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MMS 2008-006

Sperm Whale Seismic Study in the Gulf of Mexico

Synthesis Report

U.S. Department of the Interior
Minerals Management Service
Gulf of Mexico OCS Region

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ABOUT THE COVER

Cover art shows sperm whales surfacing (upper left) and breaching (upper right) in the northwest Gulf of Mexico on the 2005 S-tag cruise (photos by Craig Hayslip, Oregon State University); two sperm whales fluking near the R/V *Gyre* on the 2002 S-tag cruise (lower right; photo by Jonathan Gordon, Ecologic); and sperm whale beginning a dive in Mississippi Canyon Block 127 in the Gulf on the 2002 S-tag cruise (lower left; photo by Christoph Richter for Texas A&M University-Galveston).

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Ann Jochens	TAMU	Program Manager, PI for habitat characterization
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Aaron Thode	SIO	PI for 3-D passive acoustic tracking study
Peter Tyack	WHOI	PI for D-tag/CEE study
Bernd Würsig	TAMUG	PI for photo-ID and mesoscale survey

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SWSS Program Management

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ACRONYMS

ADCP	acoustic Doppler current profiler
AIC	Akaike Information Criterion
AMO	Atlantic Multidecadal Oscillation
AMOVA	Analysis of Molecular Variance
ANOVA	Analysis of Variance
AVHRR	Advanced Very High Resolution Radiometer
CEE	controlled exposure experiment
CoA	coefficient of association
CDT	Central Daylight Time
CTD	conductivity-temperature-depth sensor
CU	University of Colorado
CV	coefficient of variation
DAT	days after tagging
dB	decibel
DGoMB	Deep Gulf of Mexico Benthic Habitat Study
DNA	deoxyribonucleic acid
DSC	De Soto Canyon
DSL	deep-scattering layer
D-tag	Digital-recording acoustic tag (tag name and SWSS program component)
EARS	Environmental Acoustic Recording System
EEZ	Exclusive Economic Zone
EXIF	Exchangeable Image File
GOM	Gulf of Mexico
GPS	Global Positioning System
GulfCet	Gulf of Mexico Cetacean Study
HWE	Hardy Weinberg Equilibrium
IAGC	International Association of Geophysical Contractors
IFAW	International Fund for Animal Welfare
IQ	Image Quality score
IRFC	Industry Research Funders Coalition
ITM	Information Transfer Meeting
IUCN	International Union of Conservation of Nature and Natural Resources
IWC	International Whaling Commission
LCE	Loop Current eddy
mastDNA	microsatellite DNA
MED	Mediterranian Sea
MI	Markedness Index
MMS	Minerals Management Service, U.S. Department of the Interior
MMS/BS	Minerals Management Service/Biological Service
MODIS	Moderate-resolution Imaging Spectraradiometer
MPS	Mesoscale Population Study of SWSS
MR	Mississippi River
MRD	Mississippi River Delta
mtDNA	mitochondrial DNA
NAMSC	North Atlantic-Mediterranean Sea Sperm Whale Catalogue

ACRONYMS
(continued)

NAO	North Atlantic Ocean
NCDC	NOAA National Climatic Data Center
NCOM	Navy Coastal Ocean Model
NFWF	National Fish and Wildlife Foundation
NGOMNFS	Northern Gulf of Mexico ocean nowcast/forecast system
NMFS	National Marine Fisheries Service
NOAA	National Oceanic and Atmospheric Administration
NRC	National Research Council
NSEA	North Sea
NSF	National Science Foundation
OCS	Outer Continental Shelf
ONR	Office of Naval Research
OSU	Oregon State University
PAM	passive acousic monitoring
PCCS	Provincetown Center for Coastal Studies
PCR	polymerase chain reaction
PDO	Pacific Decadal Oscillation
Photo-ID	Photo-Identification
PI	Principal Investigator
POC	particulate organic carbon
POES	NOAA Polar Orbiting Environmental Satellites
PTT	platform transmitter terminal
QAIC	quasi Akaike Information Criterion
R/V	research vessel
RABI	relative acoustic backscatter intensity
RBI	relative backscatter intensity
RGS	Rio Grande Slope
RHIB	Rigid-Hulled Inflatable Boat
RMS	root mean square
SE	standard error
SeaWiFS	Sea-viewing Wide Field-of-view Sensor
SIO	Scripps Institution of Oceanography
SMM	stepwise mutation model
SRB	Science Review Board
SSC	sea surface cholorophyll
SSH	sea surface height
SSS	sea surface salinity
SST	sea surface temperature
S-tag	Satellite-tracked radio tag (tag name and SWSS program component)
SWAMP	Sperm Whale Acoustic Monitoring Program
SWFSC	Southwest Fisheries Science Center
SWSS	Sperm Whale Seismic Study
TAMU	Texas A&M University
TAMUG	Texas A&M University-Galveston

ACRONYMS
(continued)

TLP	Tension Leg Platform
UD-UK	University of Durham, UK
UD	utilization distribution
USF	University of South Florida
UStA	University of St. Andrews, UK
WHOI	Woods Hole Oceanographic Institution
WNAO	Western North Atlantic Ocean
WSE	Warm Slope Eddy
WSHC	Whale Survey and Habitat Characterization cruise
XBT	expendable bathythermograph probe

1 EXECUTIVE SUMMARY

1.1 Introduction

The U.S. Minerals Management Service (MMS) manages the oil and gas resources of the Outer Continental Shelf (OCS) in a manner that seeks "to ensure that all activities on the OCS are conducted with appropriate environmental protection and impact mitigation" (USDOI, MMS 2002). To this end, MMS sponsors studies to evaluate environmental impacts of OCS activities and to identify appropriate mitigation measures. Since the 1970s, one focus has been on the potential for impact of anthropogenic noise on marine mammals. Marine mammals are adapted to use sound in the ocean for communication, navigation, localizing and using prey, and sensing of the environment. These animals have evolved in an ocean that is filled with natural sounds. Humans began to introduce significant additional sound sources with the advent of the industrial age in the mid-nineteenth century. As the power and number of these sound sources increased, the potential for impacting marine mammals increased as well. Of concern are the potentials for negative behavioral and physiological responses to human-generated sound, at both the individual and population levels.

MMS sponsored a comprehensive literature review that detailed the state of knowledge through 1990 of human-generated and natural underwater sounds and their potential impacts on marine mammals (Richardson et al. 1991). The Office of Naval Research (ONR) then funded the conversion of this review into the classic book on *Marine Mammals and Noise* (Richardson et al. 1995). Since that time, research into the effects of noise on marine mammals has increased. Four reports of the National Research Council (NRC 1994, 2000, 2003, and 2005) provide extensive information on noise and marine mammals with recommendations for research needs. A common recommendation of these reports is to determine the normal behaviors of marine mammals and their responses to human-generated sounds (NRC 1994). Suggested was research that would study the sound exposure, as received level, at the individual animal and that would use tagging of animals to study behavior and possible responses to human-generated sound.

In the late 1980s, oil and gas activities were planned in the deepwater Gulf of Mexico (Gulf) off the continental shelf (> 200 m depth). As a result, MMS supported a series of major environmental studies beginning in 1989 to investigate the distribution and abundance of marine mammals over the continental slope waters of the northern Gulf. MMS and the National Marine Fisheries Service (NMFS) of the National Oceanic and Atmospheric Administration (NOAA) conducted aerial surveys for cetaceans over the upper continental slope in the north-central Gulf (Mullin et al. 1991). In the 1990s, the MMS-sponsored GulfCet studies used ship and aircraft visual surveys and passive acoustic techniques to survey the western and eastern parts of the northern Gulf to determine seasonal variability in the occurrence and distribution of marine mammals (Davis et al. 1998; Davis et al. 2000).

MMS recognized that, as oil and gas activities in the deepwater Gulf of Mexico increased and moved into deep water, the opportunity increased for those activities to occur in regions frequented by deepwater species of cetaceans. One species of particular concern was the sperm whale (*Physeter macrocephalus*), which is listed as endangered under the Endangered Species

Act. In 1999, MMS hosted a Gulf of Mexico Protected Species Workshop (McKay et al. 2001) to review past research, evaluate new issues, and recommend research priorities. A panel of experts identified investigation of the potential effects of sound from seismic survey operations on sperm whales as a key research priority. MMS, NMFS, and ONR then sponsored the Sperm Whale Acoustic Monitoring Program (SWAMP).

SWAMP was conducted in fiscal years 2000 and 2001 under MMS Interagency Agreement No. 15958. SWAMP essentially was a pilot study that developed new methods for studying the behavior of sperm whales and their responses to the underwater acoustic environment in support of an effort to determine the effects of seismic exploration on the animals. Most SWAMP work in the Gulf of Mexico under this Interagency Agreement concluded in September 2001. However, one additional NMFS cruise in 2003 was conducted off the U.S. Mid-Atlantic coast with partial funding under the SWAMP Interagency Agreement (Palka and Johnson 2007). Tasks on that cruise tested upgraded digital-recording acoustic tags and obtained comparative sperm whale dive data outside the Gulf (see Section 7 of the SWSS Summary Report, 2002-2004, by Jochens et al. 2006; see also Watwood et al. 2006).

During the January 2002 MMS Information Transfer Meeting (ITM) in New Orleans, LA, the International Association of Geophysical Contractors (IAGC) hosted an informal meeting to discuss future acoustic research relevant to seismic operations, and in particular, research related to understanding the effects of seismic exploration on sperm whales in the Gulf of Mexico. IAGC offered its support for sperm whale research through contribution of a seismic source vessel for controlled exposure experiments. In response, the Sperm Whale Seismic Study (SWSS) was proposed to and approved by MMS in spring 2002. In subsequent years, IAGC was joined by a number of oil and gas companies to form the Industry Research Funders Coalition (IRFC) that continued to provide contributions in support of SWSS studies.

1.2 Overview of the SWSS Study

SWSS was a multi-institutional, interdisciplinary research project supported by MMS under Cooperative Agreement 1435-01-02-CA-85186 for *Cooperative Research on Sperm Whales and their Response to Seismic Exploration in the Gulf of Mexico* through the Texas A&M Research Foundation. Texas A&M University (TAMU) provided program management and data management. The scientists who developed and implemented the scientific research plans associated with the SWSS study were from Ecologic, Oregon State University (OSU), Scripps Institution of Oceanography (SIO), TAMU, Texas A&M University-Galveston (TAMUG), University of Colorado (CU), University of Durham (UD-UK in the United Kingdom), University of Saint Andrews (UStA in the United Kingdom), University of South Florida (USF), and Woods Hole Oceanographic Institution (WHOI). Funding sponsors were MMS, National Science Foundation (NSF), ONR, IRFC, and the National Fish and Wildlife Foundation (NFWF). A five-member Science Review Board (SRB) was established in year 2. It provided recommendations and review of the SWSS Summary Report and this Synthesis Report. This board had five members: one from the federal government (NOAA), one from industry, one retired from the Marine Mammal Commission, and two from the academic community. All activities associated with sperm whales were conducted under permits issued by NMFS.

The objectives of SWSS were to

1. establish baseline information on the biology and behavior of sperm whales in the northern Gulf of Mexico,
2. characterize sperm whale habitat use in the northern Gulf of Mexico, and
3. determine possible changes in behavior of sperm whales when subjected to man-made noise, particularly from seismic airgun arrays used for offshore oil and gas exploration and geological monitoring.

To achieve each of these objectives, a set of study tasks was developed and implemented.

Five tasks were aimed at developing a better understanding of sperm whale behavior and spatial use of Gulf waters. Long-term (months to seasonal) movements and distributions of sperm whales were studied by OSU using satellite-tracked radio telemetry tags (S-tags). Short-term (hours) diving and swimming behavior and vocalizations of sperm whales were examined by WHOI using recoverable digital-recording acoustic tags (D-tags) that logged whale orientation (i.e., pitch, roll, and heading) and depth and the sounds made by and received at the whale from the environment. Medium term movements, behavior and basic biology of sperm whale groups were observed directly by Ecologic and TAMUG under the Mesoscale Population Study (MPS), which used photo-identification, photogrammetry, and passive acoustics to study sperm whale group behavior and biology and coda analysis to investigate culturally based population structure; in years 3 and 4 this mesoscale work was conducted aboard a chartered sailboat that followed whale groups, each for several days. Limited recordings of industrial sounds also were made on the MPS cruises. Visual observations of surface behavior and passive acoustic recordings of underwater vocalizations were made during all cruises as sea state conditions allowed. Biopsy samples were taken for genetic analyses by UD-UK. DNA extracted from the samples was analyzed to determine the sex of the animal and its relatedness to other individuals sampled in Gulf of Mexico groups and to sperm whales found in the North Atlantic Ocean and Mediterranean and North Seas. Diving depths and movements were examined by SIO using 3-D passive acoustic tracking techniques under development during the project.

Tasks contributing to the habitat characterization objective were three-fold. Remote sensing fields of sea surface height and ocean color were compiled from data collected by satellites in low earth orbit. These fields provided information on dynamical currents, such as generated by eddies and fronts, that can entrain chlorophyll-rich surface waters and so create conditions favorable for trophic cascade of surface production to the depths where Gulf sperm whales dive to forage (TAMU, CU, USF). *In situ* data, such as temperature, salinity, fluorescence-chlorophyll, currents, and acoustic backscatterance data, and in the fourth year fishery echosounder data, enabled further characterization of the epipelagic environment (TAMU, OSU). Limited midwater trawling was conducted on one cruise in 2003 to collect zooplankton and micronekton from 0-400, 0-600, and 0-800 m depth zones (TAMU). Habitat characterization descriptions from these data, collected by TAMU, CU, USF, and OSU, and the relation of these to the locations of sperm whales, as determined by the tag and direct observational data of OSU, WHOI, UD-UK, TAMUG, and Ecologic, allowed correlations of near-surface habitat characteristics with sperm whale usage of areas within the Gulf.

To examine potential changes in behavior of sperm whales when subjected to seismic airgun sounds, controlled exposure experiments (CEEs) were conducted by WHOI using the D-tags in conjunction with a seismic source vessel. The location and level of airgun sound delivered at the tagged sperm whale(s) were controlled by the science team. These CEEs provided data on the immediate and short-term (hours) response of sperm whales to airgun sounds compared to control non-exposure data from the same whales just before and after exposure. Longer-term avoidance or horizontal displacement behaviors of sperm whales to seismic vessel airgun sounds at much greater ranges were examined by OSU using location data from S-tags and proprietary commercial seismic shot data provided by IAGC. Opportunistic studies of behaviors in the presence and absence of airgun sounds occurring during the SWSS cruises in 2002-2003 were conducted by Ecologic.

Four reports have been completed under SWSS and are available through MMS at http://www.gomr.mms.gov/homepg/regulate/environ/techsumm/rec_pubs.html. Three Annual Reports summarize data collection activities on the cruises (Jochens and Biggs 2003, 2004, and 2006; which are OCS Study MMS 2003-069, 2004-067, and 2006-067, respectively). A Summary Report, completed in 2006, presents the results of the individual program components based on field work from 2002-2004 (Jochens et al. 2006, which is OCS Study MMS 2006-034; hereinafter called the SWSS Summary Report). Additional information is presented in the written presentation summaries given in the proceedings of the MMS ITMs of 2003, 2005 and 2007 (see Sessions 2C and 2F in McKay and Nides 2004 (OCS Study MMS 2003-073); Sessions 1F and 2F in McKay and Nides 2005 (OCS Study MMS 2005-066); and Session SWSS in McKay and Nides, In prep.). Summaries of SWAMP results are in the 2002 ITM proceedings (see Session 2F of McKay and Nides 2003 (OCS Study MMS 2003-005)) and in the 2007 summary report on cooperative research to study dive patterns of sperm whales in the Atlantic Ocean (Palka and Johnson 2007).

A brief discussion of the field measurements is presented in Section 1.3, with a fuller description given in Section 2. Sections 1.4 and 1.5, respectively, summarize the major conclusions and recommendations; details are given in Section 7 and throughout this report and the SWSS Summary Report. Section 3 gives background information on sperm whale biology, Gulf of Mexico habitat, and sound in the ocean. Sections 4, 5, and 6, respectively, present the synthesis of the population biology, habitat use, and responses of sperm whales to seismic airgun sounds. Our conclusions and some lessons-learned recommendations linked to each conclusion are summarized in Section 7, and references are given in Section 8. Sections 2 and 7 and subsections 3.1, 4.1, 5.1, and 6.1 can be read together as a concise synthesis of the SWSS project. Other subsections in Sections 3, 4, 5, and 6 provide substantial detail on various aspects of the acoustic and physical environment and sperm whale behavior in the northern Gulf of Mexico. Additional detail is provided in the SWSS Summary Report (Jochens et al. 2006), which should be read as a companion report to this Synthesis Report.

1.3 SWSS Fieldwork in 2002-2005

The SWSS study consisted of four summers of fieldwork in 2002-2005 and approximately five years of satellite tag data transmission (2002-2006), followed by analysis and synthesis. The study area was the continental slope of the northern Gulf of Mexico, with focus on the region along the 1000-m isobath between Mississippi Canyon and De Soto Canyon between 86°W and 91°W. In field year 4, the S-tag work was done in the northwest Gulf to provide information for comparison with the main study area. During SWSS, there were four S-tag cruises (2002-2005), two D-tag cruises with controlled exposure experiments using airguns on seismic vessels provided through IAGC (2002) and IRFC (2003), one cruise for a sperm whale survey and habitat characterization study conducted concurrently with the D-tag cruise in 2003, and two mesoscale population study cruises aboard a 46' Hunter sailboat (2004-2005). Data collection activities are briefly summarized here.

Cruises conducted in 2002 were in support of S-tag deployments for long term study of sperm whale movements and D-tag/CEE work for analysis of small scale sperm whale behavior patterns in the absence and presence of seismic survey sounds. The R/V *Gyre* was used for both cruises and small tag boats were launched from *Gyre* to approach and photograph and/or tag and obtain biopsy samples from sperm whales. The offshore industry work boat M/V *Rylan T*, with the shallow-water airgun boat M/V *Speculator* attached to the rear work deck, provided an airgun array with characteristics similar to those used by commercial seismic vessels in the Gulf of Mexico. The airgun array on the *Speculator* had 20 guns yielding a total volume of 1680 in^3. This ship configuration was used as the sound source for the CEEs conducted in 2002. The CEE was executed by a strict protocol that collected D-tag data before, during, and after exposure to airgun sounds. Exposure included a ramp up procedure during which sets of airgun elements in the array were gradually introduced until the full-array firing condition was reached, while the seismic source vessel moved closer to the tagged whale and its group in a manner that assured no animal would be exposed to sound levels exceeding the NMFS permit limit of 180 dB re 1 µPa (rms). Habitat characterization data collected on cruises in 2002 included currents from 153-kHz and 38-kHz acoustic Doppler current profilers (ADCP); temperature and salinity profiles using both conductivity-temperature-depth (CTD) and expendable bathythermograph (XBT) profilers; continuous, near-surface temperature, salinity, and fluorescence/chlorophyll observations; and sea surface height (SSH) fields and ocean color from remote sensing. Visual and passive acoustic observations of sperm whales also were made, tissue samples were collected for genetic analyses, and fluke photographs were taken for photo-identification. Preliminary analysis was done to consider the viability of 3-D passive acoustic tracking of sperm whales using information from the hydrophone arrays.

Cruises conducted in 2003 consisted of, concurrently, a D-tag/CEE cruise aboard the R/V *Maurice Ewing* for science operations and the M/V *Kondor Explorer* for the airgun sound source and a Whale Survey and Habitat Characterization cruise (WSHC) on the R/V *Gyre*. The airgun array on the *Kondor Explorer* had 31 guns yielding a total volume of 3090 in^3, but only 28 guns totaling 2590 in^3 were used on the D-tag/CEE cruise (DeRuiter et al. 2006). The WSHC cruise was designed to provide habitat characterization data for the time period of the D-tag/CEE cruise and to conduct sperm whale population studies from small boats launched from the R/V *Gyre.* XBT profiles of temperature in the upper 700 m were collected from the R/V *Ewing*. The WSHC and D-tag/CEE cruises were followed by an S-tag/habitat characterization cruise on the R/V *Gyre*. In addition to data types collected in 2002, a test of 3-D passive acoustic tracking was conducted from the *Kondor* and *Ewing.*

In 2004 and 2005, two cruises were conducted in each year. The first cruise included S-tag deployments from R/V *Gyre* and habitat characterization, tissue sampling for genetic analysis, visual and acoustic observations, and a 3-D passive acoustic tracking study. The second cruise used an acoustically quieter vessel, the 46' Hunter sailboat *Summer Breeze*, to gather information on the social behavior of sperm whale groups as the sailboat followed groups for 4-50 hours each. In addition, photographs, photogrammetry data, passive acoustic recordings of sperm whales, visual data, continuous near-surface temperature, and CTD profiles were collected on the sailboat cruises.

1.4 Principal Conclusions

SWSS collected a substantial body of data on sperm whales and their environment in the northern Gulf of Mexico over four years of field work. The analysis and interpretation of these data provide insights into daily and seasonal movements, abundance, group structure, diving and other behaviors, habitat characteristics and preferences, and response to airgun sounds for sperm whales in the northern Gulf of Mexico.

There are two major limitations to the SWSS study that should be kept in mind when considering the conclusions presented in this and the SWSS Summary Report. Both derive from the fact that the SWSS study area was focused along and about the 1000-m isobath in the region between Mississippi Canyon and De Soto Canyon, although one cruise was conducted in the northwest Gulf. First, this focus region has extensive human activity in the form of marine transportation, recreational activities, commercial and recreational fishing, oil and gas activities, and other anthropogenic disturbances. Thus the sperm whale population that was most studied during SWSS already may have been habituated to anthropogenic sounds, including those from seismic airgun arrays. SWSS data, therefore, should not be considered truly baseline in the sense of defining normal behavior of unexposed animals. Nevertheless, the SWSS results for the sperm whale population in this main study area do reflect a "normal" behavior in the presence of human activity for a discrete population of particular interest because its range coincides so closely with current and planned oil and gas exploration.

Second, the SWSS cruises and tagging activities were seasonally as well as spatially limited. In addition to being conducted mainly along the 1000-m isobath between the Mississippi Canyon and De Soto Canyon, SWSS cruises were conducted in June to early September. Thus the field work did not encompass the full range of the sperm whale population throughout the Gulf of Mexico in all seasons. On the other hand, the S-tag data show that spatial coverage of one or two “core populations” in the northern Gulf was fairly good. Limited observations in SWSS from areas outside the SWSS focus study area mean that results found by SWSS may not include variations, if any, in behaviors associated with other geographic regions in the Gulf. Of more concern, though, is the limited seasonal coverage. As a result fundamental information such as the seasonality and timing of breeding and whale behavior at other times of the year remain largely unknown, even though S-tag data provide some data on movements outside our main field periods.

Our principal conclusions are abstracted under each of the italicized headers that follow. Additional details and conclusions are given in Section 7 of this report and in the SWSS

Summary Report. Summary Report sections cited are so noted; all other sections cited are from this Synthesis Report.

• *SWSS results support conservation of sperm whales in the northern Gulf of Mexico as a discrete stock.*

NMFS provisionally considers the sperm whale population in the northern Gulf of Mexico as a stock distinct from the U.S. Atlantic stock (e.g., Waring et al. 2004, 2006). Results of SWSS, in particular the genetic analyses, movement patterns, photo-ID, coda vocalizations, and population structure support this stock conservation strategy. Comparisons of mitochondrial DNA (mtDNA) and other molecular markers of tissue samples from sperm whales in the northern Gulf, Mediterranean Sea, North Sea, and North Atlantic Ocean reveal a significant genetic differentiation between the Gulf of Mexico population and populations in the other three regions (Section 4.2). So far, none of the individuals photo-identified in the northern Gulf of Mexico have been matched to those in the North Atlantic and Mediterranean Sea Sperm Whale Catalogue (Section 4.7). Analyses of coda vocalizations suggest there are significant differences in repertoires between the northern Gulf of Mexico population and the populations of the rest of the Atlantic (Section 4.8; see also Section 4.3 of the SWSS Summary Report). The acoustic recordings of coda vocalizations indicate that the mixed groups in the northern Gulf of Mexico belong to an acoustic clan that is rarely encountered in other areas and, from this, it is inferred that groups from other clans enter the northern Gulf of Mexico only infrequently. Results from the one SWSS cruise in the northwestern Gulf suggest there may be a different acoustic clan in the western Gulf and so far, none of the animals photo-identified in the core study area of the north central Gulf have been matched to photo-ID images from the northwest Gulf.

• *Sperm whales are present year-round in the Gulf, with females generally having significant site fidelity and males and females exhibiting significant differences in habitat usage.*

The movements and home ranges of 52 sperm whales (33 females, 6 males, and 13 of undetermined sex) were studied using the S-tag data (Section 4.3). Results show there are no discernable seasonal migrations, but there are basin-wide movements mainly along the slope of the northern Gulf. All but one of the tagged whales stayed within the Gulf, and this individual moved into the North Atlantic and then returned to the Gulf after ~2 months. Several, thought to be males, traveled into the Bay of Campeche in the southern Gulf. There is a high degree of site-specific tenacity by many individuals, primarily females, and hence year-round usage of the home ranges, such as off the Mississippi River Delta. Repeated photo-identifications of some whales from the SWSS study area along the northern Gulf that were re-identified in several years since 1994 indicate long-term residence (Section 4.7). Photo-ID studies of these northern Gulf whales also provide no evidence of long-distance movements as no matches were found between the 285 individuals identified in the northern Gulf of Mexico (1994-2005) and the ~2500 individuals identified in the rest of the Atlantic in the North Atlantic and Mediterranean Sperm Whale Catalogue (Section 4.6; see also Section 4 of the SWSS Summary Report).

Home ranges of some females tagged in the north central Gulf overlapped with those of some females tagged in the northwestern Gulf, but the core areas of females tagged in the two locations did not. Movements of immature males had great variability, but suggest that males have larger individual home ranges and use deeper water habitats than females.

Tagging occurred generally about the 1000-m isobath. Females tagged here rarely went into waters deeper than 2000 m. In contrast, other studies have shown females, including those with calves, are present in the deeper waters (e.g., Mullin and Fulling 2004), suggesting there may be different distribution patterns for animals with possible depth preferences.

To explore habitat usage, the variables of ocean bottom depth, bottom slope, and sea surface height were examined by sex classification and meandering/transit movement type (Section 6.2 of the SWSS Summary Report). Males tended to frequent deeper water regimes than females, with a statistically significant difference of almost 300 m between the females median bottom depth (884 m) and that of the males (1171 m). Thus female sperm whales were located more frequently on the upper continental slope of the northern Gulf of Mexico. Males also were located in this region, but males also used waters with depths > 3000 m more than females did. Because of their affinity for the upper continental slope, females tended to be located where the bottom slope on average was steeper (3.06 degrees) than the slope at the locations of males (2.39 degrees). No significant differences between females and males were found in sea surface height values at animal locations, but the distributions of both sexes were best correlated with areas of negative SSH (upwelling regions). The fact that the median value of sea surface height was significantly different between meandering (-3.9 cm) and transit (-7.1 cm) locations implies that sperm whales may make differential use of cyclonic eddy interior regions than the eddy periphery.

- *The sperm whale population off the Mississippi River Delta likely has a core size of about 140 individuals.*

The genetic analyses indicate that the sperm whale population in the Gulf is unique from populations in the North Atlantic Ocean, Mediterranean Sea, and North Sea. They also indicate site fidelity of females to specific areas. Estimates of population size, based mainly on transect surveys, are approximately 1349 sperm whales Gulf-wide and a minimum abundance for the northern Gulf of 1114 (Mullin and Fulling 2004; Waring et al. 2004; a stock reassessment by NMFS (USDOC, NMFS 2007) estimates 1665 sperm whales in the northern Gulf). SWSS provided a more detailed and structured assessment of the population component located between Mississippi Canyon and De Soto Canyon using photo-identification and mark-recapture methods. Mark-recapture analysis using all available photo-ID images for the Gulf (which come mainly from SWSS and SWAMP studies) provides the best fit to a population model with an estimated population size of 281 with 95% confidence intervals of 202-434. The estimated number of members of mixed groups within the main study area, which might be considered the "core population," was 140 animals and, based on the composition of mixed groups in other areas we might expect some 88 of these animals to be females. Estimation of the proportion of calves is difficult because the typically extended calving season of sperm whales and the currently unknown calving season in the Gulf means that a clear calf size class could not be determined during SWSS summer fieldwork.

- *Gulf sperm whales seem to be smaller in individual size than sperm whales in some other oceans.*

The MPS cruises routinely used photogrammetric and passive acoustic methods to obtain size measurements of known individuals (Section 4 of the SWSS Summary Report). Results indicate the north central Gulf sperm whales on average are smaller than those measured in any other sperm whale population, including those measured using exactly the same photogrammetric method in subtropical populations in the Gulf of California (Jaquet 2006). The presence of calves with mixed groups of females indicates that north central Gulf females, with a 9-m average length, must be sexually mature. However, it is uncertain whether north central and northeastern Gulf bachelor males, which averaged 11-m length, are either physically or sexually mature. It is not known why this size difference exists, as individual size could be mediated by age, population-level genetic differences, food/nutrition, energetic differences, environmental stressors, or a combination of these. Smaller sizes may be adaptive, or they may be a cause for concern. It is also not known if this size difference exists in animals in other regions of the Gulf of Mexico, although observations by experienced observers working from small boats during the S-tag cruises indicated that the animals in the northwest Gulf seemed to be generally smaller than those in the main SWSS study area (Section 4.3).

- *Some groups of sperm whales in the Gulf were mixed-sex groups of females/immatures and others were groups of bachelor males. Typical group size for mixed groups was 10 individuals, which is smaller than group sizes in some other oceans.*

The SWSS S-tag, MPS photo-ID, and genetic relatedness data describe the social organization of the northern Gulf sperm whale population. Sperm whales seem to form small and stable units, which join other units to form groups, which in the Gulf consisted of about ten individuals. The genetic data showed that, as is common in other areas of the world, the group composition consists of mixed-sex groups and male bachelor groups (Section 4.2). Most groups were mixed-sex groups consisting of both related and unrelated females and young of both sexes. The limited S-tag data base on associations are similar to work in other areas (Whitehead 2003) indicating that associations of months occurred between females but that no long-term associations occurred between males (Section 4.5).

Not all individuals in every group were biopsied, but the group relatedness data we do have indicate that Gulf sperm whale groups are primarily composed of unrelated members. A typical group was composed of both single and multiple matrilines (i.e., where the line of descent is from common female ancestors). Without long-term association and age information, particular types of relations between group members are difficult to decipher due to the large number of possibilities available. Highly related whales (i.e., parent-offspring) were present within groups, but infrequently. When relationships were found, the most common resembled that of half-siblings or a second-order relative. The all-male bachelor groups were comprised of multiple matrilines and members were generally unrelated, although half-sibling pairs and second-order relatives were present.

The two years 2004 and 2005 studied showed a striking contrast in the distribution of different types of sperm whales and their groupings in the main study area. In summer 2004, a strong segregation was found in the distribution between groups of female/immature sperm whales and bachelor or lone males. The former were mainly found in the region south and/or west of the Mississippi River Delta and Mississippi Canyon, while the latter were mainly found in the De Soto Canyon and along the Florida slope. This basic distribution has been reported, and commented on, in SWSS and SWAMP reports. In contrast, during summer 2005, the first region lacked the mixed groups of 2004 and instead the bachelor/lone males were seen there; in fact, no members of the mixed groups "core population" were resighted. One possible cause of this change was that the oceanographic conditions between the two years were significantly different, with the discharge from the Mississippi River in 2005 being just 59% of the average summer monthly outflow (Section 3.2 reports, and comments on, this interannual difference in habitat).

• *The typical diving and underwater behaviors of the Gulf's sperm whales are similar to those of animals in other oceans.*

The SWSS study provided an extensive body of data on diving and underwater behavior of sperm whales in the Gulf of Mexico. Indeed, the detail provided in the D-tag data from the north central Gulf (SWSS), North Atlantic and Ligurian Sea has revolutionized our understanding of the underwater behavior of this species. The deep diving foraging behavior of sperm whales in the three regions was found to be similar (Watwood et al. 2006; see also Section 7.3.1 of the SWSS Summary Report). There were two dive types: dives of less than 150 m and "deep" dives to greater than 300 m. A typical deep dive consisted of four phases: descent phase, bottom phase, ascent phase, and surface phase. The dive duration typically lasted 45 min (range of 14-64 min) followed by a surface interval of 9 min. The MPS data were used to determine an independent estimate of dive duration; MPS results estimated ~55 min for the modal dive cycle (Section 4.4); this is consistent with the D-tag results. Whales descended at an average vertical velocity of 1.2 m/s, and spent on average 64% of the descent producing regular clicks, which are thought to be used in searching for prey (Watwood et al. 2006). When whales stopped descending and began the bottom phase of the dive, they started using buzzes (creaks), which are thought to represent a change in echolocation strategy as the whale attempts to capture its prey (see Miller et al. 2004a). After this foraging phase had ended, whales ascended at an average speed of 1.4 m/s. Gulf and Atlantic whales spent 72% of their time in foraging dive cycles, whereas those in the Ligurian Sea spent 97% of their time. Whales dived on average to 644 m in the Gulf of Mexico, 985 m in the North Atlantic, and 827 m in the Ligurian Sea. Under the influence of drag and buoyancy effects, the swimming behavior of sperm whales in the north central Gulf of Mexico and Ligurian Sea was found to consist of steady strokes during descent and stroke and glide behavior during ascents (Miller et al. 2004b).

• *The typical feeding and foraging behaviors of the Gulf's sperm whales are similar to those of animals in other oceans, although differences in defecation rates suggest possible differences in feeding success.*

The diving and movement behaviors of the sperm whale were related to its rapid-click buzzes as recorded on the D-tags on animals from the Gulf of Mexico and Ligurian Sea (Miller et al. 2004a). Results support the hypothesis that the buzz rates of the sperm whale can be used as a proxy for foraging activity and prey capture attempts. These data are corroborated by similar data from bats and beaked whales (Griffin 1958; Griffin et al. 1960; Johnson et al. 2004; Section

7.2 of the SWSS Summary Report). The whales spent most of the dive time at or near the bottom of the dive within one or two depth layers that likely were layers of vertically stratified prey. This result is corroborated by the 38-kHz ADCP and fishery echosounder data collected in SWSS that show dive depths corresponded to layers with elevated backscatter intensity associated with biological assemblages (Sections 5.2 and 5.3). These data also showed that whales foraging in the deep-scattering layer (DSL) at sunset exhibited movement that appeared to be associated with the diel vertical migration of the biological assemblages in the DSL, but those below the DSL did not. Most of the buzzes of the whales were produced during the bottom phase of the dives (Miller et al. 2004a). The animals actively swam and changed their orientation in the water while they were producing buzzes. The strongest activity occurred at the end of the buzz. The D-tag provides information only on the whale's orientation, movements, swim speeds, and sound production during the foraging activity. Other methods are required to study the identification, distribution and nutritional value of prey and to measure capture success rates directly.

The MPS data allowed examination of the location of each surfacing of a sperm whale group, along with typical horizontal daily displacement of sperm whales in 2004 and 2005 (Section 4.1 of the SWSS Summary Report; Section 4.4 of this report). The average horizontal daily displacement was relatively small (~35-50 km). In contrast to results for the South Pacific, the small-scale movements of the Gulf whales consisted of zigzags over a smaller area with relatively long time periods spent within a particular area. These results lead to the suggestion that Gulf sperm whales may be feeding on small but dense patches of prey. These patterns suggest a high feeding success, which is supported by the mean defecation rate, which at 20% of fluke ups, is higher than for those in the South Pacific and Galapagos.

- *In the otherwise oligotrophic Gulf of Mexico, the eddy field contributes to development of regions of locally high surface productivity that in turn may create conditions favorable for trophic cascade of surface production to the depths where Gulf sperm whales dive to forage.*

The eddy field in the Gulf of Mexico generates off-shelf conditions that transport relatively nutrient-rich, high-productivity shelf waters to the slope or upwell nutrient-rich waters from depth into the photic zone where they can fuel phytoplankton growth. SWSS results support the findings of GulfCet and SWAMP (e.g., Biggs et al. 2000, Davis et al. 2002, Biggs et al. 2005) that lead to the hypothesis that locally high chlorophyll features, particularly cyclonic eddies or eddy-induced off-margin flows, that persist for 3-4 months, provide primary production that cascades to support prey assemblages for sperm whales along the continental slope (Section 3.2). Preliminary findings from comparisons of the locations of sperm whales observed during the 2005 S-tag cruise with the acoustic backscatter from a fishery echosounder (Section 5.3) support this paradigm, as significantly higher midwater backscatter was measured when whales were locally abundant. The eddy field during SWSS varied both from year to year and within individual summers. Both sources of variability appeared to influence the encounter rates with whales (Biggs et al. 2005; Section 3.2 of this report; Section 3.1 of the SWSS Summary Report).

The interannual variability of the Mississippi River discharge itself may also have significant impact on sperm whale distributions in the main SWSS study area along the 1000-m isobath between Mississippi Canyon and De Soto Canyon. This discharge provides nutrients that result in relatively high biological productivity, which then can be transported off-shelf into the habitat of the sperm whale by the eddy field (Section 3.2). Based on the results of the 2005 MPS cruise, in 2005 sperm whales were not found in similar abundance or in the usual groupings in the main SWSS study area that were found in the GulfCet and 2002-2004 SWSS study years. The change in distribution may have been related to the lower discharge from the Mississippi River in 2005. Climate teleconnection indices may allow 5-12 month forecasts of such low river discharge conditions (see Section 5.5) and may provide an additional oceanographic condition to the eddy field that could be used to predict the areas in which sperm whales may be abundant.

A real gap in knowledge, however, is the understanding of the complex pathway by which surface productivity translates into mid- or deepwater productivity that sustains the prey field for the apex predator, the sperm whale. The actual prey species of the northern Gulf sperm whales are not known. One SWSS cruise in 2003 included limited midwater trawling to compare and contrast zooplankton and midwater fish in the 0-400 m, 0-600 m and 0-800 m depth horizons, but results were insufficient for assessing sperm whale prey fields (see Section 3.2 of the SWSS Summary Report for details). Backscatter returns from 38-kHz ADCP and fishery echo sounders are indirect indicators of potential prey patches. SWSS data showed there are backscattering layers that are deeper than the main deep scattering layer (Sections 5.2 and 5.3; see also Kaltenberg 2004). Results comparing these backscattering layers with D-tag foraging data are suggestive that these returns are indicators of the presence or absence of the sperm whale prey (Section 5.2). However, the prey field itself requires dedicated study: What species are present and used by the sperm whale? Where are they found? What are their distribution patterns in space and time? What factors affect their populations? How do physical and biological oceanographic factors affect the distribution of prey species?

- *There appeared to be no horizontal avoidance to controlled exposure of seismic airgun sounds by sperm whales in the main SWSS study area.*

The SWSS study used carefully planned controlled exposure experiments (Tyack et al. 2004) to assess whether there were behavioral changes from actual received levels from airgun sounds (Section 6.2 of this report and Section 7 of the SWSS Summary Report). The movement and sound-recording D-tag was used to record acoustic exposure and foraging behaviors of 8 sperm whales before, during and after 1-2 hr controlled sound exposures of industry-provided airgun arrays in the Gulf of Mexico in 2002 and 2003. In 2002, two CEEs were conducted involving 4 subjects. In 2003, three CEEs were completed also with a total of 4 subjects. The 8 whales for which these CEEs were conducted were exposed to maximum received sound levels between 111 to 147 dB re 1 μPa (rms) (131 to 164 dBp-p re 1 μPa) at ranges of approximately 1.4-12.6 km from the sound source.

Results showed no horizontal avoidance at the sound levels received by the D-tagged whales. These results were supported by opportunistic studies of seismic shot locations and sperm whale locations from S-tag data (Section 6.3 of this report and Section 8 of the SWSS Summary Report) and observations of whale headings observed from R/V *Gyre* before and after line starts. Vertical diving behavior also was examined. The sample sizes were insufficient to be completely confident that there were no horizontal or vertical avoidance responses. Additionally, the issue of habituation to airgun sounds is important when considering how to extend these results to sperm whales in environments with less historical seismic exploration than the Gulf of Mexico.

- *Data analysis suggests it is more likely than not that some decrease in foraging effort may occur during exposure to full-array airgun firing as compared to the post-exposure condition, at least for some individuals.*

Results of an ANOVA statistical test of the D-tag/CEE data to determine whether there were changes in foraging behavior indicated a statistically significant decrease in swimming movements during full-array exposure as compared to post-exposure periods. Likewise an ANOVA of data on the buzzes produced when whales attempt to capture prey indicated the buzz rate was lower during the exposure condition, but this effect was not statistically significant. The sample size of 7 animals that conducted foraging dives during exposure was too small to provide definitive results, in part because a planned third summer of CEEs was not incorporated into 2004 or 2005 SWSS fieldwork when the funders decided to postpone further CEE work until recommendations of the Advisory Committee on Acoustic Impacts on Marine Mammals were available.

To examine the odds-ratio of whether the limited CEE data support the conclusion of a change in behavior, Bayesian analyses were conducted. These analyses indicated that the odds favor that, during full-array exposure, there was a decrease in foraging activity of approximately 20% rather than that there was no change in foraging activity. A statistical analysis of the odds that each individual whale changed its foraging behavior during exposure demonstrated that one whale showed a statistically significant ($p<0.002$) decrease of 60%. However, the power of the test to detect small changes in foraging success was low, and no conclusions on the biological significance of these effects for an individual animal or for the population can be made from the data sets available.

- *Knowledge of the acoustic propagation and airgun sound characteristics is critical to developing the capability for accurate predictions of exposures and the modeling of potential resulting effects.*

The D-tag recordings allowed comparison of predicted with measured airgun sounds received at the animal (DeRuiter et al. 2005; Section 7.3.4 of the SWSS Summary Report). Significant differences were found between the predicted received levels and frequency bands and the actual levels and frequencies recorded by the tag. Varying oceanic conditions, such as the presence or absence of surface ducting, have important impact on the received levels and the spectra of propagated sounds, and these may explain the differences. Ray trace and parabolic equation models for sound propagation in the ocean explain the observed values quite well, but geometric spreading models did not. These results lead to the conclusions that geometric spreading models are too simplistic for predicting the received levels of signals from airgun arrays and that propagation of airgun signal can be modeled more precisely with sufficient measurement of the relevant oceanic environmental parameters. A better understanding of the broadband three-dimensional beampattern of airgun arrays would help predictive modeling. This information, in combination with data on effects of exposure, is needed for development of models to realistically assess whether effects observed are biologically significant to the population (see NRC 2005).

1.5 Recommendations

SWSS has greatly advanced our knowledge of the sperm whale population in the northern Gulf of Mexico, as the results presented in this and the SWSS Summary Report show. Nonetheless, there are a number of areas for which recommendations can be made for further study. These are presented in the context of each of the Conclusions of Section 7 and focus on knowledge gaps in basic population information, enhancements to behavioral response studies, and improvements in equipment and methods for studying sperm whale populations to allow improved conservation and understanding of the biological significance of human activities.

Gaps in basic population information remain. Basic biological information that is essential for understanding population dynamics includes estimates of population size, calving rate, and mortality rates. Additional information important for understanding population biology includes better understanding of breeding and calving seasonality and behavior, feeding/foraging success, identification of the prey species, and the trophic cascade by which near-surface productivity may drive locally higher prey fields in the depths at which sperm whales forage.

As the footprint of oil and gas exploration continues to expand in the Gulf, we believe there is a pressing need to better understand and quantify the variability of the population dynamics of the northern Gulf sperm whales, which requires long-term monitoring. SWSS met its objective of providing detailed data on sperm whales within the area of highest industrial activity, but our study was less well suited to sperm whale distributions through the entire Gulf because the SWSS study area was focused mainly along the 1000-m isobath in the region between the Mississippi Canyon and De Soto Canyon, while the sperm whale population is found from the Dry Tortugas off south Florida into the Bay of Campeche of Mexico, as well as out into the deepest waters of the Gulf. The GulfCet study comprised surveys with a broader geographic focus, but even those comprised less than 25% of the Gulf. The SWSS satellite tagging results indicate that individual whales covered much broader areas than planned for in our survey design that focused on the north central Gulf, even though S-tagging was confined to animals encountered during the summer months.

The behavioral studies of SWSS considerably advanced our knowledge of the response of individual sperm whales to activities of the seismic survey industry. Nevertheless, additional work remains to achieve the goal of a comprehensive understanding of the behavioral response of sperm whales to anthropogenic noises in the Gulf of Mexico and its biological significance. In Section 7, we recommend additional controlled exposure experiments and other behavioral response studies to increase the sample size available for analysis. Future work should include consideration of populations that have not yet been exposed to anthropogenic noises, such as from seismic source airguns. It is an open question whether the population off the Mississippi River Delta is habituated to human activity in ways that may have influenced the SWSS results.

Another area for future research is improved technology and methods. Improvements to the attachment durations of digital recording tags and additional sensors for satellite tracked tag types will enable more information to be collected at less cost. Development of methods to use opportunistic behavioral response data sets might be able to augment the controlled tests if it is possible to obtain baseline control data from whales that then are exposed to commercial surveys, which proved impossible in SWSS. Enhancements to passive acoustic monitoring methodology, both shipboard and moored, hold promise for substantial data collection opportunities. Carefully planned passive acoustic monitoring, photo-identification, and photographic mark-recapture surveys using motor-assisted sailing vessels to assess and photograph sperm whales in the years to come would provide the basis for a cost-effective, ongoing population monitoring program to provide key information required for population conservation. Improved photographic image quality, photo-matching and image analysis techniques will enhance the useful information that can be derived using photo-ID methods. The combination of these photo-ID methods with other techniques, such as satellite tagging, will allow new means of investigating sperm whale social behavior over a wide range of spatial and temporal scales.

Additional recommendations from lessons learned during SWSS are provided in the context of Section 7 of this report. But after general discussion, our six principal recommendations, without prioritization, are:

1. Continue to conserve Gulf of Mexico sperm whales as a unique stock.

2. Implement an ongoing monitoring program to continue and extend SWSS understanding of biology and behavior of Gulf whales, focused on providing information required for sperm whale population conservation.

3. Extend controlled exposure experiment work.

4. Incorporate information on the prey field of sperm whales in the Gulf of Mexico, including identification of prey species and their vertical distribution, as an integral design element of future controlled exposure experimentation.

5. Continue development of sensor and instrument capabilities, including enhancements to the D-tag and addition of new sensor capability for the S-tag.

6. Continue development of passive acoustic monitoring (PAM) techniques, so that PAM as well as visual observers are design elements in future seismic surveys.

2 OVERVIEW OF THE SPERM WHALE SEISMIC STUDY

The northern Gulf of Mexico (Gulf) is home to a population of sperm whales (*Physeter macrocephalus*), which are the most common large whale in the Gulf. Records of sperm whale encounters in the Gulf date back over one hundred years to the commercial whaling days, when there was a small fishery in the central Gulf (Townsend 1935). More recently, the distribution and abundance of sperm whales were studied as part of a number of aerial and shipboard surveys of cetaceans conducted since the 1970s (e.g., Fritts et al. 1983, Mullin et al. 1991, Davis and Fargion 1996, and Davis et al. 1998, 2000, and 2002). These surveys found sperm whales seaward of the shelf edge at various locations along the northern continental slope. Many sightings were south of the region adjacent to the Mississippi River Delta in water depths of approximately 1000 m. Aerial surveys conducted in all seasons demonstrated that sperm whales reside in the northern Gulf year-round (e.g., Mullin and Hoggard 2000).

The Sperm Whale Seismic Study (SWSS) was a five-year study of sperm whales in the northern Gulf of Mexico, their habitat, and their possible response to man-made noise. Nine cruises were conducted over four field years and were focused over the middle continental slope, centered around the 1000-m isobath. Eight of these cruises were conducted in the approximate region between ~91°W and ~86°W. This is a region that, under the influence of the discharge of the Mississippi River, has relatively biologically productive surface waters in which our cruises usually encountered dozens of sperm whales. A ninth SWSS cruise, conducted in June 2005, was in the U.S. waters of the northwestern Gulf. This report presents a synthesis of results from the SWSS study and gives recommendations for future, further study.

2.1 SWSS Background and Objectives

The core responsibilities of the Minerals Management Service (MMS) in managing the Outer Continental Shelf (OCS) activities include safe offshore operations and environmental protection. Under its environmental responsibilities, MMS seeks "to ensure that all activities on the OCS are conducted with appropriate environmental protection and impact mitigation" (USDOI, MMS 2002). To that end, the MMS sponsors studies to evaluate environmental impacts of OCS activities and to identify appropriate mitigation measures. Since the 1970s, one environmental focus has been the potential for impact of anthropogenic sound on marine mammals.

Many marine mammals are adapted to use sound in the ocean for communication, navigation, prey identification and location, and sensing of the environment. These animals have evolved in an ocean that is filled with natural sounds. Humans began to introduce additional sound sources with the advent of the industrial age in the mid-nineteenth century. As these sounds increase, the potential for impacting marine mammals increases as well. Of concern are the potentials for negative behavioral and physiological responses to human-generated sound, at both the individual and population levels (NRC 2005).

In the late 1980s, oil and gas activities were planned for development in the deepwater Gulf of Mexico off the continental shelf. As a result, MMS supported a series of major environmental studies beginning in 1989 to investigate the distribution and abundance of marine mammals over the continental slope waters (> 200 m depth) of the northern Gulf. The MMS and the National Marine Fisheries Service (NMFS) of the National Oceanic and Atmospheric Administration (NOAA) conducted aerial surveys for cetaceans over the upper continental slope in the north-central Gulf (Mullin et al. 1991). In surveys of the U.S. waters of the northern Gulf, the MMS-sponsored GulfCet studies used ships, aircraft, and passive acoustical techniques throughout the 1990s to determine seasonal variability in the occurrence and distribution of marine mammals (Davis and Fargion 1996; Davis et al. 2000).

Oil and gas activities in the deepwater region of the Gulf of Mexico have increased since the initial deepwater development in 1985 and are projected to continue to increase in coming years (e.g., French et al. 2006). Activities now extend out to regions with water depths of 800 m or more. This region is frequented by the sperm whale, which is listed as endangered under the U.S. Endangered Species Act.

In 1999, MMS hosted a Gulf of Mexico Protected Species Workshop to review past research, evaluate new issues, and recommend research priorities (McKay et al. 2001). The potential effects of noise from seismic operations on sperm whales was identified as a key research priority. MMS, NMFS, and the Office of Naval Research (ONR) sponsored the Sperm Whale Acoustic Monitoring Program (SWAMP), which was conducted in fiscal years 2000 and 2001 under the MMS Interagency Agreement No. 15958. SWAMP was a pilot study that developed methods for sperm whale tagging, began documenting a baseline on "usual" behavior of sperm whales in the northern Gulf of Mexico, and made observations on the underwater acoustic environment. This study, as well as earlier survey results, indicated that sperm whales tend to be most likely observed near the 1000-m isobath (USDOI, MMS 2002). Work in the Gulf of Mexico under this Interagency Agreement concluded in September 2001.

During the January 2002 MMS Information Transfer Meeting, the International Association of Geophysical Contractors (IAGC) hosted a discussion of future acoustic research relevant to seismic operations, and, in particular, as related to understanding the effects of seismic exploration on sperm whales in the Gulf of Mexico. IAGC offered its support for sperm whale research through contribution of a seismic source vessel for controlled exposure experiments. In response, the study entitled *Cooperative Research on Sperm Whales and their Response to Seismic Exploration in the Gulf of Mexico* was proposed to the MMS. It was approved by MMS in April 2002. The Cooperative Agreement was executed in June 2002.

The objectives of SWSS were to

(1) establish the normal behavior of sperm whales in the northern Gulf of Mexico,
(2) characterize habitat use, and
(3) determine possible changes in behavior of sperm whales when subjected to man-made noise, particularly from seismic airgun arrays.

Figure 2.1 shows the geographical location of the SWSS study area. There were two focus areas: one in the northeast between Mississippi Canyon and De Soto Canyon for cruises during summers 2002-2005 and one in the northwest corner of the Gulf for one cruise in summer 2005.

Several cruises also conducted brief surveys along the 1000-m isobath between the two focus areas.

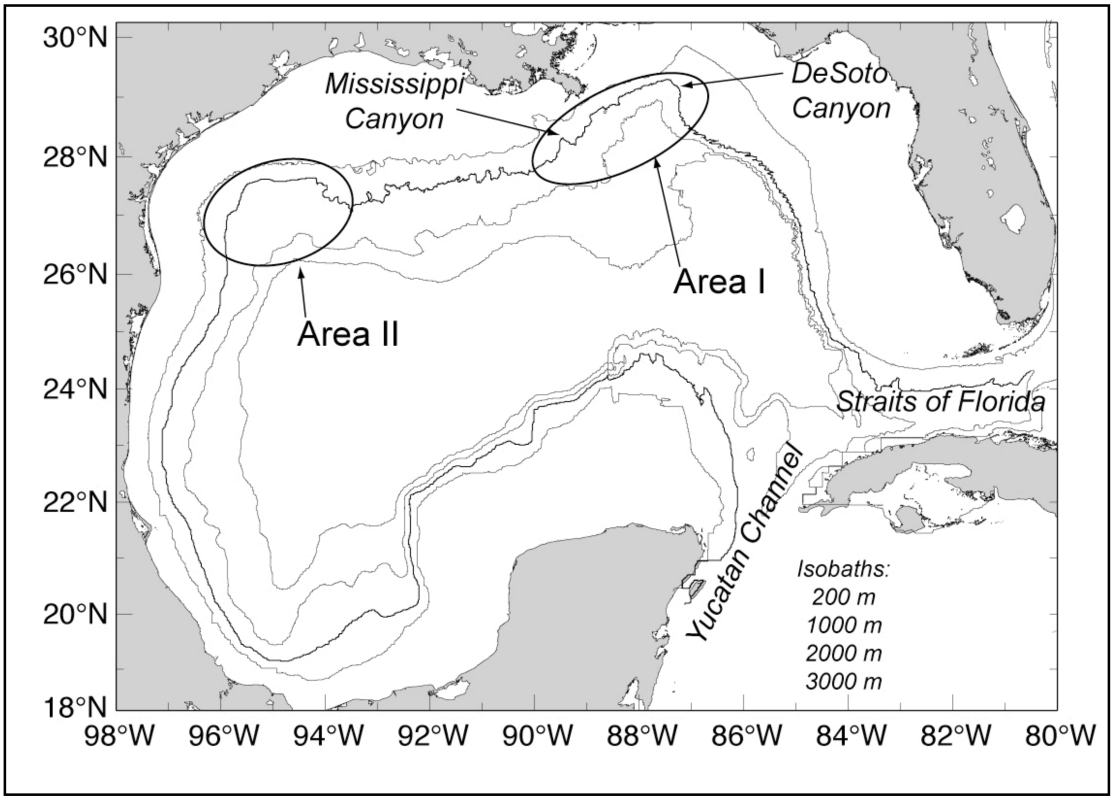

Figure 2.1. SWSS study area in the Gulf of Mexico. Area I was the focus for SWSS cruises in summers 2002-2004 and for the MPS cruise in summer 2005. Area II was the focus area for the 2005 SWSS S-tag cruise. Several cruises also conducted brief surveys along the 1000-m isobath between the two areas. Shown are the 200-m, 1000-m (thick line), 2000-m, and 3000-m isobaths.

2.2 Program Participants and Sponsors

SWSS was a multi-institutional, interdisciplinary study consisting of eight tasks performed by 17 principal scientists from 11 institutions. Principal SWSS scientists conducting the study were:

Ecologic: Jonathan Gordon (also at the University of St. Andrews, UK)
Oregon State University (OSU): Bruce Mate, Joel Ortega-Ortiz, and Kelly Benoit-Bird
Provincetown Center for Coastal Studies (PCCS): Nathalie Jaquet
Scripps Institution of Oceanography (SIO): Aaron Thode
Texas A&M University (TAMU): Ann Jochens (SWSS Program Manager), Doug Biggs, Matt Howard (SWSS Data Manager), and John Wormuth
Texas A&M University-Galveston (TAMUG): Bernd Würsig

University of Colorado (CU): Robert Leben
University of Durham, UK (UD-UK): Daniel Engelhaupt
University of St. Andrews, UK (UStA): Patrick Miller
University of South Florida (USF): Chuanmin Hu
Woods Hole Oceanographic Institution (WHOI): Peter Tyack and Mark Johnson

SWSS consisted of seven components (Table 2.1): Satellite-tracked radio tags (S-tags), Digital-recording acoustic tags (D-tags) and controlled exposure experiments (CEEs), Biopsy/genetic analyses, Habitat characterization, 3-D passive acoustic tracking, Photo-identification (photo-ID) and mesoscale population study (MPS), and Program and data management.

Table 2.1

Major Tasks in SWSS

Task	Description	Principal Investigators
Program and Data Management	Management of the program, including scientific, operational, and fiscal; oversight of preparation of deliverables; data management, including data archival	A. Jochens, TAMU, Program Manager, PI D. Biggs, TAMU, Project Scientist, co-PI M. Howard, TAMU, Data Manager
S-tag Study	S-tag logistics, data collection, data analysis, and reporting for S-tag work	B. Mate, OSU, PI J. Ortega-Ortiz, OSU, co-PI
D-tag/CEE Study	D-tag logistics, data collection, data analysis, and reporting for D-tag work	P. Tyack, WHOI, PI M. Johnson, WHOI, co-PI P. Miller, UStA/WHOI, co-PI
Mesoscale Population Study/Photo-ID	Population observations, photography, coda analysis, passive acoustic data collection, data analysis, and reporting	J. Gordon, Ecologic/UStA, PI B. Würsig, TAMUG, PI N. Jaquet, TAMUG/PCCS, co-PI
Genetic Analyses	Skin and biopsy sampling, genetic analyses for group relatedness, and reporting	D. Engelhaupt, UD-UK, PI
Habitat Characterization	Habitat characterization logistics, data collection, data analysis, remote sensing data, trawling, reporting for physical and biological habitat characterization	D. Biggs, TAMU, PI A. Jochens, TAMU, co-PI Kelly Benoit-Bird, OSU, PI - fish acoustics Chuanmin Hu, USF, PI - ocean color R. Leben, CU, PI - altimeter John Wormuth, TAMU, PI - trawling
3-D Passive Acoustic Tracking	3-D passive acoustic tracking, data analysis, and reporting	A. Thode, SIO, PI

The S-tag task was designed to evaluate the seasonal distribution of sperm whales in the northern Gulf of Mexico. Sperm whales had been sighted in the Gulf of Mexico throughout the year, but little was known about their numbers, site tenacity, and seasonal movements. Under the S-tag task, sperm whales were tagged in the northern Gulf of Mexico with a satellite-tracked radio tag (S-tag) that provided long-term (months) information on surfacing locations of the tagged individuals. Tracking by satellite was used to help identify behaviors, summer and other seasonal habitats, and, in coordination with the habitat characterization task, associations with oceanographic features. S-tag cruises were conducted in the summers of 2002 through 2005.

The D-tag task was designed to quantify diving behavior and vocalizations in Gulf sperm whales and to conduct controlled exposure experiments (CEEs) to measure reactions of these whales to air-gun sounds. A digital acoustic tag (D-tag) was applied to individual whales to provide intensive, short-term (hours) information on whale swimming behavior and to record underwater noise both from the whale and received noise from the environment. The tag recorded the sounds heard and made by the tagged whale together with its depth and orientation (i.e., pitch, roll, and heading), in a synchronized fashion throughout the dive cycle. Intensive visual and acoustic observations from a nearby research vessel recorded the social and geographical context of the whales' behavior, before, during, and after tagging. Sperm whales also were tagged with the D-tag and then exposed to sound sources from a seismic vessel and to other sound sources, such as whale codas, using playback recordings. D-tag/CEE cruises were conducted in the summers of 2002 and 2003.

The MPS/photo-identification project involved a classical, observational approach (Whitehead and Gordon 1986; Gordon 1987b) to the study of the sperm whale population in the northern Gulf of Mexico. It was conducted in summers 2002 and 2003 using small vessels launched from R/V *Gyre* for visual observations of surface behavior coupled with passive acoustic observations from the *Gyre* to find and follow the whales. In summers 2004 and 2005, it was conducted from the motor sailor, *Summer Breeze*. The research approach from the sailboat involved using passive acoustic techniques to find sperm whale assemblages, then tracking these groupings over periods that extended for several days. The study used a combination of passive acoustics and visual observation while collecting photo-ID images of whale flukes when they dive. Most sperm whale flukes are individually distinctive. This allowed mark recapture methods to be applied to provide information on a variety of parameters including population size, social organization, vital rates and movements. These techniques allowed the estimation of the size of the sperm whale population that uses the area south of the Mississippi River Delta and evaluations of their "usual behavior", their site fidelity, and their population structure.

The genetic analyses allowed study of groups of sperm whales in terms of relatedness through DNA analyses of skin/tissue samples. Skin and biopsy samples were taken during the S-tag, D-tag, and MPS cruises. The genetic analyses were used to investigate patterns of genetic structure at three hierarchical levels: 1) social structure within and between group and clusters; 2) phylogeographic structure among putative populations within the Gulf; and 3) phylogeographic structure on a global scale incorporating SWSS results with those of previously published studies with a particular focus on incorporating samples collected in the Caribbean Sea, Atlantic, and Mediterranean Sea regions.

The habitat characterization task merged methodologies from biological oceanography, physical oceanography, and remote sensing to provide an interdisciplinary description of the oceanographic habitat in which the sperm whales were encountered. Measurements on the cruises included conductivity-temperature-depth (CTD) profiles, expendable bathythermograph (XBT) profiles, current measurements and acoustic backscatter from a 153-kHz acoustic Doppler current profiler (ADCP) and a 38-kHz ADCP, near-surface underway temperature and salinity from a thermosalinograph, and continuous near-surface chlorophyll using a calibrated flow-through fluorometer. Navigation data and station locations were determined using differential Global Positioning System (GPS). Additional Gulf-wide information included sea surface height fields from satellite altimetry, sea surface temperature fields from satellite AVHRR, and sea surface chlorophyll fields derived from ocean color from SeaWiFS and MODIS. In 2003, one cruise included nighttime trawling for sperm whale prey. In 2005, one cruise included acoustic backscatter observations from 70- and 38-kHz fisheries echosounders to measure possible prey fields.

In addition to providing critical support of the tagging and survey efforts, passive acoustic techniques were used to conduct experiments for estimating whale locations underwater from their sound sources (3-D passive acoustic tracking). Other passive acoustic experiments were on use of click intervals to estimate whale size and evaluation of codas for behavioral analyses.

SWSS was supported primarily by the Minerals Management Service (MMS) of the U.S. Department of the Interior under Cooperative Agreement 1435-01-02-CA-85186. Additional support for SWSS activities was provided by the Office of Naval Research (ONR), the National Science Foundation (NSF), the National Fish and Wildlife Foundation (NFWF), and the Industry Research Funders Coalition (IRFC), which is a coalition of the IAGC and five oil and gas exploration and production companies. All activities were conducted pursuant to approved permits from the NMFS (see Jochens and Biggs 2003, 2004, and 2006 for details).

In addition to providing funding for SWSS, MMS had substantial direct involvement under this Cooperative Agreement. MMS scientists were actively involved in project oversight and coordination of study activities with academic scientists, ONR, NSF, and IRFC. They participated in the cruises on the visual and acoustic teams. MMS coordinated the Information Transfer Meetings and internal planning sessions on sperm whales and the SWSS project. Finally MMS personnel were involved in public outreach related to Gulf of Mexico marine mammals. MMS also was the lead agency for funding and decisions on program activities.

ONR, NSF, NFWF, and IRFC participation consisted of funding and direct provision of ships and materials for cruises. ONR supported tag development for both the D-tags and the S-tags used in the study. NSF provided support in year 2 through a grant to Lamont-Doherty Earth Observatory for use of the R/V *Maurice Ewing* in D-tag/CEE work for SWSS 2003. NFWF provided support for the bareboat charter and provisioning of the 46' Hunter sailboat, *Summer Breeze*, used to conduct the Mesoscale Population Study (MPS) in summer 2004. IRFC provided the non-federal match that allowed SWSS scientists to obtain the NFWF funding, as well as funding supplementary to that provided by MMS to support the Mesoscale Population Study.

The seismic source vessel was a critical component of the D-tag/CEE effort because it provided the sound source for the controlled exposure experiments. For the 2002 field year, IAGC contributed the seismic source vessel, M/V *Speculator*, mounted on the back deck of the M/V *Rylan T*, and its crew for use in the D-tag CEEs. SEAMAP, Inc., contributed a hydrophone array for the seismic source vessel during this cruise. For 2003, the IRFC contributed the seismic source vessel, M/V *Kondor Explorer*, and its crew for use in the D-tag CEEs. IRFC also provided support under SWSS for purchase of the towed hydrophone array used in the 3-D passive acoustic tracking study in 2004 and for upgrades of that array in 2005. Analysis of S-tag whale locations and seismic survey lines was supported by IRFC in 2003-2005. IRFC also provided funding support in 2005 for purchase of new depth-recording S-tags. IRFC provided separate, non-SWSS funding to OSU in support of further development of the S-tags and also provided support for calibration tests with *Kondor* airguns of the Environmental Acoustic Recording System (EARS) buoy that is part of a separate MMS-sponsored study.

A SWSS Science Review Board (SRB) was established to provide independent review of the program design and progress reports and to offer comments on the draft Synthesis Report. The SRB consisted of one federal representative (Debra Palka, NOAA), one industry representative (Phil Fontana, CGGVeritas), and three academic/science representatives with expertise in the marine mammal sciences (Daniel Costa of the University of California-Santa Cruz, Robert Hofman retired from the Marine Mammal Commission, and Doug Wartzok of Florida International University). In addition to this report, the SRB reviewed the SWSS Summary Report for 2002-2004 and provided comments that were used to improve that report.

2.3 Summary of Data Collection Activities

Table 2.2 lists the SWSS field cruises conducted in the summers of 2002 through 2005. Information on data collection methods is reported in Jochens and Biggs (2003) for 2002 cruises, Jochens and Biggs (2004) for 2003 cruises, and Jochens and Biggs (2006) for 2004-2005 cruises. Also shown in Table 2.2 is an associated, MMS-supported cruise, conducted immediately after the 2003 D-tag/CEE cruise, to calibrate the airgun array from the EARS buoy. Data collection on each SWSS cruise is described below.

Field cruises conducted in 2002 were in support of S-tag deployments for long term study of sperm whale movements and D-tag/CEE work for determination of small scale sperm whale behavior patterns in the absence and presence of seismic sounds. R/V *Gyre* was used for both cruises (Figure 2.2). Rigid-hull inflatable boats (RHIBs) were launched from *Gyre* to approach and photograph and/or tag sperm whales (Figure 2.3). The M/V *Rylan T* with the *Speculator* providing the seismic source, was used for the CEEs (Figure 2.4). The airgun array on the *Speculator* had 20 guns yielding a total volume of 1680 in^3. Habitat characterization data collection was done on both cruises. This consisted of currents from 153 kHz acoustic Doppler current profiler (ADCP), temperature and salinity profiles using both CTD and XBT profilers, continuous, near-surface temperature, salinity, and fluorescence/chlorophyll observations, and sea surface height (SSH) fields from remote sensing. Visual and passive acoustic observations were collected as were skin samples for genetic observations. Fluke photographs were taken for photo-identification. Preliminary analysis was done to assess the viability of 3-D passive acoustic tracking of sperm whales using information from the hydrophone arrays. See Jochens and Biggs (2003) for details.

Table 2.2

SWSS Cruises Conducted and Associated Data Collection Activities
(X denotes full data collection; x denotes limited data collection due to cruise limitations.)

Year	Ship	Cruise	Dates	D-tag	S-tag	Vis	PAM	HC	GA	3D	Pop
2002	R/V *Gyre*	S-tag	06/20/2002 - 07/08/2002		X	X	X	X	X		X
2002	R/V *Gyre*	D-tag	08/19/2002 - 09/15/2002	X		X	X	X	X	X	
2002	M/V *Rylan T*	CEE with *Gyre*	08/29/2002 - 09/12/2002	X		x	X				
2003	R/V *Gyre*	WSHC	05/31/2003 - 06/21/2003			X	X	X	X		X
2003	R/V *Maurice Ewing*	D-tag	06/03/2003 - 06/24/2003	X		X	X	x	X	x	
2003	M/V *Kondor Explorer*	CEE with *Ewing*	06/07/2003 - 06/22/2003	X		x	x			x	
2003	M/V *Kondor Explorer*	EARS buoy*	06/22/2003 - 06/25/2003								
2003	R/V *Gyre*	S-tag	06/26/2003 - 07/14/2003		X	X	X	X	X		
2004	R/V *Gyre*	S-tag	05/24/2004 - 06/19/2004		X	X	X	X	X	X	
2004	*Summer Breeze*	MPS	06/20/2004 - 08/15/2004			X	X	x	X		X
2005	R/V *Gyre*	S-tag	06/02/2005 - 06/30/2005		X	X	X	X	X	X	
2005	*Summer Breeze*	MPS	06/13/2005 - 08/03/2005			X	X	x	X		X

D-tag: Digital sound-recording tag deployments and CEE data collection
S-tag: Satellite-tracked radio tag deployments
MPS: Mesoscale Population Study
WSHC: Whale Survey and Habitat Characterization cruise
Vis: Visual observations of sperm whales and, opportunistically, other marine mammals
PAM: Passive acoustic monitoring for sperm whales
HC: Habitat characterization data on currents, temperature, salinity, and/or chlorophyll
GA: Genetic analyses of skin samples collected
3D: 3-D passive acoustic tracking
Pop: collection of sperm whale population and behavior data and fluke photographs
* EARS is not part of SWSS, but is a sister program supported by MMS and IRFC

Figure 2.2. The R/V *Gyre* and R2 tag boat on the S-tag cruise in 2003.

Field cruises conducted in 2003 consisted of, concurrently, a Whale Survey and Habitat Characterization cruise (WSHC) on the R/V *Gyre* and a D-tag/CEE cruise aboard the R/V *Maurice Ewing* and M/V *Kondor Explorer* (Figure 2.5). The airgun array on the *Kondor Explorer* had 31 guns yielding a total volume of 3090 in^3, but only 28 guns totaling 2590 in^3 were used on the D-tag/CEE cruise. The WSHC cruise was designed to provide habitat characterization data for the time period of the D-tag/CEE cruise and to conduct sperm whale population studies from small boats launched from the R/V *Gyre.* These two cruises were followed by an S-tag/habitat characterization cruise on the R/V *Gyre*. In addition to data types collected in 2002, a test of 3-D passive acoustic tracking was conducted from the *Kondor* and *Ewing*. Habitat characterization data collection on the D-tag/CEE cruise was limited to XBT profiles of temperature and remote sensing data. See Jochens and Biggs (2004) for details.

Figure 2.3. RHIBs used on SWSS cruises. Shown are (A) the R2 configured for D-tag work in 2002, (b) OSU tag boat, *Puffin*, off to deploy S-tags in 2005, (C) R2 configured for photo-identification work on the 2005 S-tag cruise, and (D) deployment of the tag boat from the R/V *Gyre* on the 2005 S-tag cruise.

Figure 2.4. Seismic source vessel used on the 2002 D-tag/CEE cruise. The M/V *Rylan T* with the coastal seismic source vessel *Speculator* mounted on the back deck (upper) and airgun action through BigEye binoculars during a 2002 controlled exposure experiment (lower). The cable on the right is the tow cable for the SEAMAP passive acoustic array.

Figure 2.5. Vessels used on the 2003 D-tag/CEE cruise. Shown are the science operations vessel, the R/V *Maurice Ewing* (upper), and the seismic source vessel, M/V *Kondor Explorer* (lower).

In 2004 and 2005, S-tag and MPS cruises were conducted in each summer. In addition to sea surface height fields, sea surface ocean color imagery derived from satellite observations was used in planning and implementing these two cruises. The S-tag cruises included S-tag deployments from R/V *Gyre* with a full complement of habitat characterization data, biopsy sampling, visual and acoustic observations, and a full 3-D passive acoustic tracking study. The MPS cruises consisted of use of a quiet vessel, the 46' Hunter sailboat *Summer Breeze*, to study sperm whales using classical techniques (Figure 2.6; see Whitehead and Gordon 1986; Gordon 1987b). Scientists studied the social behavior of sperm whale groups as they followed as series of group for 1-3 days each. In addition to photographs, photogrammetry, passive acoustic recordings, and visual data, continuous near-surface temperature and CTD profiles were collected to ~50-m depth on these cruises. See Jochens and Biggs (2006) for details. A planned third summer of CEE experiments was not incorporated into the 2004 or 2005 SWSS fieldwork because SWSS federal funders decided to postpone additional CEE fieldwork until the recommendations of the Advisory Committee on Acoustic Impacts on Marine Mammals were available (see Advisory Committee on Acoustic Impacts on Marine Mammals 2006 and Marine Mammal Commission 2007). SWSS industry partners concurred, so no seismic vessel was provided to continue or extend CEE work in the Gulf in 2004 or 2005.

Figure 2.6. The 46' Hunter sailboat, *Summer Breeze*, used on the 2004 and 2005 MPS cruises.

2.4 Report Organization

The three annual reports for the Sperm Whale Seismic Study (SWSS) detail the program objectives, tasks, and participants, and the data collection and processing methods for the S-tag, D-tag/CEE, WSHC, and MPS cruises, as well as presenting preliminary technical discussions (Jochens and Biggs 2003, 2004, 2006). The SWSS Summary Report, 2002-2004, presents results by program elements, without extensive synthesis (Jochens et al. 2006). This report presents a synthesis for the SWSS project. Additional information is given in the written presentation summaries in the proceedings of the MMS Information Transfer Meetings (ITM) of 2003, 2005, and 2007 (McKay and Nides 2004, Sessions 2C and 2F; 2005, Sessions 1F and 2F; and 2007, SWSS Session). Information on SWAMP is available in the 2002 ITM proceedings (McKay and Nides 2003, Session 2F). All reports are available through MMS at the URL: *http://www.gomr.mms.gov/homepg/regulate/environ/techsumm/rec_pubs.html*.

Section 1 is the Executive Summary of the report. Section 2 gives an overview of the SWSS project, its participants and objectives, and a brief summary of the cruises and data collection activities. Section 3 provides an introduction to sperm whales and their environment in the Gulf of Mexico, as well as to sound in the ocean. Population characteristics are discussed in Section 4, and habitat use is described in section 5. Consideration of the responses of sperm whales to seismic airgun sounds is presented in Section 6. Section 7 gives the conclusions and recommendations. References are provided in Section 8.

Sections 2 and 7 and subsections 3.1, 4.1, 5.1, and 6.1 can be read together as a concise synthesis of the SWSS project. Other subsections in Sections 3, 4, 5, and 6 provide substantial detail on various aspects of the acoustic and physical environment and sperm whale biology, ecology, and behavior in the Gulf of Mexico.

3 INTRODUCTION TO SPERM WHALES IN THE GULF OF MEXICO

The sperm whale is the only endangered great whale that is common in the Gulf of Mexico. Among the characteristics of the Gulf that likely provide the food web structure necessary to sustain such a population are the contribution of the Mississippi River discharge to the biological productivity of oceanic waters and the eddy field that can transport this productivity off-shelf into the deep waters where the sperm whale resides. The concern of SWSS was to examine the sperm whale within this environment and to assess the response of the whale to sounds from seismic airgun arrays in an ocean that is filled with natural and other anthropogenic sounds. This chapter provides brief overviews of the sperm whale (Section 3.1), the physical and biological habitat (Section 3.2), and the acoustical environment of the Gulf (Section 3.3).

3.1 Introduction to the Sperm Whale

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General Information

Sperm whales (*Physeter macrocephalus*, or “blower, large-headed” derived from Greek) are the largest of the toothed whales, and also the largest toothed creature on Earth. They are highly sexually dimorphic, with males an average of about 15 m, and females about 11 m long; but larger specimens have been recorded in both sexes (Best 1979). Sperm whales have an enormous blunt head comprising about 25 to 35% of their body length. This head houses spermaceti oil, with similar density as seawater. We now know that, as first postulated by Norris and Harvey (1972), click sounds reflect off the skull and a front-of-head internal air-lined sac to reverberate from front to back (and to the front again) of this oil-filled head (Cranford 1999). This system gives each click a sub-click “mushy” structure that may enhance aspects of echolocation, and also has been used by others to determine sizes of clicking animals (Gordon 1991).

Sperm whales occur throughout much of deep water of the world’s oceans. Females and calves of both sexes tend to stay in the tropics and subtropics, while large males travel to cold-temperate and even polar waters. Females become sexually mature at about age 10, but males do not become fully sexually/socially mature until they are almost 30 years old. Thus, there is a high female to male reproductive ratio. Females routinely dive to about 500-800 m to feed on squid and fishes, while males tend to dive deeper. Maximum depths of dives may be greater than 2 km, but these are likely to be exceptions (Best 1979). A recent study by Watwood et al. (2006), supported in part by the SWSS project, reported on digital tag data from 37 whales: average dive cycle was 45 min below and 9 min breathing at surface, with >72% of time spent foraging.

Sperm whales come close to shore in some areas where the continental shelf is close to shore, such as due to escarpments or canyons. For example, off Kaikoura, New Zealand, there is a year-round gathering of maturing males, with individual males staying there up to about 10 years (Richter 2002). It is assumed that they came from female-calf groups in the tropics when they became too old to live with their mothers, and will leave towards higher latitudes to feed, and to intercept females in estrus in lower latitudes as they mature. They are “biding their time” in those productive waters. There are similar aggregations in other, at times even much more shallow, waters (e.g., off Long Island New York, in waters only 41-68 m deep, Scott and Sadove 1997).

One frequently asked question is “How many sperm whales are there?” This is a difficult question to answer, for estimates of sperm whale populations are imprecise, and rely on a mixture of catch-per-unit effort, age-specific and length-specific data gathering techniques, mark-recapture techniques (as employed by photography in the present studies), and aerial and shipboard surveys, as have traditionally been carried out in the past twenty years in U.S. waters including the Gulf of Mexico. Whitehead (2002, 2003) summarized these data, and came up with the most believable estimate available of approximately 300 to 450 thousand sperm whales in all the world’s oceans and seas.

Despite this apparently “robust” number worldwide, it represents many different non-interbreeding populations, and some of these are quite small. Sperm whales are listed as “Endangered” under the U.S. Endangered Species Act, due to numbers off U.S. coasts being quite small, at an estimated about 5000 off the northeastern U.S. (Waring et al. 2006), as few as about 1200 off California, Oregon, and Washington states (Barlow 1997), and about 1300 in the oceanic northern Gulf of Mexico (Mullin and Fulling 2004; Waring et al. 2006). Nevertheless, density of sperm whales off the eastern U.S. coast, at about 17 per 1000 km^2, is higher than has been reported elsewhere (Whitehead 2002). We stress that all of these estimates are imprecise, and shall get back to the Gulf of Mexico estimate later.

While there are numerous stories of sperm whales feeding on giant squid (Family Architeuthidae), these large deep-living squid are major prey in only two known sperm whale feeding areas, off the Azores and Hawai’i (Whitehead 2003), although they are taken now and then elsewhere (Ruiz-Cooley et al. 2006). While fishes are also taken, generally smaller and mostly active squid of 13 other Families form major and variable, by area, parts of diets. Overall, adult males have a more broad diet than do adult females, probably because of males’ deeper dive capabilities and larger seasonal migrations (Whitehead 2003). Off New Zealand, Iceland, and the northern North Pacific and Atlantic, fish form major parts of (especially male) sperm whale diet (Kawakami 1980).

We know much about diets of sperm whales, largely from the whaling literature of “factory whaling” of the early to middle part of the 20th Century. However, it is not known how sperm whales actually catch their prey. Sperm whales alter their acoustic output related to foraging, so we have some building data on when prey are taken. They have large conical teeth in the underslung thin lower jaw only, which teeth fit into sockets of the upper jaw. Perfectly well-fed sperm whales have been found with deformed and broken jaws that would make the grasping of prey impossible. It is surmised that sperm whales approach their prey and then suck them in, a supposition recently gaining credence by detailed analyses of the hyoid apparatus that functions importantly in suck-feeding dwarf/pygmy sperm whales of the Family Kogiidae, which have a somewhat similar (but not perfectly similar) upper body morphology to that of sperm whales (Bloodworth and Marshall 2005). Suction feeding would not negate the possibility that whales also rapidly surge towards their intended prey, in ram-feeding manner. An ambush strategy of attracting prey to the sperm whales' white lips (perhaps enhanced by bioluminescence of squid fed on previously) also seems plausible, and would operate in efficient manner with suction feeding (Gaskin 1967).

It has been known since the 19th Century that sperm whales form social units of females and young of both sexes, and that there are often-lone "roving" males (Clark 1887). The fierce protective nature of presumed mothers towards calves when threatened by harpoons was described, and – indeed – the *modus operandi* of whalers among female groups was to secure calves first so that mothers would not dive and escape.

Until recently, the most complete description of social organization came from Best (1979), who described all-male groups (as "bachelors" of variable physical and group sizes), juveniles, and mixed schools. Because almost all of Best's information came from whaling data, he obtained excellent information on physiologically immature *vs.* mature males at certain sizes, and whether females were pre-reproductive, pregnant, lactating, or reproductively resting. He described an apparent polygynous social system, with males attaching themselves to mixed schools largely composed of females and their offspring, and surmised that this polygyny was similar to that described by Bartholomew (1970) for the harem-like situation of several highly sexually dimorphic otariids (eared seals) and two species of phocids (true seals), the elephant seals (*Mirounga sp.*).

Whitehead (2003) and Gordon (1998) ushered in the modern era of studying sperm whale behavior, vocalizations, foraging patterns, movements, and social organization by largely benign techniques of photo-identification, sound recordings, and focal group and focal animal descriptors. They did so from a sailboat, at first off Sri Lanka, and Whitehead and colleagues later on in the tropical Pacific (summarized in Gordon 1998 and Whitehead 2003).

The wealth of new information to come from photo-identifcation and focal follow studies like these is staggering. It was learned that the mixed school is a female-based social unit of one dozen or more, with largely related individuals staying together for long periods of times, and less related individuals meeting now and then as casual acquaintances (for example, Whitehead et al. 1991). Males rove widely, apparently searching for females in estrus, and then often staying with the female-based groups for only short times of hours to days. This is not the classic "harem" and "master bull" situation described by Bartholomew (1970) for pinnipeds, but is instead a long-term matriarchal system of mothers taking care of their young. Since females may stay with their mother's group, this also brings up the capability for close female-based relatives to share in the taking care of nursing calves, and thus there is "auntying" behavior related to dive synchrony of some and indications of alloparental care ("babysitting") by others (Whitehead 1996a). The amount of male roving or staying with a matriarchate may be dependent on matriarchal group size, how many females are in estrus at one time, whether females allow non-reproductive matings, and the distances needed to travel between matriarchates (Whitehead 1990, 1998).

Groups of matriarchates in broadly similar areas from year to year, and fewer reproductive males than females (since males become mature much later), may lead to reproductive decline in certain years when, for example, food becomes scarce due to an El Niño Southern Oscillation event, females move, and the few reproductive males available cannot find them. Whitehead and colleagues speculate that such a scenario played out off the Galapagos several years ago, aggravated by low number of males harking back to whaling days of the 1950's - 1970's, and with abnormally low reproductive rates already since years of heavy whaling (Whitehead 2003).

When long-lived large-brained animals travel, feed, and socialize together, youngsters have the chance to learn from their mothers and other elders, and may then pass this information on to their offspring. This is the essence of culture, and it is now reasonably well established (one must be able to distinguish a learned behavior from a genetically transmitted one) that bottlenose dolphins (*Tursiops* sp.), humpback whales (*Megaptera novaeangliae*), killer whales (*Orcinus orca*), and sperm whales exhibit strong elements of culture. For sperm whales, culture may come in part through learned sequences of click sounds or codas shared among clans. These shared sound types may be a part of shared feeding habits, dive lengths, types of near-surface activities, or other behaviors (Whitehead 2003).

Some aspects of culture are not necessarily positive for animals in the face of human-caused (or other) environmental change. Much culture may have been erased due to wholesale whaling of cultural units, and animals culturally adapted to feed or live in a particular way or place may not efficiently adapt to the need for rapidly making changes. This has been described in human societies (for example, Flannery 1994), and may impact on cetaceans as well (Whitehead et al. 2004). Culture can even get whales into trouble with humans, such as the learned behavior of killer and sperm whales to take salmon from long line fisheries off Alaska (Thode 2004a, b).

Sperm Whales in the Gulf

Sperm whales of the Gulf of Mexico did not receive the attentions of sophisticated studies of occurrence, habitat use patterns, and behaviors until relatively recently, during the "Fritts" aerial surveys by the U.S. Fish and Wildlife Service, 1979-1981 (Collum and Fritts 1985); National Marine Fisheries Service (NMFS) aerial surveys that began with continental slope censuses in 1983; NMFS boat-based surveys that began in 1990; and Minerals Management Service/USGS Biological Research Division (MMS/BRD) surveys from 1991-1997 (Figures 3.1.1 and 3.1.2). The latter MMS/BRD surveys (for example, Davis et al. 1998, 2002) were the most comprehensive ones until the present SWSS studies of the new Century. They also, as the present work, included photo-identification and behavioral descriptions. It became apparent during these studies that sperm whales are by far the most common large cetacean in the Gulf.

From genetic data largely derived during SWSS, Engelhaupt (2004) and Engelhaupt and Hoelzel (Section 4.2) showed that Gulf of Mexico sperm whales form an isolated or near-isolated population separate from the adjacent open waters of the North Atlantic. These data, as almost all gathered to date, rely almost exclusively on sperm whales from the northern Gulf, with greatest density along and deeper than the 1000 m depth contour, and do not adequately represent sperm whales that may occur regularly in the central, western, southern, or eastern Gulf (for example, Ortega-Ortiz 2003). It is very likely, though, that sperm whales of the north-central Gulf, present there throughout the year (Davis et al. 1998), are more numerous than in other parts of the Gulf.

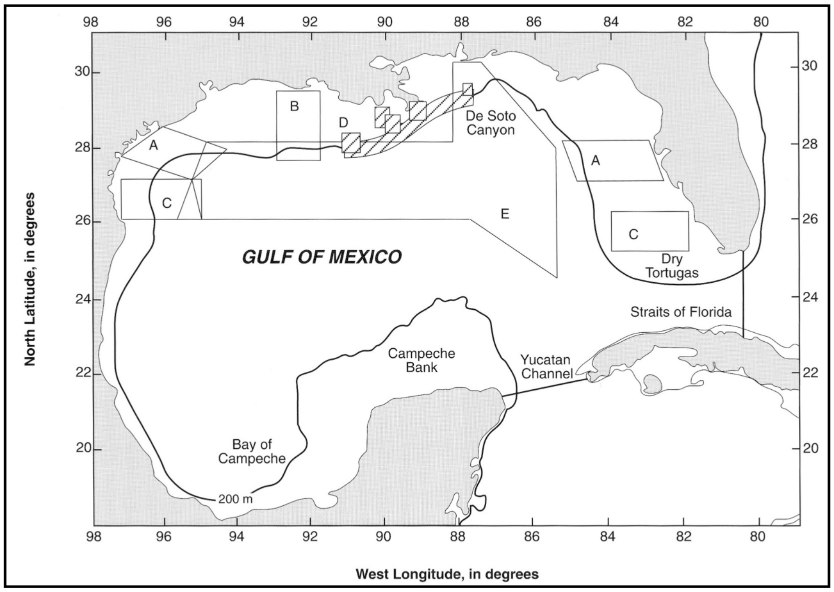

Figure 3.1.1. Locations of survey blocks from various studies. "A", "B", and "C" represent the Fritts surveys; "D" coastal surveys of 1989-1990 (hatched); and "E" NMFS surveys of 1990-1994. Courtesy Cartographic Service Unit, Department of Geography, Texas A&M University; and Würsig et al. 2000.

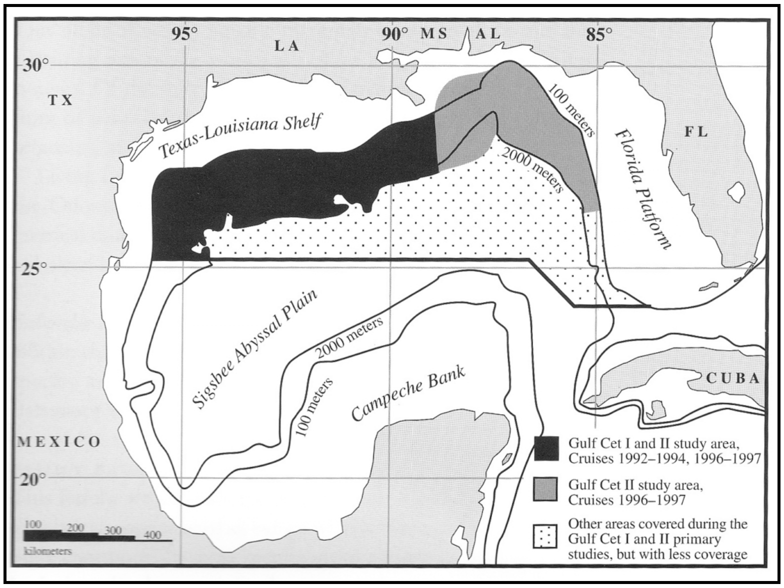

Figure 3.1.2. The GulfCet I and GulfCet II study areas, 1992-1997. There have been multiple other smaller studies in the northern as well as southern (Mexican) Gulf, not represented here. Map by Donald Frazier, and Würsig et al. 2000.

As was mentioned for worldwide population estimates, we do not know how many sperm whales there are in the northern Gulf, nor the entire Gulf. This is exacerbated by the fact that numbers and distributions can change, as they did in the anomalous low productivity and low sperm whale year of 2005 in the northern Gulf (further described in Sections 4.3, 4.6, 4.7, and 5.5). In this case, we assume that the animals moved elsewhere in the Gulf, and were simply not sighted due to our limited area of research coverage. Nevertheless, a current (and "believable") estimate derived largely from line transect surveys, is of approximately 1349 (Coefficient of Variation=0.23) sperm whales Gulf-wide, and a minimum abundance estimate for the northern Gulf of 1114 (Mullin and Fulling 2004, Waring et al. 2006).

While it was already hinted from GulfCet studies (Biggs et al. 2000), Biggs et al. (2005) recently showed that distribution of sperm whales is correlated with mesoscale physical features such as eddies associated with the Gulf of Mexico Loop Current that enters through the Yucatan Channel and exits at the Strait of Florida. Such eddies, perhaps especially the shear zones between warm and cold eddies, present locally increased primary productivity. Primary productivity is likely to be closely associated, perhaps often with a lag in time, with greater sperm whale prey. This topic is explored in more detail in Section 5 of this report. Jaquet and Whitehead (1996) suggested a similar association of sperm whales with environmental features and productivity in the South Pacific, and stressed that it is important to accurately assess scales of space and time for biologically most-meaningful comparisons. Jaquet and Gendron (2002) found some correlation with sperm whale aggregations and jumbo squid (*Dosidicus gigas*) in the Gulf of California, and it will be of interest to search for similar associations in the Gulf of Mexico.

It was noticed since at least the early 1990's that sperm whales of the northern Gulf appeared quite small, with no or at least very few fully mature "large" males (Würsig, personal observation). That animals, possibly even mature females, tend to be smaller than elsewhere was suggested from photogrammetric data (Jaquet 2006). Engelhaupt and Hoelzel (Section 4.2) found from genetic sampling of 150 sperm whales in the northern Gulf, that 72% were females and 28% were males. This is not an unexpected ratio, as sperm whale matriarchal groups are known to be most common in more tropical latitudes, and adult males are relatively rare there. Furthermore, it was the researchers' overall impression that males that were sampled genetically did not appear to be fully mature. However, the very existence of matriarchal groups with young animals indicates that reproductive males are coming into the area at times, although they were undetected by SWSS research efforts.

The recent Engelhaupt and Hoelzel study (Section 4.2) is the first to shed light on group composition of sperm whales in the northern Gulf. As had been suggested previously (Weller et al. 2000, Würsig et al. 2000) but is now indicated more strongly, most encountered groups fit a mixed-sex model of unrelated and, to a lesser degree, related adult females and young of both sexes. However, apparent all-male "bachelor groups" (*sensu* Best 1979) used the same lower latitude feeding grounds of the northern Gulf, and this result is somewhat unexpected in light of published research from elsewhere, where all male groups are in generally higher latitudes than the matriarchal societies (summarized by Whitehead 2003). Mate and Ortega-Ortiz (Section 4.3) showed from satellite-tracked whales that females had core areas averaging around 8000 km^2, while males had core areas approximately 5 times as large. Two males traveled across much of the extent of the Gulf, and one even went into the open Atlantic Ocean. These data agree with the general assessments of habitat use patterns of matriarchal societies vs. maturing and especially mature males elsewhere, and are not at all surprising.

It is not yet known what are the major prey of sperm whales in the northern Gulf, although we assume that there is much variability depending on habitat and aspects of productivity. Miller et al (Section 5.2) and Benoit-Bird and Ortega-Ortiz (Section 5.3) showed that sperm whales travel to depths of high potential prey density, and that they often forage below the uppermost deep scattering layer that migrates vertically on a diel basis. Thus, it is likely that sperm whales feed both day and night, simply because they are able to sustain long dives. Watwood et al. (2006) studied dive depths with D-tags as associated with click-rate/type indicators of foraging in three regions: the Mediterranean Ligurian Sea (12 deployments), the open Atlantic Ocean (8 deployments), and the northern Gulf (29 deployments). While there were no significant differences among areas for duration of foraging dives and overall duration of foraging, Gulf of Mexico sperm whales dove less deeply (average = 644 m) than in the Ligurian Sea and Atlantic Ocean (827 and 985 m, respectively). We caution that while such data from individual tags is of value, they are short term (lasting only about 3 to 6.5 hrs. per tag deployment), and thereby represent "snapshots" of behavior that need to be corroborated by other observational and telemetry tagging means.

3.2 Overview of Physical and Biological Oceanographic Habitat

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3.2.1 Introduction

In this section, we present general aspects of the physical circulation and the remotely sensed biological habitat in the Gulf of Mexico, and we comment on how the average conditions vary in both time and space. In preparing this synopsis, we have drawn upon oceanographic data collected in summers 2002-2005 over the continental slope along the ship track of the research vessel R/V *Gyre* during SWSS visual and acoustic surveys for sperm whales. We have supplemented these ship data with sea surface height (SSH), sea surface temperature (SST), and sea surface chlorophyll (SSC) data that are sensed remotely in near-real-time from satellites in earth orbit and with predictions from a Gulf of Mexico nowcast/forecast model. Our purpose here is to highlight when and where summer-to-summer differences in the basin-wide physical and biological oceanographic conditions occurred along the 1000-m isobath of the northern Gulf.

In Section 5.5 of this synthesis report, we focus on climatic drivers for the variations in physical and biological habitat in summers 2002-2005. Section 4.3 will describe the ranges traveled by some nearly six dozen sperm whales after they were radio-tagged in summers 2002-2005.

Combined ship and satellite measurements tell us that on average about 3 x 10^7 m^3 s^{-1} (30 Sverdrups) of warm, salty water of Caribbean origin enters the Gulf of Mexico through the Yucatan Channel, flows north into the eastern Gulf of Mexico, and then turns clockwise to exit the Gulf through the Straits of Florida (Sturges et al. 2005). The intrusions of this subtropical Loop Current inflow can be monitored by altimeters in earth orbit. Altimeter data for the Gulf have demonstrated that the metrics of Loop Current velocity and geometry vary stochastically from year to year (Leben 2005). About every 9-15 months, the turbulence in this inflow causes the separation of an anticyclonic Loop Current Eddy (LCE). We summarize here how these LCEs influenced the circulation along the continental margin of the northern Gulf in summers 2002-2005, and argue that the eddy field in combination with interannual variations in Mississippi River discharge resulted in striking summer-to-summer differences during 2002-2005 in along-margin salinity and the locations of off-margin flow.

Biggs and Ressler (2001) reviewed the deepwater biological literature to demonstrate that the peripheral regions of high-velocity surface currents that surround Gulf eddies are often “hot spots” of higher-than-average primary production, which may develop in response to the nutrient enrichment from cross-isopycnal mixing. They reported that elevated zooplankton and fish stocks, in turn, appear to concentrate in such areas, and in upwelling regions of semi-permanent mesoscale cyclonic circulation. They also reported that cyclonic eddies that form and propagate along the Loop Current margin may be especially important in biological recruitment and retention. We will show how relative acoustic backscatter intensity data, which can be collected by a hull-mounted acoustic Doppler current meter (ADCP), allowed study of subsurface biological scattering from layers of zooplankton-size and fish-size targets during the visual and acoustic surveys for sperm whales in 2002-2005.

3.2.2 Methods

In summers 2002-2005, TAMU R/V *Gyre* dropped XBTs and logged ADCP data while carrying out visual and passive-acoustic surveys for sperm whales along the 1000-m isobath of the northern Gulf. The research vessel also made CTD casts, particularly when/where the XBT and ADCP data indicated the surveys were passing into or out of anticyclonic and/or cyclonic slope eddies. The fine-scale resolution of the ship surveys, when combined with the meso-scale resolution of remote sensing surveys of SSH and ocean color, document there was summer-to-summer variability in the intensity and geographic location of Loop Current eddies, warm slope eddies, and areas of cyclonic circulation over this middle slope region of the northern Gulf. Biggs et al. (2005) summarized how these variations forced striking year-to-year differences in 2002 and 2003 in the locations along the 1000-m isobath where there was on-margin and off-margin flow, and in locations where sperm whales were encountered along the 1000-m isobath (see also Section 3.1 of the SWSS Summary Report in Jochens et al. 2006). In this synopsis, we summarize the summer 2004 and 2005 conditions to continue and extend that previous analysis.

For the basin-wide views of SSH and sea surface salinity (SSS) that are presented as Figures 3.2.1 and 3.2.2 in this overview, we have utilized the model outputs from an experimental real-time northern Gulf of Mexico ocean nowcast/forecast system (NGOMNFS). NGOMNFS is a fully automated end-to-end ocean prediction system that is run at the US Naval Research Laboratory, Oceanography Division, at the Stennis Space Center. This is a 1/72 degree (~1.9 km resolution), 38-level sigma-z data-assimilating ocean simulation based on the Navy Coastal Ocean Model (NCOM). Real-time data come from satellite altimeter SSH and SST, and three hourly surface heat fluxes, including solar radiation, wind stresses, and sea level air pressure, are applied for surface forcing (Ko et al. 2003). There are 116 rivers or freshwater runoff points, each with daily to weekly discharge data, that are included in the NGOMNFS forcing. Once the nowcast/forecast visualizations are produced, they are posted to the NRL internet website: *http://www.7320.nrlssc.navy.mil/IASNFS_WWW/NGOMNFS_WWW/NGOMNFS.html.*

The NGOMNFS model does not incorporate SSC data as a boundary condition, nor does it nowcast/forecast SSC fields. But for this basin-wide overview, we compare the NGOMNFS model output sea surface salinity (SSS) fields with the appropriate biweekly composites of basin-wide SSC imagery processed by our colleagues Hu and Müller-Karger at USF. They archived SeaWiFS composites for the seven year period October 1997 - September 2004 as an appendix to the report by Biggs et al. (2005); they also provided the biweekly composite image for June 2005.

Acoustic backscatter data that allow one to visualize the depth of subsurface biological deep scattering layers (DSLs) were collected concurrently with ADCP measurements of current speed and direction from R/V *Gyre* in summers 2002-2005. These were the first-ever biological backscatter surveys with a 38-kHz ADCP in the Gulf of Mexico, which we found can measure relative acoustic backscatter intensity (RABI) as deep as 1300 meters. The daytime depth of the main deep scattering layer at 400-500 m was easily resolved, and some secondary, deeper layers of locally high backscatter were seen down to 800 m. Theses by Kaltenberg (2004) and Azzara (2006) have detailed the general patterns and described how these patterns vary in time and space, using backscatter measurements in summers 2002 and 2003, and in summers 2004 and 2005, respectively. The objectives of their thesis research were 1) to determine how to analyze RABI from the instrument to resolve scattering layers, and 2) to survey for secondary, deeper layers of locally high backscatter that might indicate the presence of potential prey species in the 600 to 1000 m deep foraging range for Gulf of Mexico sperm whales.

3.2.3 Results

Basin-wide Views of Sea Surface Height

In each of the summers 2002-2005, SSH along the continental slope of the northern Gulf was generally 5-20 cm lower than the average SSH for the basin. This is shown in false color by the predominance of dark blue shades along the 1000-m isobath in each of the four panels of Figure 3.2.1, compared with what would be light blue to green to yellow false color were the region to be at close to background (zero anomaly) SSH. Lower than average SSH is indicative of cyclonic (upwelling or biological oasis) conditions along the 1000-m isobath. Higher than average SSH, which is characteristic of the Loop Current and the LCEs that separate from this tropical inflow, is indicative of anticyclonic (downwelling or biological desert) conditions.

In two of the four summers 2002-2005, the Loop Current extended so far north that its northernmost extension or a recently shed LCE reached the 1000-m isobath close off Mississippi River delta. Panel B of Figure 3.2.1 shows recently-separated LCE-S (a.k.a. "Eddy Sargassum") just SE of the delta in summer 2003, where it interacted with the upper continental slope between 90°W and 86°W. Look closely at Panel B to see that in early June 2003, the NW periphery of LCE-S extends up slope to almost the 500-m isobath in Mississippi Canyon. As Biggs et al. (2005) verified from shipboard measurements, this interaction flushed the canyon with low-nutrient, biologically impoverished Caribbean water that was advected north when LCE-S was still attached to the Loop Current. A similar on-margin flow of Caribbean water is evident in early June 2005, when an LCE still attached to the main Loop Current again flushed the 1000-m isobath southeast of the Mississippi River Delta with biologically impoverished blue water (Panel D of Figure 3.2.1).

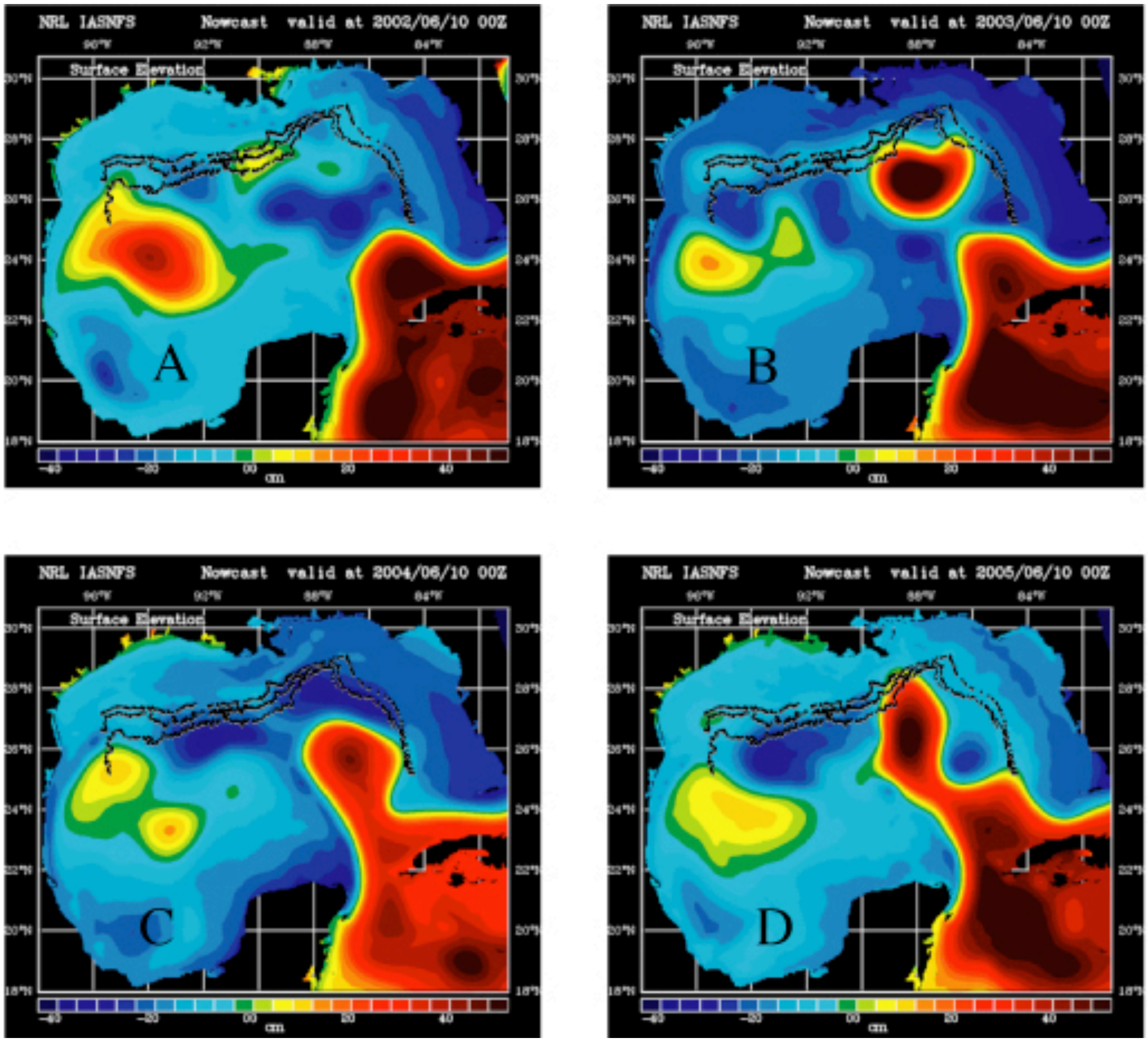

Figure 3.2.1. Basin-wide views of sea surface height in early June in each of summers A) 2002, B) 2003, C) 2004, and D) 2005. These are model outputs from an experimental real-time northern Gulf of Mexico ocean nowcast/forecast system (NGOMNFS). The 500, 1000, and 1500 m bathymetry is indicated.

After they separate from the Loop Current, most LCEs drift west and eventually end up in the "eddy graveyard" in the far northwestern Gulf. In early June of each of summers 2002-2005, Figure 3.2.1 shows that an area of elevated SSH was centered near 24°N in the far western Gulf. The warm eddy region that was largest in size and highest in SSH in the far western Gulf in these four summers occurred in June 2002 (Panel A of Figure 3.2.1), after "Quick Eddy" and "Eddy QE2" that were shed from the Loop Current in February-March 2002 combined and ended up in the northern part of the Bay of Campeche. In subsequent summers 2003-2005, these LCEs in the far western Gulf were much smaller in size and less elevated in SSH (Panels B, C, and D of Figure 3.2.1). Because none of our SWSS surveys extended south of 26°N, however, we cannot confirm whether this eddy graveyard in the far western Gulf was a region of locally low sperm whale abundance. We have only anecdotal evidence from the trajectories of radio-tagged whales that few S-tagged animals ventured into the region south of 24°N (see Section 4.3).

Basin-wide Views of Sea Surface Salinity

Summer-to-summer variability in the intensity and geographic location of the Loop Current, LCEs, warm slope eddies, and areas of cyclonic circulation over the continental margin of the northern Gulf, in combination with summer-to-summer differences in the volume of Mississippi River discharge, forced differences in the locations along the slope where there was on-margin and off-margin flow. During summers 2002-2004 when normal or above average volumes of freshwater were discharged onto the continental shelf, flow at the shelf-slope break was mostly off-margin and the eddy field over the middle slope often entrained this low salinity shelf water and transported it out into very deep water. Panels A, B, and C in Figure 3.2.2 show that salinity < 35 stretched for large areas along the 1000-m isobath, and that some of this low salinity water was carried into deeper water as eddies mediated its transport off margin as surface jets and squirts. During summer 2005, when drought conditions reduced river discharge well below average, flow was mostly on-margin and the salinity was > 35.5 for large areas along the 1000-m isobath. The striking exception to this generality was summer 2003, when LCE-S interacted with the continental margin south of the Mississippi River Delta and pumped Caribbean water with surface salinity > 35.5 into Mississippi Canyon (compare Panel B in Figures 3.2.1 and 3.2.2).

The average cumulative monthly Mississippi River discharge for May of the last 26 years 1980-2005 was 57.5 ± 20.9 km^3. Figure 3.2.3 illustrates that the annually highest monthly cumulative Mississippi River discharge generally occurs in March-April-May, and the lowest in August-September-October. Because flow gauged by the U.S. Army Corps of Engineers at this location takes about 1-2 weeks to enter the Gulf, we regard the cumulative May discharge as a proxy for the volume of freshwater on the continental shelf in the month of June. Table 3.2.1 shows that cumulative river discharge in summers 2002, 2003 and 2004 ranged from about 12% below to 18% above average. However, cumulative discharge in May 2005 was only 59% of average and so was more than one standard deviation less than the average May discharge for the period 1980-2005. As a result, in summer 2005 only in the eastern reaches of De Soto Canyon and in the far western Gulf was surface salinity over the upper slope reduced to < 35.5 (Panel D, Figure 3.2.2). In the east the lower salinity continental shelf water was pulled offshore by entrainment into the LCE that was still attached to the Loop Current, and in the far western Gulf by the enhanced off-margin surface flow set up by a counter-rotating cyclone-anticyclone eddy modon pair.

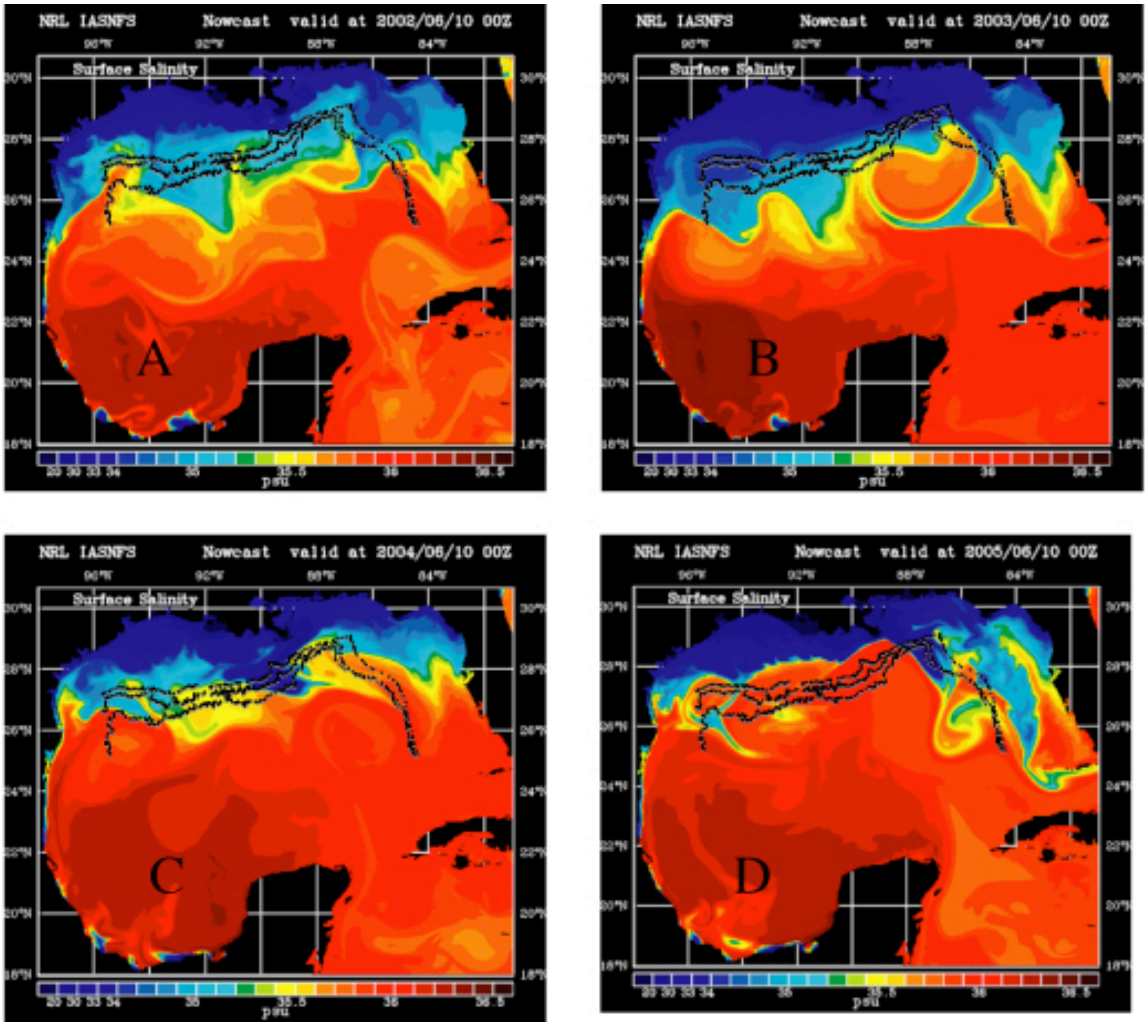

Figure 3.2.2. Basin-wide views of sea surface salinity in early June in each of summers A) 2002, B) 2003, C) 2004, and D) 2005. These are model outputs from an experimental real-time northern Gulf of Mexico ocean nowcast/forecast system (NGOMNFS). The 500, 1000, and 1500 m bathymetry is indicated.

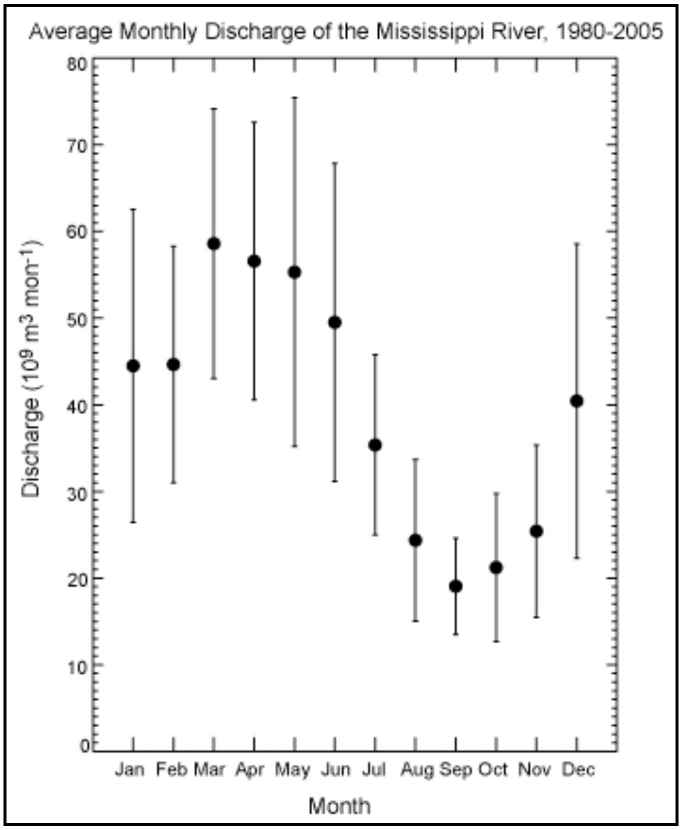

Figure 3.2.3. Monthly mean discharge of the Mississippi River at Tarbert Landing, MS, (as km^3 per month, plus or minus one standard deviation) for the period, 1980-2005. Data from the U.S. Army Corps of Engineers.

Table 3.2.1

Mississippi River Freshwater Discharge to the Northern Gulf of Mexico in May, as Gauged by the U.S. Army Corps of Engineers at Tarbert Landing, Mississippi

Year	May Discharge (km^3)	Discharge as % of mean for May
2002	68.1	118%
2003	56.4	98%
2004	50.5	88%
2005	34.0	59%

Basin-wide views of Sea Surface Chlorophyll

The four panels of Figure 3.2.4 show basin-wide views of SSC for early June 2002-2005. The inverse spatial and temporal correlation between SSS and SSC is very high, so that as a result locally low SSS generally corresponds to locally high SSC, and vice versa. In other words, low salinity water almost always corresponds to “green” or “brown” water, and high salinity water almost always corresponds to “blue” water. Because the low salinity boundary condition started with higher concentrations of river-derived essential plant nutrients, these “green” or “brown” waters are biological oases, while the high salinity boundary condition or “blue” water is generally a biological desert because it is nutrient-impoverished.

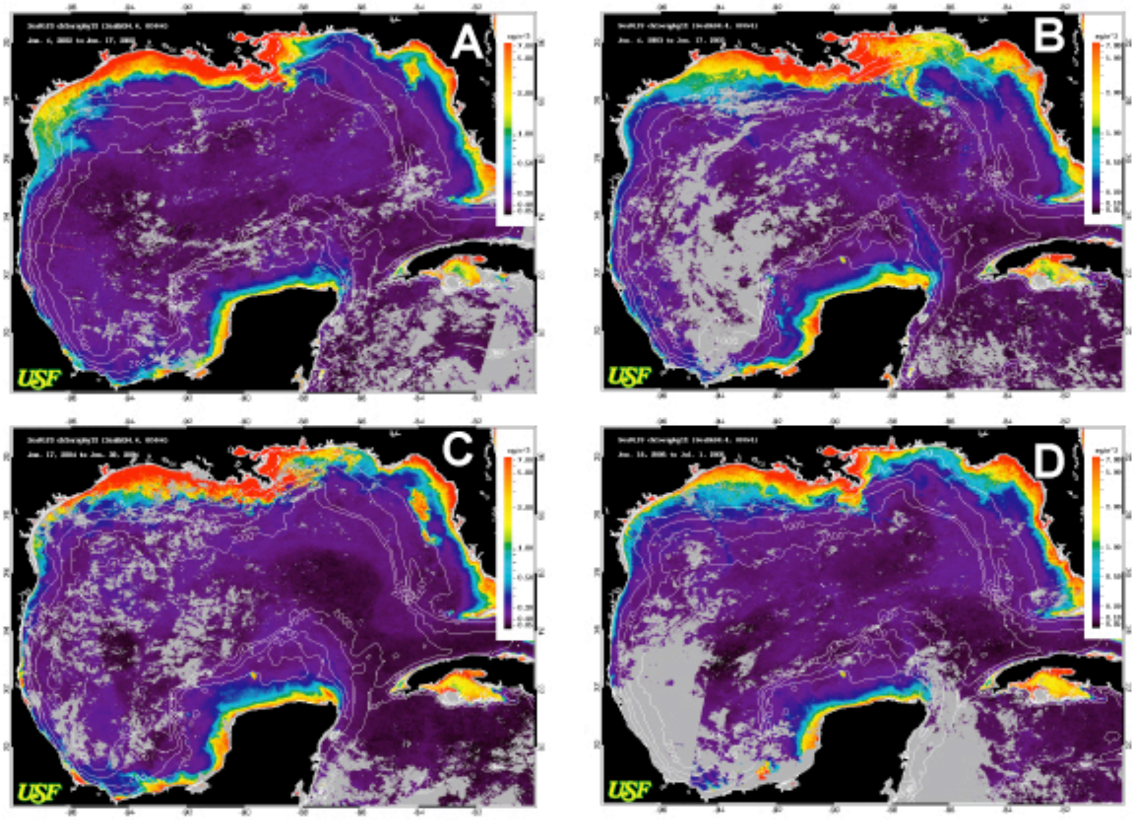

Figure 3.2.4. Basin-wide, biweekly composite views of sea surface chlorophyll in early June in each of summers A) 2002, B) 2003, C) 2004, and D) 2005.

Subsurface Acoustic Backscatter

Figure 3.2.5 (after Azzara 2006) presents an example of a running plot of relative acoustic backscatter intensity (RABI) from the 38-kHz ADCP. This figure shows data collected in summer 2005 beginning about two hours after sunrise to just before sunset on 9 June. The main daytime deep scattering layer (DSL) can be seen at 400-500 m, as can secondary scattering layers below this depth. When the ship was underway at speeds > 6 knots, the RABI signal is degraded (these periods show up as vertical lines of high signal, but which are in fact low RABI signal-to-noise). The best data were collected when ship speeds were < 4 knots. As sunset approaches, the upward vertical migration of the some of the biological scatterers that comprise the main daytime DSL is evident, beginning about 9 hours into the record (about 17:26 local time) and continuing until the record ends at dusk, at 20:16.

Figure 3.2.6 (from Kaltenberg 2004) presents a comparison of the depth of the main daytime DSL in a region of anticyclonic circulation (middle panel) with that in a region of cyclonic circulation (bottom panel). Both running plots of RABI begin at local midnight and continue for 24 hours. Both show the before-dawn downward migration of biological scatterers from surface waters into the main DSL, and the upward migration of some of these scatterers again near dusk. Kaltenberg (2004) could find no marked differences in the daytime depth of the main DSL in these two boundary conditions of circulation, or in its daytime vertical thickness, although she reported that overall RABI was generally higher in the upper 500 m in cyclonic than in anticyclonic circulations. Kaltenberg (2004) also reported that secondary, deeper DSLs were present below the daytime depth of the main DSL roughly 2/3 of the survey days in water depths of 600-1000 m, compared to only about 1/5 of the time that surveys spent in water depths > 1000 m. She also noted that secondary, deeper DSLs were more often seen when SWSS surveys in summers 2002 and 2003 were in cyclonic (lower SSH) circulations than in anticyclonic (high SSH) circulations.

Figure 3.2.7 (after Azzara 2006) presents running plots of 38-kHz ADCP RABI collected over water depths of 700-1000 m in summer 2004, over water depths > 1300 m in summer 2004, and inside an area of cyclonic circulation over water depth about 1300 m in summer 2005. All three panels show the presence of secondary, deeper DSLs below the daytime depth of the main DSL. Azzara (2006) emphasized that RABI was generally higher throughout the water column, making the main daytime DSL less distinct, when SWSS fieldwork in 2004 and 2005 surveyed the middle slope (water depths 600-900 m) than when fieldwork was in deep water (water depths > 1200 m). Most of the summer 2005 fieldwork was in an area of cyclonic circulation (low SSH, high SSC), and Azzara's data show that RABI there generally indicates the presence of secondary, deeper DSLs below the daytime depth of the main DSL.

3.2.4 Discussion

Because summer 2005 was a drought year, Mississippi River discharge during May was only 59% of average and only 69% of average for the three month period of May-June-July than those in previous summers 2002-2004. Because of this low river discharge, combined with the fact that the Loop Current had penetrated far north into the eastern Gulf, most of the 1000-m isobath in summer 2005 was flushed by biologically-impoverished, high SSS, blue water, and fewer sperm whales were encountered in summer 2005 along the 1000-m isobath of the northern Gulf than in previous summers 2002-2004. Whales were locally abundant only in and around an area of cyclonic circulation (biological oasis) in the far western Gulf. These western Gulf whales were not animals that had been seen in previous summers along the central and eastern parts of the northern Gulf. Photo-ID of the animals encountered in the cyclone in 2005 gave only 3 matches with animals seen in previous summers 2002-2004. This suggests that most animals regularly seen along the 1000-m isobath in previous summers 2002-2004 had gone elsewhere (perhaps out into deeper water), rather than migrating west into the far western Gulf and the cyclonic conditions there. The combination of genetic data (Section 4.2), radio-tagged trajectory data (Section 4.3), and photo-ID data (Sections 4.4, 4.5, and 4.6) generally support this hypothesis.

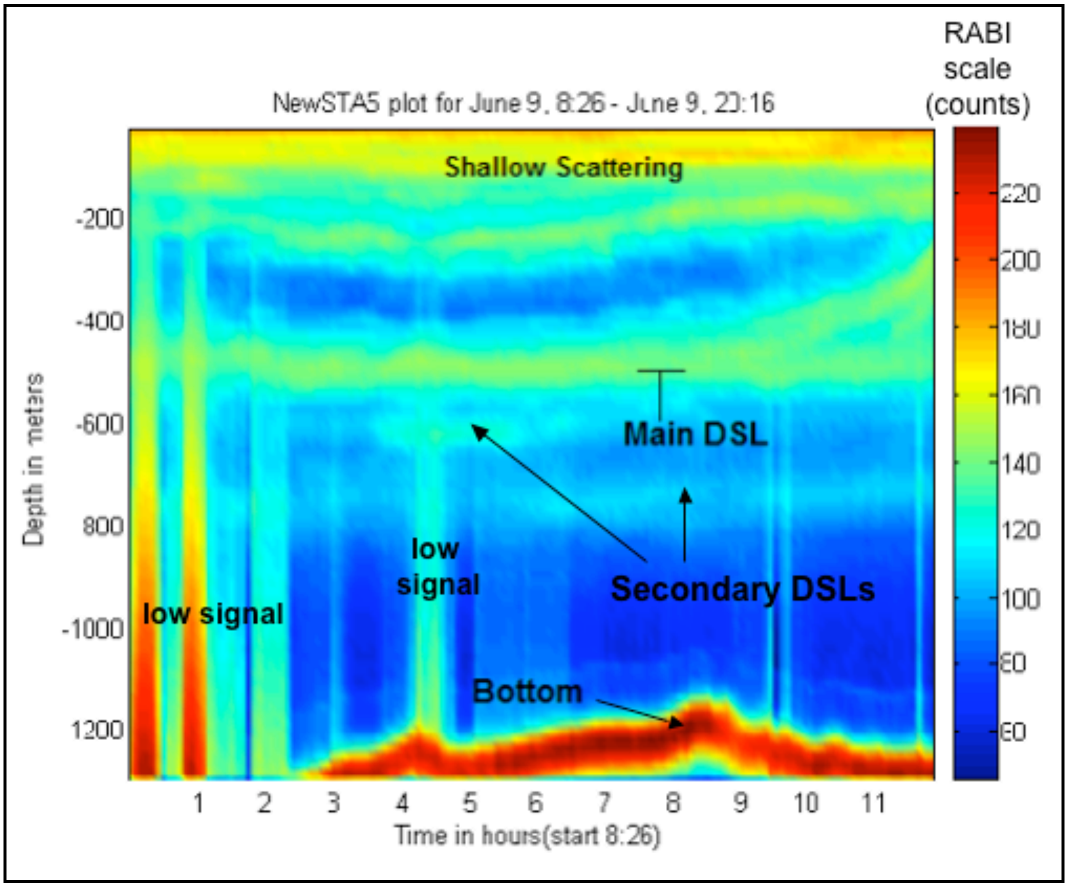

Figure 3.2.5. Example of 38-kHz ADCP Relative Acoustic Backscatter Intensity (RABI) running plot, showing data collected in summer 2005 from about two hours after sunrise to just before sunset on 9 June. The main daytime deep scattering layer (Main DSL) can be seen at 400-500 m, as can some secondary scattering layers below this depth. Times the ship was underway at speeds > 6 knots show up as vertical lines of low signal to noise; the best data were collected when ship speeds were < 4 knots. After Azzara (2006).

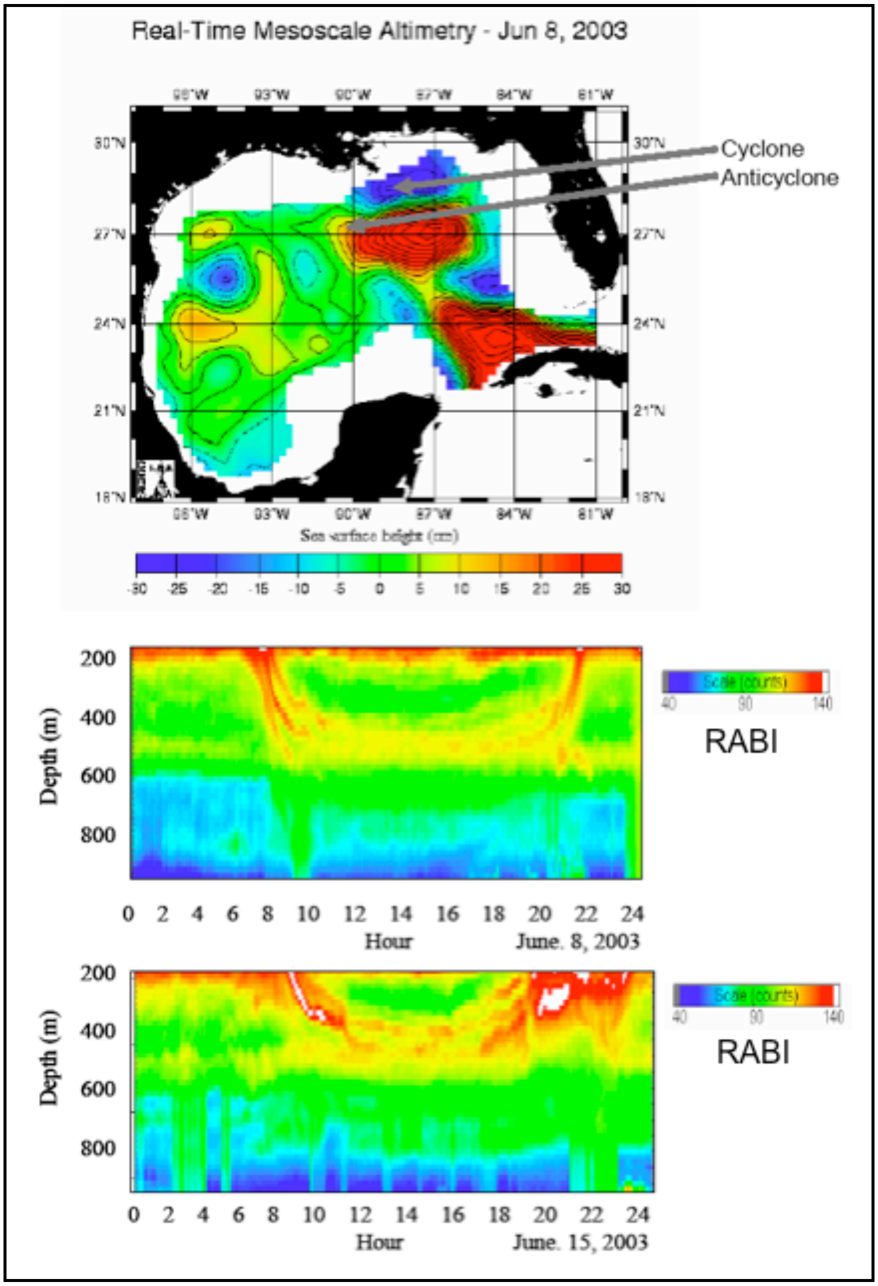

Figure 3.2.6. Running plots of 38-kHz ADCP RABI beginning at local midnight in an area of anticyclonic (high SSH) circulation (middle panel) and of cyclonic (low SSH) circulation (bottom panel) during summer 2003. After Kaltenberg (2004).

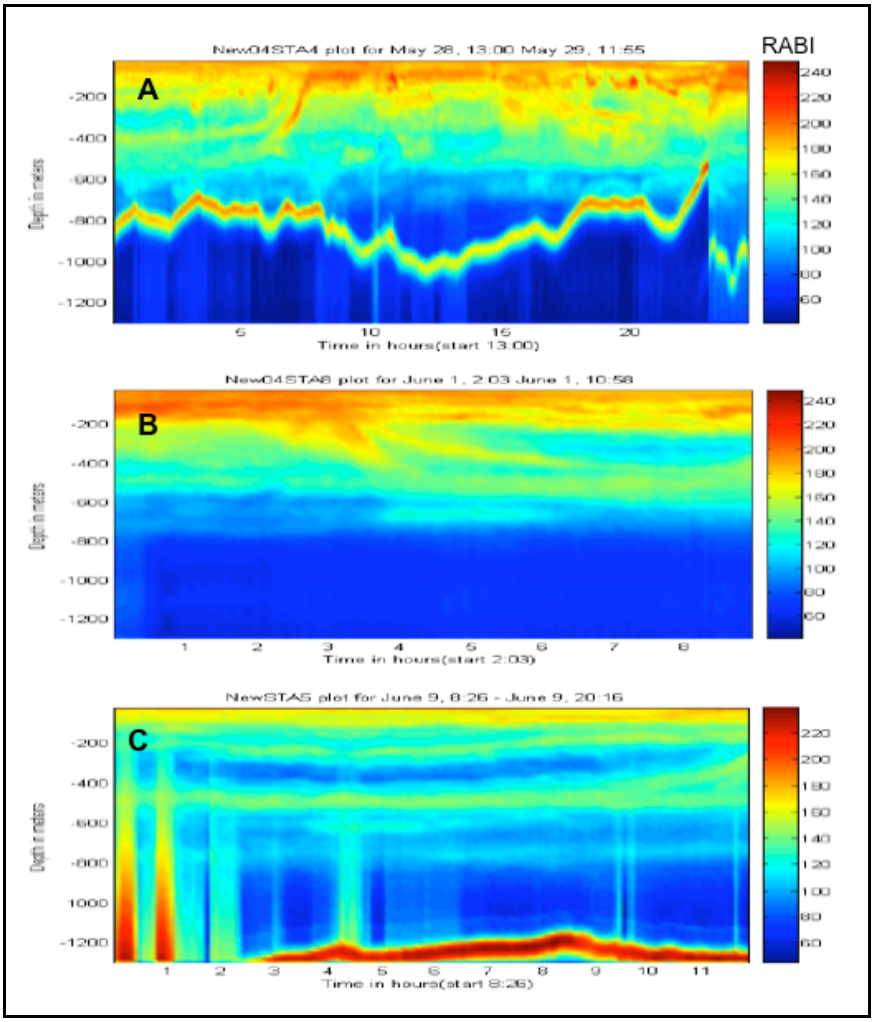

Figure 3.2.7. Running plots of 38-kHz ADCP RABI collected A) over water depths of 700-1000 m in summer 2004; B) over water depths > 1300 m in summer 2004; C) inside an area of cyclonic circulation over water depths of 1200-1300 m in summer 2005. After Azzara (2006).

The acoustic backscatter data of Kaltenberg (2004) and Azzara (2006) show that biological scatterers are generally aggregated into a daytime main DSL that occurs at depths of 400-500 m. This main DSL occurs at about the same depth in cyclonic as well as anticyclonic eddies, and some of the scatterers in both kinds of eddies migrate shallower at night and return again before dawn the next morning. Based on D-tag data (Watwood et al. 2006) we think that most Gulf of Mexico sperm whales generally dive to depths > 500 m both day and night. Most animals thus apparently are not keying their foraging behavior to the main DSL. The secondary, deeper scattering layers that show up as faint RABI signals below the main DSL may be the target of deep foraging whales, or these secondary, deeper scattering layers may be prey items that are fed upon by the deep-living prey that the whales are diving to find (see also Section 5.2). Better vertical resolution than is available from the 38-kHz ADCP at depths greater than 500 m is beginning to answer such questions (see Section 5.3).

3.3 Background on the Acoustical Environment in the Gulf of Mexico

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Electromagnetic (light) and mechanical (sound) wave energy transmits information in the atmosphere and ocean. Unlike the atmosphere, the ocean is essentially opaque to light, which is attenuated within a few tens of meters from its source in water. Sound energy, however, propagates efficiently over large distances, making the ocean acoustically transparent (e.g., Medwin 2005). The propagation paths are largely determined by the sound speed structure of the water column and the characteristics of the interfaces between the atmosphere and ocean and the seafloor and the ocean. Provided here is a brief summary of the sound speed structure in the Gulf of Mexico and effects on propagation. The complexities of sound transmission in the ocean are not given. Interested readers should refer to standard works such as Urick (1975), Clay and Medwin (1977), and Medwin (2005) for details.

Sound Speed Structure: Sound travels at speeds of the order of 1500 m s^{-1} in sea water as compared to approximately 340 m s^{-1} in air at sea level. Sound is transmitted through the water at speeds that are dependent upon temperature, pressure and salinity. Sound speed increases with increasing pressure, temperature, or salinity. In the Gulf of Mexico, as is typical of other subtropical waters, the speed increases with depth in the upper mixed layer due to the increase of pressure. In the main thermocline, the characteristic rapid decrease in temperature results in a decrease in sound speed. Below the main thermocline, where temperature gradients are small, the increase in pressure with depth again results in an increase in sound speed. Salinity typically has a lesser effect on sound speed and usually is not a controlling parameter. These characteristic patterns can be seen in Figure 3.3.1, which shows the sound speeds with depth that were derived from CTD measurements taken during the SWSS cruises in 2002-2005. These are typical of patterns observed in the Gulf of Mexico from historical measurements (see, e.g., Caruthers et al. 2002). During the SWSS project, sperm whales were frequently encountered in water depths on the order of 1 km or less. From Figure 3.3.1, one sees that under these circumstances the sound speed minimum, if it exists, would be at or near the ocean bottom, with the consequence that sound speed monotonically decreases with depth in the ocean column, except at depths shallower than the surface thermocline (20 m or less).

The actual speed at a given time and place in the ocean varies, especially in the upper 1000 m that is influenced by eddy features and seasonal variations such as in river discharge and heating and cooling. In the Gulf, sound speeds near the surface fluctuate seasonally, with typical values of 1530 m s^{-1} or less in winter and 1550 m s^{-1} in summer (U.S. Dept. of the Navy, Naval Oceanographic Office 1972). The Mississippi River discharge can be seen in the near surface waters as low sound speeds, particularly near the coast (U.S. Dept. of the Navy, Naval Oceanographic Office 1972). Anticyclonic circulation features, such as the Loop Current and Loop Current Eddies, have warm cores that result in higher sound speeds than in surrounding waters; cyclonic features with cold cores have the opposite (e.g., Jochens 1989; Caruthers et al. 2002; Renteria 1978). The variation in sound speed at a given depth is greatest in the main thermocline (Figure 3.3.1; Caruthers et al. 2002).

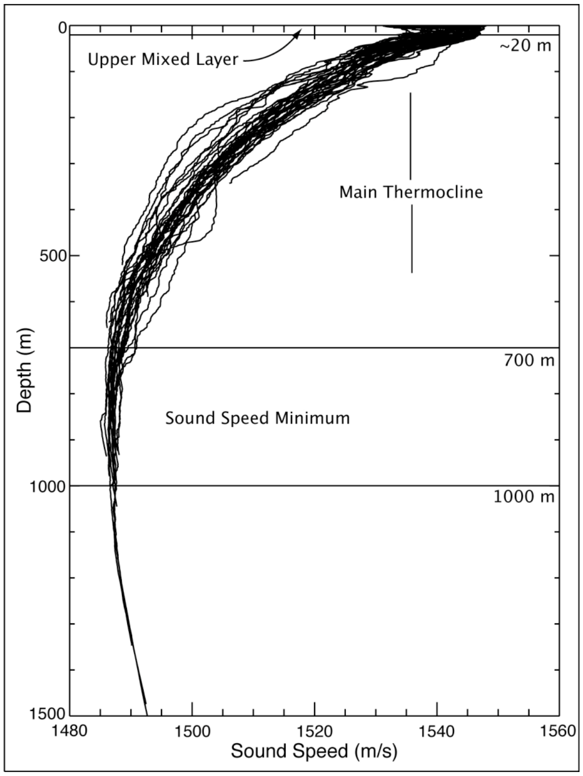


Figure 3.3.1. Sound speed profiles from the SWSS study area in summers 2002-2005. Profiles were derived from pressure, temperature, and conductivity measurements made using a SeaCat CTD at stations on SWSS cruises.

Sound waves traveling through the water are refracted when they encounter changes in the sound speed environment. They are bent toward regions of lower sound speed. Off the shelf, a deep sound speed minimum is found in the Gulf at about 800 to 1000 m depth with speeds of about 1485 m s^{-1} (e.g., U.S. Dept. of the Navy, Naval Oceanographic Office 1972; Renteria 1978; Caruthers et al. 2002). Such a minimum was found during the SWSS cruises (Figure 3.3.1). The minimum forms the axis of the deep sound channel within the Gulf. Sounds can travel very long distances through the sound channel because of the refraction of sound back towards the minimum, provided that the ocean floor lies deeper than the sound speed minimum.

Sound energy also is affected by encounters with the boundaries at the sea surface and sea floor. At these interfaces, sound energy can be attenuated, scattered, and/or reflected. At the sea floor, the type of sediment present strongly affects how much acoustic energy gets reflected from the bottom, and how much is either directly absorbed by the sediment or transmitted into the bottom. These factors in turn determine the effective absorption characteristics for long range propagation. At depths of 1 km or greater the ocean bottom composition generally consists of a mix of carbonaceous and terrestrial sediments (see for example the USGS GLORIA Geology Interpretation map at *http://coastalmap.marine.usgs.gov/gloria/gomex/geology.html*).

In general, fine-grained sediments such as silt or carbonaceous deposits absorb sound quite well, at a rate of 1 dB per acoustic wavelength traveled in the sediment. Historical sound speed profiles from the area generally contain a sound speed minimum at depths between 700-900 meters. Thus at water depths of around 1000 m the sound speed profile will tend to refract acoustic energy into an acoustically absorptive ocean floor, and a fairly high effective attenuation rate for sound would be expected. In deeper water the sound speed minimum is much further away from the ocean floor, thus more acoustic energy may be refracted away from the ocean floor into the sound speed minimum channel, attenuating the sound less.

At ranges less than one water depth from the acoustic source, the sound field intensity varies roughly as the inverse square of the range to the source, a situation described as “spherical spreading” conditions. In ocean acoustics the decrease in acoustic intensity with distance is generally described in terms of transmission loss which is defined as the ratio of the acoustic intensity at the measurement point to the theoretical intensity at a point 1 meter away from the source. It is convenient to describe this loss on a logarithmic scale known as the decibel (dB) scale. An increase of 10 dB in transmission loss represents a factor of ten reduction in signal level, while an increase of 20 dB represents a factor of 100 reduction.

When the acoustic wavelength of interest is not small compared to the depth of the source in the ocean, this inverse-square drop-off is modulated by interference effects between the surface-reflected path and direct path that produce a fringe pattern known as the “Lloyd’s Mirror Effect” (Jensen et al. 1994). When a low-frequency source is very close to the ocean surface, the net effect of these interferences is that the sound field near surface is nearly cancelled out, and that sound propagating vertically away from the surface is reinforced, creating a directional source.

At ranges greater than one water depth the influence of the ocean bottom can become important, as is the case in the Gulf of Mexico. As a result of interactions with boundaries and with the sound speed structure, sounds emitted from a source can travel to receivers on direct, reflected, and refracted pathways. The interference between these paths can create a complex transmission loss pattern in range and depth. Over the past thirty years sophisticated modeling techniques have been developed to model sound propagation as a function of source and receiver depth, sound speed profile, and ocean bottom characteristics. An example of the output of such a code is given in Figure 3.3.2, showing the expected transmission loss from a single 2-kHz source at 8-m depth in a 600-m deep ocean using a typical sound speed profile from Figure 3.3.1 and an ocean bottom composed of silt. Directional properties of an airgun array have been incorporated into this simulation. The bottom contains acoustic parameters representative of sand. Note how the acoustic paths radiating from the source are not straight, but curve down towards the bottom. In water depths where sperm whales were frequently encountered, i.e., 1-km depth or less, the local sound speed profile reaches its minimum near the ocean bottom (Figure 3.3.1). Thus the entire water column tends to refract sound toward the ocean bottom, which explains the curvature of the visible ray paths. The fact that sound speed profiles at these water depths are downward-refracting has a major impact on the propagation ranges of acoustic signals.

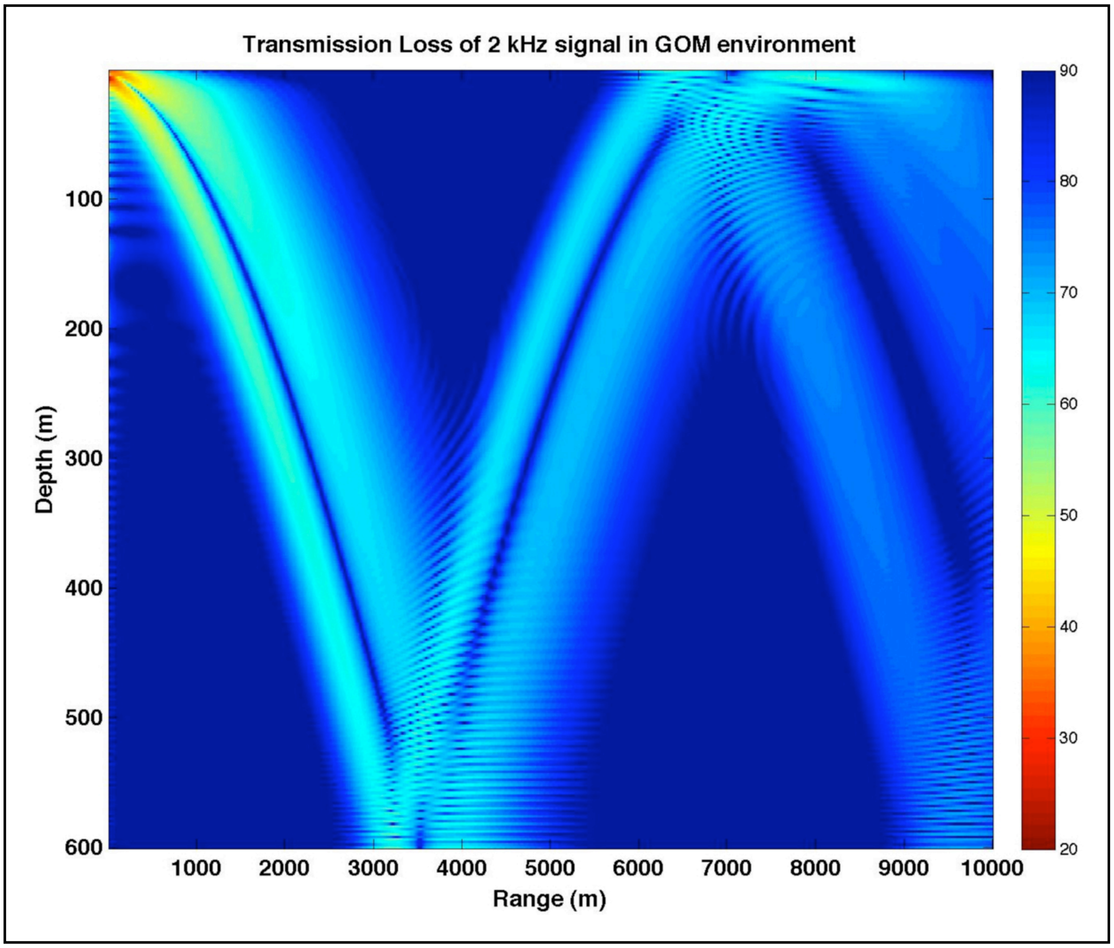


Figure 3.3.2. Output from a normal sound propagation model. Shown is the expected transmission from an omnidirectional 2-kHz source at 8-m depth in a 600 m deep ocean, using a typical sound speed profile from Figure 3.3.1 and a silty bottom. The colorscale is 20 times the logarithm of the ratio of the received field to that at a hypothetical 1 m distance from the source.

Sound Sources: Marine mammals have evolved to exploit the use of sound to sense and survive in their oceanic environment. With the advent of the industrial age, humans have introduced more sound into the ocean than was present from the "natural" sources that existed as marine mammals evolved their hearing physiologies (e.g., NRC 2003). Concern has arisen about what the effects of anthropogenic sounds might be on the marine mammals that inhabit the world's oceans. Provided here is a brief summary of natural and anthropogenic sources of sounds. Details can be found in the works by Richardson et al. (1995), NRC (1994, 2000, 2003, and 2005), and references given therein.

MMS sponsored a comprehensive literature review that detailed the state of the worldwide knowledge through 1990 of human-generated and natural underwater noise and impacts on marine mammals (Richardson et al. 1991). The Office of Naval Research (ONR) then funded a project to convert the review into the book by Richardson et al. (1995). Since that time, research into the effects of noise on marine mammals has increased. Four reports of the National Research Council (NRC 1994, 2000, 2003, and 2005) provide extensive information on and references to noise and marine mammals with recommendations for research needs. A common recommendation of these reports was to determine the normal behaviors of marine mammals and their responses to human-generated sounds (NRC 1994). Suggested was research that would study the sound exposure, as received level, at the individual animal and that would allow tagging of animals for study of behavior and possible responses to human-generated sound.

There are many sources of natural sounds in the ocean. These include wind, waves, storms, rain and hail, currents, bubbles, turbulence, seismic activity (earthquakes, undersea volcanoes), ice (not in the Gulf), and marine life (see, e.g., Wenz 1962). Table 3.3.1 shows the energy bands of various sources of sound in the ocean (NRC 2003; Richardson et al. 1995; Whitehead 2003). Plate 1 in NRC (2003) provides a graphical representation of the general categories given in this table.

Sound levels, like transmission loss, are often also presented logarithmically in terms of decibels (dB), by taking 20 times the logarithm of the ratio of the source pressure to 1 μPa. There are various conventions for defining the level of a sound. For impulsive sounds, the peak pressure, peak-to-peak pressure is often used, although time-integrated measurements have been presented as being more representative of quantities that impact marine mammal hearing (Madsen 2005). Continuous sounds are often expressed in terms of their frequency components as a power spectrum or power spectral density. Thus an impulsive sound recorded with a peak level of 1 Pa would be described as having a level of 120 dB re 1 μPa peak-to-peak.

To describe the actual intensity of sound produced by a source, one needs to define a reference distance. By convention a reference distance of 1 m is typically used. Thus a source that would produce a 1 Pa peak amplitude pressure wave 1 m from the source would have a source level of 120 dB re 1 μPa @ 1m peak-to-peak. The intricacies of reporting sound levels accurately can get quite complex, and Richardson et al. (1995) go into further details.

The dominant source of non-human sounds in the frequencies from 1 Hz to 100 kHz, which includes the frequencies of sperm whale clicks, is from the action of the wind at the sea surface that generates waves and increases bubble production (e.g., NRC 2003). Extreme storms, such as the hurricanes that are prevalent in the Gulf, generate substantial noise at these frequencies. Newcomb et al. (2005) compared underwater ambient noise levels with wind speeds generated by passage of Tropical Storm Isidore and Hurricane Lili through the north-central Gulf of Mexico. They found ambient noise levels during the storm of about 70 dB re 1 μPa at a frequency of 1 kHz and about 60 dB re 1 μPa at a frequency of 5.5 kHz as compared to non-storm levels of approximately 53 dB re 1 μPa at 1 kHz and 43 dB re 1 μPa at 5.5 kHz. Their results agreed well with the findings of Wenz (1962) for Beaufort sea states of 5-8. Newcomb et al. (2004) found that a tropical storm in the Gulf may have influenced sperm whales to move out of an area under the storm's influence.

Table 3.3.1

Frequency Bands for Selected Sound Sources in the Ocean
(NRC 2003; Richardson et al. 1995; Madsen et al. 2002a)

Sound Source	Dominant Frequency Bands	Source Level
Natural Physical Sources		
Wind-generated ocean surface waves	1 Hz to 100 kHz	
Bubble oscillations and spray	100 Hz - 20 kHz	
Microseisms	< 10 Hz	
Thermal noise (molecular agitation)	> 10 kHz	
Precipitation (rain and hail)	~100 Hz to 20 kHz	
Atmospheric sources (thunder)	10 Hz to 1 kHz	
Earthquakes, volcanoes	1-100 Hz	
Sediment transport over seafloor	1 kHz to > 200 kHz	
Deep ocean turbulence	1-20 Hz	
Non-human Biological Sources		
Biological organisms	12 Hz to >100 kHz	
Fish	< 1 kHz	
Marine mammals	< 10 Hz to > 200 kHz	
Sperm whales	100 Hz to 70 kHz	
Sperm whale clicks	5 - 25 kHz	223 dB re 1 µPa @ 1 m
Anthropogenic Sources		
Shipping and industrial activity	10 Hz - 10 kHz	
Ocean traffic	10 Hz - 1 kHz	
Ship propellers	1 - 20 Hz	
Commercial sonars (fish finders, depth sounders)	3-200 kHz	
Geophysical seismic surveys (airguns)	1 Hz - 1 kHz	
Airguns: peak pressure levels	5-300 Hz	260 dB re 1 µPa @ 1 m

Whitehead summarized the characteristics of sperm whale clicks as "sharp-onset, broadband, impulsive vocalizations." The energy of the clicks occurs at frequencies between 5 and 25 kHz (Madsen et al. 2002a; Goold and Jones 1995). The clicks are very intense, up to 223 dB peak to peak re 1 µPa @ 1m from the source (Møhl et al. 2000). An example of the time-series structure and spectrogram of a sperm whale click is shown in Figure 3.3.3. These vocalizations are used for echolocation and communication (Whitehead 2003).

Anthropogenic sounds come from many human activities on and in the oceans (Figure 3.3.4). Ships of all types (e.g., recreational, fishing, crew boats, research vessels, cargo, tankers, and military) are a major source of noise in the ocean (NRC 2003). Industrial activity, such as platform construction and drilling (e.g., Figure 3.3.5), also contributes to the noise levels. An examination of the frequencies of sound energy generated by various natural and anthropogenic sources shows that the anthropogenic sounds fill the full range of frequencies of natural sounds

(Table 3.3.1). This points out the possible masking effect that anthropogenic sounds may have on natural sounds. The effects of masking on the ability of marine mammals to detect sound cues in the environment is one of the major concerns associated with the increase in anthropogenic noise (Wartzok et al. 2004.).

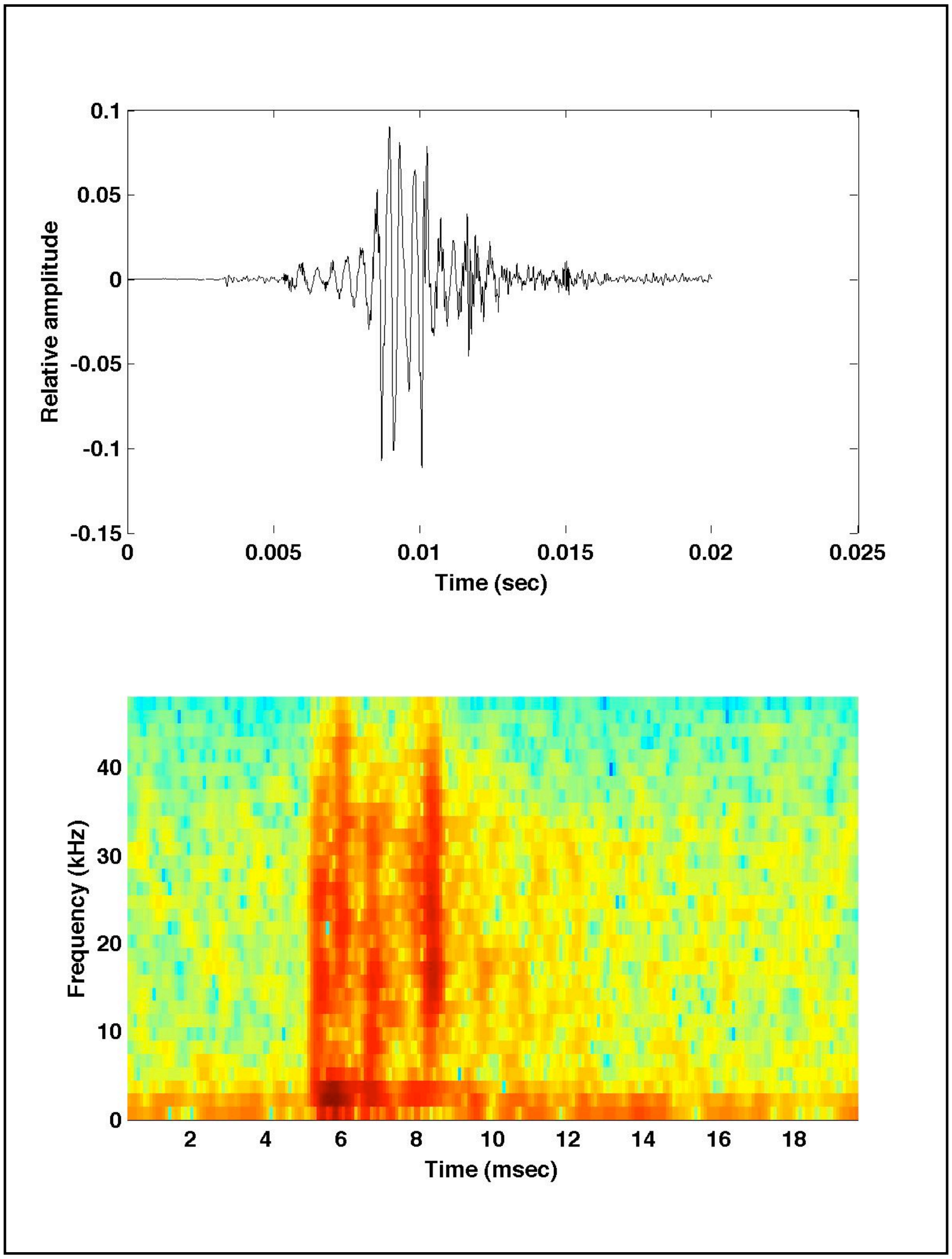


Figure 3.3.3. Time-series structure (upper) and spectrogram (lower) of a sperm whale click.

Figure 3.3.4. Sources of anthropogenic sounds in the Gulf of Mexico include offshore industrial structures, industrial vessels, cruise liners, and fishing yachts. The middle and lower photos show sperm whales who were actively diving to forage in a weed line region off the Mississippi River Delta in July 2003. (Upper photo by Jonathan Gordon of Ecologic on the 2005 MPS cruise; lower two photos by Joel Ortega-Ortiz of Oregon State University on the 2003 S-tag cruise.)

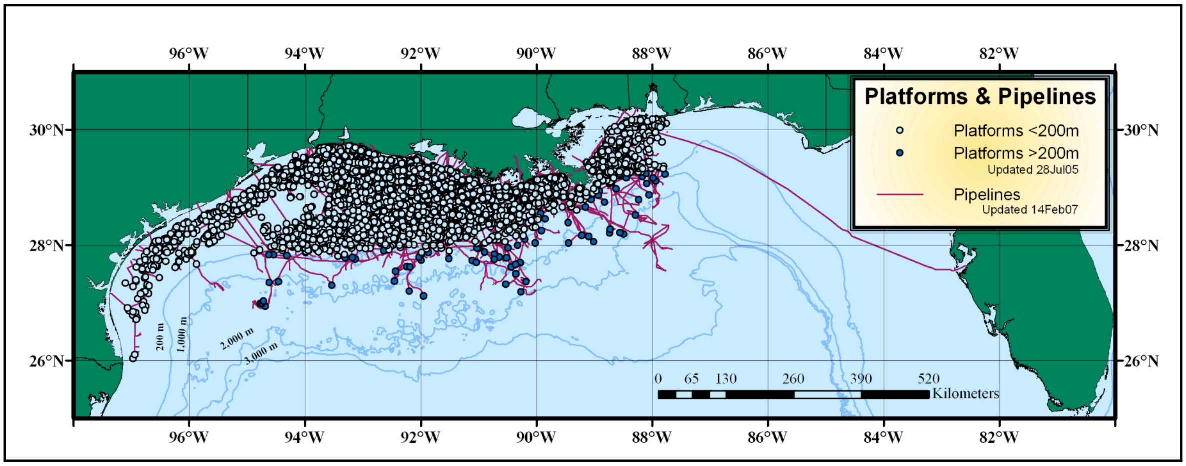


Figure 3.3.5. Platforms and pipelines in federal waters of the northern Gulf of Mexico. Notice the number that are now off the continental shelf in waters deeper than 200 m.

The spectrum (distribution of sound energy over frequency) is just one of the characteristics of a sound source. The variability over time (intermittent or continuous) and the intensity are other important characteristics. Anthropogenic sounds are of concern for their potential to cause both physical damage and modifications to behavior of marine mammals (see Wartzok et al. 2004 and NRC 2003 for reviews of potential effects). As stated in the NRC (2005) report, a key question is at what point might noise cause biologically significant impacts to a population.

The oil and gas resource in the Gulf of Mexico is an important source of the hydrocarbons used to fuel the U.S. economy. Over the last 30 years, exploration has moved farther offshore and into the deep water environment where the sperm whale lives (see, e.g., French et al. 2006). Discoveries have lead to increasing construction of platforms and pipelines off the continental shelf in the northern Gulf (Figure 3.3.5).

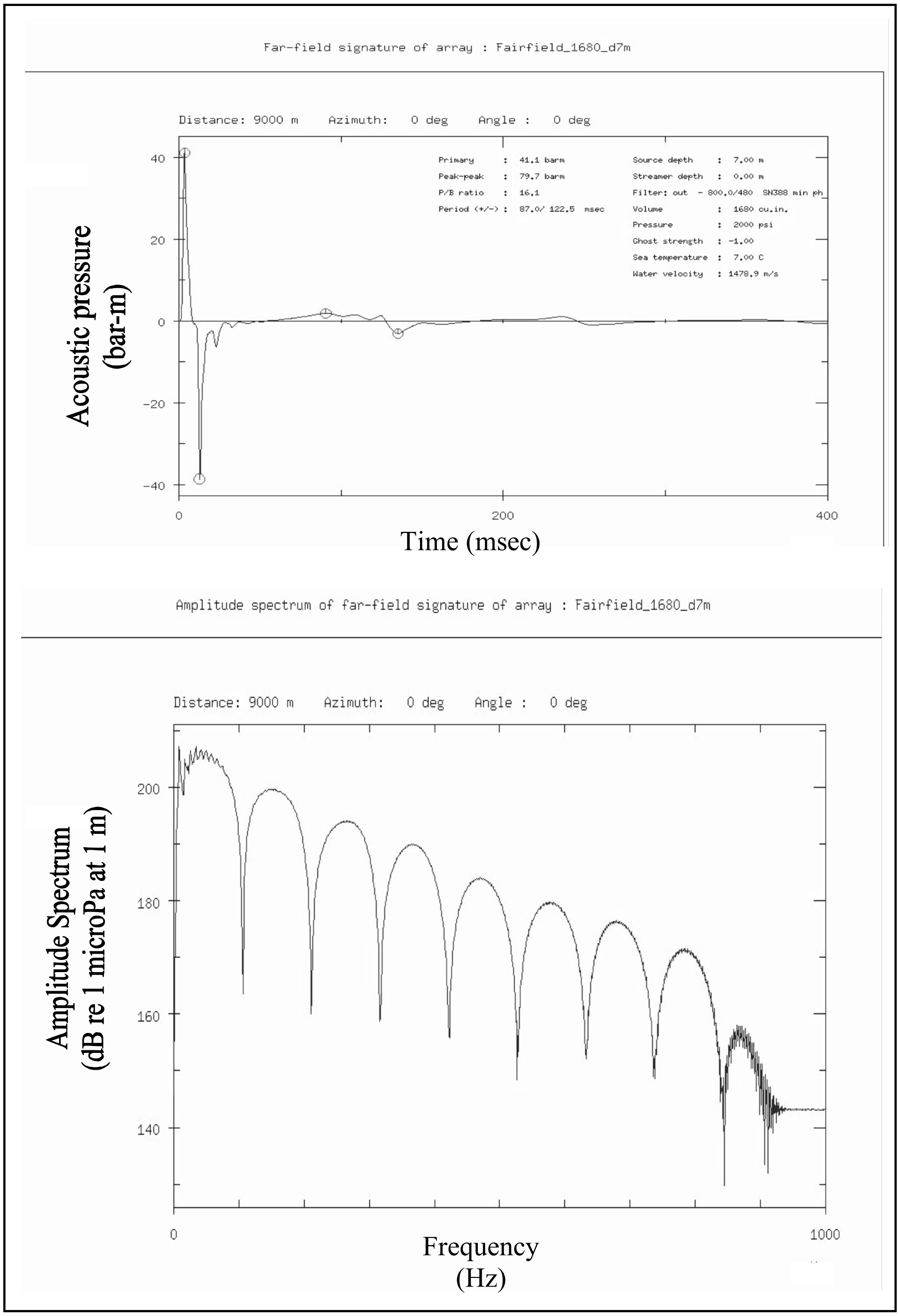
A major tool for exploration is the geophysical seismic survey. Seismic reflection profiling is used to obtain information on the geological structures beneath the sea floor. Sound pressure waves are transmitted into the ocean at the sea surface by airguns on seismic vessels, which also have streamers with hydrophones listening for the reflected sound returns. The airguns emit a volume of air under high pressure to create the sound pressure wave (Figure 3.3.6). The acoustic output depends on the number of airguns in an array, the operating pressure, and the cube root of the volume of the array (see Caldwell and Dragoset 2000, Dragoset 2000, and Richardson et al. 1995 for discussion of airgun arrays and their acoustic properties). The peak sound pulse levels from airgun arrays are greater than continuous sounds from ships and industrial sources (Richardson et al. 1995).

As the exploration for oil and gas in the Gulf has moved farther offshore, there has been a dramatic increase in the number of 3-D seismic surveys conducted in the deepwaters of the Gulf

(French et al. 2006). The concern over possible physical or behavioral effects on sperm whales from the seismic surveys was a primary motivation for the SWSS study.

The IAGC provided a representative airgun array source for use in the controlled exposure experiments conducted by the WHOI research group on D-tag. In 2002, this airgun array on the M/V *Speculator* mounted on the back deck of the M/V *Rylan T*, consisted of 20 external sleeve type airguns arranged on two separate gun strings (10 guns per string). The array volume totaled 1680 in^3 and had areal dimensions of 8 m long by 7 m wide. It produced a nearly identical acoustic signature as that of a deepwater 3-D airgun array at the distances required to be maintained from the whales on the 2002 D-tag/CEE cruise. Airguns were towed at a depth of 6 m. A schematic of the system is shown in Figure 3.3.7. The array produced a vertical far-field signature with a theoretical point source response of 258 dB re 1 µPa in the 3 to 800 Hz frequency band. For the 2003 D-tag/CEE cruise, the IRFC provided the M/V *Kondor Explorer*. Its airgun array consisted of 28 active guns with areal dimensions of 15 m long by 10 m wide, a total volume of 2590 in^3, and output a point-source equivalent level of 261 dB re 1 µPa at 1 m (peak-peak) in the 3-218 Hz frequency band (DeRuiter et al. 2006). DeRuiter et al. (2006) includes further discussion of the airgun arrays used in SWSS, as well as an analysis of modeled acoustic propagation of the pulses to sperm whale receivers.

Figure 3.3.6. Source of Fairfield *Speculator* in use during 2002 SWSS D-tag/CEE cruise. The airgun array had a total volume of 1680 in^3.



Primary : 41.1 barm
Peak-peak : 79.7 barm
P/B ratio : 16.1
Period (+/-) : 87.0/ 122.5 msec
Source depth : 7.00 m
Streamer depth : 0.00 m
Filter: out - 800.0/480 SN388 min ph
Volume : 1680 cu.in.
Pressure : 2000 psi
Ghost strength : -1.00
Sea temperature : 7.00 C
Water velocity : 1478.9 m/s

Figure 3.3.7. Characteristics of the 1680 in^3 Fairfield airgun array used on the 2002 D-tag/CEE cruise. Shown are (upper) the far-field signature of the array and (lower) the amplitude spectrum of the far-field signature.

3.4 Acoustic Recordings Made in the Vicinity of Deep Water Drilling Rigs and Oil Platforms in the Gulf of Mexico

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3.4.1 Introduction and Background

The acoustical characteristics of a range of drilling and production platforms have been measured and published (see for example Richardson et al. 1995, and references therein). However, the production of oil in extremely deep water in the Gulf of Mexico involves new technology and engineering, and we are not aware of published noise characteristics for these activities. In 2002, in the course of photo-id and telemetry studies in the Gulf of Mexico conducted as part of the SWSS project, we occasionally heard prominent tonal noise in the vicinity of oil and gas industrial structures. For example, particularly strong tonals were heard on 26 June 2002; although we were close to the URSA Tension Leg Platform (TLP) at the time, we do not know what operations, from URSA or another structure, were occurring in the area. The sperm whale studies were conducted using a combination of a large mother ship, the R/V *Gyre*, and smaller rigid hulled inflatable boats (RHIBs) that were used to track and approach whales for photo-id or tagging. The tonal sounds were picked up on simple hand held directional hydrophones, which were used on the RHIBs to locate and track sperm whales. We gained the impression that these noises were quite intense, and they interfered with our ability to track sperm whales. However, we had no means of making recordings from the RHIBs at that time. The *Gyre* did have towed hydrophones and recording systems but her ability to monitor lower frequencies was compromised by the vessel's own noise, and she was unable to approach closer than several miles away from the industrial structures. Thus, although no recordings were made in 2002, these episodes brought the noise generated by drilling rigs and production platforms to our attention.

In 2003 a simple recording system was provided for use on RHIBs operating from *Gyre*. In 2004 and 2005 a 46' motor sailing vessel was used as a platform for mark recapture studies. This vessel was much quieter than the *Gyre* and could also approach close to oil and gas industrial structures. It was decided therefore that we should take advantage of any opportunities to make recordings of noise from these structures in the Gulf of Mexico as and when they arose. The oil and gas offshore operators agreed to assist us in these efforts by providing information on their activities at the times recordings were being made.

3.4.2 Methods

In 2003 opportunities for recording only occurred when the RHIB had been launched, usually to photo-id whales, and this resulted in very few recordings. In 2004 and 2005, if our sailing vessel's other activities brought it to within a few miles of an oil and gas industrial structure and conditions allowed, we would close with the structure and make recordings at ranges within approximately 1 km of it. These activities occurred only during daylight hours, at times when whales were not being tracked, the weather was good, and other operational considerations allowed. Usually we would manage to talk to personnel on the rig or platform via marine VHF radio and explain our work to them. Personnel would be questioned about any activities that might be associated with the underwater noise recorded, and the information was logged.

To make recordings, the sailing vessel would usually be closed down to "quiet ship" and allowed to drift or sail slowly on a course away from the rig or platform. Ranges to the closest part of the structure were measured regularly using a laser range finder and recorded approximately once per minute.

3.4.3 Equipment

The recording system available on the RHIBs in 2003 consisted of two HTI-96-Min Series hydrophones with preamps (Hi-Tech Inc) and a Magrec HP27ST monitoring and conditioning unit with recordings being made as wav files at a sampling rate of 48 kHz using a Creative Nomad Jukebox 3 personal stereo. This system had a close to flat frequency response between 10 Hz and 24 kHz.

On the sailing vessel in 2004 and 2005, recordings were made on either or both of two systems. The first was the vessel's main towed hydrophone system. This consisted of a stereo pair of hydrophones, separated by 3 m, mounted within a 10-m long, 22-mm diameter oil-filled polyurethane tube. Each hydrophone comprised a Benthos AQ4 element and a Magrec HP02 broadband preamplifier. The preamplifier has a low cut filter to de-emphasize low frequency vessel and sea noise that was configured to provide -6 dB of gain at 100 Hz. A depth sensor was included close to these hydrophones, and depth was recorded automatically every 30 seconds. The tow cable length was usually 100 m. Hydrophone signals were conditioned and amplified using a Magrec HP27ST stereo monitoring unit. Recordings were made to computer files using an MAudio sound card with a 48-kHz sampling rate using the Logger program. This system was not calibrated, although the AQ4 and HP02 are characterized by the manufactures. The system response was approximately flat (within 3 dB) over the range 100 Hz to 15 kHz.

A second system on the motor sailor consisted of a single calibrated Reson TC403 spherical hydrophone with a 20-m cable length and a Reson VP2000 voltage preamplifier and filter unit (EC6081); recordings were made using a National Instruments DAQ A1-16E digital acquisition card running in a laptop computer. The sensitivity of this system was calibrated and was close to flat between 1 Hz and 80 kHz. Sound was sampled at a rate of 100 kHz. Recordings were made using the Ishmael sound analysis program (written by David Mellinger).

The capabilities of the two systems were quite complimentary. The vessel's towed hydrophone system was always deployed and could be operated in poor weather conditions. Being streamlined and at a substantial depth, this hydrophone was less vulnerable to surface noise and did not require the vessel to be near stationary. However the system was not calibrated, low frequencies were filtered and the precise location of the hydrophone at the end of a long cable was often not known. The calibrated system had a better bandwidth and it was calibrated, but it was not part of the vessel's main system and was more difficult to deploy.

Spectrograms and spectral plots were made using Matlab routines.

3.4.4 Results

A single recording was made of noise from a drilling rig in 2003 at a range of around 5 nautical miles (determined by the *Gyre*'s radar). In the course of the 2004 and 2005 SWSS photo-ID cruises, we were able to complete 11 recording sessions close to drilling rigs and production platforms. Table 3.4.1 summarizes the recordings.

Most production platforms were very quiet. In some cases little could be discerned above background noise except for faint machinery noise. These noises were not sufficiently prominent in spectra to allow meaningful received levels to be calculated. Often support vessel or sports fishing vessels also were in the area, either moving or stopped on station. These vessels were often a more significant source of noise than was the machinery noise from the production platforms.

The only recording that seemed similar to the strong tonal noise heard in 2002 was the recording made at a range of around 5 nautical miles from an unidentified drilling rig in 2003. Figure 3.4.1 shows the spectrogram and spectral plot of this recording. These results show a pronounced and constant tonal at 260 Hz.

Significant noise was recorded during two encounters with drilling rigs. On one occasion, during the approach to the Ocean Lexington on 29 June 2004, noise was heard coming from the drilling rig. A recording was made using the towed hydrophone system. However, the noise ceased before the vessel came within range and the calibrated system could be deployed, so it was not possible to measure absolute sound pressure levels. We can only characterize the frequency distribution of the noise (Figure 3.4.2). The noise consisted of pulses lasting for approximately 4 seconds with approximately 1.5 seconds between pulses. Noise was broadband with a band of emphasized frequency at around 8 kHz. The drilling rig was contacted via VHF radio, and the research team was informed that it was not drilling, but was engaged in "vibrating cold tubing".

During the recording on 2 August 2004 in the vicinity of the Discovery Enterprise drill ship, some machinery noise was recorded. From radio contact with the bridge, we found out that the ship was running powerful pumps, and this operation was the likely cause of noise. Plots for this recording are shown in Figure 3.4.3. The noise was continuous with peak levels at ~600 Hz and 3 kHz. Many emphasized frequency bands were evident at a spacing of approximately 250 Hz.

3.4.5 Discussion

Strong tonal noise, apparently emanating from drilling rigs, was heard in the Gulf of Mexico on several occasions but opportunities to make calibrated recording of these events did not occur. Good recordings were made of some other examples of prominent acoustic signals in the vicinity of drilling rigs, which were not drilling at the time.

Table 3.4.1

Summary of Recordings Made Close to Oil Production Platforms and Drilling Rigs in the Gulf of Mexico During 2004 and 2005
(Maximum and minimum distances are from research vessel to platform of interest)

Time in UTC (dd/mm/yyyy hh:mm)	**Latitude (°N)**	**Longitude (°W)**	**Structure Name**	**Drilling or Production Structure**	**Comments**	**Max Distance (m)**	**Min Distance (m)**
						While recordings were made	
19/06/2003 21:22	27.7321	90.460	Not Identified	D	Recordings made while with sperm whales at a range of ~5 nautical miles from an unidentified drilling rig	~9000	~9000
28/06/2004 17:04	28.4018	89.4524	Medusa	P		850	300
28/06/2004 18:51	28.3699	89.4124	Ocean Lexington	D	Not drilling; vibrating cold tubing	517	473
24/06/2004 18:02	29.2376	87.7653	Petronius (ENSCO25)	P	Moored supply vessel and sports fishing boat present	not recorded	not recorded
04/07/2004 18:38	28.1558	89.1089	MC-509A URSA	P		260	162
25/07/2004 09:36	28.1470	89.1100	URSA TLP	P		480	528
02/08/2004 15:33	28.2074	88.7315	Devils Tower #1175	P		454	368
02/08/2004 13:04	28.1985	88.4915	Drilling Ship Enterprise	D	Not drilling; concreting casings with powerful pumps running	582	730
27/07/2005 17:02	27.7936	90.6865	Ocean Saratoga	D		215	520
27/07/2005 17:34	27.7981	90.6416	158A Brutus TLP Green Canyon 158	P		92	512
27/07/2005 18:37	27.7784	90.5189	GC 205 Genesis	P		122	302
28/07/2005 02:26	27.6552	90.1905	Ocean America	D		not recorded	not recorded

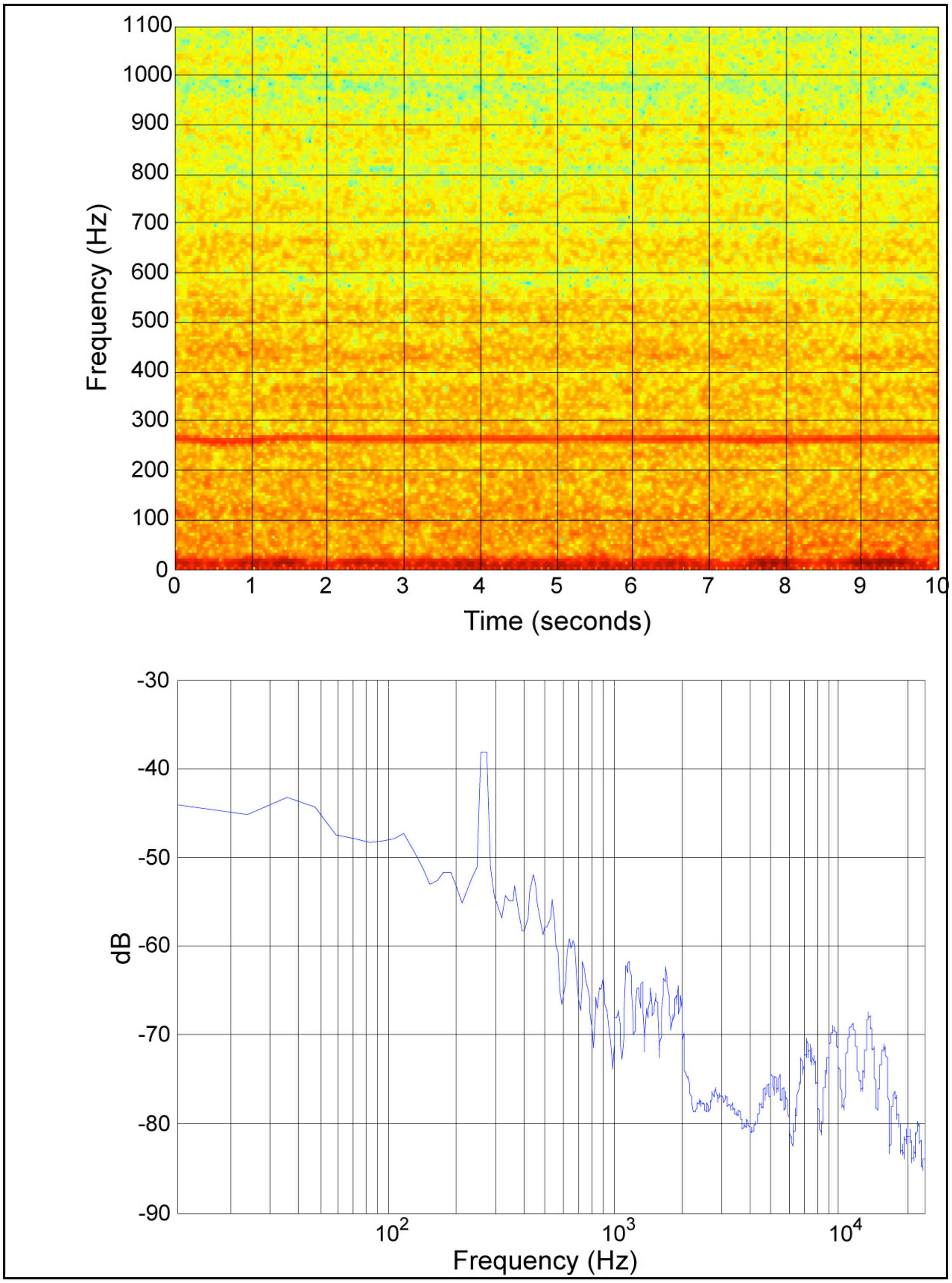

Figure 3.4.1. Spectrogram (upper panel) and spectrum (lower panel) of a recording from an unidentified drilling rig made at a range of ~5 nautical miles. The continuous tone has a spectral peak at ~260 Hz. (Fourier analysis parameters: Hamming window, FFT length 4096.)

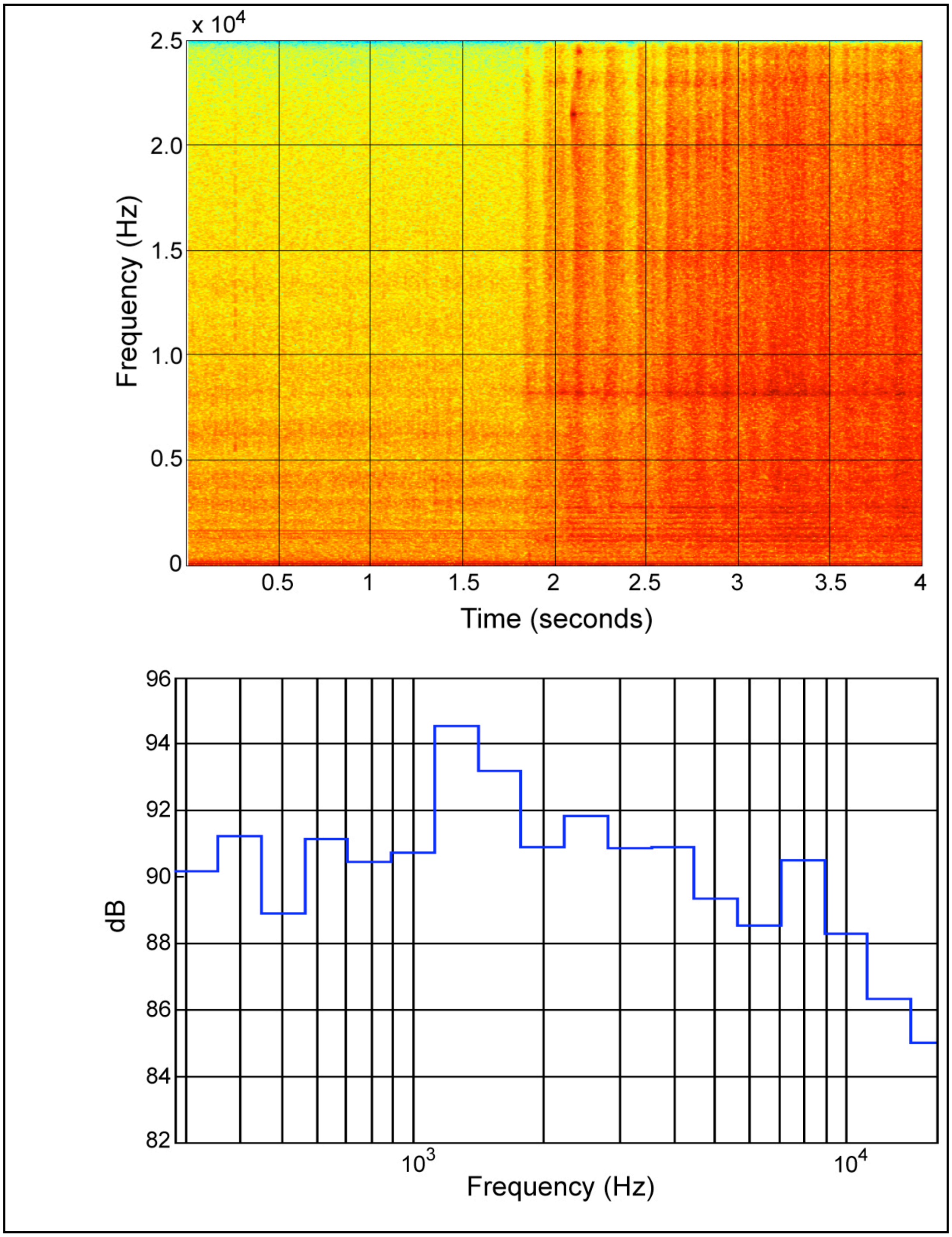

Figure 3.4.2. Spectrogram of the beginning of a noise pulse recording from (upper panel) and one-third octave band noise levels of received noise off (lower panel) the *Ocean Lexington* drill ship on 28 June 2004. Note that the one third octave band noise levels are not absolute levels. (Fourier analysis parameters: Blackman Harris Window, FFT length 1024.)

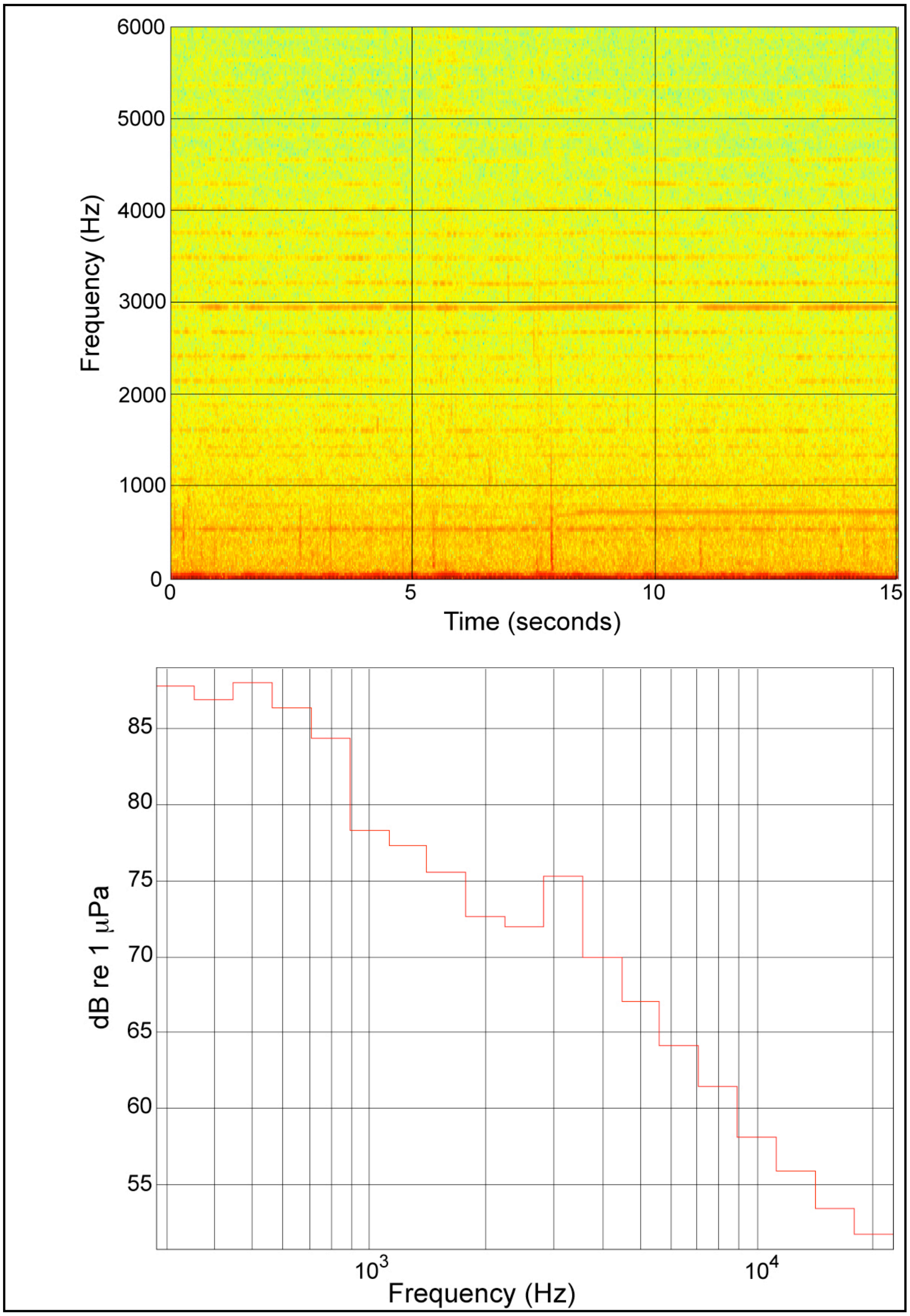

Figure 3.4.3. Spectrogram (upper panel) and absolute received one-third octave band sound levels (lower panel) of a recording made in the vicinity of *Discovery Enterprise* on 2 August 2004 while it was operating powerful pumps. Range to the closest part of the drilling ship at this time was 626 m. (Fourier analysis parameters: Blackman-Harris window, 2048 FFT length.

We found no indications that production platforms produce high levels of noise during normal operations, though it must be noted that our sampling sessions were rather short. It is possible that the strong tonal sounds heard in the vicinity of the URSA TLP in 2002 came from an associated drilling operation rather than the production platform itself.

During this activity we were able to make relatively short recordings on occasions when we happened to be close to an oil and gas structure and other operational factors allowed. This has been a sensible initial exercise, allowing us to make exploratory recordings during an existing activity at virtually no additional cost. However, it is clearly very far from providing a comprehensive description of the noise output of any of these structures. It is also evident that noise production from these structures is episodic and varies with the activities being conducted. Thus, long periods of monitoring in conjunction with detailed information about rig and platform operations will be required to fully characterize noise output associated with different activities.

Production platforms often have mooring buoys in their vicinity. A sensible way to achieve long term acoustic monitoring at a low cost would be to deploy an autonomous recorder on one of these moorings while maintaining a log of platform operations and of activities of vessels in the area.

Acoustic monitoring to capture the output of drilling rigs might need to extend over considerable time to cover the various activities involved in drilling and should be conducted in close collaboration with the drilling engineers so that different noise signatures can be associated with particular activities. Properly equipped, the type of motor sailing vessel we utilized in 2004-2005 might be a suitable platform for such a monitoring effort, as it can be operated silently, is sufficiently small and maneuverable to safely work close to platforms and rigs, and represents a very cost effective means of spending extended periods at sea.

4 POPULATION BIOLOGY OF SPERM WHALES IN THE NORTHERN GULF OF MEXICO

4.1 Synopsis of Population Biology of Sperm Whales in the Northern Gulf

Investigations of the molecular ecology for sperm whales have allowed new insights into associations among groups of animals and their seasonal movements. From genetic analyses of the tissue samples from 150 individuals that are summarized in Chapter 4.2 by Engelhaupt and Hoelzel, we have learned that individuals in most groups of sperm whales were half-siblings. Specifically, highly related whales (i.e., parent-offspring) were present within groups, but were infrequent. Individuals biopsied during the course of D-tag and S-tag fieldwork were almost three times more likely to type as females than as males, although this was not unexpected given what appears to be a preference for tropical and sub-tropical waters by female mixed groups.

The bachelor groups of all-male individuals that were sometimes encountered were comprised of multiple matrilines and members were generally unrelated, although cases for half-sibling pairs were present. Overall, the molecular ecology data support the delineation of the northern Gulf of Mexico into a female-dominated stock that is genetically distinct from the Western North Atlantic, Mediterranean, or North Sea putative populations. This genetic evidence is strongly supported by the site-fidelity information that is summarized in Sections 4.3-4.7. Engelhaupt and Hoelzel conclude that the Gulf population requires proper conservation to ensure stock survival.

Coda analyses also show the high degree of separation between northern Gulf and western Atlantic sperm whales. Codas are patterned series of clicks, often given as exchanges, and are the principal recognized form of acoustic communication among sperm whales. To look for the geographical variation of sperm whale coda repertoires in the North Atlantic, recordings from the northern Gulf were analyzed and compared with those from the Azores, Caribbean, and Sargasso Sea (Ricardo Antunes, Ph.D. dissertation in progress; see also Section 4.8). The majority of the northern Gulf repertoires showed separation from the Atlantic repertoires, with three exceptions. Single repertoires from Cuba and Panama clustered together with a single northern Gulf repertoire, and one repertoire from the western Gulf of Mexico clustered with some Caribbean ones, suggesting some link between these areas. Another northern Gulf repertoire showed more similarity with Azorean, Sargasso Sea and Iceland repertoires which in general tended to cluster together. These acoustic communication results document that sperm whale coda repertoires are geographically structured in the Atlantic Ocean and its surrounding seas, suggesting that as found for the Pacific Ocean, sperm whales populations in the Atlantic are culturally structured. Coda analyses support the idea that for this species, cultural variation should be considered for conservation and management, particularly for those spatial and time scales in which genetic variation is more homogeneous.

The combination of genetic analyses and coda analyses with satellite-monitored tagging techniques provided information on what are perceived to be social "units" comprised of related and unrelated whales that move together and split apart through space and time on a scale never before documented in such detail. As Mate and Ortega summarize in Section 4.3, females outfitted with S-tags usually ranged approximately 200 km around the tagging location, generally zigzagging across the upper continental slope. S-tagged males demonstrated more variability in their movements and greater use of water > 3000 m deep than S-tagged females.

The multiple years of radio telemetry locations from 57 S-tag deployments in 2001-2005 allow movement paths of satellite-tracked individuals to be categorized in terms of ocean bottom depth, bottom slope traversed, and whether the movement was meandering or transit. As reported in Section 6.2 of the SWSS Summary Report (2006), statistically significant differences (Mann-Whitney-Wilcoxon test; $p < 0.05$) were observed in the median values of bottom depth and bottom slope with a sample size of about one thousand S-tag locations. Females ($n = 798$) were found over median bottom depths of 884 meters and median bottom slope of 3.06 degrees, consistent with upper continental slope, while males ($n = 214$) were found over median bottom depths of 1171 meters and bottom slope of 2.39 degrees, consistent with their greater use of the lower continental slope and abyssal plain. Significant differences also were observed in the median depth for locations assigned to meandering and transit move types (median = 895 m and 968 m, respectively) although median bottom slope was not different between meandering and transit.

On the other hand and as detailed in Section 4.3 of the present report, the S-tag movement paths also suggest that female (and most male) movements in the Gulf of Mexico are not "migrations" (routine seasonal movements which are repeated annually), although such movements are still likely linked to changes in food availability. For example, synchronous movement of five females away from their tagging site in summer 2002 were evident as a series of concurrent peaks > 300 km in the displacement curves from mid-August through early November 2002 (see Figure 4.3.31a in Section 4.3). The synchrony in their movement may indicate a social bond rather than a population-wide seasonal migration since other females remained near the tagging location (curves with displacement values < 200 km) during the same period. Differences in habitat use and movement patterns have been reported between sympatric groups of female and immature male sperm whales from different vocal clans (Whitehead and Rendell 2004). SWSS results indicate differences in habitat use and movement patterns between females and males, as well as between individuals of the same sex. Future analysis of codas and other sperm whale vocalization recordings made during the tagging cruises may indicate whether differences between individuals or groups are related to vocal clan structure.

S-tag data demonstrate that home ranges of some females tagged in the north central Gulf (off the Mississippi River Delta and in the Mississippi Canyon) and some tagged in the northwestern Gulf overlapped; however core areas of females tagged in those two locations did not. Home range of two males included female core areas in both the central and western Gulf. Sperm whale core areas identified from satellite tracking locations generally overlapped with areas where whales were tagged (off the Mississippi River Delta and in the northwestern Gulf). Female groups showed affinity for areas where they were tagged in the summer, and remained there for months at a time. Therefore, distribution and home range conclusions derived from tagging data are greatly influenced by tagging location. Single site tagging studies could generate a significantly biased basin-wide picture of distribution and movements. Females tracked in this study rarely visited waters deeper than 2000 m where groups of sperm whales with calves have been observed on several occasions (Mullin et al. 2004), suggesting that female whales sighted offshore have different distribution patterns.

The male sperm whales encountered during SWSS summer field seasons in the northern Gulf were small compared to sexually mature males in the Atlantic or Pacific. In their cruise reports, the D-tag field team estimated that three of the individuals they tagged in 2002 and 2003 were in the size range of 12.5-14 m, but none of the 53 individuals that were outfitted with radio tags or biopsied during S-tag cruises were estimated to be larger than 12 m in overall length (see Section 4.3). From measurement photos taken of tail flukes between 2002 and 2004, the MPS field team estimated that only 3 of 78 individuals were 12 m or more in overall length (see Figures 4.1.19 and 4.1.20 in the SWSS Summary Report). Size was also estimated during MPS cruises using an acoustic technique that Gordon (1991) had proposed and that uses click interpulse interval (IPI) as a proxy for the length of the spermaceti organ inside the head. Jaquet (2006) explained how such initial IPI times were recorded using portable, directional hydrophones as an individual was beginning a foraging dive. She reported there was a positive correlation between these IPI times and overall body length of Gulf sperm whales estimated using photogrammetric methods.

Based on the fluke size to overall length allometric relationship derived from the 2002-2004 data, Jaquet (2006) concluded that northern Gulf males averaged only about 10.6 m in length. Because the males encountered were so small, the S-tag field teams judged that none of the males they radio-tagged or biopsied were both physically and sexually mature (Section 4.3). But even though no physically mature males were affirmatively identified on SWSS cruises, the presence of matriarchal groups with young animals indicates breeding males must be present in the northern Gulf for at least part of the year.

S-tag results showed that, despite their surprisingly small overall individual lengths, the largest-sized lone male whales and the groups of bachelor males traversed large areas of the Gulf. For example, S-tagged male #2505725 had the longest track of any individual whale (see Figure 4.3.18 in Section 4.3), providing locations for 607 days. His movements were different from other whales: he traveled into the North Atlantic for 2+ months, used the Bay of Campeche as winter/spring range during two consecutive years, and did not spend the summers of 2002 and 2003 in the same area of the northern Gulf. Based on morphometric data from other sperm whale populations outside the Gulf of Mexico and a size estimate of this whale (11 m) relative to the length of the tag boat, the S-tag team concluded that he was potentially large enough to be considered sexually mature, but not large enough to be a successful breeding bull.

A combination of genetic information with satellite-tracking (S-tag) data was also used for social structure analysis of sperm whales. As Ortega et al. (Section 4.5) explain, S-tag data allowed identification of social relationships, over time scales of months, between whales tagged on the same year. Although sperm whale aggregations are not cohesive and stable over time, it has been suggested that they are socially important, because individuals within the aggregation can likely hear one another (Whitehead 2003). The maximum distance between individuals criterion (8.3 km) used by Ortega et al. (Section 4.5) to identify association events is well within the range of aggregations mentioned above. Based on the coefficient of association, 18 female whales were assigned to six social units. Ortega et al. (Section 4.5) are confident in the assignation of eleven individuals to four social units. Although they were unable to definitively conclude on the other seven individuals and two of the social units, they consider the coefficient of association estimates as good indicators of their membership to the social units.

Gordon et al. (Section 4.4) and Richter et al. (Section 4.6) summarize mark-recapture analyses of photo-ID data to investigate population size and population social structure. Use of photographic images for mark-recapture requires that flukes are sufficiently well marked and marks are sufficiently stable to allow animals to be reliably re-identified over the time periods being considered. In fact, well-marked whales remain reliably identifiable over periods of several years validating the use of fluke photo-ID for mark-recapture studies in sperm whales. Any of the individual cruises (sightings surveys) generally provide a snapshot of animal densities over the surveyed area during the relatively short period of the survey. In contrast, mark-recapture provides an estimate of the total number of animals available to be captured within the study area between two or more sampling periods. Of course, different components of a population may vary in their availability for capture resulting in heterogeneity of capture probabilities. Gordon et al. (Section 4.4) therefore decided to use photo-ID, supplemented with other information on the structure of the population and behavior of individuals, such as telemetry data from the S-tag program, to shape their mark-recapture analysis.

The combined photo-ID and S-tag data suggest that there is a "core" population of animals centered on the Mississippi Delta/Canyon which seems to consist of mixed groups. Groups of maturing males were mainly found to the east and along the slope adjacent to Florida. Satellite tag data indicated that males roam more widely than females. S-tag and photo-ID data indicate that members of the core population remain within the Mississippi Delta/Canyon home range across years with some individuals that were first photographed during the GulfCet cruises in 1992-1993 being seen more than ten years later in 2004.

The best fits of open population models discussed by Gordon et al. (Section 4.7) suggest that the core population of mixed groups, which appear to have a range focused around the Mississippi Canyon/Delta region during the SWSS study, number around 140 animals and the larger population, including medium size males, might number around 281 animals. From data collected in 1994-2005, Richter et al. (Section 4.6) identified 285 different individuals in an ensemble total of 369 sightings, which includes repeated sightings of the same individuals in different years. Gordon et al. (Section 4.7) caution that the discovery curve clearly indicates that we have not yet identified all of the population. Therefore, the population size is expected to be considerably larger than the current number of identified individuals.

Calving rate is a useful parameter to assess in any population monitoring program because it should provide an early warning of reduced reproductive rate which might be of conservation concern. The population abundance information summarized in Section 4.7 suggests that the observed rate is in line with expectations but it also highlights that these data are difficult to collect reliably. An overall ratio of calves (which probably were a combination of young-of-the year and year-one and/or year-two individuals) to females and immature males was 0.11. This overall ratio generally agrees well with the non-Pacific field observations and with the values predicted by the model used for stock assessment by the International Whaling Commission. This suggests that calf production in the Gulf of Mexico population is in line with expectations for a healthy population. The caveat, of course, is that if animals over one year of age were included in the "calf" category, then the calving rate would be lower than this, and possibly lower than expected for a healthy population.

Group sizes in the Gulf of Mexico are considerably smaller than off Chile or the Galápagos Islands, where group sizes range between 48 and 61 individuals (Coakes and Whitehead 2004). Typical group size in our northern Gulf of Mexico study area is about one-third of those reported in Coakes and Whitehead (2004). This is the first time that such small groups have been reported for mixed sperm whale groups (compare also Whitehead 2003). Interestingly, Gulf of Mexico sperm whales also differ in other characteristics from those studied in the Pacific. Anecdotally, a newborn calf was observed in July 2006 by sports fishermen in the northwest Gulf. It appeared to be about 2 m in overall length, which is 30-40% smaller than overall lengths of 3 - 3.5 m that are reported for young sperm whale calves from other geographic locations (Whitehead 2003).

Such population-wide differences could reflect different environmental conditions, ecological adaptations, or population dynamics. However, our dataset from the Gulf of Mexico is still small compared to those from other areas, and given the large inter-annual variability we observed, it remains to be seen how well our estimates approximate long-term values. Our observations nevertheless point to an opportunity to investigate the way in which sperm whales may adapt their social behavior to suit local conditions. These differences are not only interesting for evolutionary analyses. They are also important for management purposes, since they may indicate that whales in the Gulf comprise not just a genetically distinct but an evolutionary significant unit.

4.2 Gulf of Mexico Sperm Whales – A Genetic Perspective

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The molecular ecology for sperm whales (*Physeter macrocephalus*) in the northern Gulf of Mexico (GOM) was investigated in detail using a suite of molecular markers. In addition, several genetic related aspects for the Mediterranean Sea (MED), North Sea (NSEA), the western North Atlantic Ocean (WNAO) and the collective North Atlantic Ocean (NAO) putative sperm whale populations were also described. Throughout the SWSS and preceding SWAMP projects, genetic techniques were integrated with other research projects to provide a more detailed understanding of the sperm whale population occupying the GOM. These analyses have provided new insights requiring appropriate management to ensure the survival of the northern Gulf of Mexico sperm whale stock in an area of increasing industrial activity.

Population structuring between the four putative populations, with respect to mtDNA, was highly significant and warrants the classification of each putative population as a unique stock for management purposes. The majority of Gulf of Mexico samples were from females and young males believed to be sexually immature based on rough size estimates. Incidental resampling of individuals over periods of days, months and years adds support for site-fidelity to the northern Gulf of Mexico exhibited by at least some whales. Although our sample set compares a more restricted geographic area than previous studies, the lack of significant nuclear differentiation between neighboring populations suggests that sexually mature males disperse from their natal populations and spread their genes to the more philopatric females. The genetic information is in agreement with satellite-tagging, photo-ID and coda-structuring results suggesting significant site-fidelity over time exhibited by females, with more large-scale movements exhibited by some males (e.g., Sections 4.3 and 4.4).

The genetic composition of Gulf of Mexico sperm whale groups fits the mixed sex and bachelor group type so common in other areas of the world. Relatedness within the Gulf of Mexico female-dominated groups was significantly greater than that found between groups, but still was surprisingly low and composed of both single and multiple matrilines. Highly related whales (i.e., parent-offspring) were present within groups, but infrequent. The most common relationship found was that of half-siblings. The all-male bachelor groups were comprised of multiple matrilines and members were generally unrelated, although cases for half-sibling pairs were present. The combination of genetic analysis with satellite-monitored tagging techniques provided information on what are perceived to be social 'units' comprised of related and unrelated whales that move together and split apart through space and time on a scale never seen before in such detail (see Section 4.5).

4.2.1 General Introduction

Several species of cetaceans are notoriously difficult to study as they spend the majority of their time underwater and inhabit deepwater offshore areas that require high-cost means to gain even a glimpse into their rather secretive lives. While data gathered by researchers aboard whaling vessels primarily between 1950 and 1980 did provide basic information with regards to reproduction, morphology and movement patterns through the use of discovery tag recaptures, an accurate assessment of social and population structure among free-ranging sperm whales (*Physeter macrocephalus*) proved elusive (Best 1979; Ivashin 1981; Rice 1989). Pioneering efforts by Whitehead and Gordon that began in the 1980s provided the initial non-lethal steps towards unraveling fine-scale social and population structure details for free-ranging whales (e.g., Gordon 1987a; Whitehead 1989; Whitehead 1995). Whitehead's long-term study of sperm whales found off the Galapagos Islands and Ecuador provides one of the most significant contributions towards understanding how free-ranging sperm whales live (Whitehead 2003).

The incorporation of molecular markers is a relatively young technique that has the potential to provide a wealth of information with respect to both social and population structure for 'difficult to study' species. With the advent of the polymerase chain reaction (PCR) analytical method, minute amounts of DNA collected from sources ranging from skin to bone can be replicated to produce a viable sample for analysis. The analysis of nuclear DNA, mtDNA and sex-specific genetic markers provides information on identity (Paetkau and Strobeck 1994), gender (Berube and Palsboll 1996), kinship (Blouin et al. 1996; Richard et al. 1996; Ralls et al. 2001), mating systems (Girman et al. 1997; Fabiani 2002), reproductive success (Gemmell et al. 2001), philopatry and dispersal (Lyrholm and Gyllensten 1998; Lyrholm et al. 1999; Fabiani et al. 2003).

Use of Molecular Techniques to Study Cetaceans

Population Structure

The allocation of endangered species into particular 'stocks' or populations based solely on geographic boundaries seems illogical for most marine mammals given their huge potential for movement. Only by combining a variety of techniques ranging from satellite-monitored tracking (see Section 4.3), coda structuring (see Section 4.8; also 4.3 of the SWSS Summary Report), site-fidelity using photo-ID techniques (see Section 4.4) and genetic analyses will we provide a more suitable means of assessing biologically significant population subdivisions. With respect to genetic analysis, significant subdivisions within and among populations seen via an examination of gene frequencies provides a fundamental tool for the management of exploited and protected species. The differentiation of gene frequencies within and among populations can be a result of gene flow via migration of individuals or their gametes, random genetic drift, natural and sexual selection modes, mutations, and genetic recombination opportunities that have been mediated by the mating system (Avise 1994).

Female philopatry and male dispersal are the expected patterns of dispersion for mammalian species based on theoretical considerations (Greenwood 1980). The differences in dispersal between males and females may influence how populations are structured from a genetic perspective. Population structure affected by gender-based dispersal is particularly visible when one compares the haploid and maternally inherited mtDNA with the bi-parental nuclear genome (Avise 1994). If females are philopatric and males disperse, then one expects to find more variation between putative populations with respect to mtDNA and less variation with respect to nuclear DNA. Previous cetacean studies on humpback whales (*Megaptera novaeangliae*; Palumbi and Baker 1994; Baker et al. 1998), fin whales (*Balaenoptera physalus*; Berube et al. 1998) and sperm whales (Lyrholm et al. 1999) using genetic techniques based on mtDNA and nuclear DNA provide valid support for this sex-biased dispersal scenario. Lyrholm et al.'s (1999) sperm whale study examined population structure on a very broad global scale by comparing a collective set of samples from the North Pacific, North Atlantic and Southern hemisphere oceanic populations. Whether geographic structuring was present within geographic areas of the North Atlantic Ocean was untested and thus deemed a priority for sperm whale management related issues.

Group Composition

Sperm whale mixed groups tend to be found in low latitude warmer waters while young all-male bachelor groups and solitary males tend to frequent higher latitudes (Rice 1989). Upon reaching sexual and physical maturity, males return to lower latitudes to breed with females (Best 1979; Rice 1989; Whitehead 1993). Berzin's (1972) idea of sperm whales forming a 'harem band' mating system, with a male dominating a group of females, has since been replaced with a widely accepted polygynous system where sexually mature males only temporarily associate with groups of females in estrous (Best 1979; Rice 1989; Whitehead 1993; Christal and Whitehead 1997; Lyrholm et al. 1999; Whitehead and Weilgart 2000). The early studies that identified long-term relationships between females (Ohsumi 1971), the presence of juveniles and calves of both sexes and adult females (Best 1979) and what appeared to be cooperation among individuals within groups (Caldwell and Caldwell 1966) led several researchers towards the premature conclusion that sperm whale groups were strictly matrilineal in structure. While it has been noted that the banding together of females into groups may indeed support cooperative foraging, communal care of calves, and provide a collective defense mechanism to defend against predators (Best 1979; Arnbom et al. 1987; Whitehead et al. 1991; Whitehead 1996a); a purely matrilineal group structure where females remain with their mothers has since been rejected (Richard et al. 1996; Lyrholm and Gyllensten 1998; Christal 1998). The stable social unit appears to present the most probable case for highly related members, although transfers of unrelated whales between units does exist (Christal 1998). In addition to avoiding inbreeding with one another, close kin in vertebrates tend to cooperate and associate more than unrelated individuals (Emlen 1997). The extent of kinship structure that underlies the observed social behavior of sperm whale groups is fundamental towards understanding the evolution of social organization and may have important implications as to how to best manage putative populations (Pamilo 1989; Queller and Goodnight 1989).

Study Aims

As a result of the lack of required information available for management to base decisions on, the primary objective of the genetic component of the SWAMP and SWSS research projects was to describe the genetic structure for the northern Gulf of Mexico stock of endangered sperm whales with respect to both group composition and population structure. In particular, group and cluster compositions were examined from both a gender and genetic relatedness perspective, while the assessment of mtDNA and nuclear DNA genotypes within and between putative populations were analyzed to provide resolution with respect to how stocks are structured genetically.

This study aimed to describe the following aspects:

1. Genetic structure of four putative geographic sperm whale populations: Previous results for sperm whale population structuring on a global scale based on both matrilineal and bi-parental genetic markers are consistent with the expectation of greater female than male philopatry in this species (Lyrholm and Gyllensten 1998; Bond 1999; Lyrholm et al. 1999). A sufficient sample size allowed for an examination of structuring within sub-areas of the North Pacific (Lyrholm et al. 1999), however, genetic structuring within areas of the North Atlantic and Southern hemisphere was not possible due to the lack of sample material.

This study quantifies the level of geographic structuring and genetic variation among five putative sperm whale populations located in the Gulf of Mexico, Mediterranean Sea, North Sea, western North Atlantic Ocean and the collective North Atlantic Ocean by examining the maternally inherited mtDNA and multiple polymorphic microsatellite loci from the bi-parental nuclear genome. This comparison provides a genetic perspective towards understanding how male and female patterns of dispersal influence population structure within this species. Finally, this study provides an important insight as to what extent sexually mature males may be distributing their genes to multiple geographic populations. If sexually mature roving males spread their genes to multiple geographic populations, then this should have consequences on the level of nuclear DNA variation that is present within and between populations.

2. Composition of sperm whale groups and clusters in the northern Gulf of Mexico and the North Sea: Sperm whales exhibit a cosmopolitan distribution with females and young males remaining in more tropical and subtropical waters, while larger males increase their range into more polar latitudes as they age and grow (Best 1979; Leatherwood and Reeves 1983; Rice 1989). Apart from the solitary or occasionally paired sexually and physically mature males, sperm whales are most often found in mixed sex and all male (bachelor) groups (Best 1979; Whitehead and

Arnbom 1987; Rice 1989; Childerhouse et al. 1995). Previous genetic-based findings suggest a significant level of relatedness among female dominated mixed sex social group members (Richard et al. 1996; Lyrholm et al. 1996, 1999; Christal 1998; Bond 1999). A better comprehension of the relatively unstudied groups found in the northern Gulf of Mexico stock was deemed an important and necessary step towards understanding the extent of group structure for these speculated 'resident' whales.

This study utilized molecular markers to combine gender information, maternal lineages and genetic relatedness among individuals sampled from both clusters and groups to provide a more detailed assessment of how groups and clusters of sperm whales within the northern Gulf of Mexico are composed. Relatedness values were tested for members found both within and between groups and clusters to assess whether genetic patterns influence social structure (pending long-term association analyses). This was particularly important with respect to understanding how multiple whales that were both biopsy sampled and tagged with OSU's satellite-monitored radio transmitters move together or split apart through space and time (see Section 4.5).

4.2.2 Materials and Methods

The collection of tissue samples from free-ranging and stranded sperm whales was conducted under Marine Mammal Protection Act/Endangered Species Act permit #909-1465 and #909-1726. Tissue collection for free-ranging and stranded sperm whales, DNA extraction, DNA processing and data analysis methods are described in extensive detail in Engelhaupt (2004).

4.2.3 Results

Sampling Locations and Duplicate Samples – Gulf of Mexico

A total of 236 tissue samples comprised of biopsies (N = 175) and sloughed skin (N = 61) were collected from free-ranging sperm whales located in the northern Gulf of Mexico during one 2000 NMFS cruise (Figure 4.2.1) and six SWAMP and SWSS research cruises conducted during 2000–2005 (Figures 4.2.2 through 4.2.8). Of these, 24 samples were collected from sloughed skin that had opportunistically adhered to the WHOI D-tag suction cups, 47 samples were of whales sampled by biopsy dart or sloughed skin collection after OSU satellite-monitored tags had been attached and two samples were collected by biopsy dart from whales with an OSU B-Probe attached. A further four samples were collected from dead stranded whales in the Gulf (Texas: N = 2, Louisiana: N = 1, Florida: N = 1).

Of the 236 tissue samples collected from free-ranging sperm whales, 80 samples were determined to be genetic duplicates as per the criteria outlined in Engelhaupt (2004) and 6 were deemed unreliable due to poor quality and quantity DNA – a result that is common with sloughed skin samples. This left a total of 150 unique free-ranging Gulf of Mexico individual whales and four individual whales that had stranded on the beaches along the northern Gulf of Mexico making a grand total of 154 whales for population and group composition comparisons.

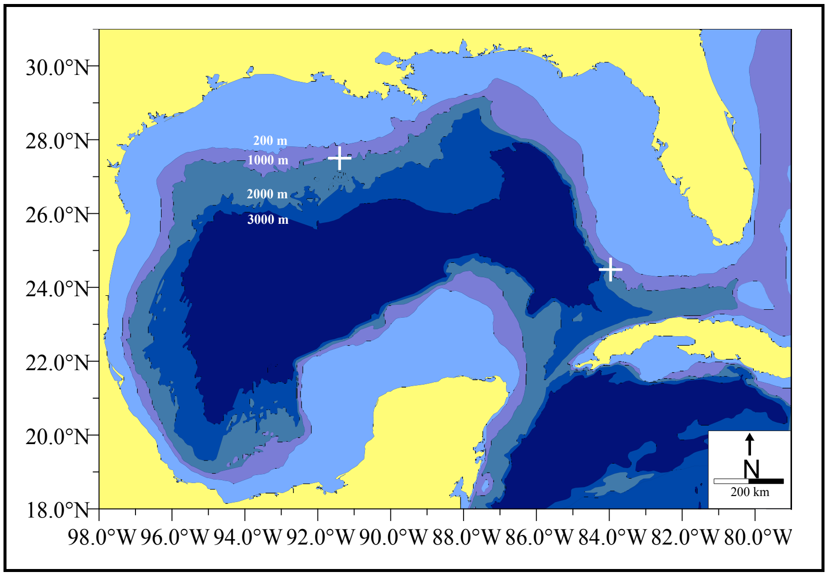

Figure 4.2.1. Gulf biopsy sampling locations during the May 2000 NMFS marine mammal survey cruise are depicted as white crosses. Depth contours of 200, 1000, 2000 and 3000 m are illustrated in shades of blue.

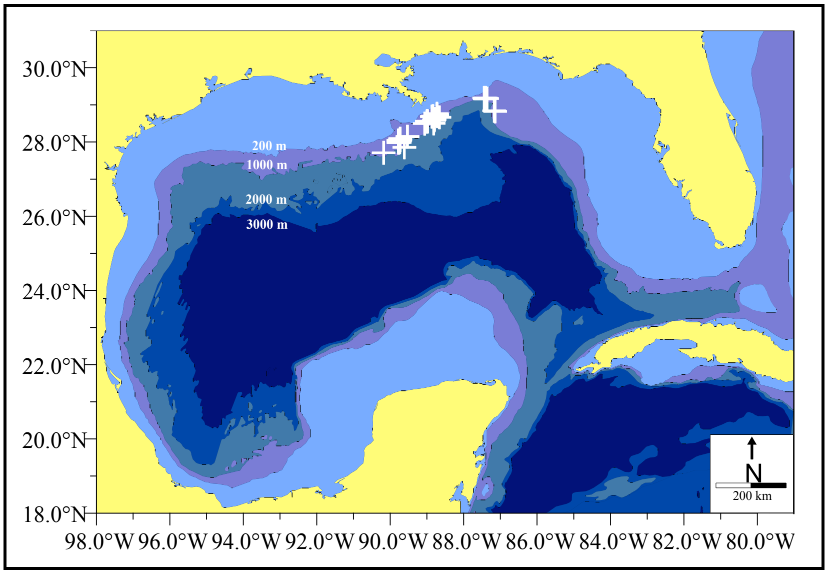

Figure 4.2.2. Gulf biopsy and sloughed skin sampling locations during the SW2K July-August 2000 SWAMP cruises are depicted as white crosses. Depth contours of 200, 1000, 2000 and 3000 m are illustrated in shades of blue.

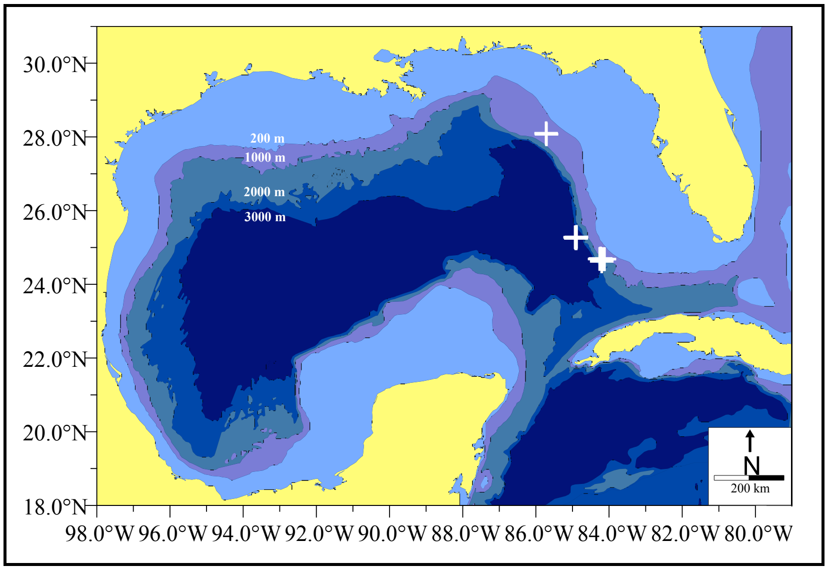

Figure 4.2.3. Gulf biopsy and sloughed skin sampling locations during the SW2K1 March-April 2001 SWAMP spring cruise are depicted as white crosses. Depth contours of 200, 1000, 2000 and 3000 m are illustrated in shades of blue.

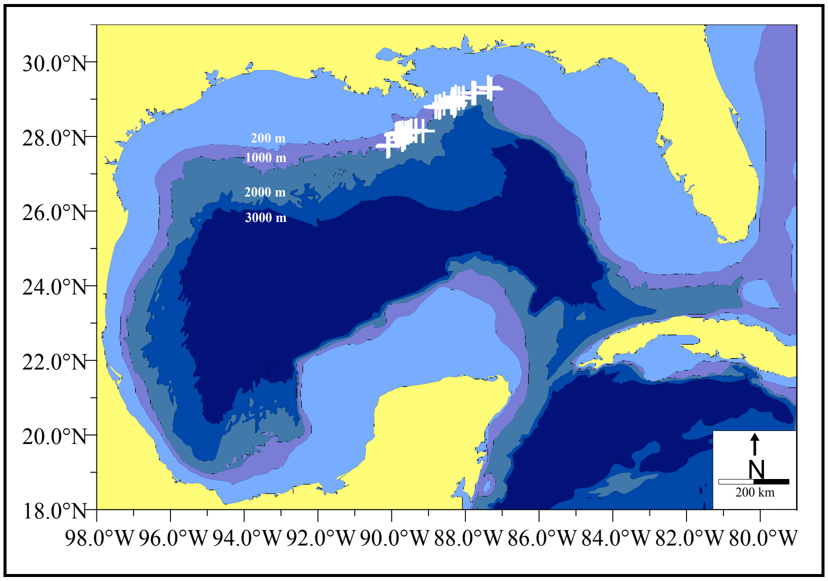

Figure 4.2.4. Gulf biopsy and sloughed skin sampling locations during the SW2K1 July-August 2001 SWAMP summer cruise are depicted as white crosses. Depth contours of 200, 1000, 2000 and 3000 m are illustrated in shades of blue.

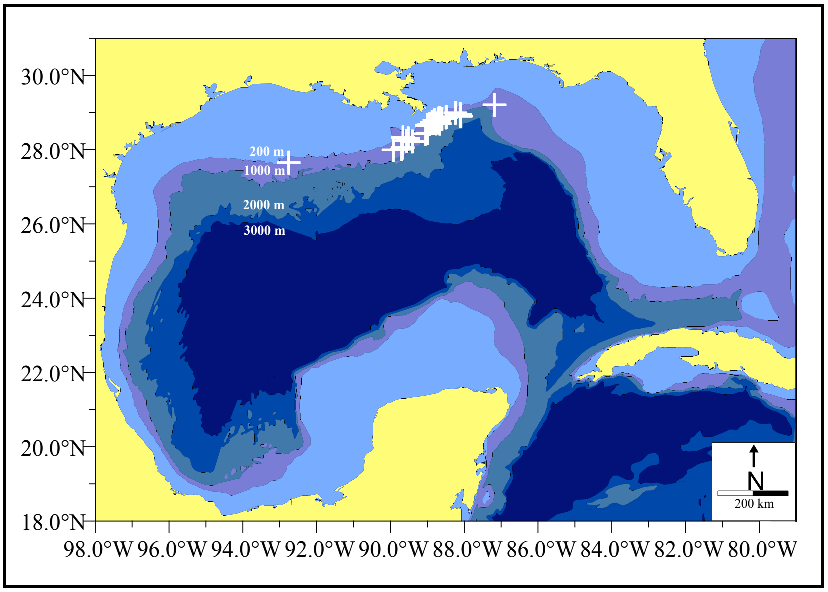

Figure 4.2.5. Gulf biopsy and sloughed skin sampling locations during the SWSS 2002 summer cruises are depicted as white crosses. Depth contours of 200, 1000, 2000 and 3000 m are illustrated in shades of blue.

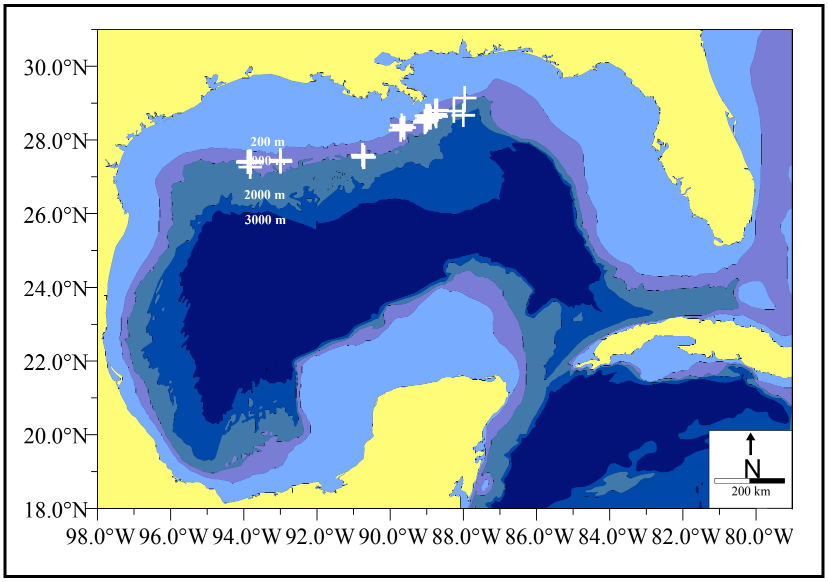

Figure 4.2.6. Gulf biopsy and sloughed skin sampling locations during the SWSS May-June 2003 summer cruises are depicted as white crosses. Depth contours of 200, 1000, 2000 and 3000 m are illustrated in shades of blue.

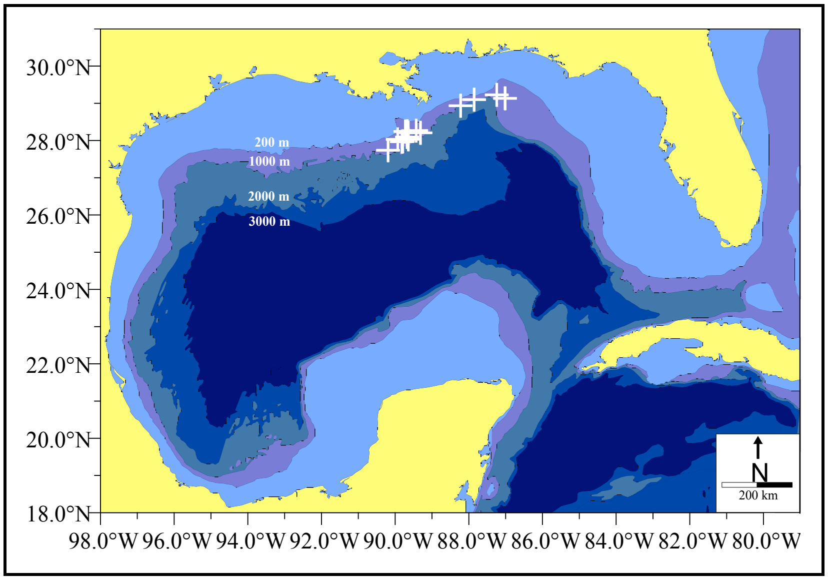

Figure 4.2.7. Gulf biopsy and sloughed skin sampling locations during the SWSS May-June and June-August 2004 summer cruises are depicted as white crosses. Depth contours of 200, 1000, 2000 and 3000 m are illustrated in shades of blue.

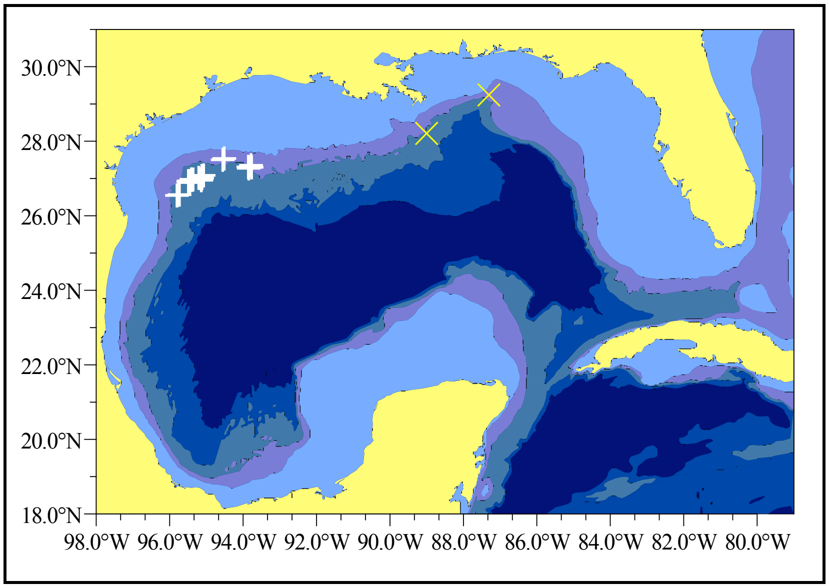

Figure 4.2.8. Gulf biopsy and sloughed skin sampling locations during the SWSS May-June 2005 summer cruise are depicted as white crosses. Biopsy samples collected during the 2005 Mesoscale cruise are depicted as yellow crosses. Depth contours of 200, 1000, 2000 and 3000 m are illustrated in shades of blue.

Surface Reactions to Biopsy Sampling

An assessment of behavioral reactions to biopsy sampling showed that the majority of reactions were generally mild and short-term "startle" responses similar to those described by Whitehead et al. (1990) (Engelhaupt 2004). No significant difference in behavioral reactions was observed between males and females. Although the sample size was small, no visible reactions to biopsy darting of the flukes were noticed and repeat biopsy events on the same individuals did not lead to increasing responses. Overall, these results are in agreement with previous studies performed on numerous cetacean species including sperm whales.

Gender Determination

Gulf of Mexico: For each of the 150 free-ranging Gulf sperm whales, gender was determined for 145 samples using the ZFX/ZFY technique described by Berube and Palsboll (1996). Male (n=2) and female (n=2) strandings with known gender from the GOM and NSEA were included in the analysis and utilized as a means of confirmation for PCR amplifications. In the Gulf of Mexico, the sex ratio of females to males was 2.54:1 (~72% females and 28% males), which is significantly different than an expected ratio of 1:1 (X^2=28.36, p<0.001). This is not unexpected though given what appears to be a preference for lower-latitude waters by female mixed groups (Best 1979; Rice 1989). None of the males that were sampled appeared to be both physically and sexually mature based on very rough length estimates compared to the RHIB and morphological characteristics (e.g., pronounced heads: heads that appear swollen with a distinct ridge behind the base of the skull). However, several of these 'young' males may have been either in or nearing sexual maturity based on these same rough size estimates and compared to Best's (1979) sexual maturity estimates.

Population Comparisons

Sample Size Reductions ('All' and 'Restricted' Sample Sets)

Population comparisons – sample numbers and parameters. Previous studies suggest that high levels of relatedness found within sperm whale groups could potentially bias statistical testing when examining geographic population structuring (Richard et al. 1996; Lyrholm et al. 1999; Bond 1999). As a result, population comparisons using mtDNA and microsatellite DNA (msatDNA) loci were performed using two datasets – 'all' and '*restricted*'. Two methods used to eliminate close kin from the *restricted* population structure estimates are described in detail in Engelhaupt (2004).

The 'all' dataset included all sampled individuals within each of three geographic areas (mtDNA: GOM: N=153, MED: N=38, NSEA: N=19; msatDNA: GOM: N=83, MED: N=22, NSEA: N=20). The '*restricted*' dataset consisted of individuals that were 'pruned' to eliminate potential close kin (mtDNA: GOM: N=40, MED: N=7, NSEA: N=16; msatDNA: GOM: N=40, MED: N=8, NSEA: N=18). Sample sizes differed from the original collected numbers due to failure of poor quality and quantity samples to be sequenced for the control region and failure for the majority of the 16 microsatellites to amplify correctly. An additional analysis for mtDNA sequence results was set up that compared the GOM and MED populations against a WNAO and an overall NAO population. The NAO population is a compilation of data from published studies including samples distributed throughout the western and eastern NAO and the NSEA in addition to free-ranging and stranded whale samples collected from the North Sea, WNAO, Caribbean and Sargasso Seas. The NAO incorporated sequences from the NSEA (N=19), Caribbean, Sargasso and WNAO (N=84) with those of Lyrholm and Gyllensten's (1998) published NAO sequences (N=47). The total number of samples used to represent the 'all' dataset for the collective NAO was 150. The NAO 'all' dataset was unable to be split into a *'restricted'* dataset at this stage due to difficulties associated with comparing microsatellites used for determining kinship between multiple laboratories. However no differences were seen in previous tests comparing 'all' and 'restricted' mtDNA sequences from regions (Engelhaupt 2004).

While a sufficient number of samples remained for the GOM and NSEA datasets, the reduction of possible relatives within the putative MED population significantly reduced the number of individuals used for microsatellite analyses from 22 to *8*. Although the MED '*restricted*' data set was included in population comparisons, caution should be taken when interpreting results obtained from small sample sizes.

Mitochondrial DNA

Genetic diversity estimates: Sequences from this study for 340 individual sperm whales from the GOM, MED, NSEA, WNAO and NAO were compared at the 399bp segment from the 5' control region with twenty-three sperm whale haplotypes (organized as letters A through W and Lyr. 4) provided by Sarah Mesnick of NOAA's Southwest Fisheries Science Center (SWFSC) using the program Mega 2.0 (*http://www.megasoftware.net*) to determine unique haplotypes within the five geographic regions. The SWFSC data include Lyrholm and Gyllensten's (1998) forty-seven previously sequenced samples and resulting haplotypes collected in areas throughout the NAO as well as all other haplotypes discovered to date that occur for sperm whales on a global scale.

For this study, six (1.5%) polymorphic nucleotide sites defining a total of only seven unique lineages were found between the GOM, MED, NSEA and NAO (Table 4.2.1). All nucleotide substitutions between haplotypes were transitions.

Shared haplotypes, distribution of haplotypes and haplotype frequencies are provided in Table 4.2.2. On a global scale, the three most common haplotypes were 'A', 'B', and 'C' (Lyrholm and Gyllensten 1998). While these three haplotypes clearly dominated the NAO (Lyrholm and Gyllensten 1998), haplotype X was the most common (69%) in the GOM with haplotype 'Y' being unique to the GOM. Interestingly, haplotype 'X' was only found once amongst the 150 NAO samples possibly suggesting this whale may have emigrated from the GOM population. A total of five haplotypes ('A', 'B', 'C', 'X' and 'Y') occurred in the GOM; all samples collected from the MED were represented by a single haplotype ('C'); three haplotypes ('A', 'B' and 'C') occurred in the NSEA samples; and six haplotypes ('A', 'B', 'C', 'X', 'Lyr4' and 'N') were present in the NAO data. Although 'A' and 'B' do occur in the GOM, NSEA, WNAO and the NAO, only the 'C' haplotype was distributed across all geographic regions.

Table 4.2.1

Haplotypes with Corresponding Variable Sites
(For 399 base pairs of the mtDNA control region for sperm whales distributed throughout the GOM, MED, NSEA, WNAO and NAO. Dots indicate nucleotide equivalence with the reference sequence (HapA) above.)

Haplotype	Variable Sites					
	62	121	207	272	288	319
Hap A	C	C	A	A	A	G
Hap B	T	.	.	.	.	.
Hap C	T	.	.	.	G	.
Hap Lyr4	.	T	.	.	.	.
Hap N	T	.	.	.	.	A
Hap X	T	.	G	.	G	.
Hap Y	T	.	G	G	G	.

Table 4.2.2

Haplotype Frequencies for Four Geographic Putative Populations
(The left number indicates the 'all' data set and the right italicized number indicates the '*restricted*' subset.)

Haplotype	**GOM**	**MED**	**NSEA**	**WNAO**	**NAO**
A	0.026 / *0.000*	0.000 / *0.000*	0.421 / *0.438*	0.430	0.413 / *0.388*
B	0.150 / *0.225*	0.000 / *0.000*	0.105 / *0.125*	0.095	0.127 / *0.194*
C	0.072 / *0.100*	1.000 / *1.000*	0.474 / *0.438*	0.440	0.420 / *0.373*
Lyr4	0.000 / *0.000*	0.000 / *0.000*	0.000 / *0.000*	0.012	0.013 / *0.015*
N	0.000 / *0.000*	0.000 / *0.000*	0.000 / *0.000*	0.012	0.020 / *0.030*
X	0.686 / *0.575*	0.000 / *0.000*	0.000 / *0.000*	0.012	0.007 / *0.000*
Y	0.065 / *0.100*	0.000 / *0.000*	0.000 / *0.000*	0.000	0.000 / *0.000*
Total	153 / *40*	38 / *7*	19 /*16*	84	150 / *67*

Gene (or haplotype) diversity (h) and nucleotide diversity (π) for each population were unusually low across each of the four 'all' and '*restricted*' populations datasets (Table 4.2.3). Very similar results were reported by Lyrholm et al. (1996) and Lyrholm and Gyllensten (1998). The GOM, NSEA, WNAO and the NAO populations all possessed similar low levels of gene diversity. Nucleotide diversity was also extremely low and constant across the GOM, NSEA, WNAO and NAO populations (0.2% to 0.3% ± 0.2).

The results of Tajima's D for each 'all' and 'restricted' population (excluding the MED due to total lack of polymorphism) were non-significant ($p > 0.05$), suggesting that this locus is not under selection. Fu's F_S test confirmed these results ($p > 0.10$ for each population).

Genetic differentiation between populations: An exact test of population subdivision revealed significant differentiation between all populations for comparisons done for both the all and *restricted* datasets (p-value = 0.000 ± 0.000), with the exception of the MED-NSEA (p-value = 0.049 ± 0.001) and MED-NAO (0.041 ± 0.002) '*restricted*' comparisons (Table 4.2.4). As previously stated, no comparisons were made between the WNAO and the NAO or the NAO and the NSEA because the collective NAO dataset possesses all of the sequences from the WNAO and the NSEA populations. After correction with sequential Bonferroni, the MED-NSEA and the MED-NAO '*restricted*' datasets were non-significant, suggesting no differentiation between the two. This result may be a consequence of the '*restricted*' dataset's small sample size (N=7) for the MED.

Table 4.2.3

Haplotype Diversity (*h*), Nucleotide Diversity (π) ± Standard Deviation and the Mean Number of Pairwise Differences ± Standard Deviation Within Four Geographic Populations
(*Restricted* dataset numbers are in italics.)

Location	Dataset	*n*	Haplotype Diversity (*h*)	Nucleotide Diversity (π)
GOM	all	153	0.500	0.002 ± 0.002
	restricted	*40*	*0.614*	*0.003 ± 0.002*
MED	all	38	0.000	0.000 ± 0.000
	restricted	*7*	*0.000*	*0.000 ± 0.000*
NSEA	all	19	0.620	0.003 ± 0.002
	restricted	*16*	*0.642*	*0.003 ± 0.002*
NAO	all	150	0.640	0.003 ± 0.002
	restricted	*67*	*0.682*	*0.003 ± 0.002*
WNAO	all	84	0.620	0.003 ± 0.002
Total	all	222	0.752	0.003 ± 0.002
	restricted	*130*	*0.776*	*0.003 ± 0.002*

Table 4.2.4

Exact Test *P*-values for Population Comparisons
(Datasets are divided into all and *restricted* material. *P*-values significant at the 0.05 level after sequential Bonferroni correction are in bold type and marked with an '*'.)

	Dataset	*N*	GOM	MED
GOM	all	153	—	
	restricted	*40*		
MED	all	38	0.000 ± 0.000	—
	restricted	*7*	*0.000 ± 0.000*	
NSEA	all	19	0.000 ± 0.000	0.000 ± 0.000
	restricted	*16*	*0.000 ± 0.000*	***0.049 ± 0.001****
NAO	all	150	0.000 ± 0.000	0.000 ± 0.000
	restricted	*67*	*0.000 ± 0.000*	***0.041 ± 0.002****
WNAO	all	84	0.000 ± 0.000	0.000 ± 0.000

F_{ST} and F_{ST} measures of genetic differentiation were calculated for the sequenced fragment based on conventional F-statistics and the Tamura-Nei distance measures respectively. A comparison between the GOM, MED and NSEA populations was performed first. A second comparison between the GOM, MED, WNAO and NAO was then performed.

AMOVA results, incorporating F_{ST}, suggest that the primary source of variation (55.04%/*59.55%*) for the GOM, MED and NSEA 'all' and '*restricted*' samples originates within populations and 44.96%/*40.55%* of the variation is attributed to among population variation. As expected, similar results were obtained when we examined the within population variation (60.60%) and among population variation (39.40%) for the GOM, MED, NSEA, WNAO and NAO comparison. All pairwise calculated values, apart from for the MED-NSEA '*restricted*' population comparison, proved highly significant ($p < 0.01$) for both F_{ST} and F_{ST} genetic differentiation measures (Table 4.2.5). After correcting for multiple comparisons using the sequential Bonferroni correction, the MED-NSEA '*restricted*' comparison was no longer significant at $p < 0.05$. Overall, rather high F_{ST} and F_{ST} values showed extensive differentiation between the GOM, NSEA, MED, WNAO and NAO with respect to both the 'all' and '*restricted*' population comparisons.

Table 4.2.5

mtDNA Population Comparison Among Three Geographic Areas of GOM, MED, and NAO (F_{ST} values are presented in the lower left matrix and F_{ST} values for are presented in the upper right matrix. '*Restricted*' dataset values are in italics and provided below the 'all' dataset values. Statistically significant p-values based on 10,000 permutations of the data and after Bonferroni corrections are marked with an asterisk ($p < 0.05$ = *; $p < 0.01$ = **; $p < 0.001$***).

	GOM	**MED**	**NSEA**	**NAO**	**WNAO**
GOM	—	0.460*** *0.334***	0.488*** *0.420****	0.481*** *0.432****	0.482***
MED	0.626*** *0.511****	—	0.564*** *0.365*	0.368*** *0.333***	0.393***
NSEA	0.427*** *0.326****	0.526*** *0.319*	—	—	
NAO	0.391*** *0.292****	0.331*** *0.279***	—	—	—
wNAO	0.409***	0.363***	—	—	—

Microsatellite Results

All population differentiation analyses using nuclear DNA 'microsatellite' markers between the GOM, MED and the NSEA were conducted on two sets of data – 'all' and '*restricted*'. An overall comparison between the GOM, MED, NSEA, WNAO and NAO populations are pending the results of an ongoing collaboration to score genotypes between laboratories and will be presented in a future publication.

Microsatellite Genetic Diversity Within Populations:

1. Linkage Disequilibrium & Hardy Weinberg Equilibrium (HWE) Deviation. Sixteen microsatellite loci were analyzed for 125 individuals from three different geographic locations. Linkage disequilibrium was tested for each pair of loci within each of the three putative geographic populations and across the data as a whole to ensure that loci were independent of one another. Eleven locus pairs in the 'all' dataset (GOM=9, MED=1, NSEA=1) showed linkage disequilibrium with a p-value < 0.05. After correcting the given p-values with the sequential Bonferroni adjustment for multiple comparisons, the resulting p-values were non-significant for the 'all' population; therefore no association between alleles at different loci was assumed in subsequent analyses.

Estimations of HWE deviation were performed for each population at each locus by testing for heterozygote deficiency and excess within populations and on a global scale. After sequential Bonferroni adjustments were made to the existing p-values, significant deviation ($p < 0.05$) from HWE with respect to heterozygosity deficiency remained at locus EV37 (GOM '*restricted*', MED 'all' and MED '*restricted*' datasets) and EV104 for the GOM 'all' and the MED 'all' and '*restricted*' datasets.

2. Microsatellite allele frequency variation among geographic populations. Under HWE, the observed and expected heterozygosity should be similar in value. Discrepancy between the two may be a result of non-random mating or inbreeding, null alleles or the Wahlund effect. Mean observed and expected levels of heterozygosity over all 16 loci across all 6 datasets are shown in Table 4.2.6.

Total alleles across all three populations for both the 'all' and '*restricted*' datasets was 174 and *163* respectively. The GOM 'all' and '*restricted*' datasets contained the largest number of scored alleles (total alleles = 164 and *151* respectively), while the MED showed the lowest amount (total alleles = 100 and *78* respectively). This result is most likely directly attributed to the difference in sample sizes between geographic areas. Allele sizes didn't appear to differ drastically between populations and were similar to values produced by both Lyrholm et al. (1999) and Bond (1999). Several loci exhibited higher levels of polymorphism than others in both the 'all' (allele range = 3–24 alleles/locus) and '*restricted*' (allele range = *3–21* alleles/locus) datasets and the mean number of alleles/locus over all sixteen loci across all individuals in all populations for each dataset was 10.88 and *10.19* respectively. The percentage of private alleles (*pa*) observed per population and per dataset was as follows: GOM (*pa* = 19.0%, *15.3%*); MED (*pa* = 0.5%, *0.0%*); and NSEA (*pa* = 5.2%, *4.9%*). Overall, private alleles occurred more frequently within the GOM population, but at rather low frequencies across all three populations and both datasets ($pa \leq 0.078$ and $pa \leq 0.075$ respectively).

Table 4.2.6

Mean Observed and Expected Heterozygosity Levels for Each Population's Respective Dataset

Heterozygosity	**Gulf of Mexico**		**Mediterranean Sea**		**North Sea**	
	All	*Restricted*	All	*Restricted*	All	*Restricted*
H_O	0.742 ±0.162	*0.750* ±*0.186*	0.651 ±0.240	*0.648* ±*0.314*	0.742 ±0.158	*0.741* ±*0.155*
H_E	0.752 ±0.133	*0.759* ±*0.143*	0.687 ±0.211	*0.671* ±*0.258*	0.762 ±0.142	*0.766* ±*0.145*

Population Genetic Differentiation:

1. Allelic and Genotypic Distributions. An exact test used to test allelic distribution in different populations (null hypothesis: that allelic distribution is identical across populations) yielded results consistent with population differentiation. However, results may be due to low power at some loci. The extent of significant genetic differentiation between putative populations depended on the locus that was screened. Comparisons for each 'all' dataset population pair across all loci using Fisher's method revealed highly significant *p*-values ($p < 0.001$) for both the GOM-MED and the MED-NSEA. Comparisons for each '*restricted*' dataset population pair across all loci using Fisher's method revealed significant *p*-values ($p < 0.01$) for both the GOM-MED and the MED-NSEA.

Tests of genotypic differentiation (null hypothesis: the genotypic distribution is identical across populations) were also performed and the results confirmed several of the previous genetic results. Several loci that differentiated pairs of populations in both datasets continued to differentiate them at significant levels ($p < 0.05$ after seq. Bonferroni correction). Comparisons for each 'all' dataset population pairs across all loci using Fisher's method revealed highly significant *p*-values ($p < 0.001$) for both the GOM-MED and the MED-NSEA before and after sequential Bonferroni corrections. Comparisons for each '*restricted*' dataset population pair across all loci using Fisher's method revealed significant *p*-values ($p < 0.01$) for both the GOM-MED and the MED-NSEA before and after sequential Bonferroni corrections.

2. Population Structure. The extent of genetic differences that lead to genetic structuring between populations was tested using F_{ST}, theta (θ), R_{ST} and Rho_{ST} statistical measures. Each measures the extent of genetic variation that can be attributed to the genetic differences between each population pair. R_{ST} (Slatkin 1995) and Rho_{ST}, the latter being an unbiased analogue to R_{ST} developed by Goodman (1997), were developed specifically for microsatellites and take the stepwise mutation model (SMM; Shriver et al. 1993) model into account when calculating differentiation. Based on previous sperm whale genetic and behavioral findings, our null hypothesis was that variation observed in nuclear markers (i.e., microsatellites) between putative

populations would be low or non-existent, a result that is suggestive of male dispersal between populations.

F_{ST} and θ estimates for the GOM-MED and the MED-NSEA comparisons each showed low, but significant ($p < 0.01$), differentiation between populations in the 'all' and '*restricted*' datasets before and after sequential Bonferroni corrections were implemented (Table 4.2.7). Pairwise results for R_{ST} and Rho_{ST} are also provided in Table 4.2.7. Rho_{ST} over all populations was 0.020 (95% CI: 0.018 – 0.058; $p < 0.01$) and *0.014* (95% CI: 0.013 – 0.083; $p > 0.05$) for the 'all' and '*restricted*' datasets respectively.

Testing for a recent bottleneck event using the Wilcoxon test in the program BOTTLENECK 1.2.02 also showed some evidence of heterozygosity excess within the GOM population ($p = 0.007$), but not the MED or NSEA populations ($p = 0.058$).

Table 4.2.7

Pairwise Comparisons and Distance Measurements for the GOM, MED and NSEA Populations Using F_{ST}, θ, $R_{ST}(S)$, Rho_{ST}
('*Restricted*' dataset values are in italics and provided below the 'all' dataset values. Statistically significant p-values after Bonferroni corrections are marked with an asterisk ($0.01 < p < 0.05$ = *; $0.001 < p < 0.01$ = **; $p < 0.001$***.)

	F_{ST}	θ	$R_{ST}S$	Rho_{ST}
GOM-MED	0.033*** *0.032****	0.035** *0.037***	0.052*** *0.078***	0.037*** *0.047*
GOM-NSEA	0.000 *-0.005*	0.000 *-0.005*	0.009 *0.015*	0.004 *0.004*
MED-NSEA	0.030*** *0.031***	0.030** *0.033***	0.030 *0.047*	0.031 *0.038*

3. <u>Sex-biased dispersal</u>. As previously described, genetic differentiation was highly significant among the GOM, MED, NSEA, and NAO samples for the mtDNA control region sequences, but only the MED population showed significant differentiation for the microsatellite DNA loci. Sex-biased dispersal results are in agreement with females being the more philopatric sex and males dispersing from their natal populations (Table 4.2.8). Although F_{ST} was slightly higher among females than males, it was non-significant ($p > 0.05$). However, sperm whale population comparisons using nuclear markers show little to no significant differentiation with respect to nuclear DNA and this may have a direct effect on F_{ST} testing for sex-biased dispersal. The

variance assignment test provided an expected higher value for males (the dispersers) than for the females (the more philopatric sex), although values were slightly above the non-significant threshold ($p = 0.081$). The mean assignment test, F_{IS} and H_S were all highly significant ($p < 0.01$) and provided values in accordance with males dispersing.

Table 4.2.8

Sex-biased Dispersal Results for Males and Females with Respect to F_{IS}, F_{ST}, H_O, H_S, Mean Assignment and Variance Assignment

	n	F_{IS}	F_{ST}	H_O	H_S	**Mean Assignment**	**Variance Assignment**
Females	66	-0.004*	0.043	0.738	0.735*	0.785*	14.278
Males	59	0.049*	0.016	0.713	0.750*	-0.878*	16.010

**p*-value < 0.01

Genetic Composition of GOM Groups

Composition of Groups

Members from nineteen groups of whales (G0 – G18) were sampled throughout the Mississippi River Canyon, De Soto Canyon and Dry Tortugas areas during the spring and summer 2000 and 2001 field seasons (Figure 4.2.9). The boundaries of the specified areas are arbitrary given the enormous potential for large-scale movement possessed by individual sperm whales (Best 1979; Ivashin 1981; Kasuya and Miyashita 1988; Rice 1989; Dufault and Whitehead 1998). No distinctively 'large' whales were found within the study area, giving the impression that physically mature adult males either were not present during the study periods or that mature, breeding males are present but are smaller in the Gulf than in other areas that have been studied. Additional details on group composition are provided in Engelhaupt (2004).

Composition of Satellite-Tagged Groups: After the SWAMP cruises during 2000 and 2001, efforts were made to combine biopsy sampling and satellite-monitored tagging to allow for an in-depth examination of how related and un-related individuals within a group maintain associations through time and space. A detailed comparison of genetic relatedness with extremely fine-scale association and movement patterns over days to months for all whales tagged and sampled during 2002–2005 SWSS cruises is described in Ortega-Ortiz et al. (in preparation) (see also Section 4.5).

Gender composition of groups: The sexual composition of groups G0 to G18 was examined using molecular techniques. The majority (72.3%) of whales sampled in these groups were sexed as females. The males were generally scattered throughout, although there were three cases of all male groups (G6, G7 and G8). These males were thought to be sexually immature based on their estimated sizes. By limiting the dataset to include only groups that have ≥ 50% of their estimated group size sampled, only groups G0, G1, G3, G4, G5, G6, G7, G8 and G18 were retained. This more conservative approach results in 66.6% of the nine groups fitting a mixed sex social group scenario and 33.3% fitting the bachelor group scenario. Of these nine groups, 67.5% of all individuals were females and 32.5% were males.

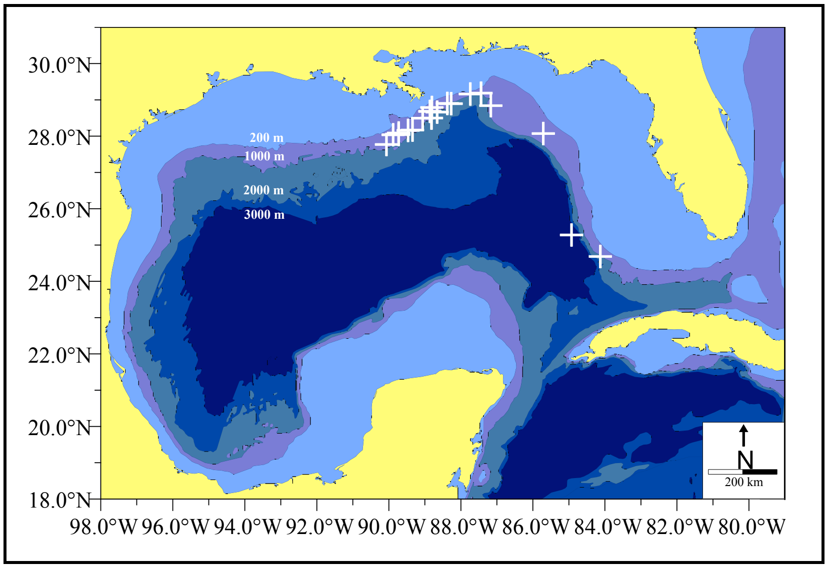

Figure 4.2.9. Locations of 19 groups (G0-G18) sampled in the northern GOM during 2000-2001 are represented by white crosses. Depth contours of 200, 1000, 2000 and 3000 m are illustrated in shades of blue.

Pairwise and group relatedness estimates: All groups were tested as separate entities to provide estimates of relatedness. Estimates of relatedness were determined based on *restricted* and all allele frequency datasets as previously described. Incorporating both datasets allowed a qualitative assessment of the relative importance of background alleles when calculating R-values. Relatedness measurements ranged from -1.0 to +1.0 with positive values signifying two individuals sharing more alleles that were identical by descent than expected by chance, whereas negative R-values were indicative of two individuals sharing fewer such alleles than expected by chance. When populations are in Hardy-Weinberg equilibrium, relatedness coefficients should average 0.50 for first-order relatives (e.g., parent-offspring and full-sibling pairs), 0.25 for second-order relatives (e.g., half-sibs, grandparent-grandchild, and aunt/uncle-niece/nephew) and 0.00 for pairs of randomly chosen individuals that are not related. Relatedness values among all nineteen groups ranged from *-0.130* to *0.278* for the restricted dataset and -0.155 to 0.270 for the all dataset. The mean group relatedness estimate among all 19 groups was *0.067* (s*td. dev.=0.123*) and 0.073 (std. dev.=0.113) for the *restricted* and all datasets respectively. Pairwise relatedness estimates were obtained for all individual members within their respective group.

Estimates of relatedness for all (n=139) pairwise combinations found within each of the 19 groups ranged from *-0.284* to *0.675* and -0.285 to 0.666 with an overall mean of *0.063* (std. dev.=0.193) and 0.054 (std. dev.=0.192) for the *restricted* and all datasets respectively. Both the *restricted* and all means were not significantly different than an R-value of 0.000 (*restricted* Wilcoxon-Mann-Whitney: $U=83.5$, $p=0.813_{20,000}$ (where the subscript = Monte Carlo resampling size); all Wilcoxon-Mann-Whitney: $U=76$, $p=0.905_{20,000}$), which is indicative of non-relatedness among individuals. The distribution of group R-values was centered near zero and suggests individuals within groups generally are not directly or closely related.

Relatedness values for whales found within groups were compared to relatedness levels for whales found between groups to determine whether relatedness is significantly higher within rather than between group members. The mean R-value for all (n=2,556) pairwise relatedness comparisons possible between groups G0-G18 was -0.013 (std. dev. = 0.138) and *-0.003* (*std. dev. = 0.137*) for the all and *restricted* datasets respectively. A highly significant difference (*restricted* Wilcoxon-Mann-Whitney: $U = 144863$, $p = 0.000_{20,000}$; all Wilcoxon-Mann-Whitney: $U = 143977$, $p = 0.000_{20,000}$) in mean relatedness values was found for whales within vs. between groups with respect to both the *restricted* and all datasets suggesting that whales within a group are more related to one another than to whales found in other groups.

The following relatedness estimate data describes two groups of whales where > 2 members of the group were both sampled and tagged with OSU satellite-monitored tags. Age-classes (immature and adult) were estimated based on visual observations only. No young calves were sampled or tagged during this study. Detailed association and kinship information is provided in Ortega-Ortiz et al. in preparation; see also Section 4.5.

> <u>Group G20</u> contained approximately 18 whales, of which four immature males and one adult female were sampled. Two individual males (02070103 and 02070104) within the group shared the same haplotype (C), while the other three whales carried the A, B and X haplotypes. The group estimates of relatedness were *-0.011* (*restricted*) and -0.025 (all). Pairwise relatedness estimates among group individuals ranged from *-0.242* to *0.110* (*restricted*) and -0.279 to 0.110 (all). The female (02070105) shared neither a haplotype nor a strong relatedness value with any of the young males.
>
> <u>Group G22</u> contained approximately eleven whales, of which seven adult females were sampled. All whales within the group shared the same 'X' haplotype. The group estimates of relatedness were *-0.014* (*restricted*) and -0.040 (all). Pairwise relatedness estimates among group individuals ranged from *-0.327* to *0.390* (*restricted*) and -0.364 to 0.353 (all). Interestingly, four whales (00071904, 00071907, 00071908 and 00071909) were previously sampled two years earlier in July 2000 when they were members of group G3.

Matriline composition within groups: All sperm whales sampled in the northern Gulf of Mexico contained one of five haplotypes (A, B, C, X and Y). To date, no additional lineages have been found in samples throughout the GOM. Figure 4.2.10 represents the percentage of sampled members haplotypes (B, C, X and Y) within each of the Gulf groups.

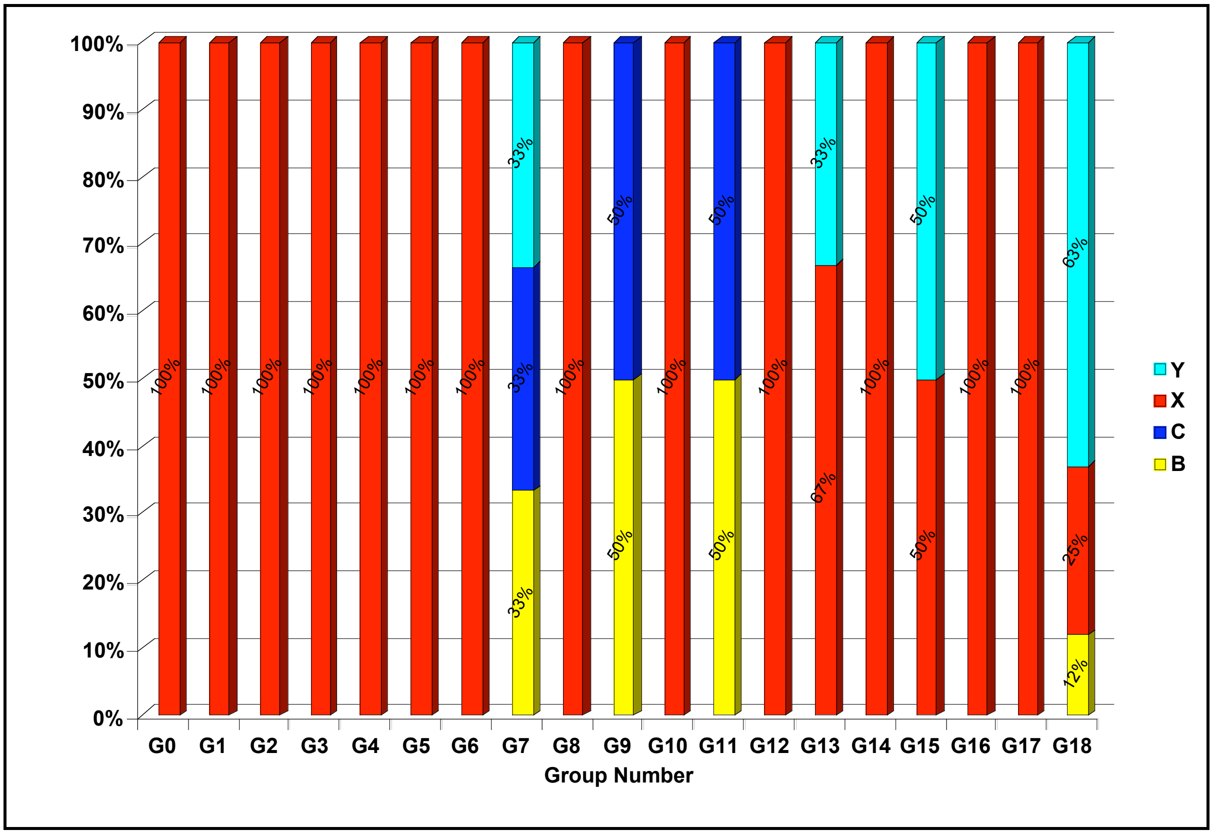

Figure 4.2.10. Percentage of haplotypes B, C, X and Y within the 19 GOM groups.

Putative highly related pairs within groups: Highly related pairs (e.g., mother-offspring, full-siblings, half-siblings and grandparent-grandchild) within groups were identified via an examination of R-values determined with Relatedness 5.0.2 and Kinship 1.3.1 software. Alleles shared across 16 polymorphic loci between possible pairs were examined by eye. Out of 76 individuals comprising 19 groups, only nineteen potential highly related pairs were identified within 12 of the 19 groups. Of the nine groups with ≥ 50% of their members sampled, six groups contained highly related pairs within their respective group. Degrees of relatedness between relations were tested for three scenarios – parent-offspring, full-siblings and half-siblings using the likelihood method previously described. Due to the lack of additional long-term behavioral information, relatedness values could not provide further clarification about which relationship between individuals was the correct one. Certain relationships that tested positive for mother-offspring or full-siblings pairs were discarded after comparing mtDNA haplotypes. For example, the female pair 01032602 / 01032603 that passes for a full-sibling pair ($p < 0.01$) cannot be correct as they come from two different maternal lineages ('B' and 'C' respectively). However, the likelihood of this pair being half-sisters that are related via paternal lines remains plausible ($p < 0.001$).

Nine pairs show R-values that represent parent-offspring, full-siblings or half-siblings based on log-likelihood testing. Interestingly, two of the all male groups (G6 and G8) contained potential full-sibling pairs. None of the members of the two sampled pairs were considered to be both sexually and physically mature based on estimated sizes.. Given the similar estimated length observed in the field, gestation period and growth curve data presented by Best (1979), the most likely scenario would be that these two whales are related at the half-sibling level (sharing a common mother or father – either is possible in this case).

Genetic Composition of Clusters

Clusters vary from groups mainly with respect to the behavior exhibited and the distance separating whales at the surface. Two individuals from each of six clusters (A, B, C, E, F and G), three from cluster D and four from cluster I were sampled using biopsy and sloughed skin collection methods. All clusters described here were imbedded within groups and therefore share the same locations as six of the 19 groups seen in Figure 4.2.9. Additional information such as cluster sizes, number of samples/cluster, gender, haplotype and relatedness values are provided in Engelhaupt (2004). Given the cluster size range of two to ten whales, it is clear that not all clusters were sampled in their entirety and caution should be taken when interpreting the results. However, clusters C, F and G were sampled in full.

Gender composition of clusters: Fifteen females (78.9%) and four males (21.1%) sampled from eight free-ranging clusters in the northern Gulf of Mexico were confirmed using molecular sexing methods. Females within a given cluster varied from juveniles to adults (based on approximate sizes estimated from small boat personnel), while all males within a cluster were considered sexually immature based on estimated sizes. If we limit our dataset to incorporate only clusters that have ≥ 50% or more of their estimated cluster size sampled, then we retain clusters A through G. Only three of these seven clusters were sampled in their entirety. This more conservative approach results in four clusters comprised of females only, two clusters including males and females and only one containing all males. Of these seven clusters, 73.3% of all individuals sampled while in a cluster formation were females and 26.6% were males. Although it would appear that clusters in the northern Gulf are primarily composed of females and/or female-young male combinations, this may simply be a result of the full Gulf sample set being dominated by females.

Pairwise and cluster relatedness estimates: All clusters were tested as separate entities to provide estimates of relatedness. Individual cluster relatedness values over all eight clusters ranged from *-0.119* to *0.585* for the *restricted* dataset and -0.135 to 0.584 for the all dataset. The mean cluster relatedness estimate over all eight clusters was *0.206* (s*td. dev. = 0.289*) and 0.193 (std. dev. = 0.293) for the *restricted* and all datasets respectively. Pairwise relatedness estimates were obtained for all individual members within their respective cluster. Estimates of relatedness for all 15 pairwise combinations within each of the nine clusters ranged from *-0.224* to *0.585* and -0.241 to 0.584 with an overall mean of *0.100* (std. dev. = 0.263) and 0.084 (std. dev. = 0.266) for the *restricted* and all datasets respectively. These means were not statistically different than an R-value of 0.000 (*restricted* Wilcoxon-Mann-Whitney: $U = 8$, $p = 1.000_{20,000}$; all Wilcoxon-Mann-Whitney: $U = 7$, $p = 1.000_{20,000}$), which is indicative of non-relatedness among individuals. The distribution of all cluster R-values was centered near zero, which suggests that individuals within clusters were not highly related.

Potential relative pairs within clusters: First order relative pairs within clusters were identified upon an examination of R-values determined with Relatedness 5.0.2 and Kinship 1.3.1 software. Out of 19 individuals comprising eight clusters, only three potential highly related pairs were identified within three separate clusters (C, F and G). One pair was from the male only cluster G. Potential parent-offspring relationships were only possible within clusters C and F as cluster G was composed of two young males. Both pairs in clusters C and F shared alleles at 16 of 16 loci and provided significant likelihood results for each relationship tested. The male sampled in cluster F was deemed immature based on estimated size. Cluster G could be composed of either full or half-sibs. The two males sampled in cluster G were believed to be immature based on estimated size.

Cluster vs. group comparisons: The mean relatedness value for whales found within clusters was compared to the mean relatedness level for whales found within groups to determine whether relatedness is higher within clusters rather than groups. No significant difference (*restricted* Wilcoxon-Mann-Whitney: $U = 1030$, $p = 0.942_{20,000}$; all Wilcoxon-Mann-Whitney: $U = 1051$, $p = 0.959_{20,000}$) was found when clusters A-I were compared with the mean relatedness values of whales found within groups G0-G18. This suggests that clusters and groups share a low level of relatedness among members.

4.2.4 Summary of Results and Recommendations for Future Research

The research conducted during both the SWAMP and SWSS projects provides a detailed understanding of the molecular ecology for sperm whales occupying the northern Gulf of Mexico (GOM) in addition to describing genetic details for the putative populations located in the Mediterranean Sea (MED), North Sea (NSEA), western North Atlantic Ocean (WNAO) and collective North Atlantic Ocean (NAO). Population structuring between geographic locations, with respect to mtDNA, was highly significant and warrants the classification of each putative population as unique stocks for management purposes. The genetic composition of GOM sperm whale groups fits the previously described scenarios for both mixed sex and bachelor groups located in other areas of the world. Given the limited sample sizes in all areas, it is not possible to rule out the existence of other more or less discrete population stocks or population segments in the Gulf.

Genetic Structure of Four Putative Geographic Sperm Whale Populations

The northern GOM stock is currently listed as a separate stock from that of the western NAO (Waring et al. 2001, 2002, 2004, and 2006). At present, this appears to be based solely on geographic boundaries. Prior to this research, distribution and abundance surveys found sperm whales present year-round throughout the northern GOM which may be a strong indication of philopatry by some whales to an area (Davis et al. 1998). Molecular sexing results indicate that the majority of samples obtained from the Gulf were from immature males and females and adult females. If the expected pattern for mammalian dispersion (Greenwood 1980) holds true and female sperm whales are philopatric to particular geographic areas as indicated by surveys and resightings of individuals within an area over time (Weller et al. 2000), then population structuring with respect to the maternally inherited mtDNA genome may be visible between putative populations (barring extensive emigration and immigration between geographic locations). Although variation and diversity between locations were low, the highly significant level of structuring with respect to this examination of 399 base pairs of the mtDNA control region supports previous genetic results suggesting a significant degree of female philopatry between ocean basins (Lyrholm and Gyllensten 1998). This study's comparison of mtDNA haplotypes between regions proved highly significant with respect to genetic differentiation measures (F_{ST} range = *0.279* (*restricted*) to 0.626 (all); F_{ST} range = *0.333* (*restricted*) to 0.564 (all)) and was consistent with Lyrholm and Gyllensten (1998) results which provided evidence of mitochondrial genetic differentiation between regional populations on a world-wide scale. This is not specific to sperm whales though and has been described for a variety of other marine mammals (see Hoelzel et al. 2002b for a comparative review). While Lyrholm's global-scale study found low mtDNA variation between oceans, this study provides a novel finding in the form of two unique haplotypes ('X' and 'Y') only found among whales sampled in the GOM and WNAO (haplotype 'X' occurring only once in the WNAO). Interestingly, testing for relatedness between the WNAO sample that possessed haplotype X and any of the GOM samples failed to show any sign of first-order relation linking this sample to a GOM whale. The majority of whales sampled in the GOM carry Haplotype 'X'. Also unique was the fact that all samples sequenced from the MED contained only one haplotype ('C'). Although haplotype 'C' was the most common haplotype among all the NAO samples, the total lack of haplotype and nucleotide diversity within the MED sample set may be a clear indication of population isolation, small effective population size or bottleneck event that has reduced maternal lineages (Baker et al. 1999; Hoelzel et al. 2002a; Lyrholm et al. 1996).

Also in agreement with Greenwood (1980), the lack of strong significant nuclear differentiation between neighboring populations suggests that sexually mature males disperse from their natal populations and spread their genes to the more philopatric females. F_{ST}, R_{ST} and Rho_{ST} values (< 0.08), although significant, indicated minimal genetic differentiation between the GOM-MED and the MED-NSEA (significant for F_{ST} only) populations with respect to nuclear differentiation. By testing for sex-biased dispersal, our F_{IS}, H_S and mean assignment results were all in agreement with males being the dispersers and females being the more site-faithful of the sexes. However, larger sample sizes are required to increase the power of these tests (Goudet et al. 2002). While Lyrholm et al. (1999) has already provided evidence for sex-biased dispersal occurring on a global scale, our sample set compares a more restricted geographic area and only includes populations that border the NAO.

Overall, our population structure results support the delineation of the northern Gulf of Mexico into a female-dominated stock that is genetically distinct from the WNAO, NAO, MED and NSEA putative populations (Engelhaupt et al., in preparation). Our genetic evidence is strongly supported by the site-fidelity and coda structuring information presented Sections 4.3, 4.4, and 4.8 of this report and Section 4.3 of the SWSS Summary Report. As such, human activities that may adversely affect the GOM population require proper management to ensure whale stock survival. While the putative population in the MED lacks any mtDNA variation among sampled members, only further sampling in conjunction with additional studies focusing on contaminant analysis, site-fidelity, movement patterns and habitat use will provide a more thorough understanding with regards to questions of isolation.

Recommendations for Future Research – Population Structure

A continuation and extension of multi-faceted research techniques in multiple locations (i.e., the southern, eastern and western Gulf of Mexico, the Caribbean Sea, the MED, throughout the western and eastern NAO and NSEA) would provide further detail needed to accurately describe levels of both population and possibly subpopulation structuring. Mate et al.'s (2006, in review; see also Section 4.3) extensive analysis using satellite-monitored tracking tags strongly supports the idea that movement among female sperm whales is extremely limited and that whales found within particular geographic areas (western and central Gulf of Mexico) prefer separate 'core areas', this is a key factor that may result in subpopulation structuring with respect to the mtDNA genome if sample size in the western Gulf is increased. The movement of tagged males can be more extensive (see Section 4.3; Mate et al. 2006, in review) and supports the concept of male-mediated gene flow between oceans, but requires tagging and sampling of what are believed to be sexually mature males based on accurate size estimates. The occurrence of haplotype 'X' in the WNAO suggests some degree (however minute) of emigration may be occurring by Gulf of Mexico females. The ability to 'bridge the gaps' between geographic areas would provide valuable information about the extent of gene flow within and among geographic locations and better define stock boundaries for regulatory purposes. The development and incorporation of Y-chromosome genetic markers would allow for an assessment of whether genetic variation between males from different geographic populations exists in addition to quantifying levels of relatedness between males from multiple geographic locations. Dedicated efforts to sample large physically and sexually mature males generally found at higher latitudes as well as at lower latitudes during what we believe is the breeding season would provide further clues as to how males disperse from their natal populations and spread their genes to the more philopatric females. The compilation of genetic studies via collaboration amongst researchers around the globe provides important answers with regards to previously unknown questions. Calibrations are currently underway to combine our microsatellite allele size results with those of published data (i.e., Lyrholm et al. 1999) on sperm whale microsatellites to provide a more detailed picture as to how these three putative populations fit into the global sperm whale nuclear DNA picture. Further sampling in conjunction with additional research focusing on contaminant analysis, site-fidelity, movement patterns, habitat use and coda structure among clans will provide a proper understanding of how to properly manage existing sperm whale populations.

Composition of Sperm Whale Groups and Clusters in the Northern Gulf of Mexico

Based on preliminary length estimates and group size estimates conducted during the GulfCet I and GulfCet II cruises, sperm whale groups encountered in the northern Gulf of Mexico were assumed to contain adult females and immatures and calves of both sexes (Davis et al. 1998; Weller et al. 2000; Würsig et al. 2000). In order to accurately assess group type and relatedness among whales within and between groups, this study compared a greater number of polymorphic microsatellites (N=13-16) than previous sperm whale studies, analyzed the highly variable mtDNA control region to describe maternal lineages and incorporated gender results based on molecular sexing techniques. Although our assessment of group composition generally lacked the required long-term association data (aside from those groups and units described in Ortega-Ortiz et al. in preparation; see Section 4.5) and total group sampling to fully understand social structure within GOM groups, both poorly and well-sampled (≥ 50%) group results were quite comparable with gender and relatedness findings suggesting that the majority of groups encountered in the GOM fit the mixed-sex group scenario comprised of both related and unrelated adult females and young of both sexes (Engelhaupt and Hoelzel, in preparation). The occurrence of what seems to be all-male bachelor groups utilizing the same low-latitude feeding grounds as the female mixed-sex groups in the GOM was unexpected.

Relatedness within groups was surprisingly low, but significantly greater than relatedness found between groups. This result is consistent with other sperm whale studies that have focused on both groups and units (Richard et al. 1996; Christal 1998; Bond 1999). There were instances of first-order kin pairs present among sampled group members; however, they were not as frequent as one would expect within a previously described matrilineal species where females show high levels of care for their offspring (Whitehead and Weilgart 2000). Interestingly, groups were composed of both single and multiple (up to 3 in some instances) matrilines. Individuals that shared numerous alleles across multiple loci, but carried different mtDNA haplotypes were assumed to be related at the level of half-siblings via a common paternal line or perhaps grandmother/grandchild (no large males that could be grandfathers were present in the study site) if they shared the same haplotype. Bond (1999) described half-sibling relationships as the most common for mixed sex groups in the Azores and our findings for the Gulf of Mexico appear quite similar. However, the Azores groups were predominantly composed of related individuals (Bond 1999) while the GOM group relatedness values imply that groups are primarily composed of unrelated members.

The sampling of clusters was undertaken on an opportunistic basis. Clusters contained both single and multiple (up to 3) haplotypes and relatedness results among clustered members indicated that clustered whales were no different than whales found within groups.

Recommendations for Future Research – Group Composition

Unfortunately, the Gulf of Mexico lacks extensive long-term (i.e., multi-year) association data required to accurately describe social affiliations among group members. Aside from the data presented in Section 4.5 regarding satellite-monitored tagging results with kinship estimates, our data on group composition is currently unable to imply whether whales sampled within groups are constant companions or simply casual acquaintances that mix with permanent group members on a temporary basis (Whitehead et al. 1991). However, incidental resampling of whales over periods of months to years, does suggest certain whales within groups maintain close affiliations over time. Future work must build on the continued integration of photo-ID, photogrammetry and biopsy sampling in order to combine relatedness issues with association patterns between whales of an accurately known age class over long (several years) durations. The combination of biopsy sampling and satellite-monitored tagging will continue to provide one of the most in-depth examinations of how related and non-related whales sampled within a group either move apart or stay together through space and time. This combination of techniques promises an extremely fine-scale assessment into the daily lives of sperm whales utilizing the northern GOM and surrounding seas.

4.3 Home Range and Seasonal Movements

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4.3.1 Introduction

Information on movement patterns is important to understand the ecology of animals. Movement can subtract from or add to the number of individuals in a local population, alter the outcome of inter- and intra-species interactions, and influence genetic variability (Turchin 1998). Therefore, knowledge of movement patterns is critical to adequately manage animal populations. In the case of sperm whales (*Physeter macrocephalus*), lack of detailed long-term observations has made stock definition for management purposes difficult and controversial (Donovan 1991; Dufault et al. 1999).

Presence of sperm whales in the Gulf of Mexico is known from whaling records from the late 1700s to early 1900s (Townsend 1935), opportunistic sightings and stranding data (Jefferson and Schiro 1997), and dedicated aerial and shipboard surveys (Collum and Fritts 1985; Mullin et al. 1994; Jefferson 1996; Sparks 1997; Biggs et al. 2000; Mullin and Hoggard 2000; Mullin and Fulling 2004). Based on year-round occurrence of strandings, opportunistic sightings, and whaling catches, Schmidly (1981) hypothesized that sperm whales in the Gulf may constitute a distinct stock. Although more information is needed to substantiate stock differentiation, Gulf sperm whales have been considered a separate stock for regulatory purposes (Waring et al. 2002, 2004, 2006). Systematic seasonal aerial surveys have confirmed year-round occurrence of sperm whales in the northern Gulf (Mullin and Hoggard 2000; Mullin and Fulling 2004; Mullin et al. 2004). Although sperm whale sightings are more common during the summer months than in winter, data from both opportunistic sightings and systematic surveys do not show a definitive seasonal distribution pattern (Jefferson and Schiro 1997; Mullin et al. 2004), and the low number of winter sightings may result from reduced effort and poorer sighting conditions in that season.

In contrast with the information on distribution, abundance and habitat characterization obtained from shipboard surveys in the last 15 years (Mulling et al. 1994; Davis et al. 1998; Baumgartner et al. 2001; Davis et al. 2002; Mullin and Fulling 2004), published data regarding movement patterns and site fidelity are limited (Weller et al. 2000). Photo-identification from two shipboard surveys in 1994 and 1996 indicated that some sperm whales maintained a level of interannual site fidelity to waters offshore the Mississippi River Delta (MRD). Out of 37 identified whales, four were sighted both years, and distance between interannual sightings ranged from 36.6 to 46.2 km (Weller et al. 2000). However, as Weller et al. (2000) indicate, it is unknown whether individuals or groups reside in the Gulf year-round, are transient in the region, or migrate to and from other nearby basins where sperm whale presence has been documented.

Adult female and immature sperm whales are found in tropical and subtropical waters, whereas adult males spend most of their time in colder waters at high latitudes and only visit tropical waters to reproduce (Best 1979; Whitehead and Arnbom 1987; Whitehead 2003). Whaling ship logbook records show concentrations of sperm whale captures in certain areas, called “grounds” by the whalers (Townsend 1935). Sperm whale grounds are approximately 1,000 km across and generally coincide with areas of high chlorophyll concentration, high secondary productivity and steep bottom slope (Jaquet and Whitehead 1996; Jaquet et al. 1996). Female and immature sperm whales usually remain in a whaling ground, restricted to ranges of about 1000-1500 km over 10-year periods (Berzin 1972; Gambell 1972; Ivashin 1983; Dufault et al. 1999; Whitehead 2003). However, sometimes they move much further and interchange may occur between stocks that have been considered discrete for management purposes (Best 1969; Kasuya and Miyashita 1988; Donovan 1991; Dufault and Whitehead 1995a; Dufault et al. 1999). While improvements in genetic analysis will help resolve stock structure of sperm whales (e.g., Lyrholm et al. 1999; Engelhaupt 2004), as Dufault et al. (1999) point out, "to effectively conserve and manage sperm whales in the face of substantial anthropogenic disturbance, we need new and good information on modal and exceptional movement patterns over a range of timescales."

Whale movement patterns have been identified from data gathered through several methods: implanting "Discovery"-type marks in the whale body and recovering the marks during whaling operations (e.g., Best 1969; Clarke et al. 1978; Ivashin 1983; Kasuya and Miyashita 1988), tracking whales by signals from acoustic- or radio-tags (Watkins et al. 1993; Watkins et al. 1999) and analyzing individual identification records (Whitehead 2001). These methods have characterized whale movements at different scales. "Discovery" marks provide time and space displacement from mark deployment to mark recovery. In contrast, tracking studies provide detailed information on movements for periods from a few hours (e.g., Whitehead 1996b; Whitehead and Rendel 2004) up to 21 days (Watkins et al. 1999). Analysis of individual identifications has provided information on sperm whale movement patterns over periods as long as a few years; however, this method requires substantial data sets to obtain precise estimates (Whitehead 2001).

Satellite-monitored radio tracking has been successfully used to study movements of several species of large whales, including sperm whales (e.g., Watkins et al. 1996; Mate et al. 1997; Mate et al. 1998; Mate et al. 1999; Watkins et al. 1999; Mate et al. 2000; Heide-Jørgensen et al. 2001a; Watkins et al. 2002; Etnoyer et al. 2006; Zerbini et al. 2006; Mate et al. 2007), and provides information that would be difficult to obtain by other methods or would otherwise require huge field efforts to develop large datasets and many years to elucidate. In this section we describe the seasonal movement patterns and home range of sperm whales in the Gulf of Mexico determined by satellite-tracking radio-tagged individuals.

4.3.2 Methods

Implantable tags with UHF radio transmitters were deployed on 57 sperm whales in the northern Gulf between 2001 and 2005. Tagged whales were tracked through the Argos satellite-based system, which is carried aboard the US National Oceanic and Atmospheric Administration (NOAA) Polar Orbiting Environmental Satellites (POES). We deployed four tags in 2001 during a cruise for the Sperm Whale Acoustic Monitoring Program (SWAMP) conducted by NMFS. The other 53 tags (N = 18, 15, 8 and 12 respectively) were deployed on four cruises conducted each summer in 2002-2005, as part of the Sperm Whale Seismic Study (SWSS) funded by Minerals Management Service and administered by Texas A&M University. Whales were tagged off MRD in 2001-2004 and in the northwestern Gulf in 2005 (Figure 4.3.1). Tagging was conducted from a 6.7-m rigid-hulled inflatable boat (RHIB) launched from the NOAA ship

Gordon Gunter during SWAMP and a similar 6.4-m RHIB launched from the Texas A&M research vessel *Gyre* during SWSS cruises. We approached whales at a range of 1.5-2.5 meters. Tags were deployed with a Barnett 150-pound crossbow during the first cruise; for all other cruises an air-powered applicator (Heide-Jørgensen et al. 2001b) was used. Tags in this study were similar in design to those used on blue whales (Etnoyer et al. 2004; Etnoyer et al. 2006) and right whales (Baumgartner and Mate 2005) consisting of Telonics ST-15 UHF transmitters housed in stainless steel cylinders (19 cm long by 1.9 cm in diameter). Double-edged blades were mounted in one end, with a flexible whip antenna (16 cm long) and saltwater conductivity switch (6.5 cm long) mounted in the other end (Mate et al. 2007). The tag housing was coated with long-term release antibiotic (Gentomycin sulfate in a methacrylate compound) to reduce the possibility of infection. During the 2005 SWSS cruise, two tags equipped with a Telonics ST-21 transmitter were deployed with depth sensors to determine dive habitats (Irvine and Mate in preparation). In order to conserve power and maximize battery life, the tags were programmed to transmit only when out of the water, during four one-hour periods when the NOAA POES were most likely to be overhead. The tags transmitted every day during 2001. In 2002 the same daily transmission cycle was used for the first 90 days and then every third or fourth day resulting in subsequent locations being > 3 days apart. ST-15 tags deployed in 2003-2005 were programmed with a single transmission cycle: one day on and three days off. The two ST-21 transmitters deployed in 2005 were programmed to transmit daily.

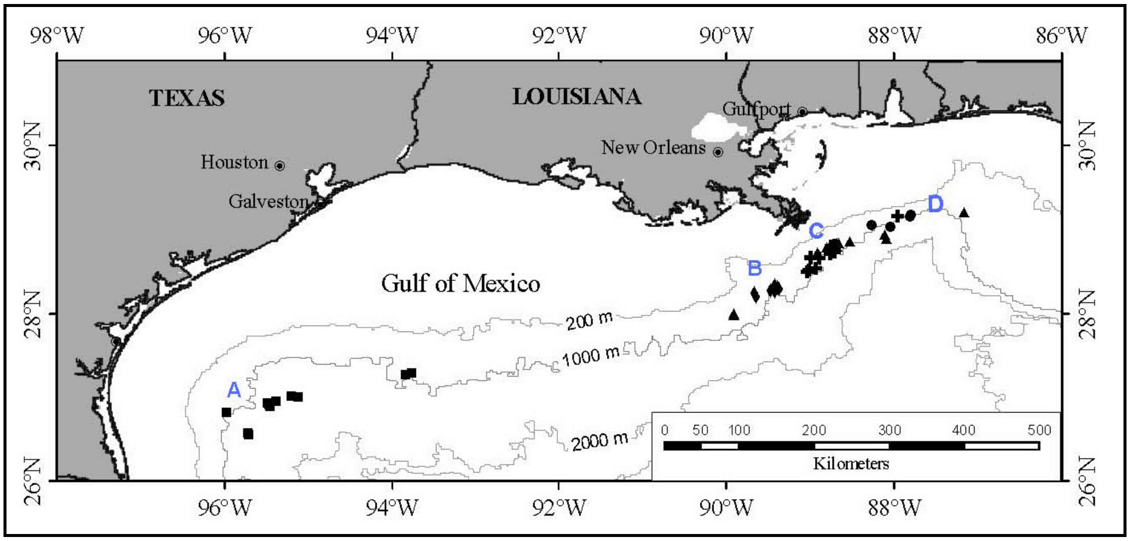

Figure 4.3.1. Deployment locations of satellite-monitored radio transmitters. Year of deployment is indicated with circles for 2001, triangles for 2002, crosses for 2003, diamonds for 2004, and squares for 2005. Regions of interest are: A) Rio Grande Slope (RGS), B) Mississippi Canyon (MC), C) Mississippi River Delta (MRD), and D) De Soto Canyon (DSC). Contour lines indicate 200, 1000, 2000, and 3000 m bottom depth.

Tags deployed in 2003-2005 had color coded antennas to facilitate identification during resightings. Additionally, whenever possible we obtained fluke photographs for individual identification and skin biopsies for genetic analysis. Animal size was estimated by those in the tagging boat comparing the whale to the length of the boat during the tagging approach. Sex-linked genetic markers were used to determine gender. Tissue collection, DNA extraction, DNA processing and data analysis methods are described in extensive detail in Engelhaupt (2004; see also Section 4.2).

The locations of radio tagged whales were calculated by Service Argos from Doppler shift of transmissions created by the speed of the satellite passing overhead (Harris et al. 1990). Location accuracy depends upon the timing and number of messages received during the satellite's passage through reception range (maximum of 16 minutes). Argos estimates accuracy and assigns each location to one of eight classes. Sixty-eight percent of location classes 1, 2, and 3 (abbreviated LC-1, LC-2, and LC-3) are predicted to be within 1.0, 0.35, and 0.15 km, respectively. Location classes 0, A, B, Z and X have no predicted accuracy and are considered low quality (Mate et al. 1997). We retained the largest number of locations possible without compromising accuracy. For this purpose, we calculated the straight-line distance along the surface of the ocean and travel speed between consecutive locations and added a "buffer zone" with a radius of 11.5 km to low quality locations, 1 km to LC-1 locations, and no buffer to LC-2 and LC-3. We based the radius of the buffer zone on previous testing which showed that 95% of Argos-estimated LC-0 locations for ST-15 transmitters were within 11.5 km of the actual location (Mate et al. 1997). Removal of locations to minimize errors then proceeded in several steps:

1. Locations with buffer areas entirely on land were removed.

2. Locations with speeds < 6 km/h (when less than 12 hours apart) or <3.5km/h (when greater than 12 hours apart) between them were retained. If speeds were greater, the sum of the two location buffer values was subtracted from the total distance between them and the speed recalculated. If the new value fit the criteria, both locations were retained; otherwise, the location with the lower LC quality was removed. If the locations had the same quality, the one whose removal minimized distance traveled was eliminated.

3. Locations were also edited on a temporal basis. When a location with an assigned quality of less than LC-1 was 4 hours apart from another location, only one was retained. The location with the higher LC quality was chosen or, if they were both less than LC-1, the one whose removal minimized distance traveled was edited out.

4. When an LC-1 location was < 20 minutes apart from a location LC-2 or LC-3, the LC-1 location was removed. If an LC-1 location was < 20 minutes apart from another LC-1, the location whose removal minimized distance traveled was eliminated.

In the Gulf of Mexico, sperm whales are known to occur in deep waters beyond the continental shelf (e.g., Davis et al. 1998; Baumgartner et al. 2001; Davis et al. 2002). Therefore, satellite-determined locations were plotted in a geographic information system (ArcView GIS, ver. 32.), overlaid on a 2-minute latitude/longitude bottom depth grid (this is the two-minute Gridded

Global Relief Data of the 2001 ETOPO2 data set produced by the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Geophysical Data Center). Low quality locations in waters less than 200-m depth were removed.

Home ranges of satellite-tracked sperm whales were estimated using the Animal Movement Extension for ArcView (Hooge and Eichenlaub 2000) to calculate kernel utilization distribution (UD) (Worton 1989). The home range of each tagged whale was defined as the area covered by the 95% UD and high-use or “core” areas were defined by the 50% UD area. In order to avoid pseudo replication, only satellite-determined locations more than 23 hours apart were used in the home range analysis. Almost all (99.2%) high quality locations (ARGOS LC1-3) occurred over water deeper than 500 m. therefore, home range estimates were corrected by subtracting any portion of UD areas that occurred in water < 500m deep. Individual home range and core areas of all tagged whales were overlaid to identify overlap between individuals.

4.3.3 Results

Location data were received from 52 of 57 tags. Thirty-three tagged whales were females, six were males, and 18 were of undetermined sex due to the lack of biopsies (Table 4.3.1). A total of 4276 satellite-determined locations were received from Service Argos. After applying the quality selection criteria, 3,269 locations (76.4%) were retained. Forty two percent of all received locations (50% of retained locations) were of LC-1 quality or better. The number of locations retained for each individual ranged between 3 and 187 (mean = 61.8, median = 46.5). Effective tag life (i.e., time between tag deployment and reception of last satellite-determined location) ranged between 11 and 607 days (mean = 191.7, median = 133.0). Some tags transmitted past their effective life but the Argos System was unable to estimate a location for those transmissions. For example, the tag with the longest effective life (PTT #2505725) transmitted for 620 days after it was deployed but no location was estimated after 607 days.

Tagged whales ranged in estimated length from 7.5 to 12 m. Whales tagged in 2005 were smaller than whales tagged in 2002-2004. Tagged males ($\bar{x}$ = 10.5, n = 5) and females ($\bar{x}$ = 10.6, n = 9) were similar in size during 2002, the only year with a reasonable sampling of males. Photogrammetric size estimates suggest that sperm whales are smaller in the central and eastern Gulf of Mexico than in the Gulf of California, Mexico (Jaquet 2006; see also Section 4.4.4 of this report). Calves were observed in the groups of sperm whales encountered during all four years on S-tag cruises. In 2002, 7 of 16 groups that were sighted had calves (4 of the 6 groups tagged had calves). In 2003, 4 of 16 sighted groups had calves (2 of the 8 groups tagged had calves). In 2004, 10 of 17 groups that were sighted had calves (2 of the 4 groups tagged had calves). In 2005, 7 of 16 sighted groups had calves (4 of the 7 groups tagged had calves). Three tagged females, PTT# 2505660, 3200838, and 3700836, were accompanied by calves and were assumed to be the mothers.

Table 4.3.1

Tag Deployment Information, Active Tag Life, Maximum Displacement, Home Range and Core Area of Satellite-Tracked Sperm Whales

(Home range and core area correspond to 95% and 50% kernel utilization distribution, respectively.
N.D. = no data, tag did not transmit; F = female, M = male, U = unknown, * = adults accompanied by a calf.).

PTT# (tag#)	Sex	Whale size (m)	Deployment			Tag life (days)	Num. of locations	Maximum displacement (km)	Home range (km^2)	
			Date (GMT)	Latitude N	Longitude W				95% UD	50% UD
2102083	U	8.4	08 Aug. 2001 23:03	29.174	87.799	136.6	199	1286	113,284	21,778
2110820	U	N.D.	01 Aug. 2001 18:51	29.064	88.266	0.0	0	N.D.	N.D.	N.D.
2123030	U	N.D.	07 Aug. 2001 23:19	29.042	88.054	0.0	0	N.D.	N.D.	N.D.
2123032	U	N.D.	08 Aug. 2001 20:25	29.159	87.809	0.0	0	N.D.	N.D.	N.D.
2505647	F	11	01 Jul. 2002 21:58	28.903	88.092	135.7	71	228	27,096	3,100
2505648	M	11	28 Jun. 2002 23:03	29.207	87.178	73.0	30	539	219,547	31,576
2505649	U	10	07 Jul. 2002 20:20	28.708	88.911	371.8	101	177	12,791	2,968
2505650	M	11	01 Jul. 2002 19:48	28.956	88.109	268.0	120	923	114,146	21,304
2505654	U	10	24 Jun. 2002 23:06	27.993	89.913	122.6	43	592	83,794	11,931
2505655	U	10	03 Jul. 2002 20:47	28.839	88.687	74.6	57	535	53,518	14,382
2505660	F*	11	24 Jun. 2002 18:36	28.011	89.913	63.7	22	410	76,447	12,178
2505669	F	11	03 Jul. 2002 23:07	28.804	88.693	454.7	89	683	70,360	10,779
2505670	F	11	03 Jul. 2002 19:48	28.840	88.692	286.0	46	649	64,675	8,832
2505678	F	12	02 Jul. 2002 23:10	28.860	88.529	17.1	9	75	3,341	576
2505685	M	10	01 Jul. 2002 19:35	28.958	88.109	566.1	107	824	111,076	14,208
2505701	F	9.5	03 Jul. 2002 23:42	28.805	88.698	247.2	111	658	71,539	9,592
2505709	F	9.5	03 Jul. 2002 16:49	28.788	88.764	372.9	91	642	68,192	11,683
2505710	U	10	07 Jul. 2002 19:25	28.732	88.923	81.9	42	137	8,976	2,331
2505719	F	9.5	03 Jul. 2002 15:24	28.793	88.808	70.7	22	638	108,067	10,933
2505720	F	11	03 Jul. 2002 20:09	28.850	88.673	30.8	8	130	8,567	3,475

Table 4.3.1

Tag Deployment Information, Active Tag Life, Maximum Displacement, Home Range and Core Area of Satellite-Tracked Sperm Whales (continued)

PTT# (tag#)	Sex	Whale size (m)	Deployment			Tag life (days)	Num. of locations	Maximum displacement (km)	Home range (km^2)	
			Date (GMT)	Latitude N	Longitude W				95% UD	50% UD
2505725	M	11	01 Jul. 2002 21:40	28.903	88.099	607.3	97	2100	1,136,092	101,600
2505726	M	11.5	01 Jul. 2002 20:16	28.950	88.113	275.8	89	875	209,742	28,026
2800826	F	9.25	11 Jul. 2003 23:15	28.805	88.722	243.5	82	446	22,788	4,269
2800827	M	9.5	11 Jul. 2003 20:43	28.797	88.763	179.1	21	190	15,566	3,485
2800828	F	8.5	04 Jul. 2003 00:06	28.657	89.009	304.0	136	579	71,331	14,184
2800829	F	10	09 Jul. 2003 23:38	28.482	89.043	298.9	93	212	12,837	1,696
2800833	F	8.5	05 Jul. 2003 17:41	28.732	88.763	155.8	79	143	8,670	1,340
2800839	U	9	08 Jul. 2003 19:03	28.521	88.946	48.1	9	41	2,230	490
2800843	F	8.5	05 Jul. 2003 15:49	28.725	88.721	352.9	158	466	13,883	2,780
2801385	F	10.25	03 Jul. 2003 23:42	28.651	89.001	391.4	109	573	72,138	12,055
2805654	U	9.25	04 Jul. 2003 00:21	28.667	89.007	79.9	32	587	76,656	19,934
2805678	F	10.25	11 Jul. 2003 20:17	28.787	88.758	218.1	74	778	112,156	31,298
2805710	U	9.5	07 Jul. 2003 20:15	28.652	88.908	408.7	148	701	86,864	13,811
2805719	F	8.5	06 Jul. 2003 00:08	28.698	88.765	341.0	162	412	22,939	4,275
2805720	F	9.25	06 Jul. 2003 23:54	29.140	87.965	130.4	49	232	15,832	5,331
2810820	F	10	09 Jul. 2003 16:18	28.506	89.026	61.8	17	238	7,242	1,165
2823038	U	9.25	11 Jul. 2003 23:35	28.794	88.724	95.6	5	477	100,446	17,447
3200838	U*	N.D.	10 Jun. 2004 18:51	28.320	89.394	0.0	0	N.D.	N.D.	N.D.
3200841	U	N.D.	17 Jun. 2004 20:02	28.213	89.645	0.0	0	N.D.	N.D.	N.D.
3200845	U	9.5	10 Jun. 2004 17:05	28.332	89.436	91.3	16	62	4,776	729

Table 4.3.1

Tag Deployment Information, Active Tag Life, Maximum Displacement, Home Range and Core Area of Satellite-Tracked Sperm Whales (continued)

PTT# (tag#)	**Sex**	**Whale size (m)**	**Deployment**			**Tag life (days)**	**Num. of locations**	**Maximum displacement (km)**	**Home range (km^2)**	
			Date (GMT)	**Latitude N**	**Longitude W**				**95% UD**	**50% UD**
3201387	U	9	10 Jun. 2004 19:45	28.300	89.372	139.2	22	119	5,238	1,454
3201390	F	9	10 Jun. 2004 17:46	28.311	89.433	95.2	13	187	11,956	2,909
3202083	F	8.5	06 Jun. 2004 23:00	28.247	89.670	39.5	9	64	2,902	848
3205660	F	9	06 Jun. 2004 14:30	28.266	89.429	71.9	3	49	1,463	324
3205670	F	8.5	06 Jun. 2004 15:51	28.271	89.485	359.2	54	465	22,635	8,586
3700836	F*	8.5	11 Jun. 2005 15:35	26.567	95.732	128.2	38	203	23,714	6,870
3700846	F	8	21 Jun. 2005 18:52	26.931	95.484	472.2	179	263	36,019	4,354
3700847	F	8.25	27 Jun. 2005 00:53	27.288	93.775	56.4	25	123	12,301	2,359
3701386	F	8	21 Jun. 2005 19:01	26.928	95.488	97.2	35	183	16,593	2,325
3705644	F	8	21 Jun. 2005 16:59	26.950	95.402	20.7	29	100	11,415	1,826
3705648	F	7.5	21 Jun. 2005 22:46	26.891	95.458	332.6	128	610	80,727	11,009
3705650	U	8	11 Jun. 2005 14:45	26.552	95.719	56.2	19	106	12,726	5,551
3705654	F	8	28 Jun. 2005 22:52	27.017	95.208	58.9	21	153	11,543	2,930
3705701	F	7.5	24 Jun. 2005 16:15	27.274	93.845	11.2	4	74	11,063	5,322
3705709	U	8	29 Jun. 2005 15:16	26.815	95.983	126.2	31	290	18,068	2,044
3705726	F	8.5	21 Jun. 2005 23:43	26.909	95.485	292.4	94	600	90,462	15,967
3705800	F	7.75	15 Jun. 2005 14:52	27.010	95.118	33.3	47	123	14,476	3,096

After the 2001 field season, when only one of four tags (25%) was successfully attached by crossbow, and the deployment system was changed to a compressed air applicator (Heide-Jørgensen et al. 2001b; Mate et al. 2007). This resulted in more reliable deployment of tags and more consistent tag longevity, with data received from 51 of 53 whales (96%) tagged from 2002-2005. Of the 51 tags sending data, 21 (40%) lasted > 200 days, 12 (23%) lasted > 300 days, and 8 (15%) transmitted for more than one year. The tagged males (n = 6) transmitted for an average of 328.2 days while the tagged females (n = 33) transmitted an average of 186.8 days.

Nine whales were resighted 213 to 350 days ($\bar{x}$ = 316.6, S.D. = 58.62) after tagging (DAT). Two had lost their tags (197 and 31 days after transmissions had stopped on whale #2505678 at 214 DAT and #2800828 at 330 DAT) and there were no apparent signs of wounds or swelling. Three tags were still attached 104, 279 and 72 days after transmissions were no longer being received from whales #2505701 at 351 DAT, #2505719 at 350 DAT and #2505726 at 348 DAT, respectively. The remaining four tags were exposed 2-7 cm and continued to transmit 110, 73, 23, and 63 days after the last sightings of whales #2505669 at 355 DAT, #2505670 at 213 DAT, #2505709 at 350 DAT, and #2805710 at 19 DAT, respectively. One tag (on whale #2505709), which had been attached for 350 days, had worked its way nearly out of the whale (85% of tag exposed), revealing a few small white dots in a 4 cm circle where attachments had worked their way through the skin. Two gooseneck barnacles and a cluster of tunicates were attached to the tag housing (Mate et al. 2007). The whale appeared healthy and its behavior did not differ from other whales. The tag ceased transmitting 23 days after this observation, probably coinciding with the loss of the tag. Only one whale (#2505670) showed any visible effect related to the tag attachment that consisted of modest localized swelling at its last sighting (213 DAT).

Gender-based Movements

The only successful tag deployed in 2001 was on an 8.4-m whale of unknown sex (#2102083). It spent 91 days off the MRD and then moved west and south along the slope across the northern and western Gulf (Figure 4.3.2). It arrived in the Bay of Campeche 117 days after tagging, and stayed for 19 days until the transmissions ceased.

The minimum possible distance traveled by all the tracked whales (assuming rhomb line movement between consecutive retained locations of the same individual) was 155,613 km (35,598 km for those biopsied as males and 92,202 km for those biopsied as females). Speed estimates ranged from 0 to 9.6 km h^{-1}, averaged 1.35 km h^{-1} (S.D. = 1.28), and the 95 percentile was 3.69 km h^{-1}. A comparison was performed between individuals with at least 30 locations (21 females and 5 males) after the variable was log transformed to approximate a normal distribution. There were significant differences in the average speed among individuals ($p < 0.01$) and also between females and males (ANOVA with individual whale factor nested in sex factor, $p < 0.01$, $\bar{x}$ females = 1.27 km/h, $\bar{x}$ males = 1.44 km/h).

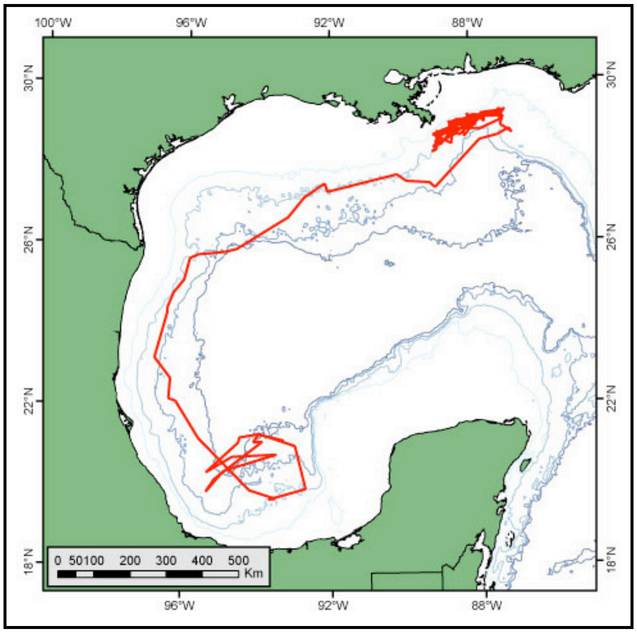

Figure 4.3.2. Trackline of sperm whale of unknown sex (PTT #2102083) tagged in 2001 off the MRD and tracked for 136 days to the Gulf of Campeche, Mexico.

Females typically ranged approximately 200 km around the tagging location zigzagging across the upper continental slope. Females were also observed > 200 km away from the tagging location but, in most cases returned to the tagging locations. One trek, involving a group of at least five females tagged on 3 July 2002 (#s 2505669, 2505670, 2505709, 2505701, and 2505719), is represented in Figures 4.3.3-4.3.5. That group left the Mississippi Canyon on 28 October 2002 and traveled together about 680 km west, along the 1000 m depth contour. On 23 September they turned and headed east to arrive near the tagging location on 10 November 2002. A sixth whale (#2505660) tagged on 24 June also traveled much the same route (Figure 4.3.5). During this same period, four other tagged whales (male #2505725; female #2505647, Figure 4.3.6; and two of unknown sex #2505710 and #2505649, Figure 4.3.7) remained within 200 km of the tagging location. Females rarely moved into deep water (Figure 4.3.8 shows one example of an exception, whale #2800828). One female whale (#2505647) spent most of its time in water depths over 2000 m, which was in deeper water than the other females (Figure 4.3.6).

The same sorts of tracks were observed for female whales in 2003 and 2004, with examples of short range movements (Figures 4.3.9-4.3.10 and 4.3.11, respectively), intermediate distances from the tagging site (Figure 4.3.12), and longer loops to the Rio Grande Slope (RGS) (Figures 4.3.13 and 4.3.14, respectively).

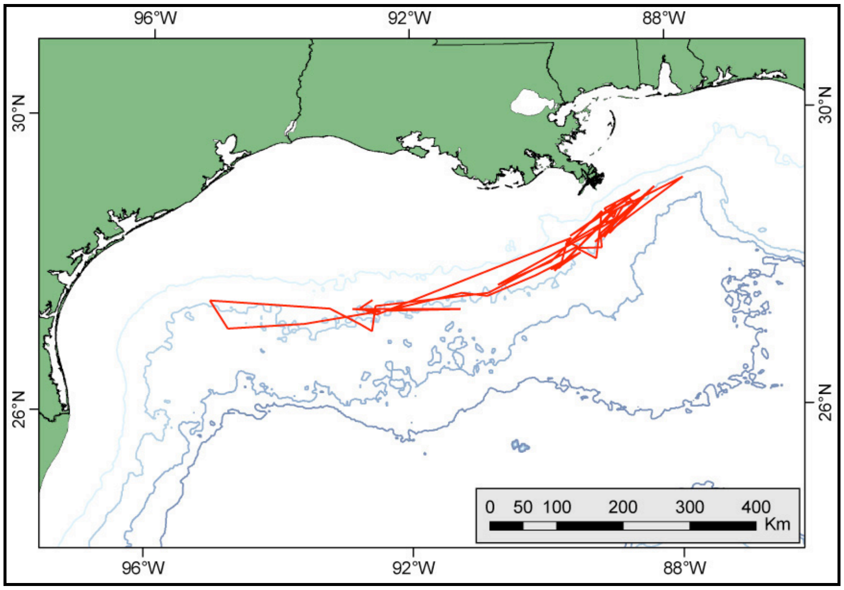

Figure 4.3.3. Trackline of female sperm whale (PTT #2505669) tagged in 2002 off the MRD to the RGS and back.

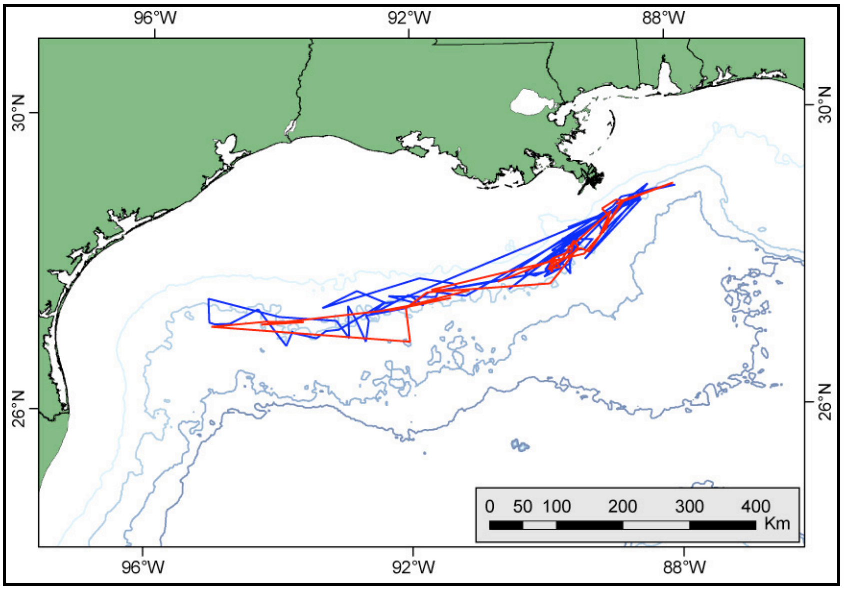

Figure 4.3.4. Trackline of two female sperm whales (PTT #2505570 and #2505709) tagged in 2002 off the MRD.

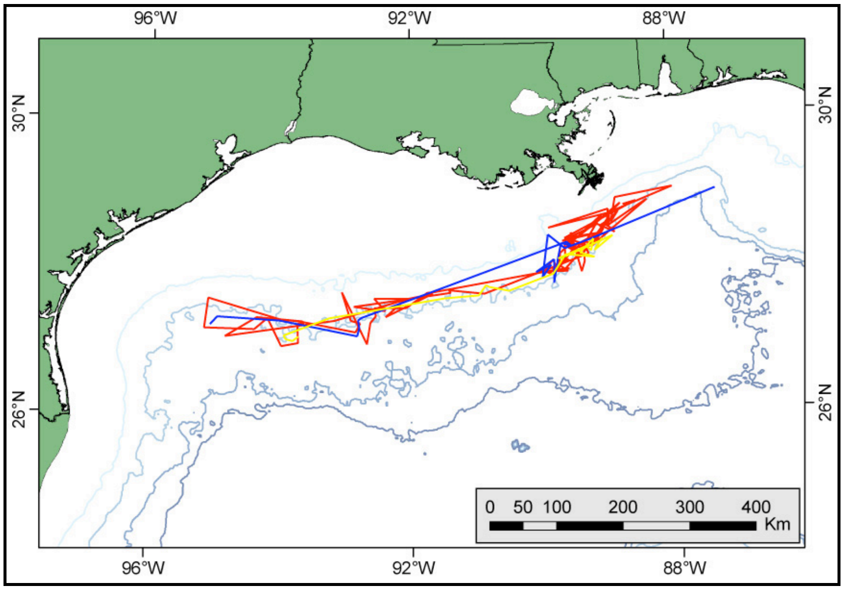

Figure 4.3.5. Trackline of three female sperm whales (PTT #2505701, #2505719, #2505660) tagged in 2002 off the MRD.

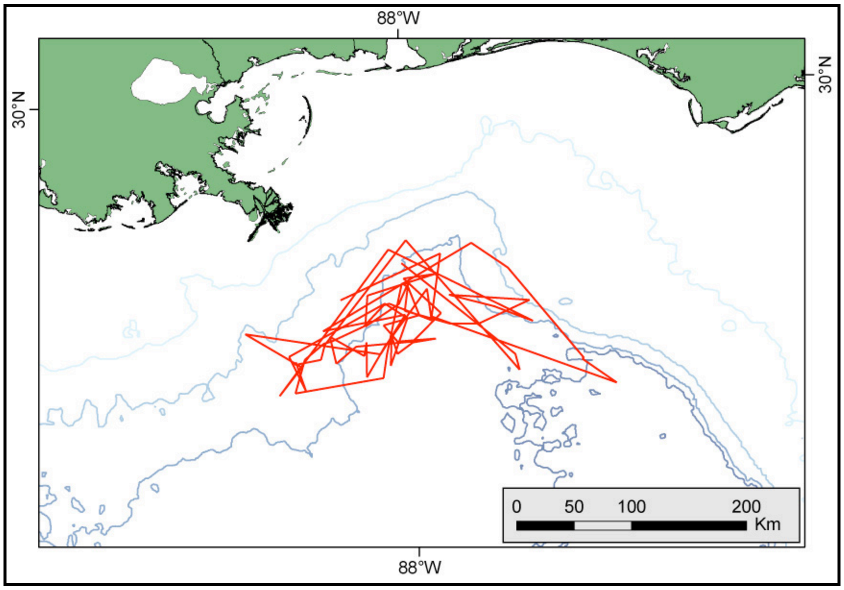

Figure 4.3.6. Trackline of female sperm whale (PTT #2505647) tagged in 2002 showing a consistent emphasis on somewhat deeper waters than most females.

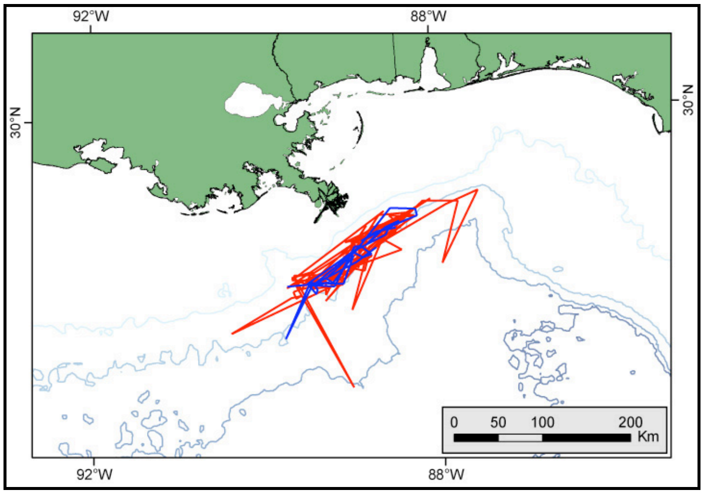

Figure 4.3.7. Trackline of two sperm whales of unknown sex (PTT #2505649, #2505710) tagged in 2002, showing localized movements near the tagging site for up to 372 days (PTT #2505649).

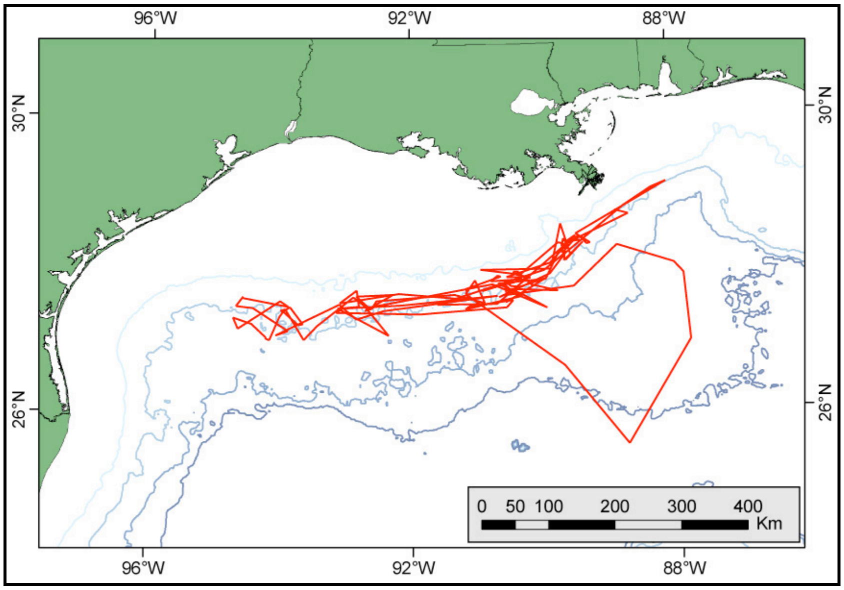

Figure 4.3.8. Trackline of female sperm whale (PTT #2800828) tagged in 2003 with a loop out into water >3000 m.

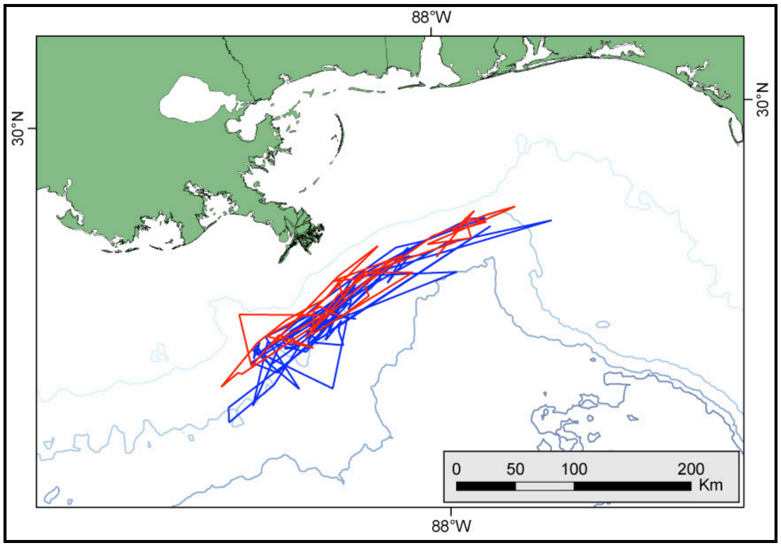

Figure 4.3.9. Trackline of two female sperm whales (PTT #2800829 and #2805720) tagged in 2003 showing localized movements near the tag site for up to 299 days (PTT #2800829).

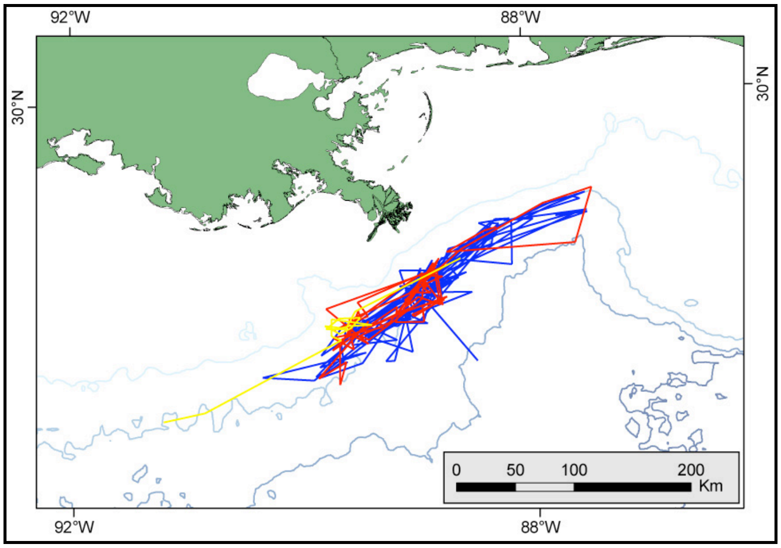

Figure 4.3.10. Trackline of three female sperm whales (PTT #2800833, #2800843, and #2810820) tagged in 2003 showing localized movements for up to 353 days (PTT #2800843).

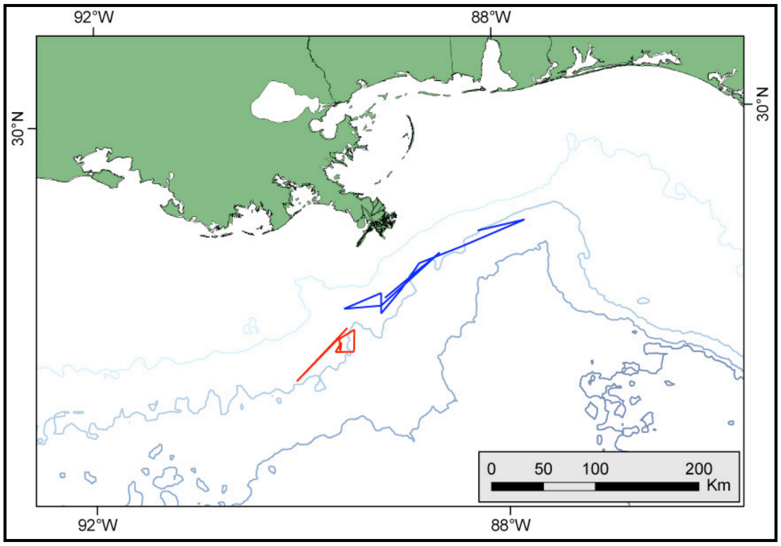

Figure 4.3.11. Trackline of two female sperm whales (PTT #3201390 and #3202083) tagged in 2004.

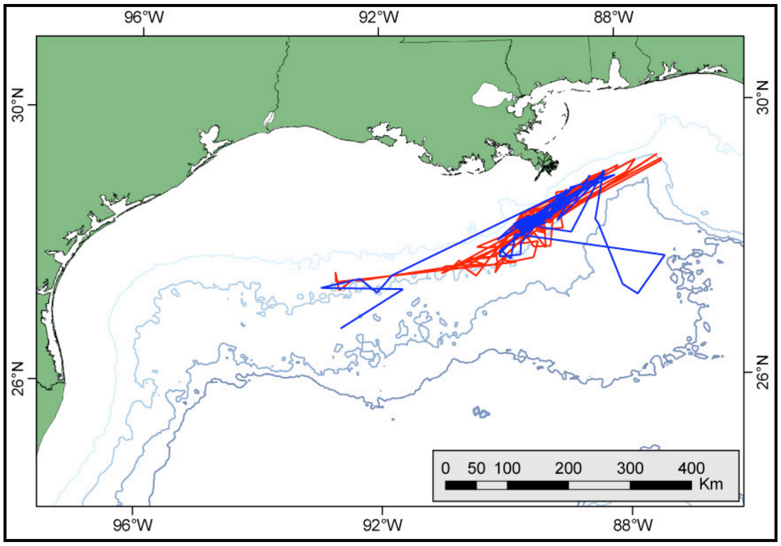

Figure 4.3.12. Trackline of two female sperm whales (PTT #3200826 and #3205719) tagged in 2003 showing a loop out into deep water >2000 m.

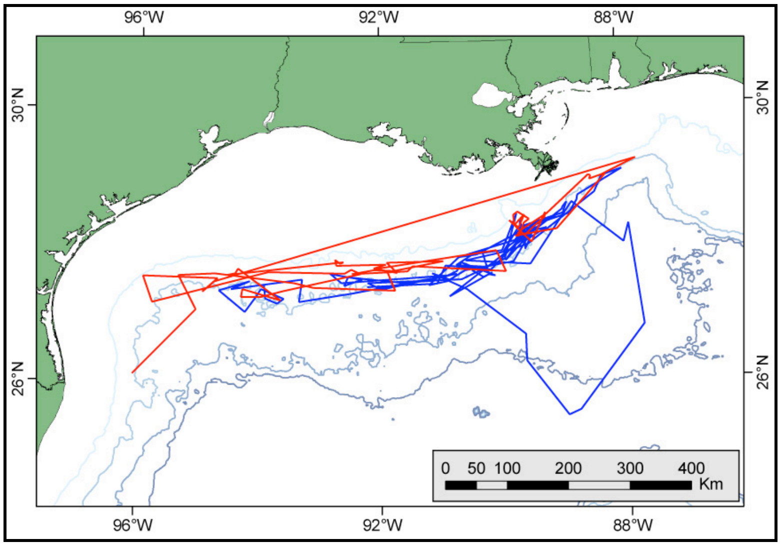

Figure 4.3.13. Trackline of two female sperm whales (PTT #3201385 and #3205678) tagged in 2003 showing their movement to the western Gulf and an offshore loop into water >3000 m.

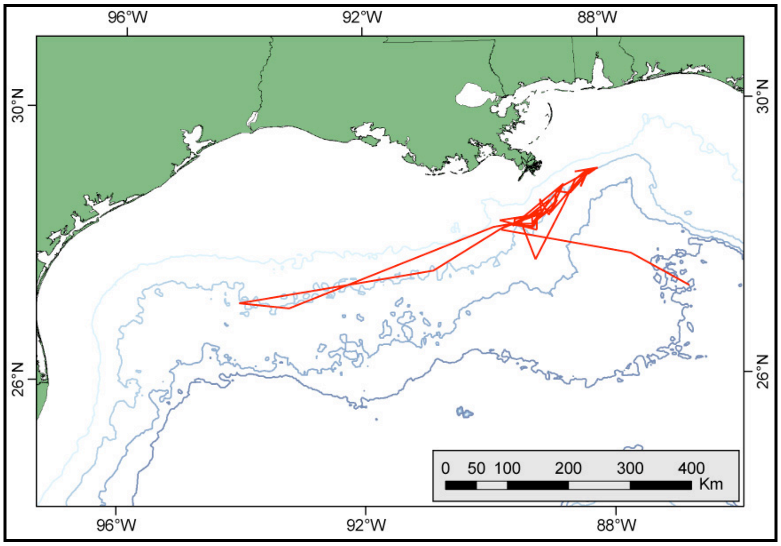

Figure 4.3.14. Trackline of female sperm whale (PTT #3205670) tagged in 2004 showing a round trip to the western Gulf and exploration to the 3000 m contour southeast of the tagging site.

Males tagged in 2002 demonstrated more variability in their movements and greater use of water > 3000 m deep than 2002 tagged females (Figure 4.3.15). Four of five whales tagged in a small group within 2.6 h on 1 July 2002 off the MRD were males (#2505650, #2505685, #2505725, and #2505426). These whales did not stay together. Two (#2505650 and #2505726) traveled together toward the western Gulf and then separated. Whale #2505726 stayed over the RGS in the western Gulf for two weeks and then returned east (Figure 4.3.16), but made another loop west later, while whale #2505650 stayed at the RGS for 208 days, until the tag stopped transmitting (Figure 4.3.17). Whale #2505685 made two looped trips, one to the water of the deep southeast Gulf, and the other to the RGS (Figure 4.3.16). Whale #2505648 did not go so far west, but made a large loop into deep water over the central Gulf (Figure 4.3.16).

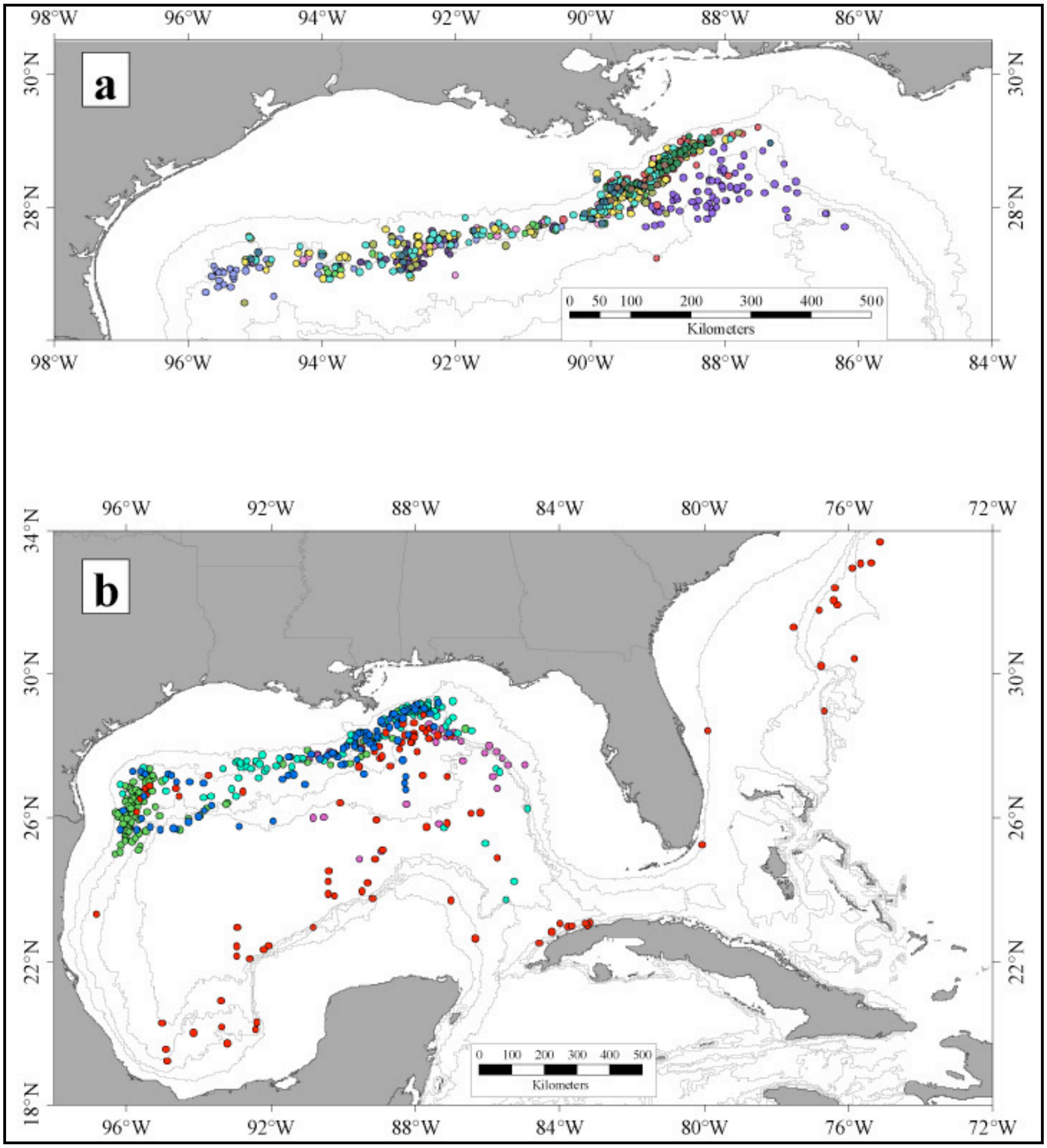

Figure 4.3.15. Satellite determined locations of female and individuals of unknown sex (a) and male (b) sperm whales tagged in 2002. Contour lines indicate 200, 1000, 2000, and 3000 m bottom depth. Colors of locations indicate different individuals.

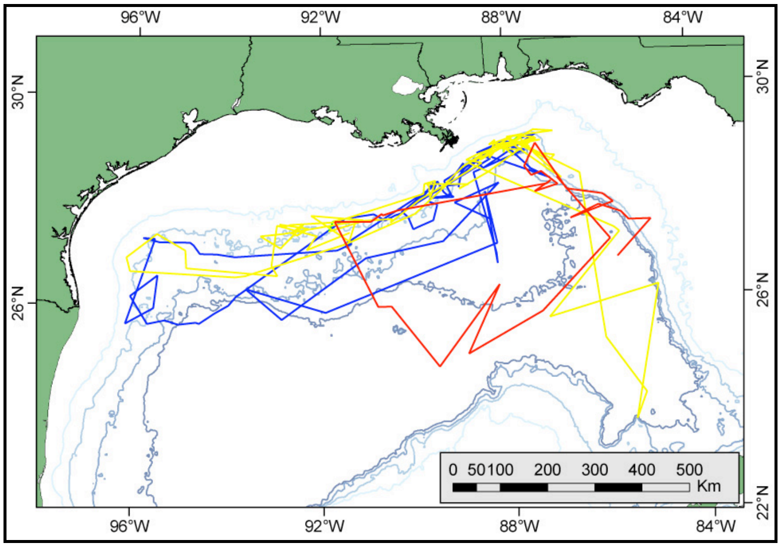

Figure 4.3.16. Trackline of three male sperm whales (PTT #2505648, #2505685, #2505726) tagged in 2002 showing their travels to water > 3000 m and two whales making round trips to the western Gulf (PTT #2505685 and #2505726).

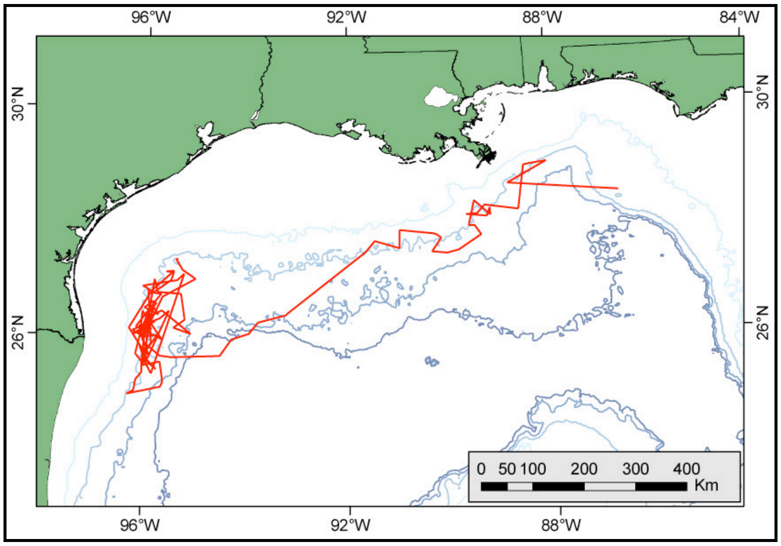

Figure 4.3.17. Trackline of male sperm whale (PTT #2505650) tagged in 2002, which traveled to the western Gulf where it spent an extended period.

Whale #2505725 visited the RGS a year after tagging and had the longest track of any individual whale (Figure 4.3.18), providing locations for 607 days. His movements were different from other whales: he traveled into the North Atlantic for 2+ months, used the Bay of Campeche as winter/spring range during two consecutive years, and did not spend the summers of 2002 and

2003 in the same area of the upper Gulf. Based on morphometric data from other areas (Best 1979) and our size estimate of this whale (11 m), we concluded that he was potentially large enough to be considered sexually mature, but not large enough to be a successful breeding bull. In contrast, the single male tagged in 2003 was tracked for the shortest time and distance of all males (Figure 4.3.19). Several of the whales of unknown gender had either little movement, as in 2004 (Figure 4.3.20) or had wide-ranging east-west movements along the upper slope in 2002 (whales #2505655 and #2505654, Figure 4.3.21) and 2003 (#2805654 and #2823038, Figure 4.3.22). Collectively, whales tagged in 2003 and 2004 (14 females, one male, and eight of unknown sex) had movements similar to those of females tagged in 2002, moving primarily east-west along the upper slope between the MRC and MRD (Figure 4.3.23a and 4.3.23b).

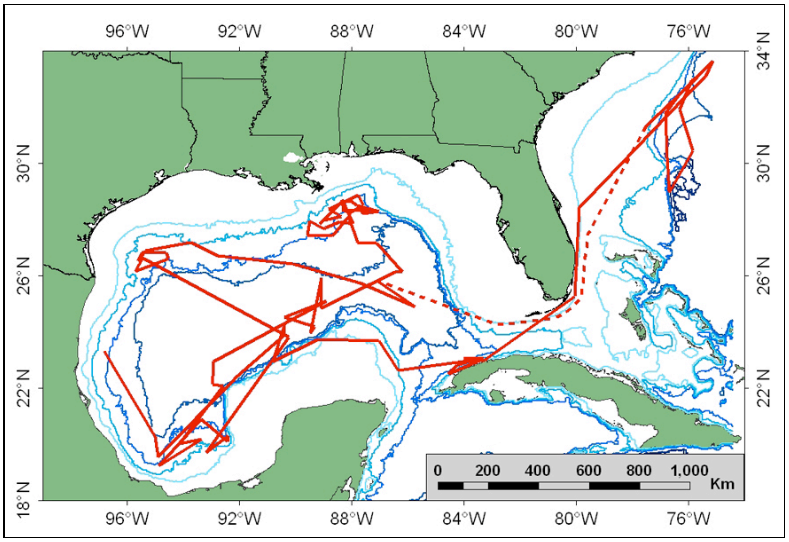

Figure 4.3.18. Trackline of male sperm whale (PTT #2505725) tagged in 2002 which transmitted for 620 days. Its movement into the North Atlantic for more than two months provides the first evidence that the Gulf of Mexico may not be a stock isolated from the North Atlantic. Its return to the Gulf included an extended stay off the northwest Cuban coast. It summered in two different regions of the upper Gulf, and visited the Gulf of Campeche twice. Dashed line indicates probable path interpolated around Florida for two consecutive locations, one inside the Gulf and the other in the North Atlantic.

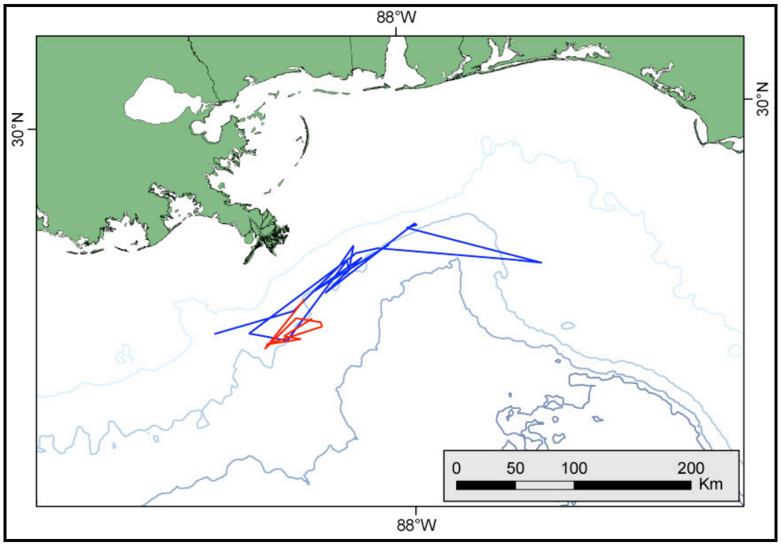

Figure 4.3.19. Trackline of a male sperm whale (PTT #2800827) and a sperm whale of unknown sex (PTT #2800839) tagged in 2003, spending extended periods near the tag site, up to 179 days (PTT #2800827).

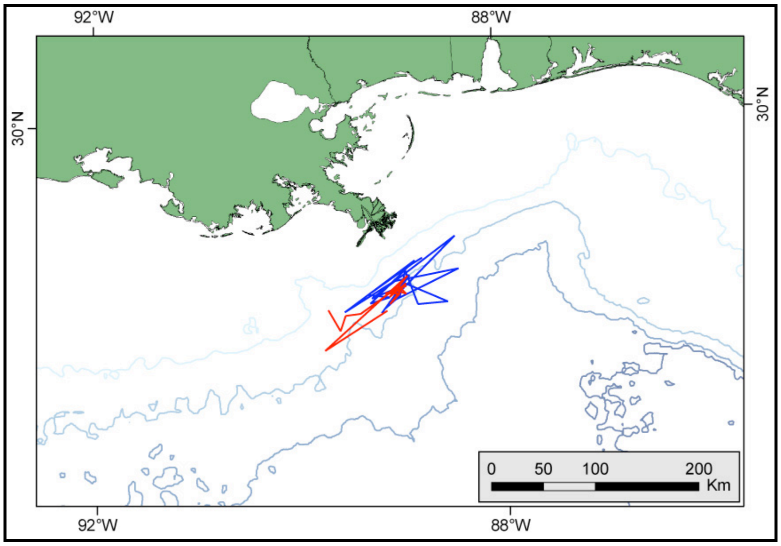

Figure 4.3.20. Tracklines of two sperm whales of unknown sex (PTT #3200845 and #3201387) tagged in 2004 showing localized movements for over 90 days each.

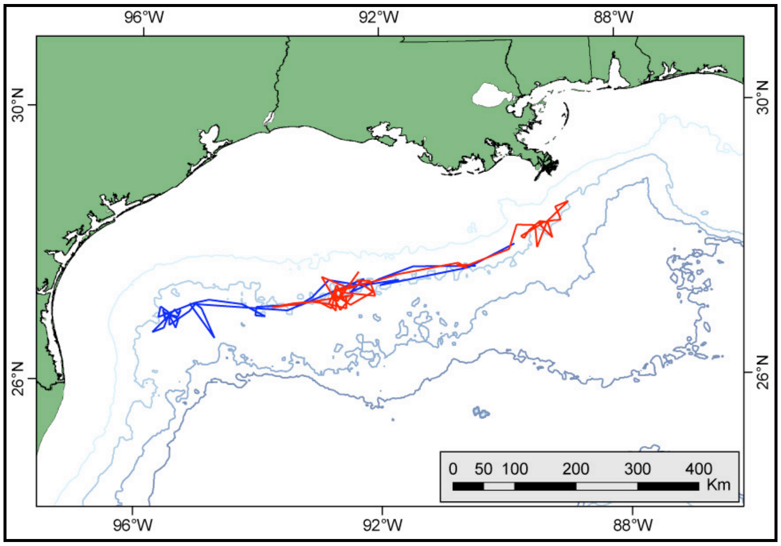

Figure 4.3.21. Tracklines of two sperm whales of unknown sex (PTT #2505655 and #2505654) tagged in 2002 showing travel to the western and far western upper slope regions of the Gulf.

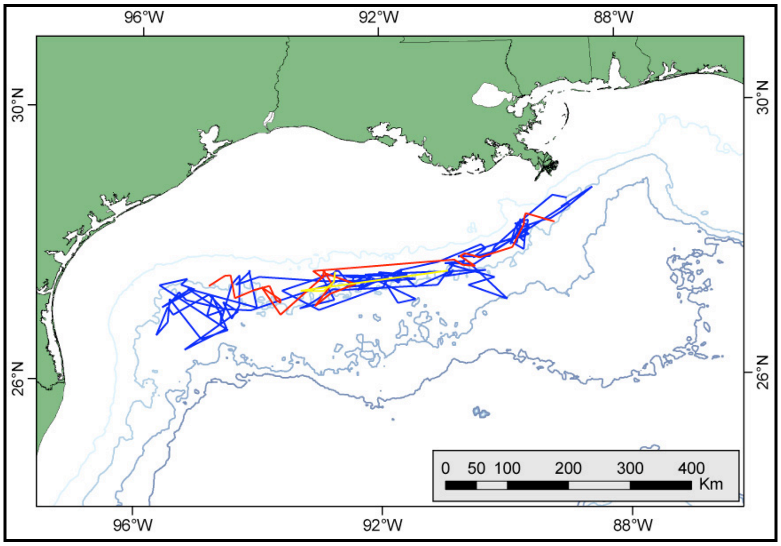

Figure 4.3.22. Tracklines of three sperm whales of unknown sex (PTT #2805654, #2805710, and #2823038) tagged in 2003 showing movements to the central and western upper slope.

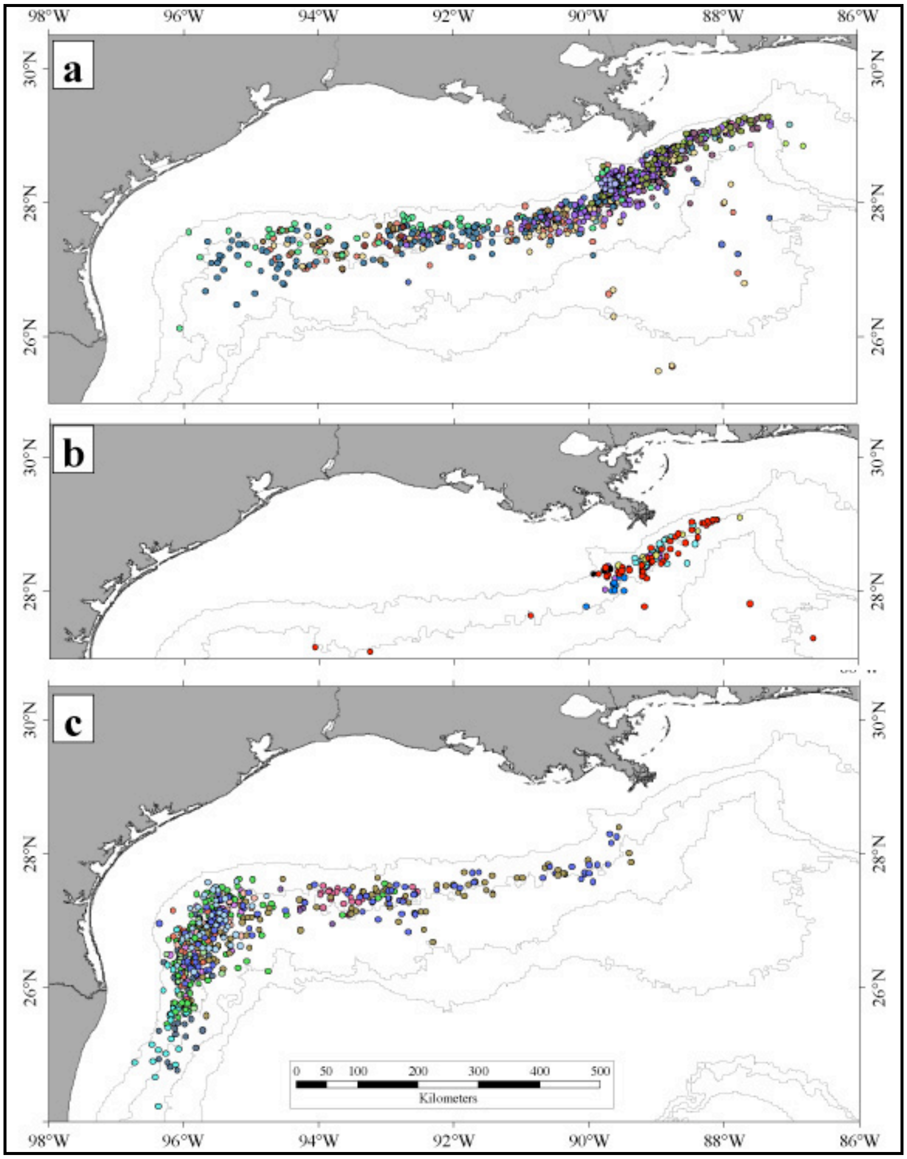

Figure 4.3.23. Satellite-determined locations of sperm whales tagged in (a) 2003, (b) 2004, and (c) 2005. Contour lines indicate 200, 1000, 2000, and 3000 m bottom depth. Colors of locations indicate different individuals.

In 2005, whales tagged in the northwestern Gulf (10 females and 4 whales of unknown sex) remained along the upper slope as well (Figure 4.3.23c) and exhibited the same general movement patterns observed for females tagged in previous years (very restricted ranges or short loops away from the tagging area) but with a different regional concentration. Female whale #3700846 spent 392 days exclusively in the western Gulf (Figure 4.3.24), as did seven other females (Figures 4.3.25-4.3.27) and two whales of unknown sex (Figure 4.3.28). Two females (#3705648 and #3704726) ranged east to the Mississippi Canyon in the winter but returned west, spending most of their time near the tagging area (Figures 4.3.29 and 4.3.30, respectively).

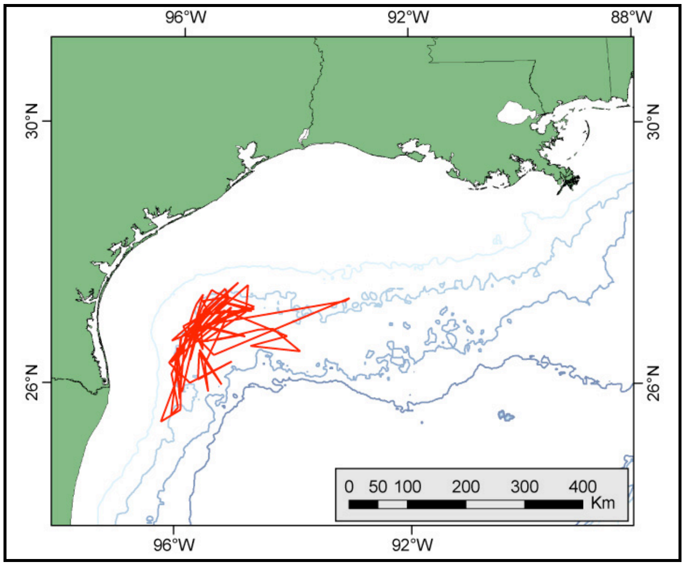

Figure 4.3.24. Trackline of female sperm whale (PTT #3700846) tagged in the northwestern Gulf of Mexico in 2005, showing localized movements up to 472 days.

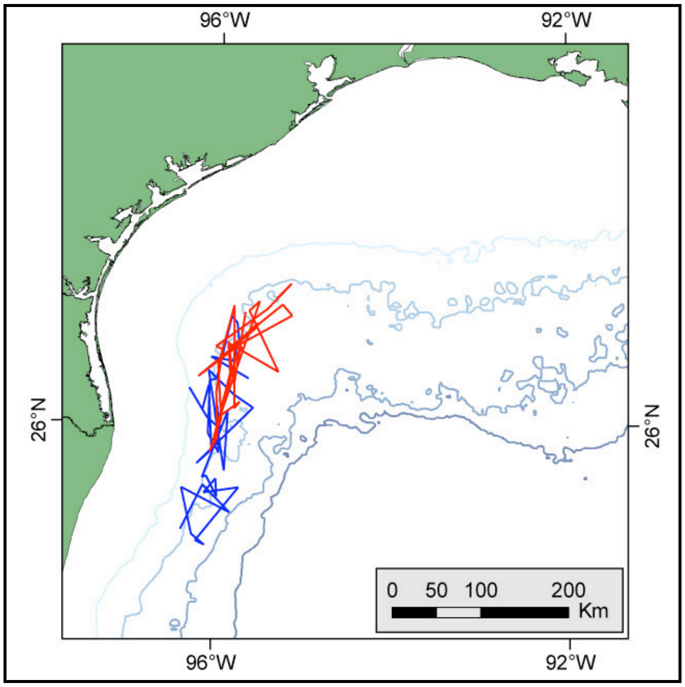

Figure 4.3.25. Trackline of two female sperm whales (PTT #3700836 and #3701386) tagged in 2005 in the northwestern Gulf, showing localized movements along the upper slope.

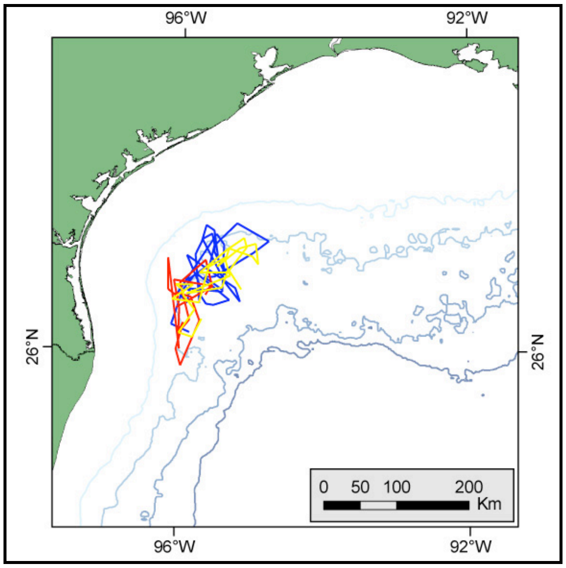

Figure 4.3.26. Trackline of three female sperm whales (PTT #3705644, #3705654, and #3705800) tagged in 2005 in the northwestern Gulf, showing localized movements along the upper slope.

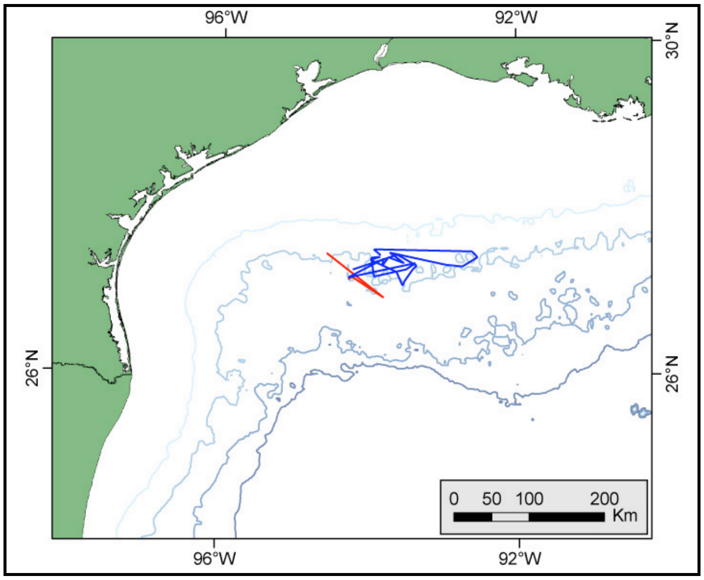

Figure 4.3.27. Trackline of two female sperm whales (PTT #3700847 and #3705701) tagged in 2005 off the Texas-Louisiana border, showing localized movements along the upper slope.

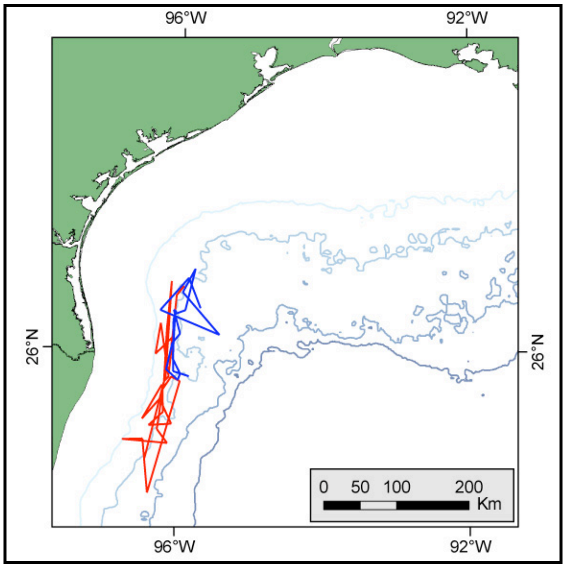

Figure 4.3.28. Trackline of two sperm whales of unknown sex (PTT #37005650 and #3705709) tagged in 2005 in the western Gulf, showing localized movements along the upper slope.

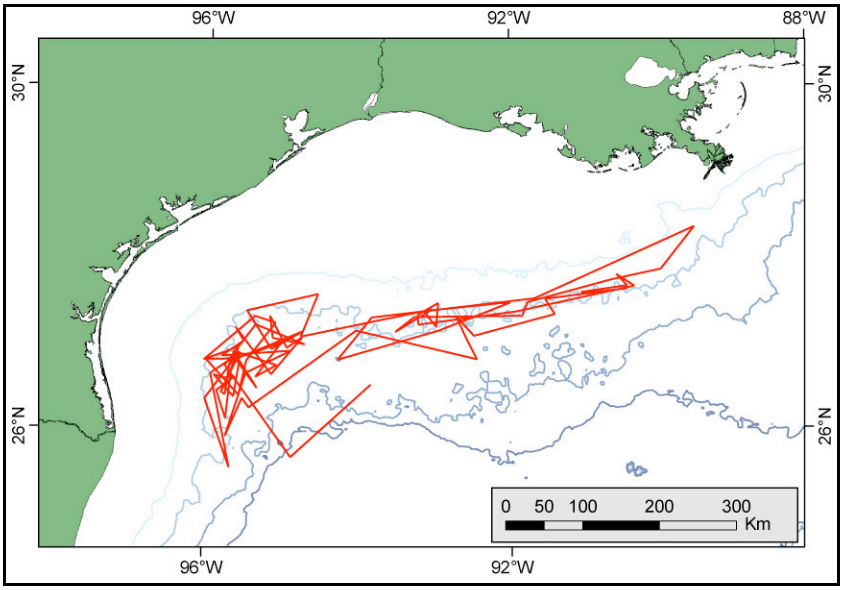

Figure 4.3.29. Trackline of female sperm whale (PTT #3705648) tagged in 2005 in the northwestern Gulf of Mexico, showing a round trip to the Mississippi Canyon.

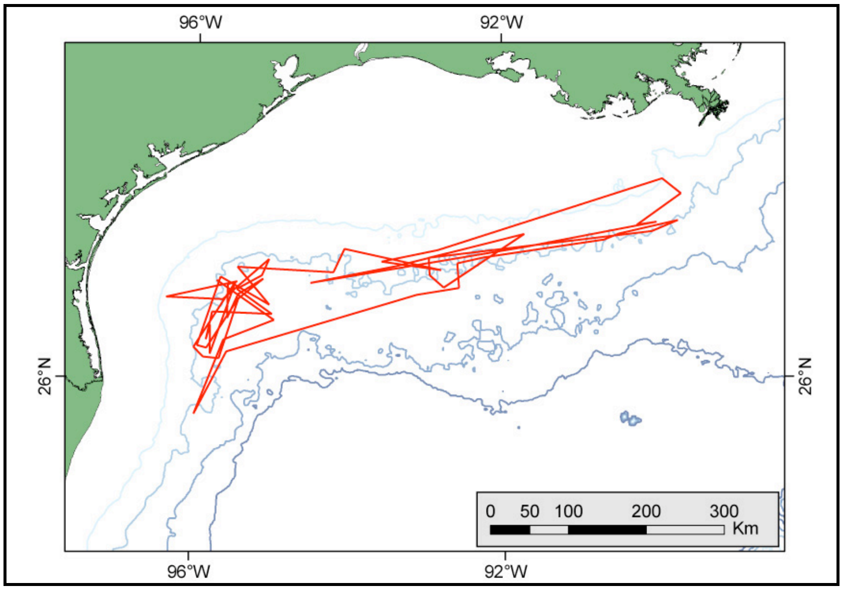

Figure 4.3.30. Trackline of a female sperm whale (PTT #3705726) tagged in 2005 in the northwestern Gulf of Mexico, showing a round trip to the Mississippi Canyon.

During the time they were tracked, female whales moved 49-778 km from the tagging location (Figure 4.3.31) while maximum displacement for males ranged from 190 to approximately 2100 km (Figure 4.3.32). The average maximum displacement away from tag deployment location was 335.4 km (S.D. = 230.97) for females and 910.3 km (S.D.= 648.80) for males. Displacement analysis identified no clear general seasonal movement pattern (Figures 4.3.31 and 4.3.32). To account for interannual variation, we examined the movements for periodicity in the three whales whose tags transmitted for more than 450 days (Figure 4.3.33). Two showed some evidence of pattern repetition. Whale #2505669, in the aforementioned group of 2002-tagged females, repeated the trip west from the MRD beginning in early August 2003 and was 406 km away from its tagging location when it stopped transmitting on 1 October 2003 (Figure 4.3.3). Male #2505685 started transmitting in late August 2002, 56 days after tagging and 366 km west of MRD (Figure 4.3.16). It kept moving west until it reached the RGS, turned around in mid-September, and arrived back at the MRD the second week of November 2002. The following year this individual left the MRD in early June on a westerly loop, returning in late November. These examples of summer-fall trips contrast with a male PTT #2505725 tagged the same year, that did not exhibit similar consistent seasonal movements except for visits to the Bay of Campeche for one month in March 2003 and a few days in early February 2004 (Figure 4.3.18).

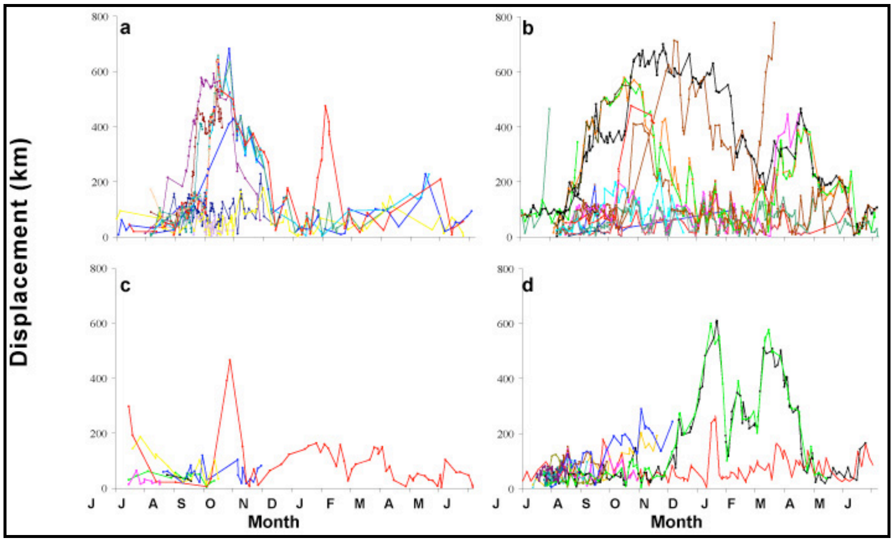

Figure 4.3.31. Displacement away from tagging location of female and unknown-sex sperm whales. Shown are whales tagged in (a) 2002, (b) 2003, (c) 2004, and (d) 2005. Time scale starts in June because most tagging took place in the summer and depicts dispersion along the year. Displacement for whales tracked for more than 12 months was wrapped around the time scale in time axis. Color of lines indicate different individuals.

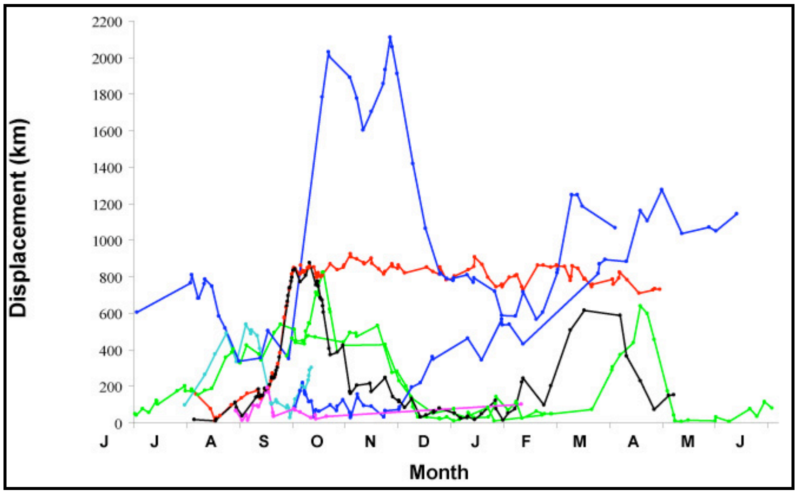

Figure 4.3.32. Displacement away from tagging location of male sperm whales tagged in 2002. Time scale starts in June because most tagging took place in the summer and depicts dispersion along the year. Displacement for whales tracked for more than 12 months was wrapped around the time scale. Displacement values higher than 1400 km for PTT #2505725 are minimum estimates following the 200 m contour around the Florida Peninsula as this individual exit the Gulf and moved into the North Atlantic. Color of lines indicate different individuals.

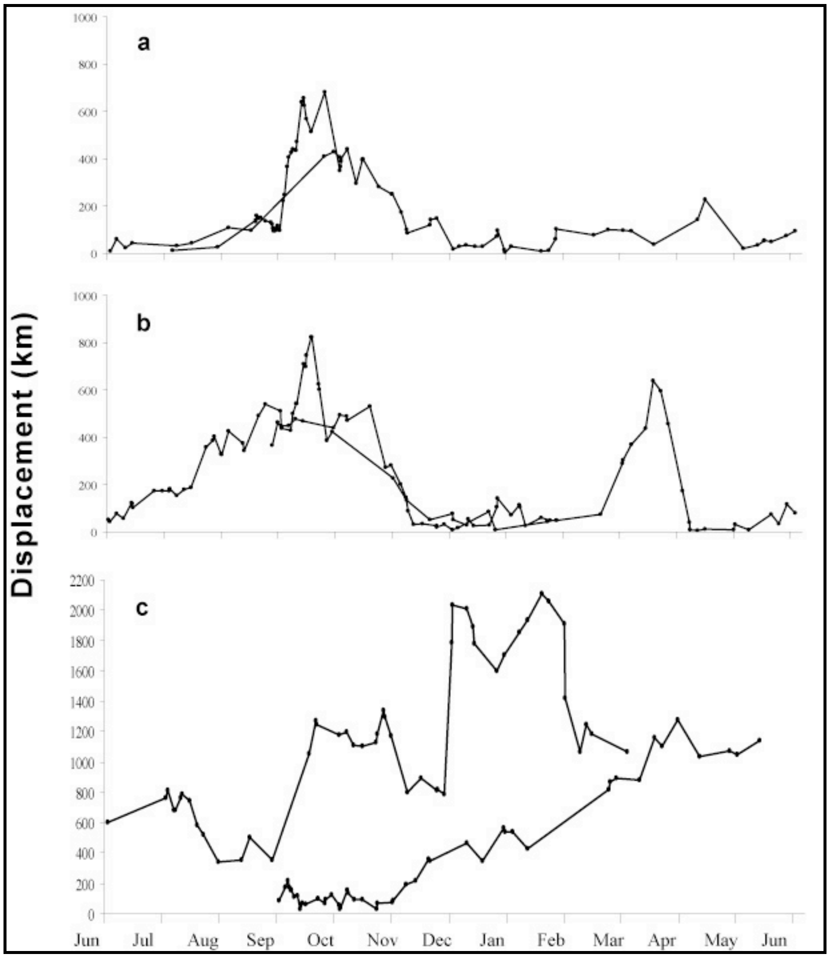

Figure 4.3.33. Displacement away from tagging location for whales tagged in 2002 and tracked >450 days. Shown are a) female PTT #2505669, b) male PTT #2505685, c) male PTT #2505725.

Seasonal distribution of satellite tracked sperm whales was examined by plotting the locations received each month for the 12 individuals (8 females, 2 males, 2 unknown) whose tags transmitted for 330 days or longer. No clear seasonal pattern of habitat use was observed (Figure 4.3.34).

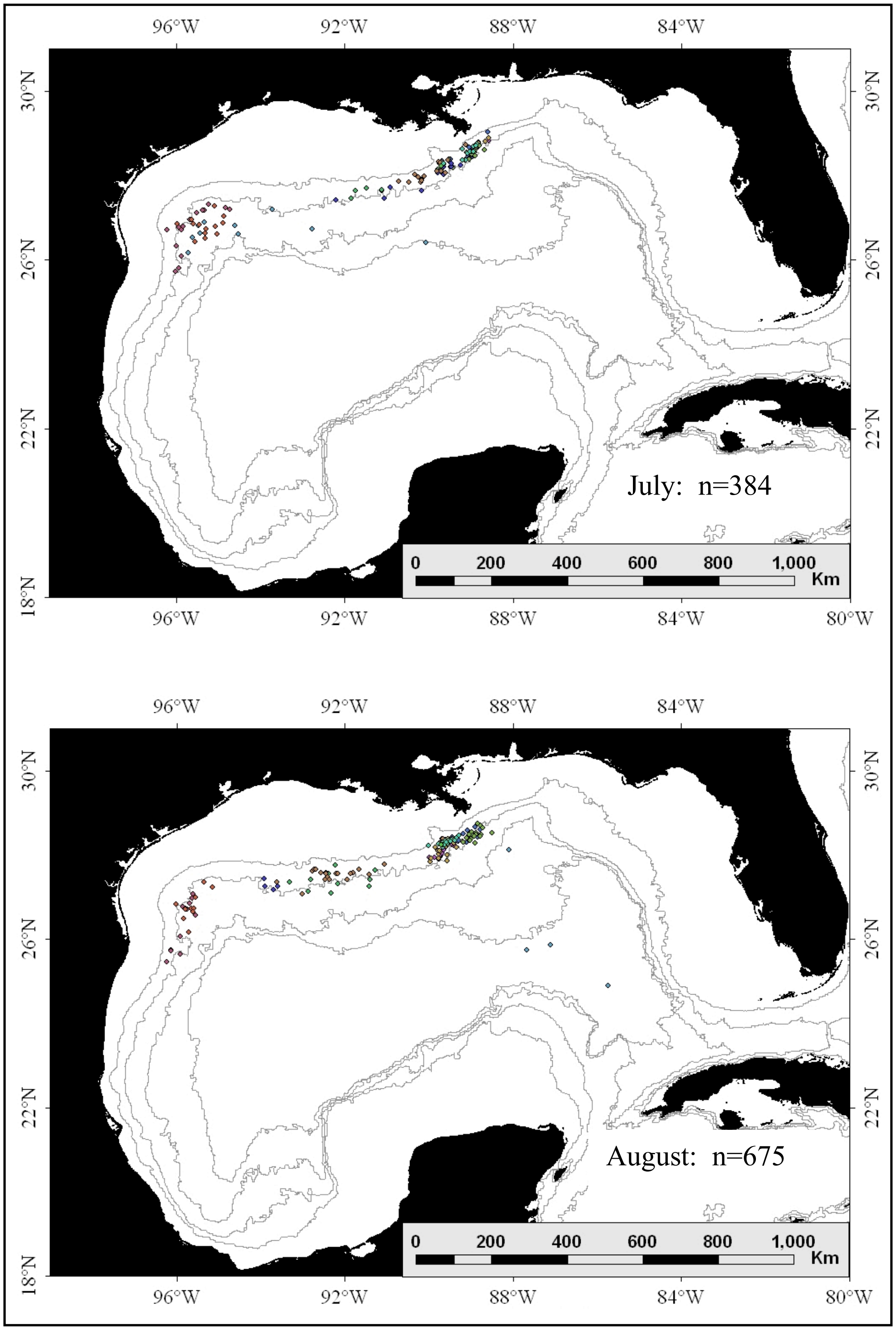

Figure 4.3.34. Satellite-determined locations received for the 12 sperm whales tracked for at least 330 days. Color of the circles indicates different individuals. In order shown are locations for July, August, September, October, November, December, January, February, March, April, May, and June. The number of locations is given.

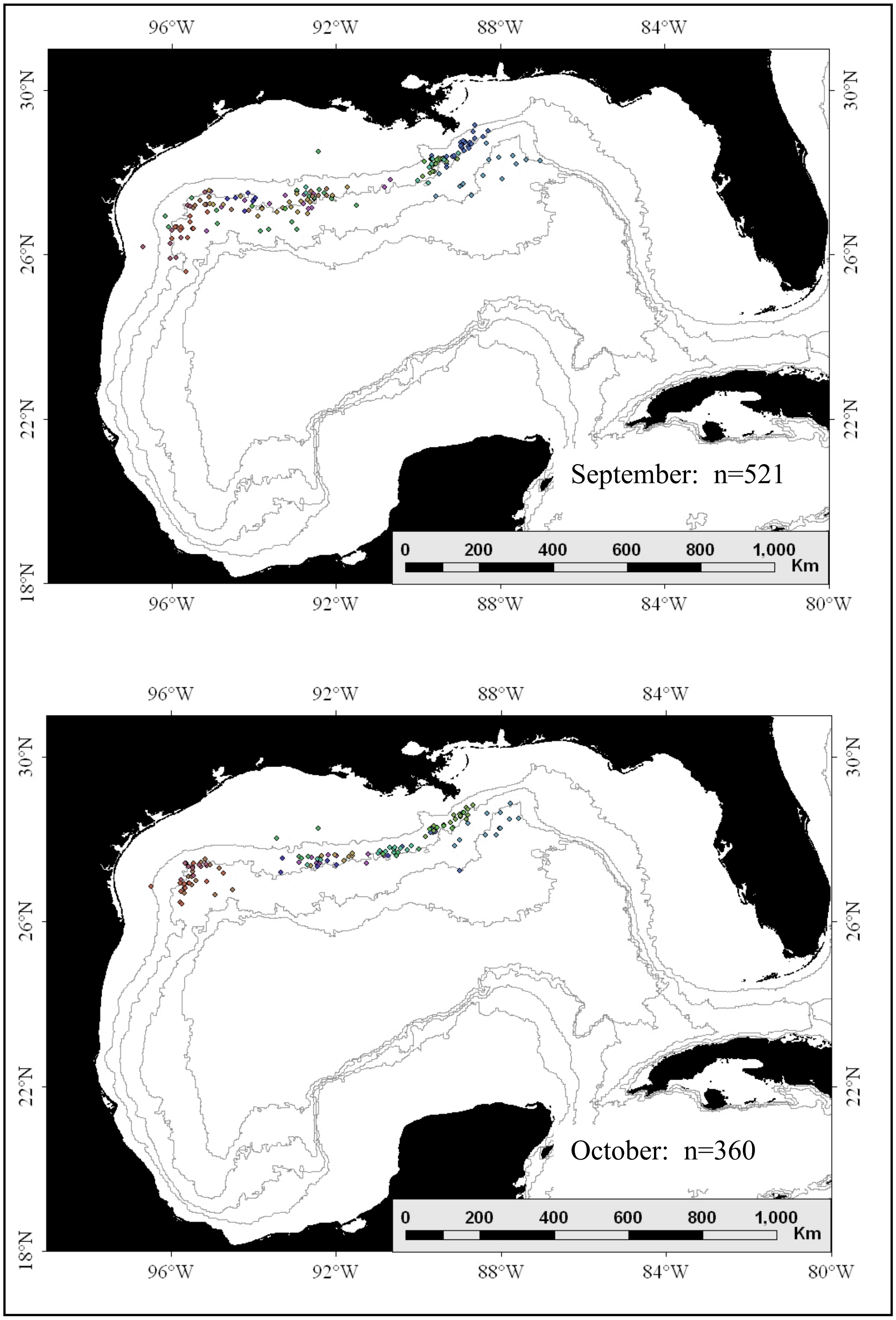

Figure 4.3.34. Satellite-determined locations received for the 12 sperm whales tracked for at least 330 days. (continued)

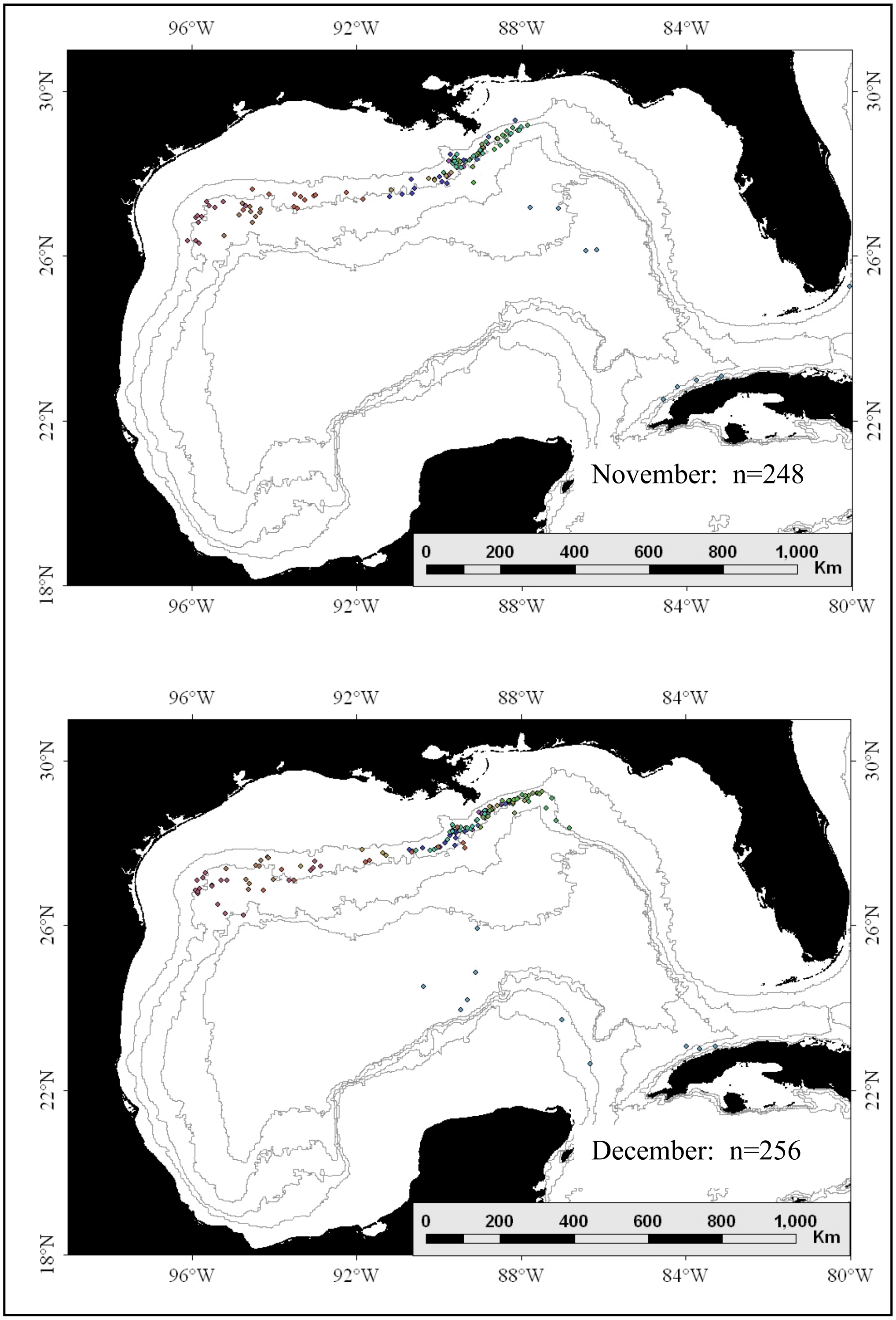

Figure 4.3.34. Satellite-determined locations received for the 12 sperm whales tracked for at least 330 days. (continued)

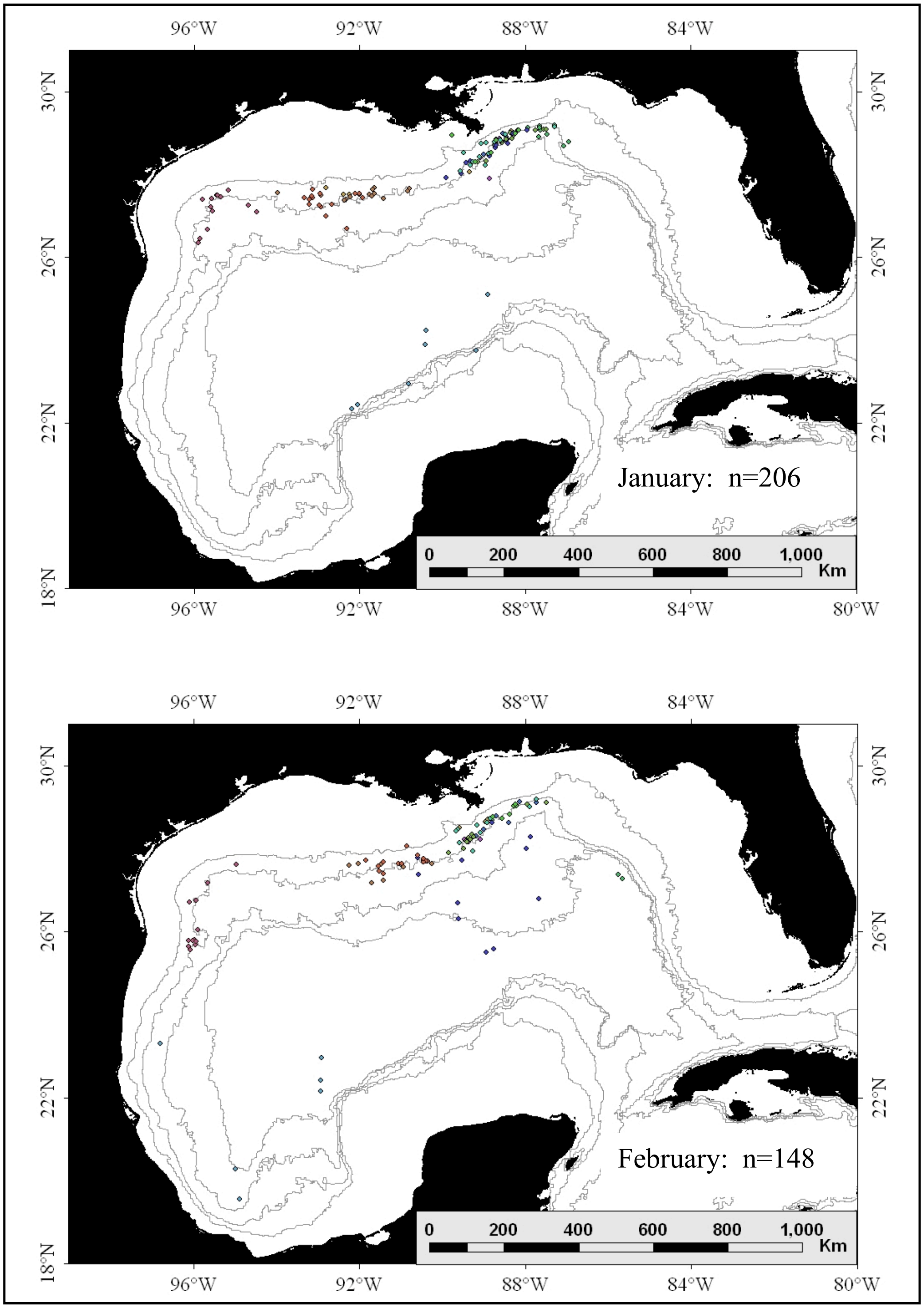

Figure 4.3.34. Satellite-determined locations received for the 12 sperm whales tracked for at least 330 days. (continued)

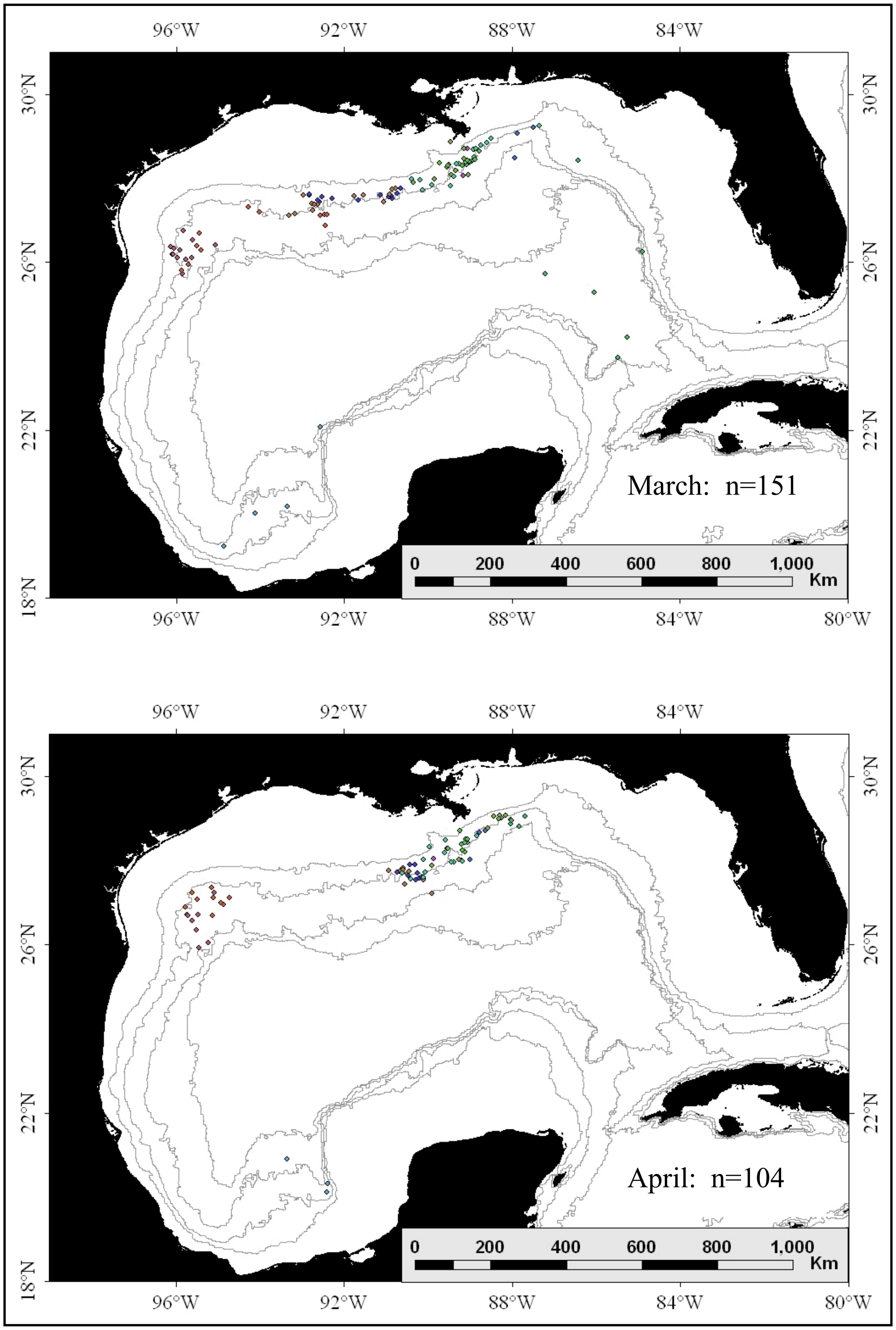

Figure 4.3.34. Satellite-determined locations received for the 12 sperm whales tracked for at least 330 days. (continued)

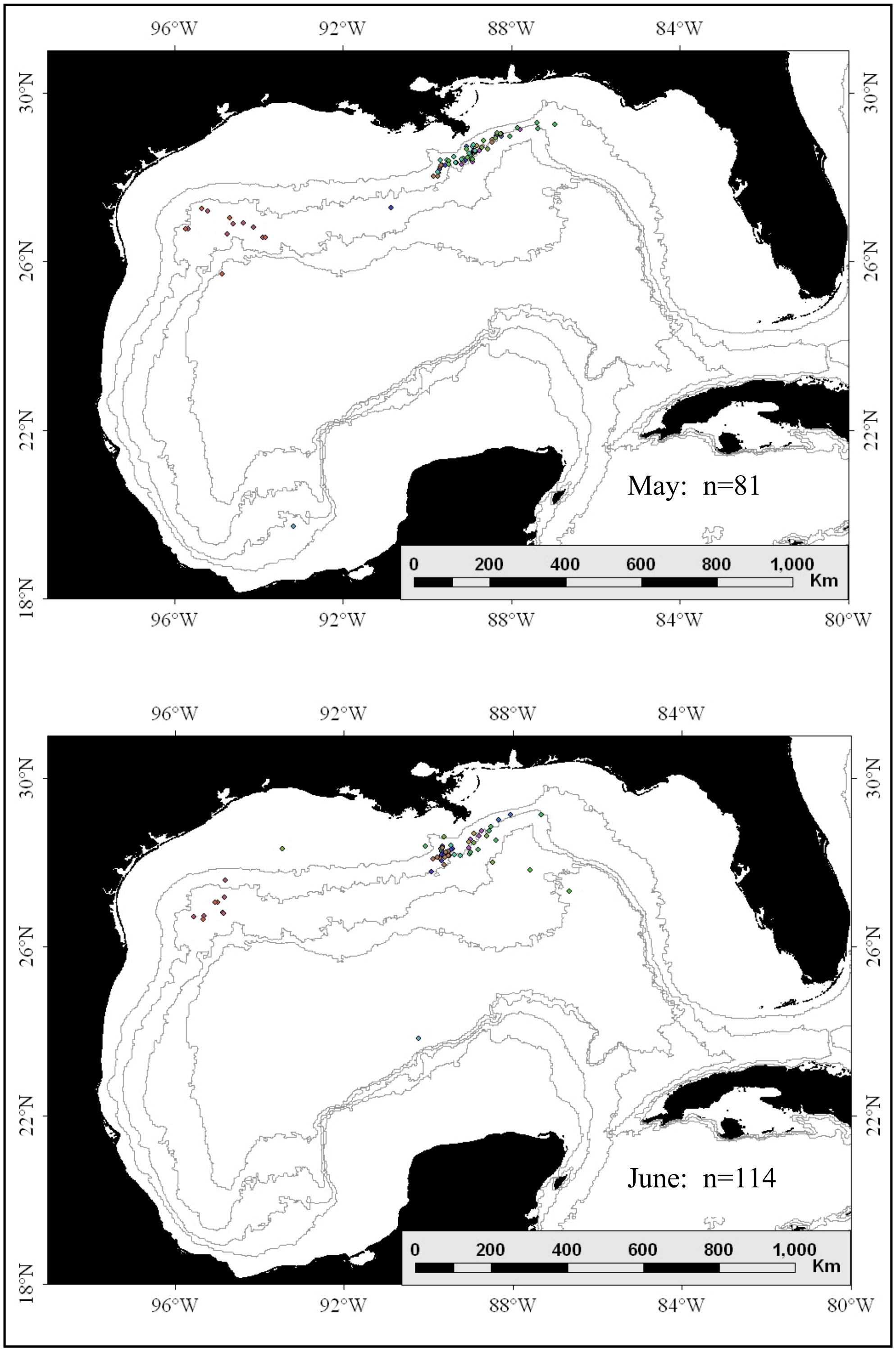

Figure 4.3.34. Satellite-determined locations received for the 12 sperm whales tracked for at least 330 days. (continued)

Home Ranges and Core Areas

Home range (95% UD probability area) varied from 1463 km^2 to 1,136,092 km^2 ($\bar{x}$ = 69,056, S.D.= 158,899). When calculated using only the values from individuals with more than 30 locations, mean home range area was 44,717 km^2 for females (n = 21, S.D.= 31,465) and 392,764 km^2 for males (n = 4, S.D. = 497,664). Despite nearly an order of magnitude of difference in the mean value between males and females, no statistical comparison was done due to the small sample size for males. Size of high utilization "core" areas (50% UD probability area) ranged from 324 km^2 to 101,600 km^2 ($\bar{x}$ = 10,256, S.D. = 15,195). The average core area was 8258 km^2 for females (n = 21, S.D. = 6,836) and 41,285 km^2 for males (n = 4, S.D. = 40,604). Core areas were found on the upper continental slope near the continental shelf edge.

A composite of home range areas for all tagged whales was 1,131,365 km^2 and comprised nearly the entire Gulf of Mexico in waters deeper than 500 m and a small portion of the US southeast North Atlantic coast (Figure 4.3.35a). Of that area, 970,902 km^2 (85.8%) was shared by 1-3 individuals, 33,516 km^2 (3.0%) by 4-6 individuals, 21,862 km^2 (1.9%) by 7-9 individuals, 16,730 km^2 (1.5%) by 10-12 individuals, and 88,353 km^2 (7.8%) by more than 12 individuals. Home range area shared by more than 12 tagged whales comprised the entire northern continental slope west of De Soto Canyon (DSC), in waters 500-2000 m deep. By contrast, the composite core area for all tagged whales occupied 12,691 km^2 along the northern slope with the area shared by a higher number of individuals concentrated in the Mississippi Canyon, MRD, and, to a lesser extent, the RGS (Figure 4.3.35b). Of the entire core area 12,190 km^2 (96.1%) was shared by 1-3 individuals, 58 km^2 (0.5%) by 4-6 individuals, 96 km^2 (0.8%) by 7-9 individuals, 113 km^2 (0.9%) by 10-12 individuals, and 230 km^2 (1.8%) by more than 12 individuals.

The composite home range area for the six tagged males was identical to that of all whales (1,131,365 km^2, Figure 4.3.36a), showing the enormous influence of their long-term and wide-ranging movements. Moreover, the vast majority of that range (66%) was the result of the most wide-ranging individual. In contrast, only 4919 km^2 (< 1%) of the home range was shared by all six males and only 90,735 km^2 (8%) was shared by three males. The composite core area for males was 32,174 km^2, just 2.8% of the home range, with primary concentration between the MRD and DSC in water 500-3000 m deep and secondarily on the RGS off of the US-Mexico border between depths of 500-2000 m (Figure 4.3.36b). No portion of the northern slope between these two areas was included in the core area, supporting its use by males for transiting only. Because few males were sampled, only two small areas were each used by more than three males: off the MRD along the 1000-m isobath where most of the males were tagged and along the central axis of DSC in water 2000+ m deep.

The home range composite area for females tagged in 2002-2004 was 140,407 km^2 (Figure 4.3.37a), just 12.4% of the composite home range for all whales, and extended along the northern slope from the Texas-Mexico border to DSC in water 500-2000 m deep. The highest use area was from Mississippi Canyon to DSC in 500-1500 m, although the shallower parts of the entire northern slope range were well used with pockets of higher use concentrating along the 1000-m contour. The core area was a narrower swath of 2150 km^2 along most of the northern 1000-m isobath, with the highest use from the Mississippi Canyon to the MRD (Figure 4.3.37b). The home range for all 2005-tagged whales was 104,362 km^2 and included the tagging area in the

RGS, in waters 500-2000 m, extending east along the 1000-m contour to the eastern edge of Mississippi Canyon (Figure 4.3.38a). As with the females tagged in the eastern Gulf, the 2005-tagged females had small areas of higher use in between the two major tagging areas, unlike the males. However, part of the highest use area for 2005-tagged whales did overlap with the core area for the males (Figure 4.3.38b). The total combined home range for females was 156,043 km^2 of which 57% (88,726 km^2) was shared by females tagged in the MRD and RGS. In contrast, only 8% (5,551 km^2) of the total combined core area (69,638 km^2) was shared by females tagged in those two regions.

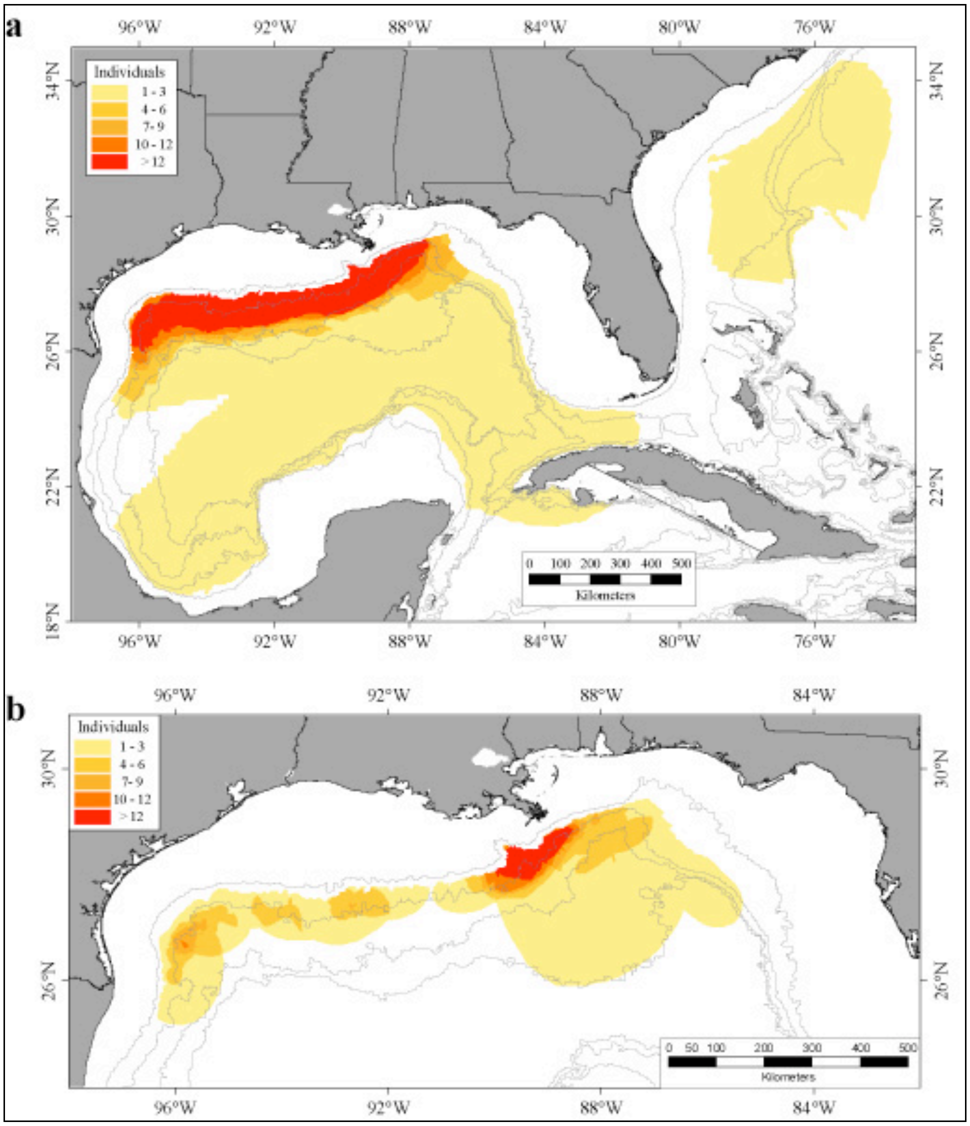

Figure 4.3.35. Home range (a) and core area (b) for all satellite-tracked sperm whales. Color contours indicate the number of whales that use the area. Line contours represent the 200, 1000, 2000, and 3000 m isobaths.

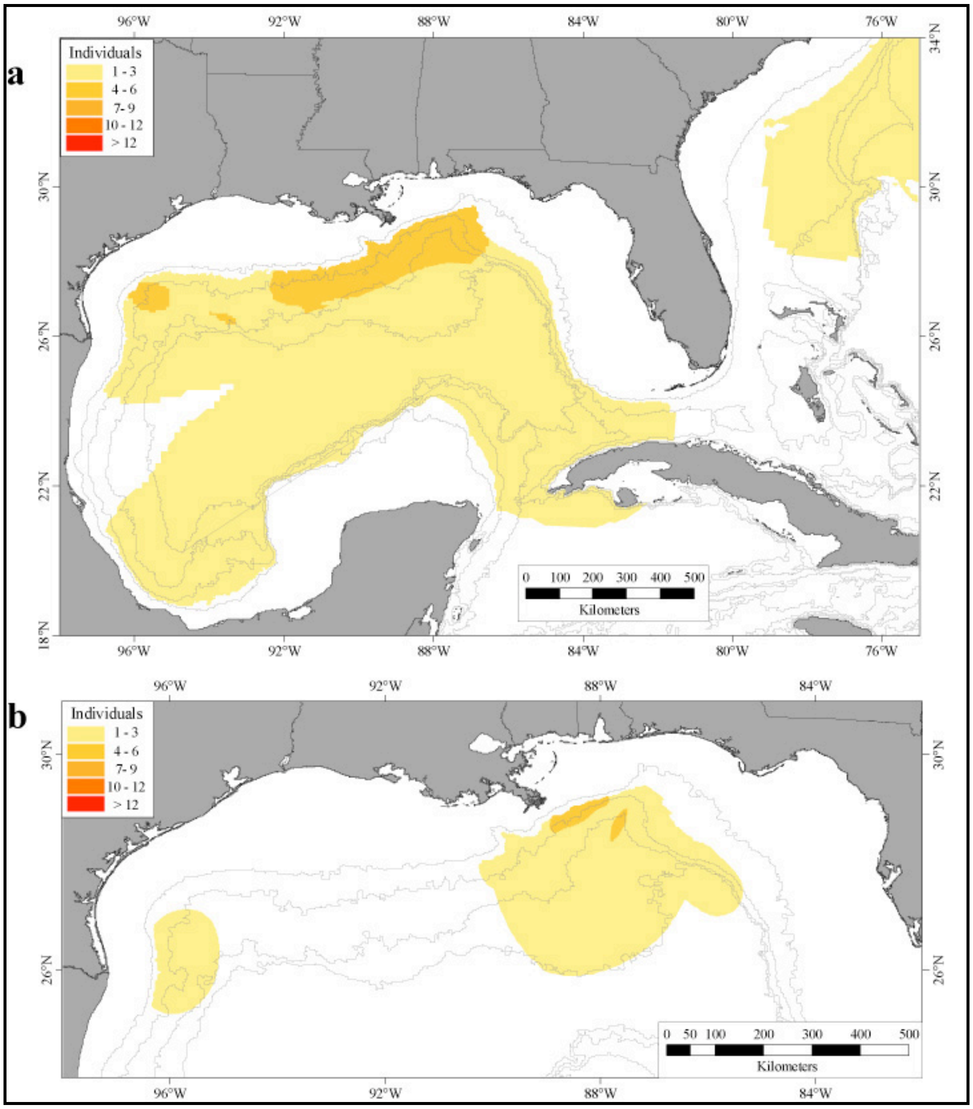

Figure 4.3.36. Home range (a) and core area (b) for satellite-tracked male sperm whales. Color contours indicate the number of whales that use the area. Line contours represent the 200, 1000, 2000, and 3000 m isobaths.

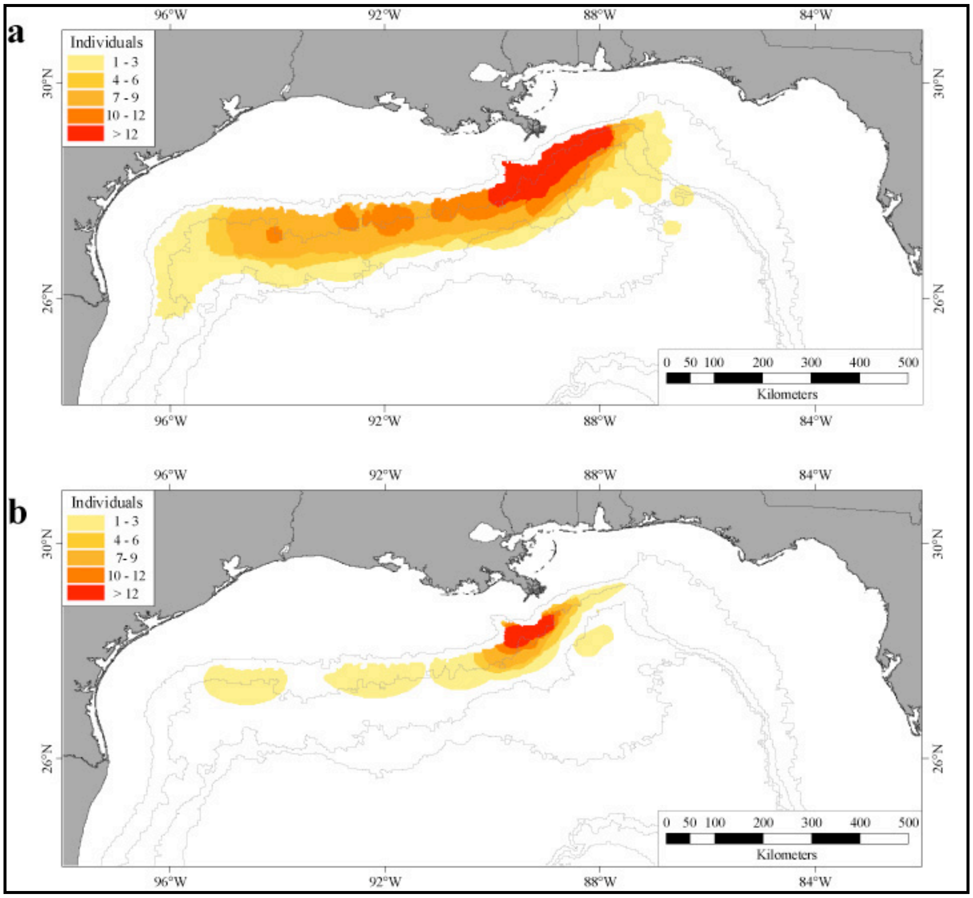

Figure 4.3.37. Home range (a) and core area (b) for 2002-2004 satellite-tracked female sperm whales. Color contours indicate the number of whales that use the area. Line contours represent the 200, 1000, 2000, and 3000 m isobaths.

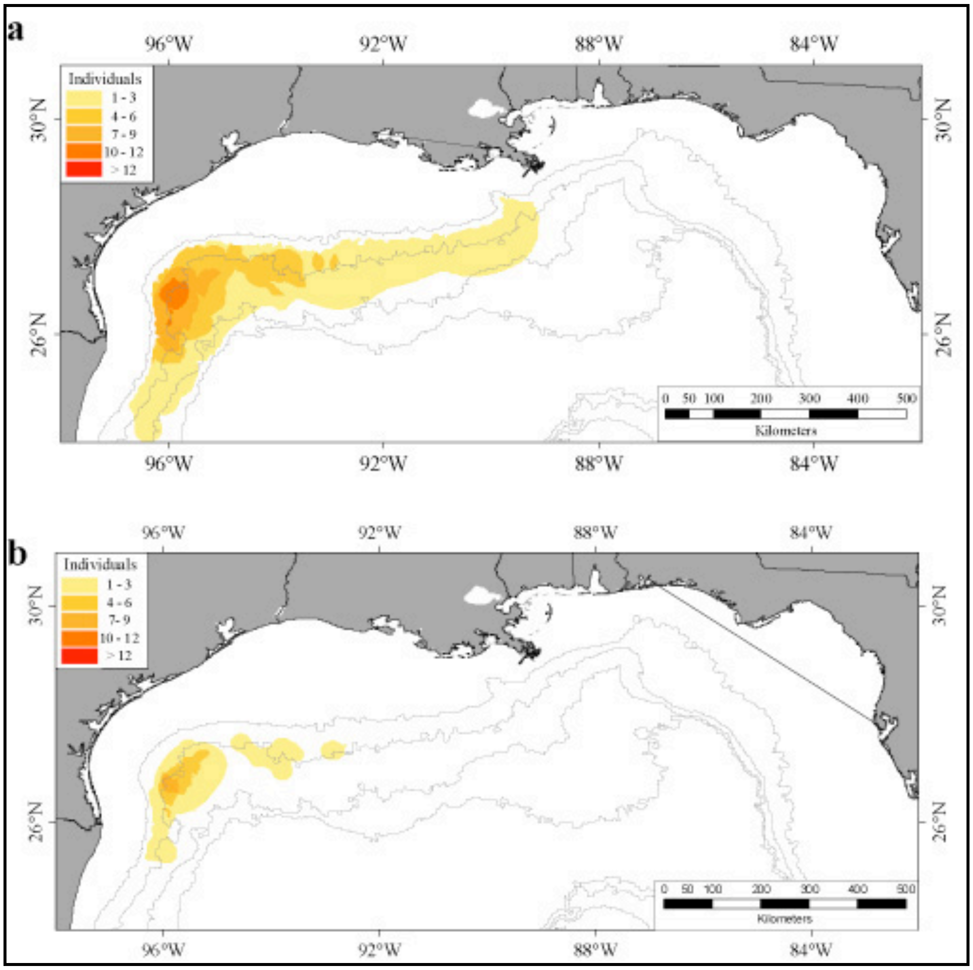

Figure 4.3.38. Home range (a) and core area (b) for all 2005 satellite-tracked sperm whales. Color contours indicate the number of whales that use the area. Line contours represent the 200, 1000, 2000, and 3000 m isobaths.

Home range estimates are dependent on the number of locations included in the analysis. Due to considerable variability in the active life of the tags, our data likely have a seasonal bias emphasizing the period immediately after tagging (summer and early fall) when most tags were active. To account for seasonal influence in home range preferences, we analyzed a subset of 12 tags on whales (8 females, 2 males, and 2 individuals of unknown sex) that were operational for more than 330 days. To compare home range estimates based on an annual cycle we limited the locations to < 375 days after tagging to reduce the influence of partial second year location data (Figure 4.3.39a). The continued prominence of the northern slope is not surprising, but the overall area home range (535,723 km^2) dropped to 47.4% of the composite home range for all whales. The small area in the Atlantic disappeared completely because male #2505725 left the Gulf only during the second year of transmission (i.e., more than 370 days after tagging). The core area for this subset of whales was 7149 km^2 (56.3% of the composite core area for all whales). Despite the small number of males in this analysis, the home range and core areas (Figure 4.3.39b) most closely resemble the distributions determined earlier for the males.

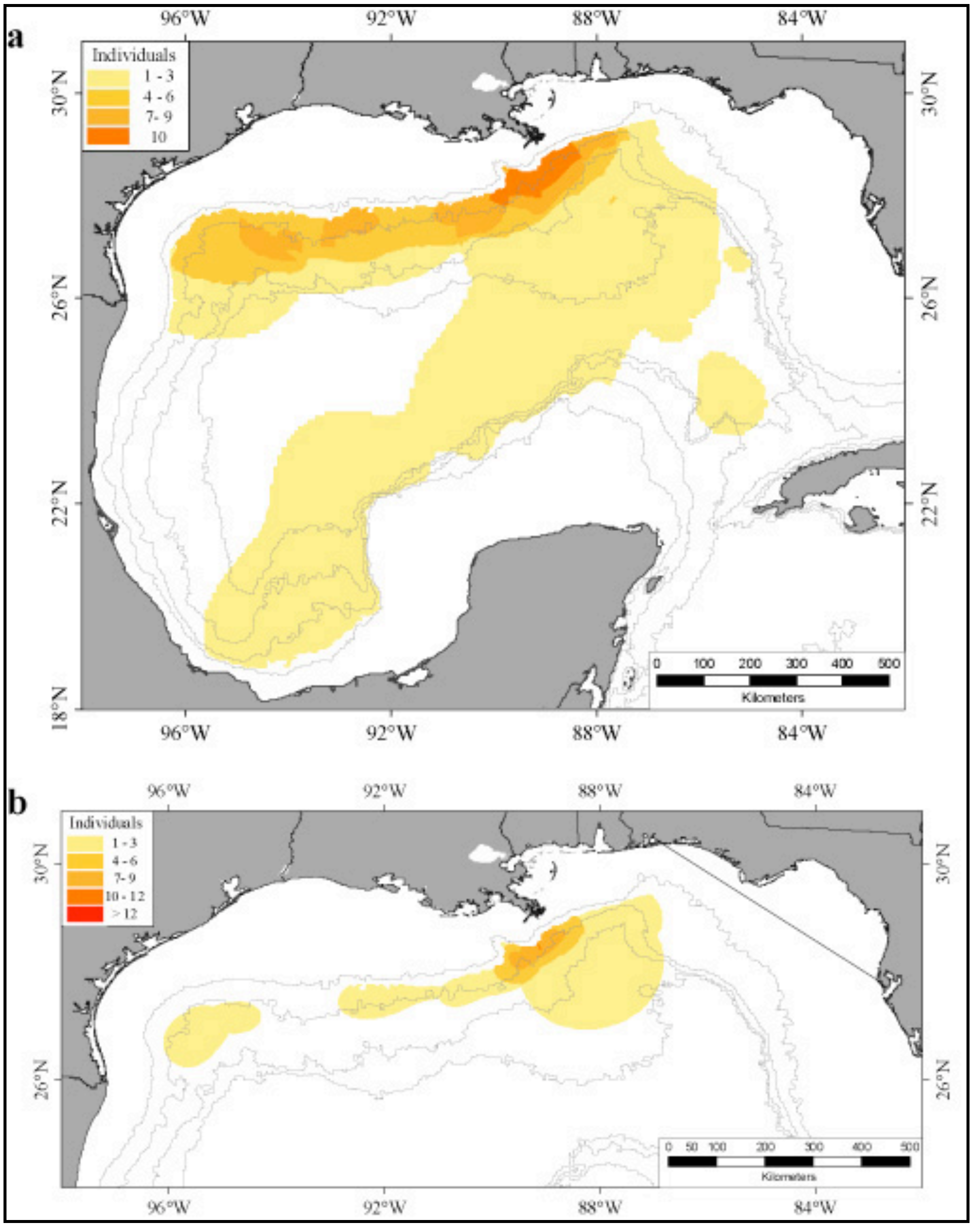

Figure 4.3.39. Home range (a) and core area (b) for the 12 sperm whales with tag life >330 days. Only data up to 375 days were used for whales with longer tag life. Color contours indicate the number of whales that use the core area. Line contours indicate 200, 1000, 2000, and 3000 m isobaths.

4.3.4 Discussion

Tags were deployed from June to early August. Due to the variation in active tag life and a progressive decrease in the number of active tags, more individuals were tracked and more locations received during the summer months. Furthermore, most of the tags were deployed in two focal areas: off the MRD and in the northwestern Gulf.

Whale speed estimated by satellite tracking was lower than speed measurements from direct observation (Whitehead 1989; Watkins et al. 1999; Whitehead 2003). This was expected since the average time between consecutive satellite-estimated locations was three days. Therefore, speed values reported here are based on the minimum distances traveled and likely underestimate the actual over-ground speed of sperm whales dramatically.

Discovery tag recoveries in the southern hemisphere more than one month after tagging showed average straight line movements of 1575 km for males (n = 17) and 690 km for females (n = 22) (Best 1979). Observations of sperm whale mixed schools and schools of small bachelors in the southern hemisphere suggest that they are sympatric even though they may be socially segregated (Gambell 1972; Best 1979). They also have similar migratory cycles, moving toward the equator in the fall and toward the subtropical convergence in spring.

Observations off the Galapagos Islands and the South Pacific showed groups of female and immature sperm whales generally moving only short distances (16 km) during 12-hour periods of presumed high feeding success and greater distances (40-55 km) during periods of presumed low feeding success (Whitehead 1996b). The inverse relationship between travel distance and feeding success (inferred from defecation rate) was strong, significant, and consistent between years. Whitehead (1996b) suggests that, due to the lack of coherence in environmental variability over scales of 500 km and more, sperm whales may use migration as their principal strategy when facing food shortages. Female and immature sperm whales photo-identified off the Galapagos Islands moved frequently to the waters off mainland Ecuador (approximately 1000 km away), occasionally to those off Panama and Peru (1500-2000 km distant), and rarely to those off Chile and the Gulf of California (> 3000 km away) (Dufault and Whitehead 1995a; Whitehead 2003). Our S-tag data suggest that female (and most male) movements in the Gulf of Mexico are not "migrations" (routine seasonal movements which are repeated annually), but are likely linked to changes in food availability (see Section 5.3 for more discussion of this hypothesis). The synchronous movement of five females away from their tagging site in 2002 can be identified as a series of concurrent peaks > 300 km in the displacement curves from mid-August through early November (Figure 4.3.31a). The synchrony in their movement may indicate a social bond rather than a population-wide seasonal migration since other females remained near the tagging location (curves with displacement values < 200 km) during the same period. Differences in habitat use and movement patterns have been reported between sympatric groups of female and immature male sperm whales from different vocal clans (Whitehead and Rendell 2004). Our results indicate differences in habitat use and movement patterns between females and males, as well as between individuals of the same sex. Future analysis of sperm whale vocalization recordings made during the tagging cruises may indicate whether differences between individuals or groups are related to vocal clan structure.

Based on a displacement of about 650 km in the Pacific Ocean over scales of years, Whitehead (2003) estimated a circular home range with a diameter of about 1444 km which yields a circular home range area of about 1,638,670 km^2. Whitehead's circular home range estimate does not coincide with the average of our kernel home range estimations (44,717 km^2 for females and 392,763 km^2 for males in the northern Gulf).

The home ranges of some females tagged in the north central Gulf (off MRD and in the Mississippi Canyon) and some tagged in the northwestern Gulf (RGS) overlapped; however, core areas of females tagged in those two locations did not. Home ranges of two males included female core areas in both the central and western Gulf. Sperm whale core areas identified from satellite tracking locations generally overlapped with areas where whales were tagged (off the MRD and in the northwestern Gulf). Female groups showed affinity for areas where they were tagged in the summer, and remained there for months at a time. Therefore, distribution and home range conclusions derived from tagging data are greatly influenced by tagging location. Single site tagging studies may generate a significantly biased basin-wide picture of distribution and movements. Females tracked in this study rarely visited waters deeper than 2000 m where groups of sperm whales with calves have been observed on several occasions (Mullin et al. 2004), suggesting that female whales sighted offshore have different distribution patterns. One female whale (#2505647, Figure 4.3.6) was tagged farther offshore than most and spent most of its time in deeper water, indicating possible gradations of whales with specific water depth preferences. Further studies are needed to resolve whether there is exchange and/or home range overlap between upper slope and offshore (> 2000 m) female sperm whales.

We consider the similar site-centric patterns observed in female whales tagged in two locations along the northern slope edge in the Gulf of Mexico to be indicative of the modal behavior for such groups. We would anticipate seeing similar patterns (core areas of about 200 km in diameter and exploratory trips under 800 km) for females at other upper slope regions, such as west of the Dry Tortugas or the Bay of Campeche. Our limited sample size provides some insight into the movements of immature males, but given the variability we observed, more data are needed for a general characterization of movements for this class. Ideally, future S-tag research would include repeated tagging of the same whales to provide data over multiple years.

The observation that none of the Gulf sperm whales outfitted with radio tags were larger than 12 m may be a result of smaller-sized whales preferring shallower waters relative to their diving ability and/or availability of suitable prey. The high site affinity of female sperm whales for specific locations in the Gulf may indicate consistency in the availability of enough food to support constant presence of sperm whales in those locations.

Satellite tag performance in this study (effective tag life and quality of locations) is unprecedented for large whales. In some cases, transmissions were received days to weeks after the last Argos-determined location but new locations could not be determined due to the poor quality or number of transmissions. This was most likely due to low battery voltage and reinforces our observations that sometimes tag attachment outlasted effective transmission life.

The data presented here provide a detailed characterization of the distribution and movement patterns in scales from days up to a year. A characterization of movement patterns at smaller temporal scales (hours to days) is presented in the Section 4.4. Future studies using new technology (such as FastLoc GPS tags) can provide data with higher resolution and accuracy of short term movements of individual whales than was possible with the SWSS S-tag. There still exists a need for studies to understand the movement patterns and habitat use of sperm whales in the GoM at larger temporal scales, which was not possible with the resolution and extent of the method we used. It would be important to determine individual interannual variations. Additional studies that re-tag, over several years, individuals representative of different age/sex composition of the population would be useful to document sperm whale movement patterns over multiple years.

4.4 Short Term Movements, Foraging and Long Term Site Fidelity of Sperm Whales in the Northern Gulf of Mexico

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4.4.1 Introduction

The movement patterns of individual animals are important biological information. Movement through space allows animals to sense different parts of their environment to search for food and mates and avoid predators, while the net results of the movements of all the animals in a population is the population's range and its relative densities within it. Movement, in conjunction with differential mating over many generations, results in genetic differences between animals that are often used to define biological populations. Movement is a parameter that can usually be measured reliably, even for animals such as marine mammals, which can be difficult to observe. Changes in location, or movement, are also often the fundamental, and sometimes the only data provided by telemetry devices. Long-term satellite telemetry of marine mammals that utilizes the Argos system has limited spatial and temporal precision. When tracking sperm whales from the Gulf of Mexico with Argos tags, locations were received once every 3 days on average with a spatial accuracy that was estimated to be better than 1 km in 68% of cases (Section 4.3). Such data are best suited for measuring temporal and spatial movements at a relatively large scale.

By contrast, digital tags provide information on scales of meters and seconds and allow tracking of 3-dimensional movement under water (e.g., see Sections 5.2 and 6.1). Finally, direct observations, such as those presented here, bridge the large spatial and temporal scales of satellite tags (e.g., Section 4.3) with the short scales of D-tags. Direct observations are in many cases available for consecutive surfacing with precision of 10s of seconds and are accurate to better than 100 m. Thus, they can complement the satellite tracking studies by providing information at finer spatial and temporal scales that can assist with the interpretation of less precise and less frequent observations from telemetry.

The satellite tracking studies (Section 4.3) show that males in the northern Gulf of Mexico may range widely, including excursions out into the Atlantic. However, females and some males (which may be members of mixed groups) have a quite restricted home range along the edge of the continental shelf of the northern Gulf of Mexico that did not extend far beyond the main study area covered here.

Identified sperm whales in the Gulf of Mexico have been resighted after periods of several years within a few miles of their original locations (e.g., Weller et al. 2000). This has been posited as evidence of strong site fidelity for at least some individuals in this population. However, research efforts within the northern Gulf of Mexico have focused on a few restricted areas, such as the Mississippi Canyon and regions offshore from the Mississippi River Delta. This effort bias needs to be accounted for in any analysis.

Foraging effort and success are exceptionally difficult to measure in sperm whales because foraging occurs at great depth where direct observation is impossible. However, sperm whales often defecate as they fluke up to initiate dives, and very rarely do so at other times while they are visible at the surface. Thus, information on foraging success has to be gleaned indirectly from buzz rate data (see Section 6.1; Watwood et al. 2006; Miller et al. 2004a) or from data on defecations per fluke up, which can be collected if whales are observed carefully, and which is also likely a reliable indicator of recent foraging success. Analysis of sperm whale tracks from the Pacific collected using methods that were similar to those employed in this study indicated that whales exhibited less direct movements over periods of several hours to days when defecation rates are higher and they might thus be assumed to be in better foraging areas (Jaquet and Whitehead 1999; Rendell et al. 2004; Whitehead 1996b). It was suggested that these more convoluted paths may have resulted as whales moved to remain within favorable food patches. Similar analysis of tracks and defecation rates from the northern Gulf of Mexico should indicate how this area compares with other study locations as a foraging site and may provide data to allow foraging behavior to be inferred from satellite telemetry data.

4.4.2 Methods

Visual and acoustic surveys for sperm whales were conducted within a study area between the 500 to 1500-m contours along the northern shelf edge of the Gulf of Mexico, between and 95.5°W and 86.5°W and along the shelf edge west of Florida as far south as 27°N. (Figure 4.4.1). Survey tracks were laid out within survey blocks in the study area to provide reasonably good coverage of blocks. Predetermined tracks were not followed as precisely as they would be in, for example, a designed line transect survey. Factors such as weather conditions and practical issues, such as the need to make passages to reach ports, often caused survey plans to be adapted. However, on the rare occasions that the boat moved towards areas where whales were known or thought to be present such survey effort was flagged in the database so that it could be removed from certain analyses.

In tropical waters sperm whales are usually found in groupings which move together and may show long term associations over periods of years. Once sperm whale assemblages were detected during the survey phase, the vessel broke survey and started to track groupings for extended periods, typically between 4 to 48 hours, using visual and acoustic methods. Whales seen at the surface were approached cautiously from behind and carefully observed to assess their size, status, and features such dorsal fin calluses. When the whales fluked up to initiate long deep dives, sequences of images were taken of their tail flukes for photo-identification purposes.

Canon EOS1D cameras and Sigma 70-300mm f4 lenses were used to collect photo-identification images.

Images were graded and scored for the extent of marking on individual flukes using an index based on an assessment of the likelihood of images being correctly matched over different time lags. The quality of images was also scored. See Section 4.7 for a detailed explanation of this grading process. The quality score integrated factors such as focus, exposure and image size to provide an assessment of an image's inherent potential to reveal marks of particular types. Images were organized in catalogues and the Phlukes matching tool (available from http://homepages.cwi.nl/~adri/europhlukes/flukes/index.html) was used to assist with matching fluke images to the existing collection. New flukes that were sufficiently well marked to allow long term identification were allocated new identification numbers and added to the data base.

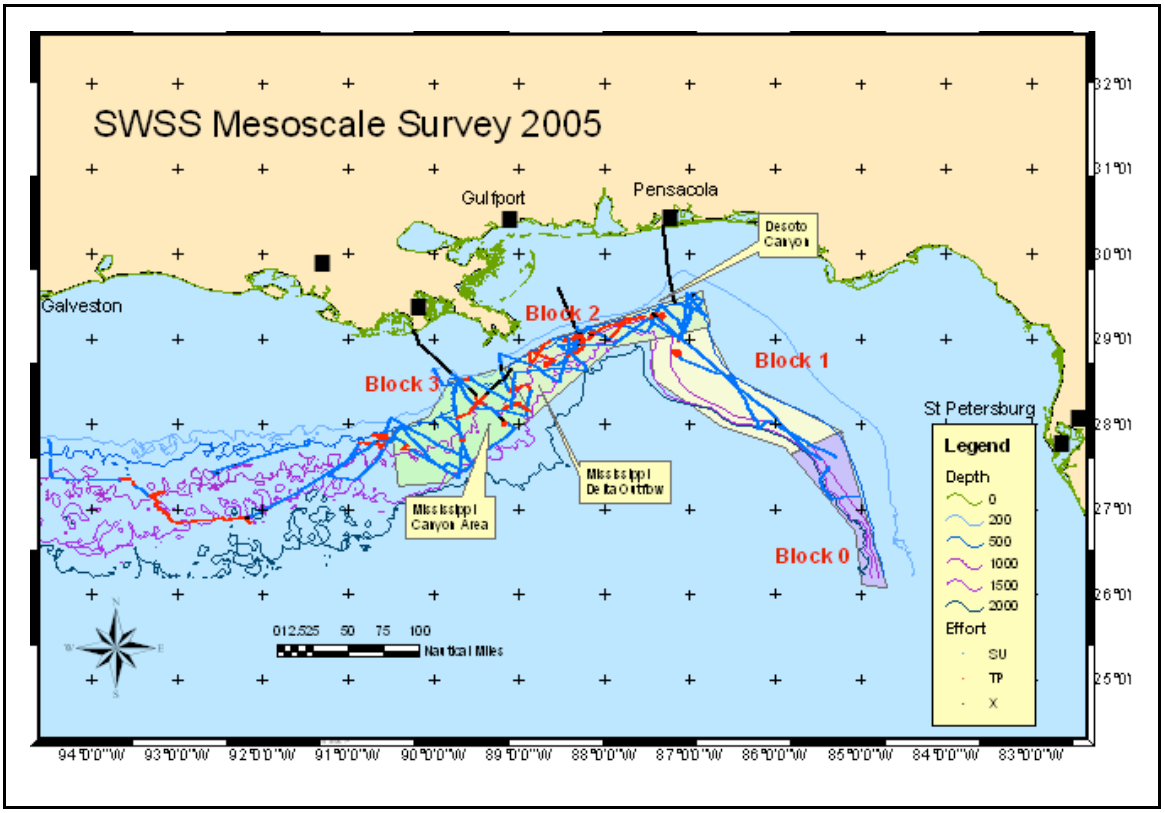

Figure 4.4.1. Plot of the 2005 SWSS Mesoscale Population Study cruise aboard the *Summer Breeze* from 13 June-3 August. The predetermined survey blocks (Blocks 0 to 3) are overlaid by the actual track of the *Summer Breeze* (thick colored lines: blue: survey mode [regular acoustic monitoring] (SU); red: tracking and photo-ID mode (TP); black: off effort or on transit (X)). Depth contours are shown with thin colored lines.

Data used here were collected from two quite different types of vessels. In 2002 and 2003, the main survey vessel was the R/V *Gyre* (60-m oceanographic vessel owned and run by Texas

A&M University). On this larger platform teams of visual observers on the vessel's flying bridge equipped with BigEye (25x150) binoculars worked in conjunction with acoustic teams monitoring towed stereo hydrophone arrays to detect and track groups of whales. Small rigid hulled inflatable boats (RHIBs) were launched to allow sperm whales at the surface to be approached close enough for photo-ID images and other data to be collected. The RHIBs used directional hydrophones to track submerged whales and were guided to clusters of whales at the surface by visual observers on the larger vessel.

In 2004 and 2005, a 46' motor sailor was used as the sole research vessel. This proved a much more effective acoustic monitoring and tracking vessel but it was not a good platform for long range visual searching. Surveys were broken when sperm whale groups were detected acoustically on the towed stereo hydrophone arrays or visually by observers using hand-held binoculars. The sailboat then followed these groups of whales acoustically and visually for periods of up to 48 hours while photo-identification images and detailed observations were collected.

At each fluke up, observers recorded whether or not the whale had defecated during fluke up, or whether it hadn't been observed sufficiently well to be able to make an assessment. It became clear that these data were not collected reliably from the RHIBs in 2002 and 2003 so only data collected from the motor sailor in 2004 and 2005 have been analyzed for defecations.

All survey vessels ran data logging software at all times which stored accurate locations of the vessel and the locations of whale fluke ups. The *Gyre* and the 46' motor sailor ran the International Fund for Animal Welfare (IFAW) "Logger" program on PCs (program written by Douglas Gillespie and made available by the International Fund for Animal Welfare) while the RHIBs collected data on "hand held" computers (HP200LX) using a custom-written program.

The boat's location each hour within periods spent tracking particular assemblages of whales was used as a measure of the overall movements of the groups. These data were also used to calculate an index of directness for each tracking period, being the sum of hourly movements divided by the net movement over the tracking period.

Comparison of the locations and times of repeated photo-identifications of the same individual were used to provide information on the movements of individual whales over a range of time scales from ~1 hour (approximately one dive cycle) to years. Movements and mean speeds were calculated and analyzed using specially written visual basic programs and commercially available parametric and nonparametric statistical packages.

Movement parameters were also calculated using modules for analysis of continuous movement in SOCPROG 2.3, a program for analyzing photo-identification data written in Matlab by Dr H. Whitehead, Dalhousie University, Canada (*http://myweb.dal.ca/hwhitehe/social.htm*). Movement analysis routines in SOCPROG implement the techniques described in Whitehead (2001).

To investigate whether individual whales showed "site fidelity" and particularly preferred locations within our main study area we analyzed only data collected along the main shelf edge study area in the northern Gulf of Mexico. Within each year we calculated a mean location for each whale. When an individual whale was identified in more than one year we compared the distance between its mean locations in the two years and the average of the distances between its mean location in the first year and the mean location of all the other identified whales in the second year. In this way we controlled for non-uniformity in the spatial coverage and the survey effort.

4.4.3 Results

Re-sightings of identified whales provided data on 1712 individual whale movements over time periods from 30 mins to years. Figure 4.4.2 shows the location of whales at the first fluke up location for all movements analyzed here. It can be seen that most of the movement data were collected off the shelf edge in the northern Gulf of Mexico.

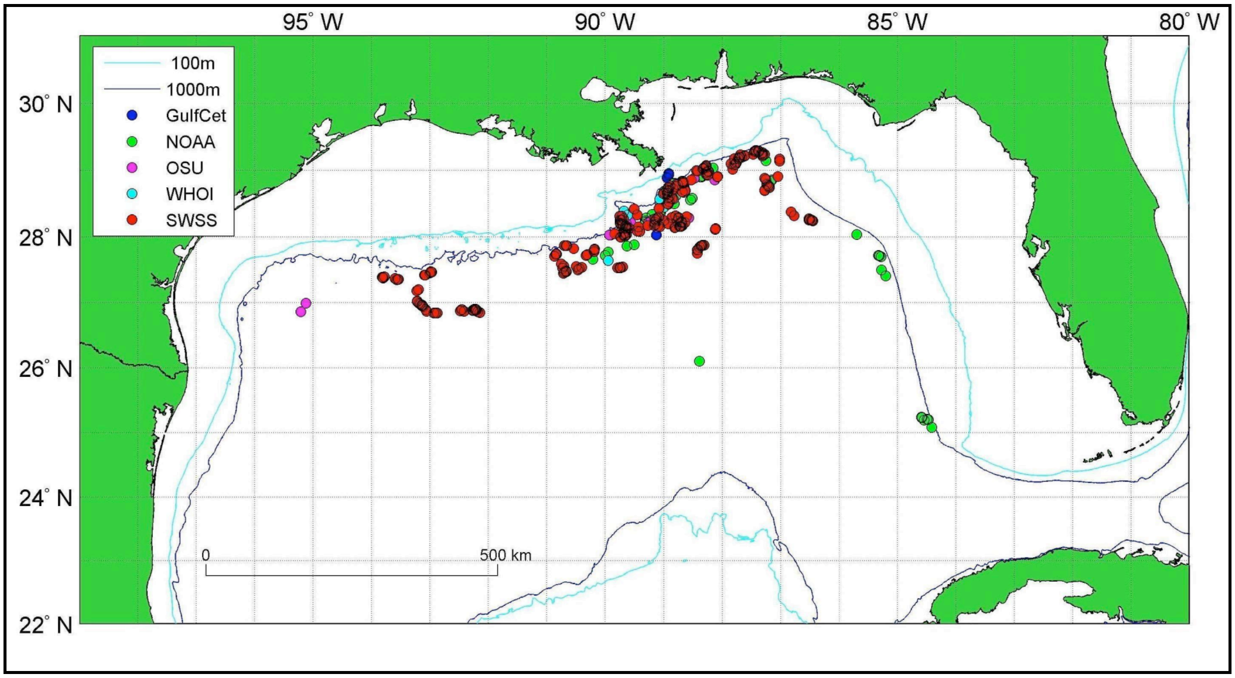

Figure 4.4.2. Locations of sperm whales at first fluke up.

A histogram of intervals between fluke ups for periods of less than 200 mins (Figure 4.4.3) shows pronounced peaks at multiples of approximately 55 minutes. This reflects the modal dive cycle time for sperm whales in this area. This dive cycle time is also the minimum time over which horizontal movement data and mean speed can be measured with these data.

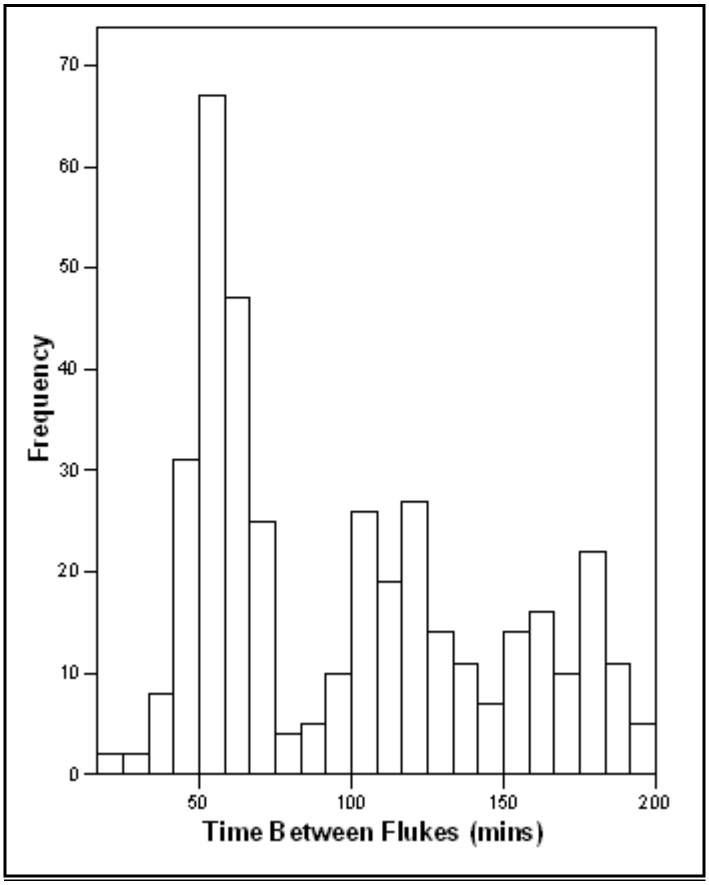

Figure 4.4.3. Histogram of time intervals between fluke ups of identified whales used to investigate movements for intervals of less than 200 mins.

Net speed between identified locations decreases with the time interval over which speed was measured (Figure 4.4.4). This is to be expected in animals that do not move in a completely straight line and very probably reflects changes in direction of movement of these animals with time. The regression in Figure 4.4.4 suggests that over a time interval of ~55 mins (modal dive cycle time) the mean speed is 3.3 km h^{-1}. The mean measured speed was 3.27 km h^{-1} with a standard deviation of 1.0 km h^{-1} for all movement over time intervals between 40 and 70 mins (approximately one dive cycle). Whales were often encountered along the edge of the continental shelf and appeared to observers in the field to move parallel to contours. This is reflected in Figure 4.4.5 which shows the direction of movement subtracted from the orientation of the depth contour at the mid point of each movement. Relative angles between direction of movements and direction of contours have been calculated and transformed so that 0 shows alignment with the orientation of the contour, -90 would be moving directly offshore, and +90 would indicate a movement directly inshore. Frequencies for angles aggregated within 10 degree bins were significantly non-uniform (Chi square = 53.4, df = 16, P <0.001) with a peak in movements in the same direction as the contours. Similarly, water depth (from ETOPO2 gridded data as in Section 4.3.2) tended to be very similar at sequential fluke up locations (within 70 mins of each other) with a mean absolute difference in depths at fluke-up locations of only 1.28% (SD = 1.22%).

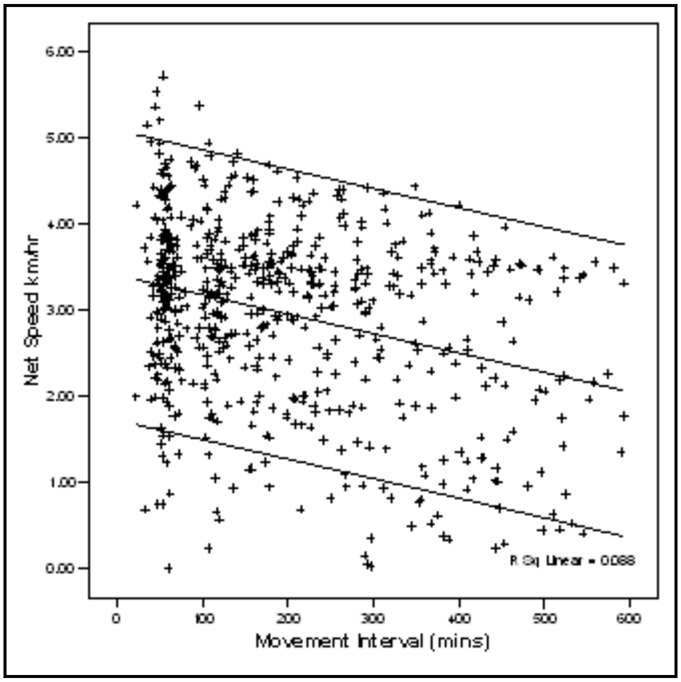

Figure 4.4.4. Plot of net speed against interval over which speed has been measured. Regression line and 95% confidence intervals are plotted.

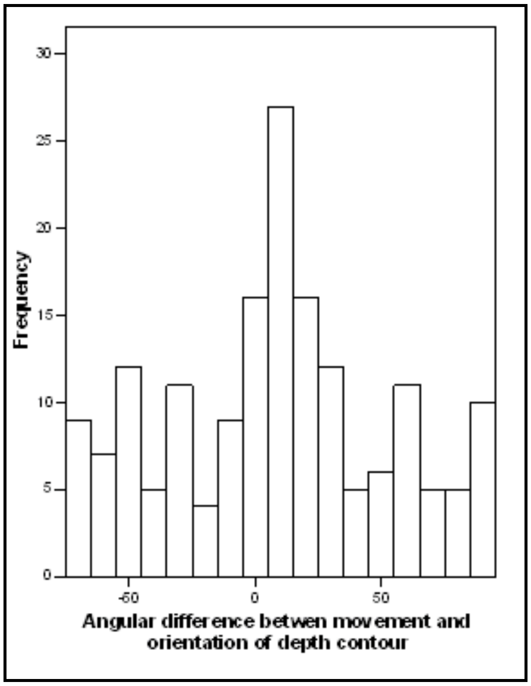

Figure 4.4.5. Histogram of angular difference between movement between two fluke up positions and the orientation of the depth contours at the mid point of the dive for movement intervals of less than 70 mins.

The whale's heading at the time of fluke up was usually noted. Whale headings were compared with the direction of movement during the subsequent dive by subtracting one from the other. Figure 4.4.6, a histogram of difference between fluke up heading and subsequent movements, indicates that heading at fluke up is a very good predictor of movement during the subsequent dive.

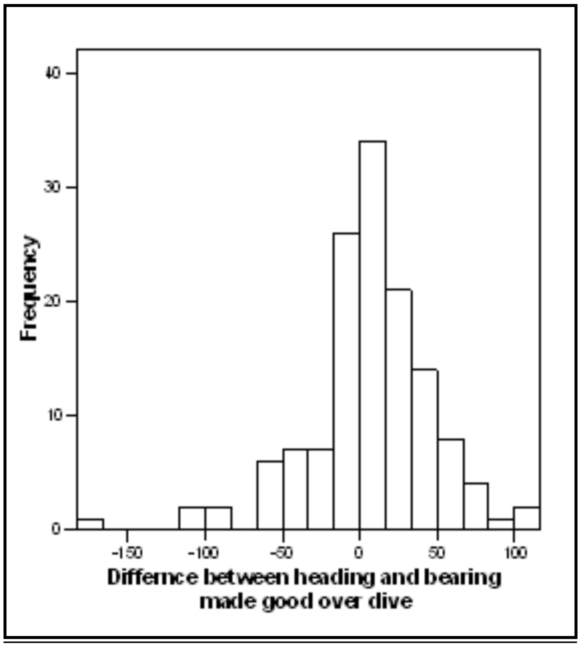

Figure 4.4.6. Histogram of angular difference between whale heading at fluke up and direction of movement over the subsequent dive.

Information on surface ocean currents was available from the output of a near real time oceanographic now-cast model for the Gulf of Mexico (Ko et al. 2003). The angular difference between whale movements and current direction for movements over period of less than 80 mins was not uniform with a preponderance of movements at ~60 and 300 degrees to the current. These peaks probably reflect the angle at which currents impinge on the shelf edge in this region and the fact that whale movements tended to be along the shelf edge (see above). Angles between movements and currents were recast between 0 degrees being perfectly aligned with the current to 180 degrees directly opposed to it. There was no tendency for whales to swim either with or against the current. As might be expected, speed of movement increased as the direction of travel increasingly became aligned with the current (Figure 4.4.7; Pearson Correlation Coefficient =-.191, P=0.018, n=153).

There was no significant relationship between speed and mean water depth for movements over periods of less than 80 mins (Pearson's correlation=0.10, P=0.891). Speed was not significantly different between years (ANOVA F=.908, df =3, P=0.439).

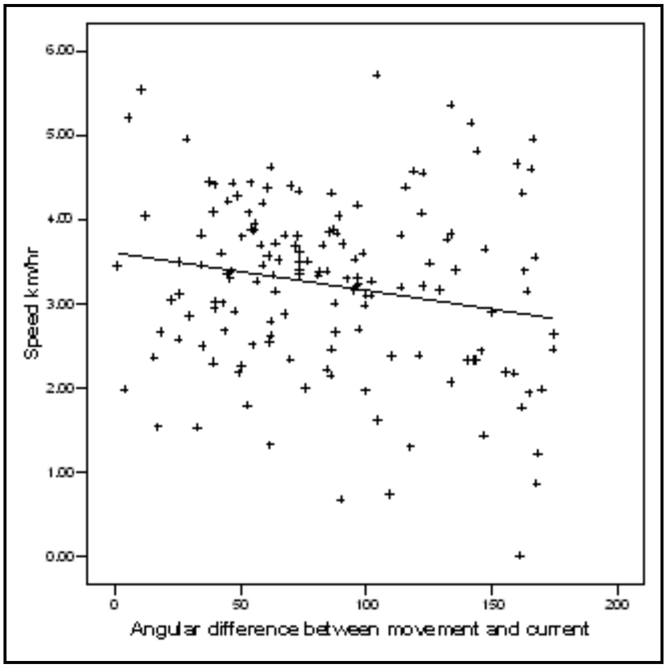

Figure 4.4.7. Plot of mean speed between fluke up locations and the relative direction of current and movement. Movements in the same direction as the current (0°) were higher than those against the current (180°).

Several different types of whales could be distinguished in the field. Most animals were encountered in mixed groups of females and young whales of both sexes. Some animals were seen to be nursing young calves within these mixed groups (see "Calf Sightings" in Section 4.7). Medium sized young whales that we presumed were maturing males were typically found in smaller groups and could be distinguished by their larger body size. In addition, the sex of some identified whales in the catalogue had been determined genetically (Dan Engelhaupt pers. comm.). Differences in mean speed over periods of less than 120 minutes were compared between different classes of whale using Kruskal Wallis non-parametric tests. Speeds measured from maturing males (mean 2.58 km h^{-1}, SD = 0.802) were significantly lower than those for adults generally (mean 3.285 km h^{-1}, SD = 1.02) and than those of nursing females (mean 3.483 km h^{-1}, SD = 0.370) (Kruskall Wallis, Chi-Square 11.578, df=2, P=0.003). The speeds of nursing females and other adults were not significantly different (Mann-Whitney, P=0.138).

Movements over longer time periods are usually analyzed as root mean square (RMS) displacements which is a more theoretically relevant measure than mean movements (Turchin 1998) and also gives a greater weight to larger movements. RMS displacements for periods of up to 24 hours based on photo-identification of individuals and summarized in two hour time blocks are shown in Figure 4.4.8. Over this time period, there is little indication that displacement is approaching an asymptote, indicating rather even movement patterns with little change in directions or double-backing over these time periods.

To investigate the movements of assemblages of whales being actively tracked over longer periods we used the location of the survey vessel every hour as an indication of the group's approximate location. Figure 4.4.9 shows squared displacements for all of the tracking periods between 2002 and 2005. There is considerable variability in dispersion rates but squared displacements usually tended to level off over periods of longer than a day or so which was usually due to groups changing their direction of movement and in some cases moving back parallel to the shelf edge.

To investigate movements over greater ranges and at larger temporal and spatial scales we analyzed all available photo-identification data from the Gulf of Mexico, including datasets from other research teams in SWSS, GulfCet and NOAA. Table 4.4.1 and Figure 4.4.10 indicate that these data cover a wider spatial and temporal scale than the more restricted dataset (from the SWSS Mesoscale cruises) analyzed above. Even so, effort outside the core study area and study periods was limited. We used continuous movement routines in SOCPROG to calculate likelihood values for RMS displacement and daily diffusion rates over extended time periods based on resighting of identified animals. Over periods in excess of years diffusion rate is low and RMS displacement asymptotes at around 300 km which may reflect the home range of the core group of sperm whales within this area.

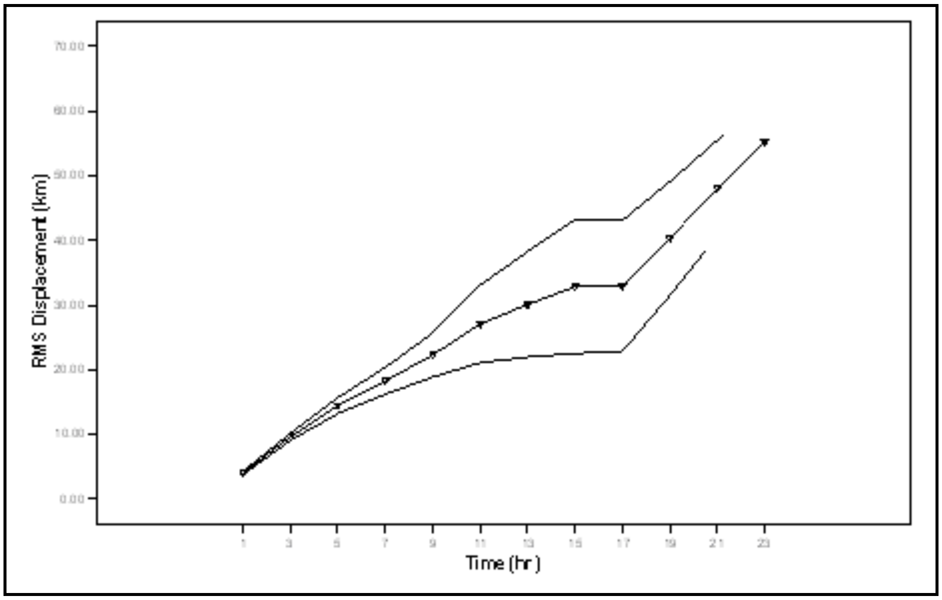

Figure 4.4.8. Root mean square displacement for individual sperm whales summarized in two hourly time blocks for periods up to 24 hours.

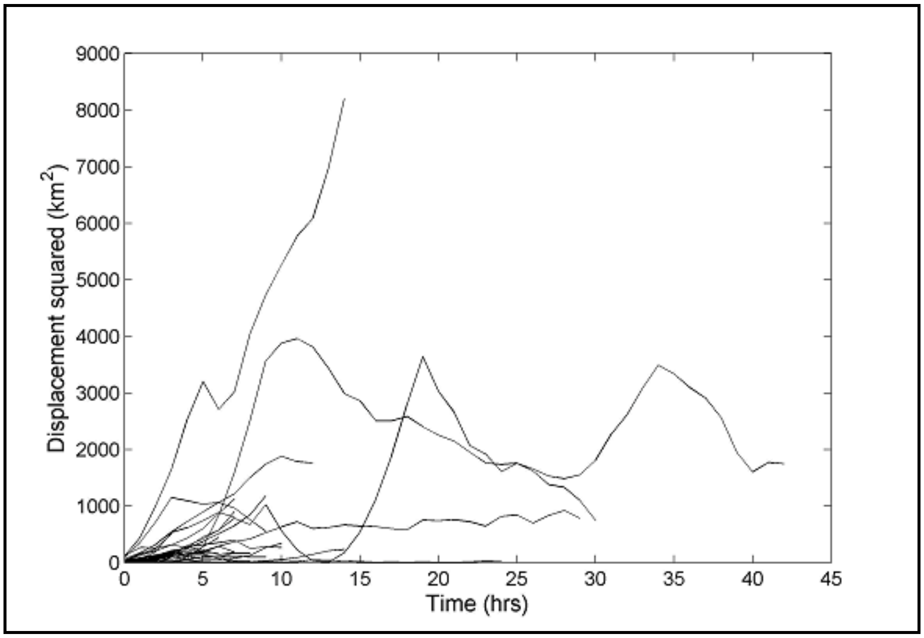

Figure 4.4.9. Squared displacement against time in hours for groups tracked between 2002 and 2005.

Table 4.4.1

Summary of Photo-ID Data, Potentially Useful Images Taken by Each Research Team in Each Year

	Year								
Contributor	1994	1996	2000	2001	2002	2003	2004	2005	Total
GulfCet	8	16							24
NOAA			39	67	12	35	15		168
SWSS S-tag					21	21	9	15	66
SWSS Mesoscale					72	173	204	138	587
Total	8	16	39	67	105	229	228	153	845

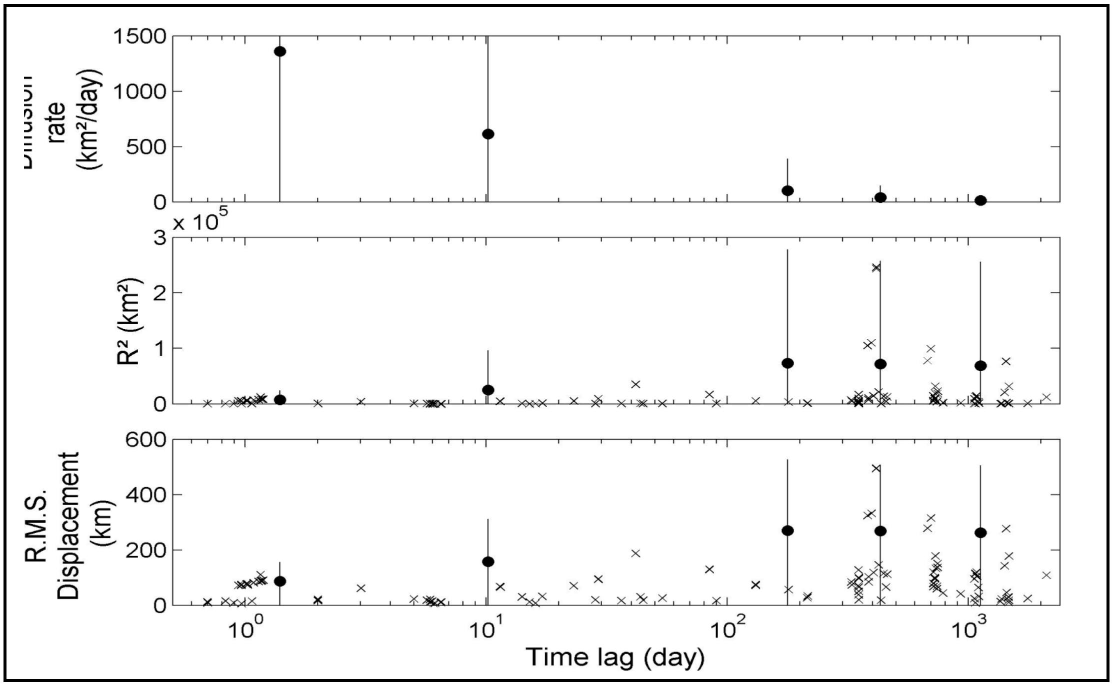

Figure 4.4.10. Results of likelihood estimation of movement using methods of Whitehead (2001) and the SOCPROG software. Panels show estimates for diffusion rate, squared displacement and root-mean squared displacement respectively. X's show actual data, circles show maximum likelihood estimates and error bars show standard errors from jackknifing with day sampling periods**.**

Weller et al. (2000) reported resighting of whales within tens of kms of their original locations after time lags of approximately 2 years. Using the full dataset (which included some of Weller et al.'s animals) we compared distance between resightings for the same animals between years for lags of 24 months or more. The longest time lags of 118, 107, 106, 106 months had distances between resightings of 15, 19, 4 and 20 kms, respectively. The median distance between 27 resightings with a lag of greater than 24 months was 43.6 kms. Of 27 resighting distances 20 were less than 100 km. A histogram of resightings distances truncated at 100 km is shown in Figure 4.4.11.

Of course, in any dataset based on resightings, the locations of sightings are totally dependent on the spatial extent of the survey effort. While this extended over much of the continental slope of the northern Gulf of Mexico more effort was focused in areas of relatively high abundance such as the Mississippi Canyon and Mississippi River Delta region. Thus, the apparent site fidelity detailed above may in part reflect the distribution of our research effort. To control for this uneven effort we compared distances between locations at which whales were re-identified in a particular year with distances to all other identifications in that year. Thus, when a whale was identified in two different years distances between the identified whale's mean location in the first year and its mean location in the second year were compared with the mean distances to all other mean locations of other identified whales in the second year. Distances between resighting mean locations were significantly less than distances between non-resighting mean locations (Figure 4.4.12: Resighting distances mean = 91.3 km, SD=74.7, n=31; Non resighting mean 167.1 km, SD=89.7, n=192; Mann Whitney U=1100.0, P=0.000).

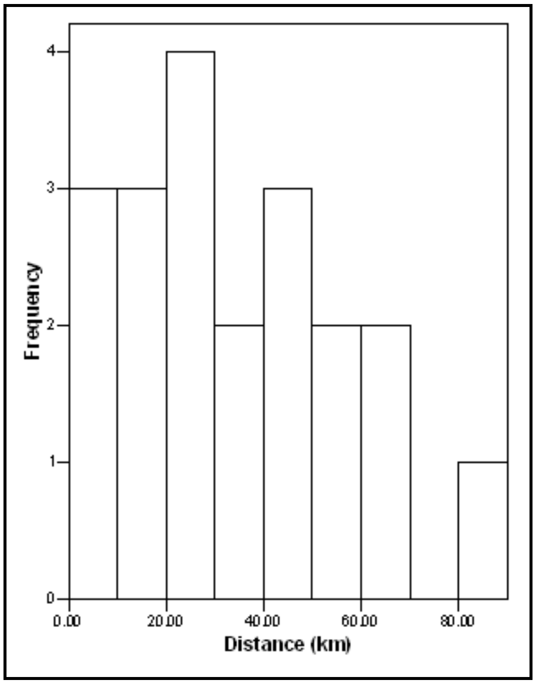

Figure 4.4.11. Distribution of 20 distances between resightings of photo-identified whales more than 24 months apart (truncated so that 7 distances greater than 100 km are not shown).

Investigations of defecation rates were restricted to data collected in 2004 and 2005 and to tracking periods for which at least 5 fluke ups were examined adequately for defecation. Overall, the mean incidence of defecation was 0.209 defecations per fluke up (based on observation of 430 fluke ups observed adequately in 2004 and 2005). Defecation rate was higher in 2004 (0.235) than in 2005 (0.148) and the overall incidence of defecation was significantly greater in 2004 as well (Chi Square=4.08, df=1, P=0.043). The mean horizontal speed over dives that were initiated by a fluke up with defecation were not significantly different from the mean speeds of dives following a non-defecation fluke up (Mann-Whitney U, z=-1.27, P=0.206).

Mean defecation rates and directivity indices were calculated for individual tracking periods. Figure 4.4.13 shows a histogram of values of the directivity index for 55 tracking periods. An index of 1 would indicate a straight line and 0 a closed track returning to the point of departure. There are some indications of a bimodal distribution as might be expected if tracking periods could be defined as foraging or non-foraging periods. However, although defecation rate increased slightly as directivity decreased, these two variables were not significantly correlated

(Pearson Correlation coefficient=-.084, P=0.748). Neither directivity indices nor mean defecation rates within tracking periods varied significantly between years (ANOVA F=0.963, P=0.334; F=1.99, P=0.170).

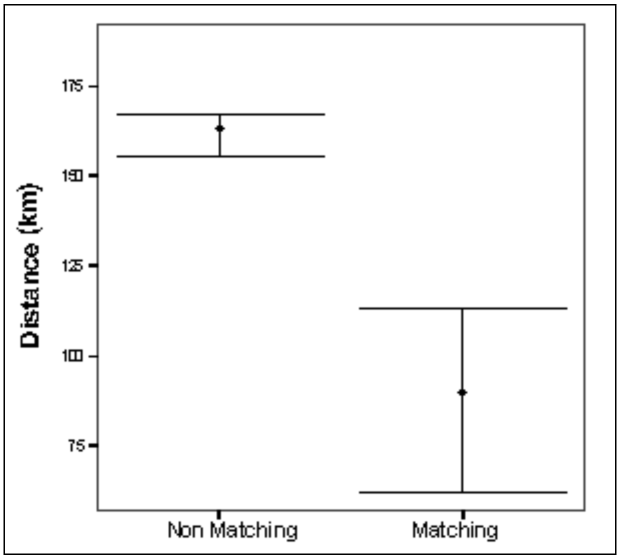

Figure 4.4.12. Distances between matching and non-matching flukes in different years in the northern Gulf of Mexico. Plot shows means and 95% confidence limits.

4.4.4 Discussion

Values for dive cycle time and movement speed are similar to those reported from other areas. The mean speed of movement reported here (3.3 km h^{-1}) is similar to that observed in mixed groups in other parts of the world (3.8 km h^{-1}, Whitehead 1989; 4.3 km h^{-1}, Whitehead 2003; 3.8 km h^{-1}, Jaquet et al. 2003). These speeds reflect net horizontal movement over a dive cycle, during which the animals have also moved a significant distance in the vertical plane and also may have executed many heading changes. It is likely that diving whales swim through the water at a speed close to their most metabolically efficient speed for transport. Miller et al. (2004b) used D-tags to measure mean swimming speeds of 5.22 km h^{-1} during descents and 5.68 km h^{-1} during ascent in dives by 5 whales in the Ligurian Sea and 18 whales in the Gulf of Mexico. As expected the speed of these movements in three dimensions over short temporal scales are somewhat higher than the horizontal speeds measured over complete dive intervals in this study.

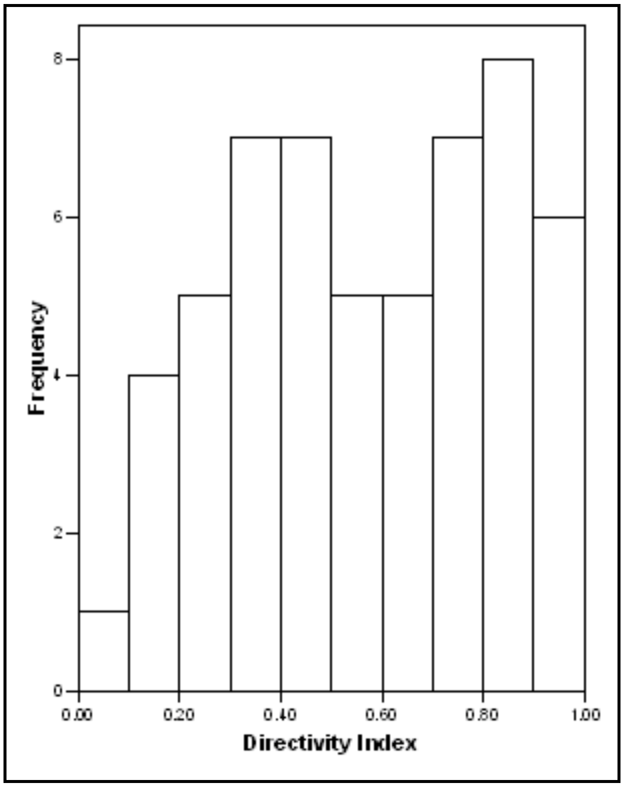

Figure 4.4.13. Directivity index for 55 tracking periods in 2004 and 2005.

With a mean speed of 2.6 km h^{-1}, the movements of males were ~20% slower than average for all whales. This is unexpected because the speed for minimum metabolic cost of transport should scale with body length and be higher for larger animals, such as males. However, other researchers have also reported lower movement rates for males. For example, mean horizontal speeds of 2 and 1.9 km h^{-1} were measured for maturing males in New Zealand by Gordon et al. (1992) and by Jaquet et al. (2000), while rates for two males radio tracked off Dominica were 2.6 and 3.5 km h^{-1} (Watkins et al. 1999). It has been reported that males are more likely to dive to and forage close to the bottom (see review in Whitehead 2003). Some maturing males tracked with D-tags in the Gulf of Mexico dove to the bottom during their dives but females were not observed to do so (Section 5.2). Lower mean horizontal speeds in males may be related to these different foraging strategies and dive patterns.

Our results also show that ocean currents affect the whale's movements; this serves as a reminder that these animals inhabit a dynamic environment. Currents may also differ in strength and direction at different depths and these factors may account for some of the variability in observations of net movements reported here. Currents may have little effect on the rate at which pelagic prey are encountered though, as both the whales and their prey are transported equally in a large body of water. Currents may be more significant, however, if prey are associated with the bottom and do not move freely in the current.

The tendency for whales to move along contours and stay within a narrow range of water depth has been noted from other areas, but not quantified. This will tend to constrain horizontal movements along a smaller elongated area rather than being spread evenly in all directions. Such considerations are relevant to calculations of dispersion and diffusion rates and should also be born in mind in models of movements to reduce the effects of location error in satellite telemetry.

The mean defecation rate observed in this area (0.209) is high compared to those observed in other regions. For example, the average defecation rate observed during a survey of the South Pacific was 0.084 (Jaquet and Whitehead 1999) and the long term mean from studies in the Galapagos area 0.032 (Whitehead 2003). Assuming the defecation rate is a proxy for successful foraging, this suggests that whales encountered in the northern Gulf of Mexico were engaged in foraging at high rates. This may be an indication that Gulf whales are feeding on a more evenly distributed prey resource than sperm whales feed on elsewhere, which in turn may support the concept that the small size of Gulf animals is an adaption to this type of prey environment. On the other hand, without any measure of defecation volume, we could not distinguish between animals that are feeding continuously on small amounts of prey and thus defecating frequently from animals that are feeding intermittently on large patches of prey. In the latter case the animals might store the energy from the feeding event and then process it in a large bolus and thus have large but less frequent defecations. In this regard, we point out that defecation rates did not correlate with directness of paths during tracking periods as has been reported from other areas. This may be because many of our tracking periods were short compared to those in studies for which this effect had been reported. It may also be the case that within this area prey are not distributed in a way that results in a correlation between path directness and defecation rate. For instance, if prey were available at consistent densities over larger spatial scales, whales may not turn as frequently as when feeding on small and well-defined prey patches.

Our analysis comparing distance between resighting of the same individuals between years suggests that even within our main study area some individual animals had smaller preferred ranges. However, the median distances between resightings (~72 km) was somewhat larger than the very small (<10 km) distances between resightings previously reported for sperm whales in this area by Weller et al. (2000).

4.5 Association Between Satellite-Tracked Individuals

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4.5.1 Introduction

Sperm whales have a complex social structure: individuals typically share their range, and may have relationships with many other individuals (Caldwell et al. 1966; Whitehead 2003). Female sperm whales form cohesive "social units" that remain together for periods of at least years

(Whitehead et al. 1991; Christal et al. 1998; Connor et al. 1998; Lyrholm and Gyllensten 1998; Whitehead 1998, 2003). Two or more social units often join over periods of days to form "groups" that move together in coordinated fashion. Within a group, individuals associate more often with members of their own social unit (Whitehead et al. 1991; Christal and Whitehead 2001). Groups of sperm whales can form "aggregations" over scales of 2-20 km. Aggregations vary considerably in temporal and spatial terms, have dynamic membership over periods of hours, and may indicate a concentration of food resources (Jaquet 1996; Whitehead and Weilgart 2000; Whitehead 2003). At larger spatial scales, sperm whales form "concentrations" which can extend for hundreds of kilometers, contain hundreds of whales, and coincide with areas of increased secondary productivity (Jaquet and Whitehead 1996; Whitehead and Weilgart 2000; Whitehead 2003). A higher level of social structure, the "vocal clan", is based on the repertoire of "codas" (Rendell and Whitehead 2003b). Sperm whale vocal clans "have ranges that span thousands of kilometers, are sympatric, contain many thousands of whales and most probably result from cultural transmission of vocal patterns. Units seem to form groups preferentially with other units of their own clan" (Rendell and Whitehead 2003b).

Although the first genetic studies of sperm whale social units showed low diversity, which suggested a matrilineal structure (Richard et al. 1996; Connor et al. 1998; Lyrholm and Gyllensten 1998), recent observations indicate that social units may not be strictly matrilineal (Christal 1998; Mesnick 2001; Rendell and Whitehead 2004). However, few social units have been analyzed for genetic relatedness, and they have all come from the same region: Galapagos Islands (Christal 1998; Mesnick 2001; Rendell and Whitehead 2004).

Interaction between pairs of individuals is the basic element of the structure of animal societies (Hinde 1976; Whitehead 1995) but recording interactions between individual sperm whales is difficult due to their long dives and extensive movement patterns. Therefore, analysis of social structure for this species has been based on associations, defined as "observations of animals in circumstances in which interactions are likely to occur" (Whitehead 2001). Photo-identification by natural marks along the trailing edge of the fluke has been the most common method used to identify individuals and determine associations between sperm whales (Whitehead and Arnbom 1987; Whitehead et al. 1991; Whitehead and Kahn 1992; Christal et al. 1998; Whitehead and Weilgart 2000; Lettevall et al. 2002; Whitehead 2003). Studies of sperm whale social structure using photo-identification techniques require several observation sessions. Moreover, if the observations are limited to just a few sessions in a particular season, several years of photo-identification data are required to accurately identify social units.

Technological advances can provide alternative methods to study social structure of animals that are difficult to observe directly. One of those technologies is telemetry. VHF radio-telemetry has been used to study social structure of terrestrial organisms (Khidas 1990; Rolstad et al. 1991) and satellite-telemetry has been successfully used to track whales (e.g., Watkins et al. 1996; Mate et al. 1997; Mate et al. 1998; Mate et al. 1999; Watkins et al. 1999; Mate et al. 2000; Heide-Jørgensen et al. 2001; Watkins et al. 2002; Etnoyer et al. 2006; Zerbini et al. 2006; Mate et al. 2007). However, the number of simultaneously monitored individuals and the active life of satellite transmitters have not been enough to analyze social structure of whales using satellite telemetry. The number of tagged individuals and the amount of locations obtained with S-tags deployed during SWSS present an opportunity to study social structure of satellite-tracked sperm whales. The objectives of this analysis were: 1) assess the feasibility of using satellite-telemetry data to determine potential interactions between tracked whales, 2) determine associations between tagged individuals, and 3) compare social structure to genetic relatedness of Gulf of Mexico sperm whales.

4.5.2 Material and Methods

Data used for this analysis are a subset that includes only the 51 whales tracked from 2002-2005 (Table 4.5.1) of the satellite-determined locations data set described in Section 4.3. Tag deployment, transmission cycle, and location filtering procedure are described in detail in Section 4.3. Whenever possible, skin samples for genetic analyses were collected from sloughed skin or with the aid of a biopsy dart. Genetic analyses examined 13 polymorphic microsatellites from the bi-parentally inherited nuclear DNA, a 399 base-pair sequence of the maternally inherited mitochondrial DNA control region, and sex-linked markers to determine sex of the individuals and relatedness among them (Section 4.2). Biopsy collection, DNA extraction, DNA processing and genetic data analysis methods are described in more detail in Engelhaupt (2004).

Satellite-determined locations of tagged sperm whales were used to determine associations, between of pairs of individuals based on spatial proximity. For this purpose, we identified "contemporary locations", i.e., satellite-determined positions of tagged whales determined from transmissions received by the satellite within a short time of each other. Distance between a pair of individual whales (dyads) was calculated for contemporary locations. In order to avoid pseudo replication, when more than one pair of contemporary locations were observed for a dyad within 24 hours, only the distance estimate from the highest quality pair of locations was included in the analysis. The proportion of contemporary locations classified as an association was evaluated as a function of time between locations and distance between individuals to determine criteria to define association events.

Simple ratio coefficients of association (CoA) between individuals (Cairns and Schwager 1987) were calculated for each dyad. CoA was estimated only for individuals that had 10 or more contemporary locations. For the tagged whales with genetic data, Mantel's test (Mantel 1967) was used to determine if there was correlation between genetic relatedness and CoA. The computer programs SOCPROG (Whitehead 1999) and MatrixTester v.2.2.3 (Hemelrijk 1990) were used to conduct a Mantel's permutation procedure to test for significance of correlation between genetic relatedness and the CoA matrices (Hemelrijk 1990). The program SOCPROG was also used to make graphic representations (sociograms) of genetic relatedness and CoA between individuals.

4.5.3 Results

Skin biopsies were obtained for 41 of the 51 individuals included in the association analysis. Thirty-three tagged whales were females, eight were males, and 10 were of undetermined sex due to the lack of biopsies (Table 4.5.1). Five haplotypes were identified among tagged whales (see Section 4.2). Haplotypes of whales tagged in 2002 were A, B, C and X (1, 1, 3, and 10, respectively; 3 individuals not determined). Individuals in subsequent years had only haplotypes X and Y (8 and 3 in 2003, and 8 and 1 in 2005, respectively). Genetic structure of sperm whale population in the Gulf of Mexico, including data of non-tagged whales, is described in Section 4.2. Tagged whales ranged in estimated length from 7.5 m to 12 m. Individuals tagged in 2005 were smaller than those tagged in 2002-2004. Mature sperm whales exhibit a high degree of sexual dimorphism, with adult males being considerably larger than females and immature males (Whitehead 2003). Males tagged during this study were not notably larger than the females. Therefore, we consider that those males were most likely immature individuals.

A total of 3052 locations were used for the analysis. After the initial filtering (quality control filter described in detail in Section 4.3), the number of locations retained for each individual ranged between 3 and 162 (mean = 59.8, median = 46). Effective tag life (i.e., time between tag deployment and reception of last satellite-determined location) ranged between 11 and 607 days (mean = 192.8, median = 130.4).

The highest percentage of contemporary locations classified as association occurred at a maximum interval of 2.5 hours between locations (Figure 4.5.1). That peak was observed for all three intervals of maximum distance between locations we evaluated (20, 8.5 and 5 km). Therefore, we used 2.5 hours as the interval to define "contemporary locations" (i.e., two locations were considered contemporary if they were observed within 2.5 hours of each other). As expected, the percentage of contemporary locations classified as association generally increased as a function of maximum distance between locations (Figure 4.5.2). However, an inflection point was observed in the curve of that function when maximum distance between locations was 8.25 km. For that reason, two whales were considered associated in a particular day if the distance between their contemporary locations was ≤ 8.3 km.

Table 4.5.1

Summary Information for Satellite Tracked Sperm Whale Individuals Included in the Association Analysis
(M = male, F = female, U = unknown. Haplotypes are indicated by letters, except for N.D. = no data.)

PTT#	Sex	Haplotype	Relatedness data?	Whale size (m)	Deployment date	Tag life (days)	Num. of locations	Contemporary locations	Associations	Social Unit
2505647	F	B	Yes	11.00	01 Jul. 2002 21:58	136	71	42	5	
2505648	M	C	Yes	11.00	28 Jun. 2002 23:03	73	30	19	0	
2505649	U	N.D.	No	10.00	07 Jul. 2002 20:20	372	101	25	11	
2505650	M	X	Yes	11.00	01 Jul. 2002 19:48	268	120	68	17	
2505654	U	X	No	10.00	24 Jun. 2002 23:06	123	43	34	1	
2505655	U	N.D.	No	10.00	03 Jul. 2002 20:47	75	57	36	21	
2505660	F	X	Yes	11.00	24 Jun. 2002 18:36	64	22	14	6	
2505669	F	X	Yes	11.00	03 Jul. 2002 23:07	455	89	60	49	***A***
2505670	F	X	Yes	11.00	03 Jul. 2002 19:48	286	46	37	44	***A***
2505678	F	X	Yes	12.00	02 Jul. 2002 23:10	17	9	4	7	
2505685	M	A	Yes	10.00	01 Jul. 2002 19:35	566	107	56	10	
2505701	F	X	Yes	9.50	03 Jul. 2002 23:42	247	111	67	61	***A***
2505709	F	X	Yes	9.50	03 Jul. 2002 16:49	373	91	58	37	***A***
2505710	U	N.D.	No	10.00	07 Jul. 2002 19:25	82	42	26	9	
2505719	F	X	Yes	9.50	03 Jul. 2002 15:24	71	22	20	23	***A?***
2505720	F	X	Yes	11.00	03 Jul. 2002 20:09	31	8	7	9	***A?***
2505725	M	C	Yes	11.00	01 Jul. 2002 21:40	607	97	49	5	
2505726	M	C	Yes	11.50	01 Jul. 2002 20:16	276	89	60	19	
2800826	F	X	Yes	9.25	11 Jul. 2003 23:15	244	82	17	11	
2800827	M	X	Yes	9.50	11 Jul. 2003 20:43	179	21	14	4	
2800828	F	X	Yes	8.50	04 Jul. 2003 00:06	304	136	83	39	***B***
2800829	F	Y	Yes	10.00	09 Jul. 2003 23:38	299	93	66	68	***C***
2800833	F	Y	Yes	8.50	05 Jul. 2003 17:41	156	79	50	59	***C***
2800839	U	N.D.	No	9.00	08 Jul. 2003 19:03	48	9	7	9	
2800843	F	Y	Yes	8.50	05 Jul. 2003 15:49	353	158	95	84	***C***
2801385	F	X	Yes	10.25	03 Jul. 2003 23:42	391	109	72	31	***B***
2805654	U	N.D.	No	9.25	04 Jul. 2003 00:21	80	32	22	11	***B?***
2805678	F	X	Yes	10.25	11 Jul. 2003 20:17	218	74	51	3	
2805710	U	N.D.	No	9.50	07 Jul. 2003 20:15	409	148	87	10	

Table 4.5.1

Summary Information for Satellite Tracked Sperm Whale Individuals Included in the Association Analysis (continued)

PTT#	Sex	Haplotype	Relatedness data?	Whale size (m)	Deployment date	Tag life (days)	Num. of locations	Contemporary locations	Associations	Social Unit
2805719	F	X	Yes	8.50	06 Jul. 2003 00:08	341	162	93	26	
2805720	F	X	Yes	9.25	06 Jul. 2003 23:54	130	49	35	12	
2810820	F	X	Yes	10.00	09 Jul. 2003 16:18	62	17	12	14	
2823038	U	N.D.	No	9.25	11 Jul. 2003 23:35	96	5	4	2	
3200845	U	N.D.	No	9.50	10 Jun. 2004 17:05	91	16	10	3	
3201387	U	N.D.	No	9.00	10 Jun. 2004 19:45	139	22	8	3	
3201390	F	0	Yes	9.00	10 Jun. 2004 17:46	95	13	7	2	
3202083	F	0	Yes	8.50	06 Jun. 2004 23:00	40	9	4	1	
3205660	F	0	Yes	9.00	06 Jun. 2004 14:30	72	3	2	1	
3205670	F	0	Yes	8.50	06 Jun. 2004 15:51	359	54	8	1	
3700836	F	X	Yes	8.50	11 Jun. 2005 15:35	128	38	24	9	***F?***
3700846	F	X	Yes	8.00	21 Jun. 2005 18:52	393	135	49	16	***E?***
3700847	F	Y	Yes	8.25	27 Jun. 2005 00:53	56	25	16	0	
3701386	F	X	Yes	8.00	21 Jun. 2005 19:01	97	35	24	15	***E?***
3705644	F	X	Yes	8.00	21 Jun. 2005 16:59	21	29	12	6	
3705648	F	X	Yes	7.50	21 Jun. 2005 22:46	333	128	19	9	***D***
3705650	U	N.D.	No	8.00	11 Jun. 2005 14:45	56	19	13	7	***F?***
3705654	F	X	Yes	8.00	28 Jun. 2005 22:52	59	21	15	3	
3705701	F	X	Yes	7.50	24 Jun. 2005 16:15	11	4	4	0	
3705709	U	N.D.	No	8.00	29 Jun. 2005 15:16	126	31	23	1	
3705726	F	X	Yes	8.50	21 Jun. 2005 23:43	292	94	44	10	***D***
3705800	F	N.D.	Yes	7.75	15 Jun. 2005 14:52	33	47	16	0	

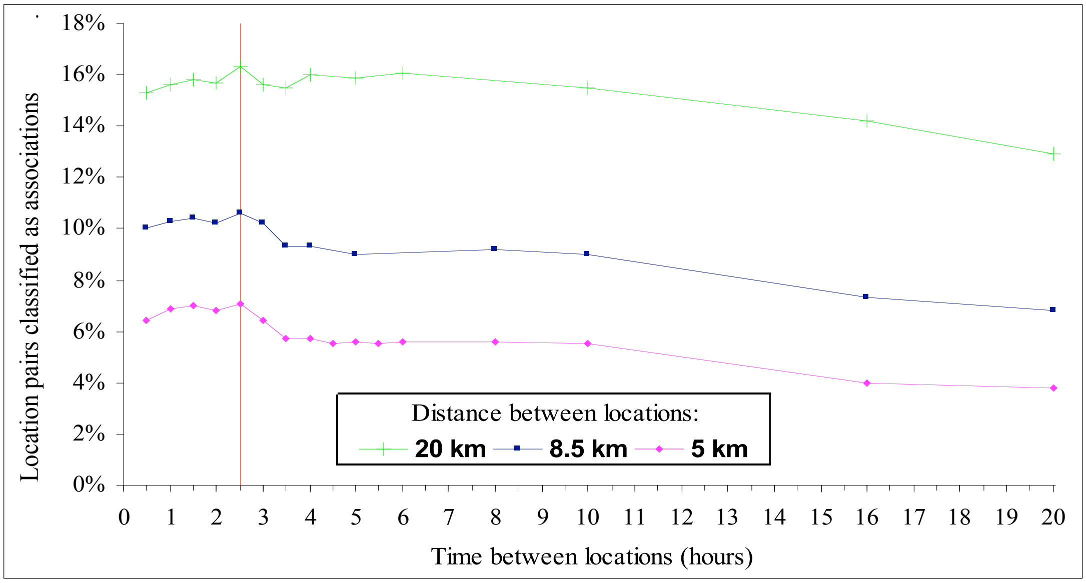

Figure 4.5.1. Proportion of contemporary location pairs classified as association events, as a function of time between locations, for three intervals of maximum distance between locations. The red vertical line indicates selected maximum time criterion (2.5 hours).

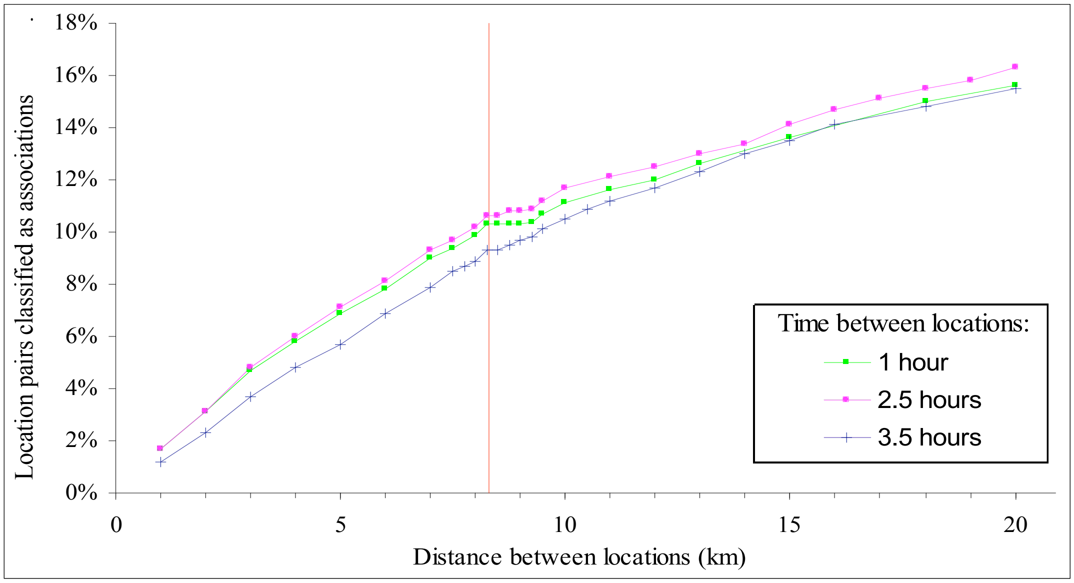

Figure 4.5.2. Proportion of contemporary location pairs classified as association events, as a function of maximum distance between locations, for three intervals of time between locations. The red vertical line indicates selected maximum distance criterion (8.3 km).

Applying the criterion of 2.5 hours between locations, we identified 652 contemporary sampling-events (i.e., when the locations of two or more different individuals were recorded within 2.5 hours of each other). Within those sampling events, we observed 2355 individual whale locations and 4183 dyad-events (i.e., occurrence of a particular pair of whales). We defined 295 association-sampling events (i.e., 24-hour period in which at least one sampling event was observed). Based on the number of individuals whose tags were active at the same time (18 in 2002, 19 in 2003, 10 in 2004, and 12 in 2005) we could have observed contemporary locations from 435 different dyads. However, we only recorded occurrence of dyad-events from 353 different pairs of individuals. After filtering out multiple occurrences of the same dyad, 3642 (87%) dyad-events were retained. Distance between simultaneous locations ranged from 0.1 to 1668.7 km (Mean = 234.82 km, Median = 153.8 km). A total of 402 dyad-events (11%) were identified as associations (within 8.3 km of each other).

On 1 July 2002, we tagged one female (tag #2505647) and four males (tags # 2505650, 2505685, 2505725, and 2505726) off the Mississippi River Delta. Males with tag numbers 2505650 and 2505726 moved away and traveled together towards the west for almost two weeks. Male number 2505685 separated from the other tagged individuals, traveled away from the tagging area, and met again at least two times, 90 and 130 days after tagging, with male number 2505726. Male with tag number 2505725 traveled with none of the other taged animals during the 607 days it was tracked. Overall, immature males did not travel together for periods of more than 20 days. The female in that group (2505647) remained near the tagging location. After tagging, she was only observed to be associated with two of the males once and twice, respectively, so the CoA between them was very low.

A group of seven females (tag numbers 2505655, 2505669, 2505670, 2505701, 2505709, 2505719, and 2505720) were tagged together on 3 July 2002. At least four of those females (2505669, 2505670, 2505701, and 2505709) traveled together for more than five months and we consider them to be part of a social unit (Figure 4.5.3). Whales with tags number 2505719 and 2505720 stayed with other members of unit "***A***" during all the time their transmitter was active, 70 and 30 days respectively. It is very likely that those two whales were also members of social unit "***A***". Tagged whale number 2505655, of unknown sex, remained with unit "***A***" for 46 days, then moved away from the group (up to 368 km in 11 days), re-encountered the group 26 days later, and then separated again until it stopped transmitting 83 days after being tagged. Maps with tracklines of individuals from social unit "***A***" are shown in Figures 4.3.3, 4.3.4, and 4.3.5.

Two other individuals tagged in 2002 (tag numbers 2505710 and 2505649) remained within 100 km from the location where they were tagged for more than 80 days (Figure 4.3.3 in Section 4.3). During that time, those two individuals had several association events which resulted in a relatively high coefficient of association (0.195). However, 2505710 stopped transmitting after 82 days. Therefore, it was not possible for us to confirm if they remained associated long enough to be considered members of the same social unit.

Two female whales tagged in 2003, tag numbers 2800828 and 2801385, traveled together for just over nine months (276 days) and were observed associated on 24 occasions (Figure 4.5.4; see also Figures 4.3.8 and 4.3.13 in Section 4.3). We consider that pair as members of social unit "***B***". The whale with tag #2805654 also traveled with the pair of unit "***B***" for 80 days, until the tag stopped transmitting. It is likely that this individual was also a member of unit "***B***". Another pair of females tagged in 2003 (tag numbers 2800833 and 2800843) traveled together for at least five months and were observed to be associated on 20 occasions (Figure 4.5.5; see also Figures 4.3.10 and 4.3.13 in Section 4.3). We assigned them membership to social unit "***C***". A female whale with tag number 2800829 had 20 and 37 associations with individuals 2800833 and 2800843, respectively. However, the travel path of whale 2800829 did not always match that of social unit "***C***" (Figure 4.5.5; see also Figure 4.3.9 in Section 4.3) and we do not consider it a member of that unit.

On 21 June 2005, we tagged five females in the western Gulf. Two of those females, tag numbers 3705648 and 3705726, remained together for at least nine months after tagging (Figure 4.5.6) and were assigned to social unit "***D***". Those two females from unit "***D***" made a five month round trip, from the Rio Grande Slope (RGS) in the west to the Mississippi Canyon in the north central Gulf (Figures 4.3.29 and 4.3.30 in Section 4.3). Another pair of females tagged on 21 June 2005, tag numbers 3700846 and 3701386, remained for three months in the RGS area, within 200 km of the tagging location (Figure 4.5.7; see also Figures 4.3.24 and 4.3.25 in Section 4.3). The tracklines of those two females during the three months were similar and eleven associations were observed between them. Although three months of traveling together may not be sufficient to conclusively identify those two individuals as members of the same social unit, we speculate that they belong to social unit "***E***". Female with tag number 3705644 was observed to be associated with whales #3700846 and 3701386 on two and three occasions, respectively, but she was only tracked for 21 days, and it is not possible to confirm if she is also a member of social unit "***E***".

Two females tagged in the western Gulf on 11 June 2005 (tag numbers 3700836 and 3705650) remained near the tagging location for almost two months and were observed associated on seven occasions, until one of the transmitters (3705650) stopped working (Figure 4.5.8; see also Figures 4.3.25 and 4.3.28 in Section 4.3). It is possible that those whales also form a social unit ("***F***") but the tracking period was not long enough to provide conclusive results.

Four pairs of whales, all of them females with relatedness values > 0.4, were considered as first-order relatives. Two pairs of females (2800828-2805678 and 3700846-3701386) which shared an allele at 13/13 loci and had the same mtDNA haplotype, are very likely parent-offspring. The other two pairs (2505719-2810820 and 2800833-2800843) also shared the same mtDNA haplotype and it is also likely that they are parent-offspring. Two pairs of first-order relatives had high CoA. Dyad 2800833-2800843 was part of social unit "***C***" while dyad 3700846-3701386 is probably part of social unit "***E***". In contrast, whales with tag numbers 2800828 and 2805678 did not have a high CoA. It was not possible to determine the CoA for the dyad 2505719-2810820 because they were tagged in different years and the active life of their transmitters did not overlap.

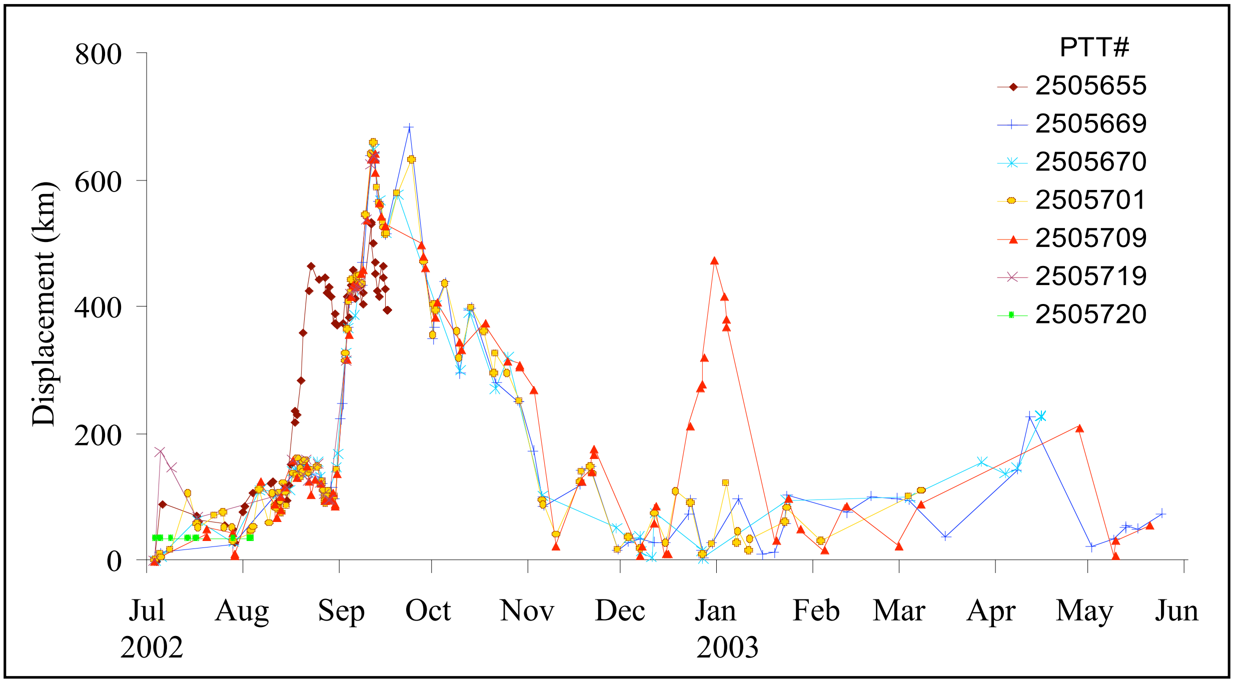

Figure 4.5.3. Displacement of social unit ***"A"*** away from tagging location.

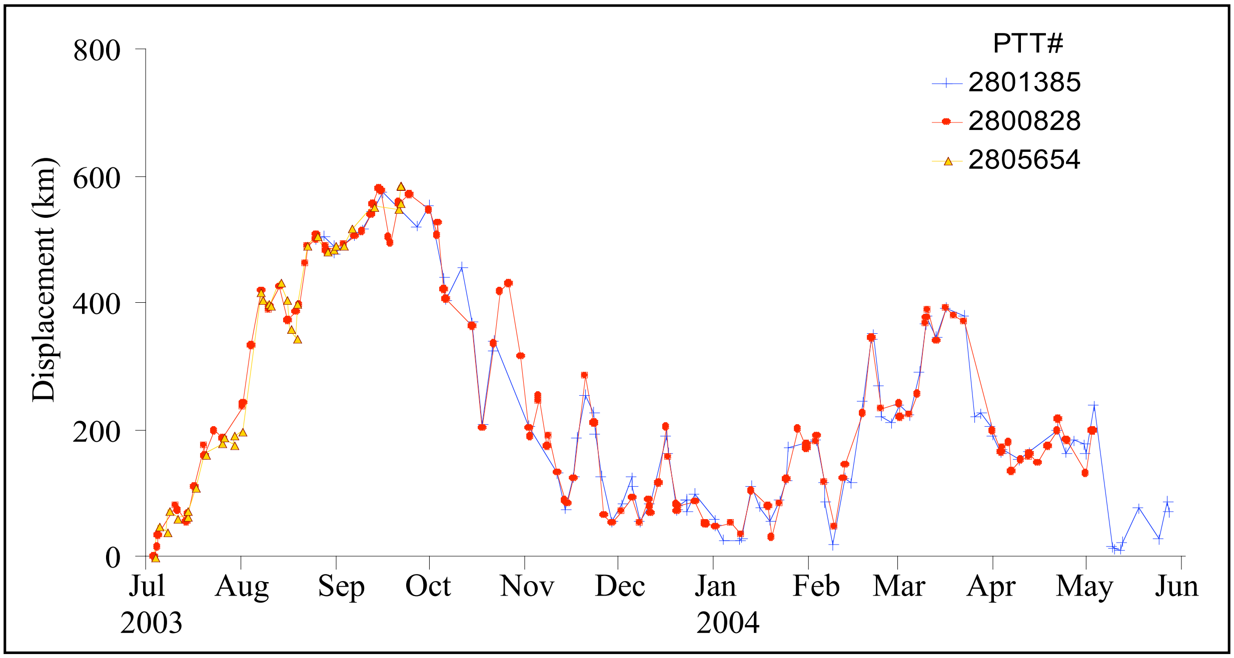

Figure 4.5.4. Displacement of social unit ***"B"*** away from tagging location.

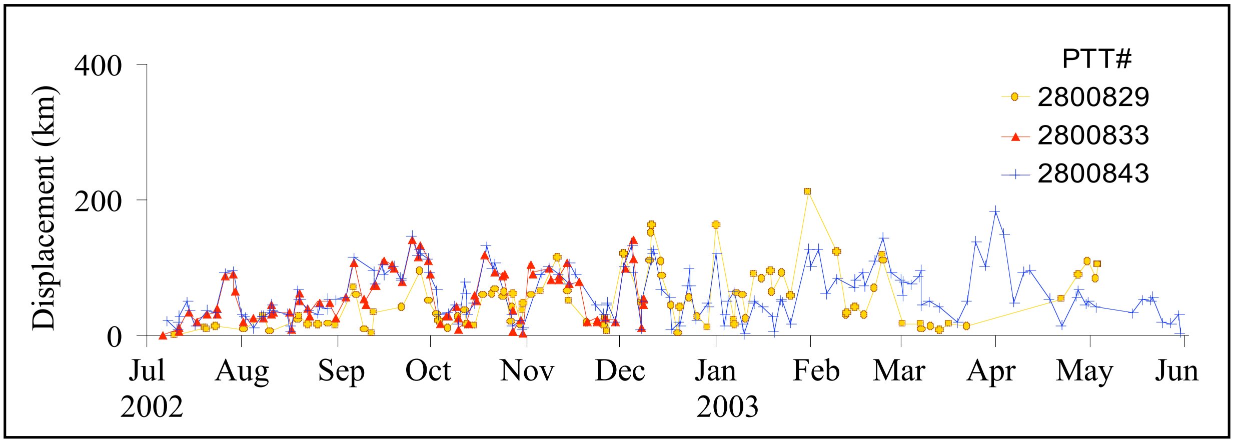

Figure 4.5.5. Displacement of social unit ***"C"*** away from tagging location.

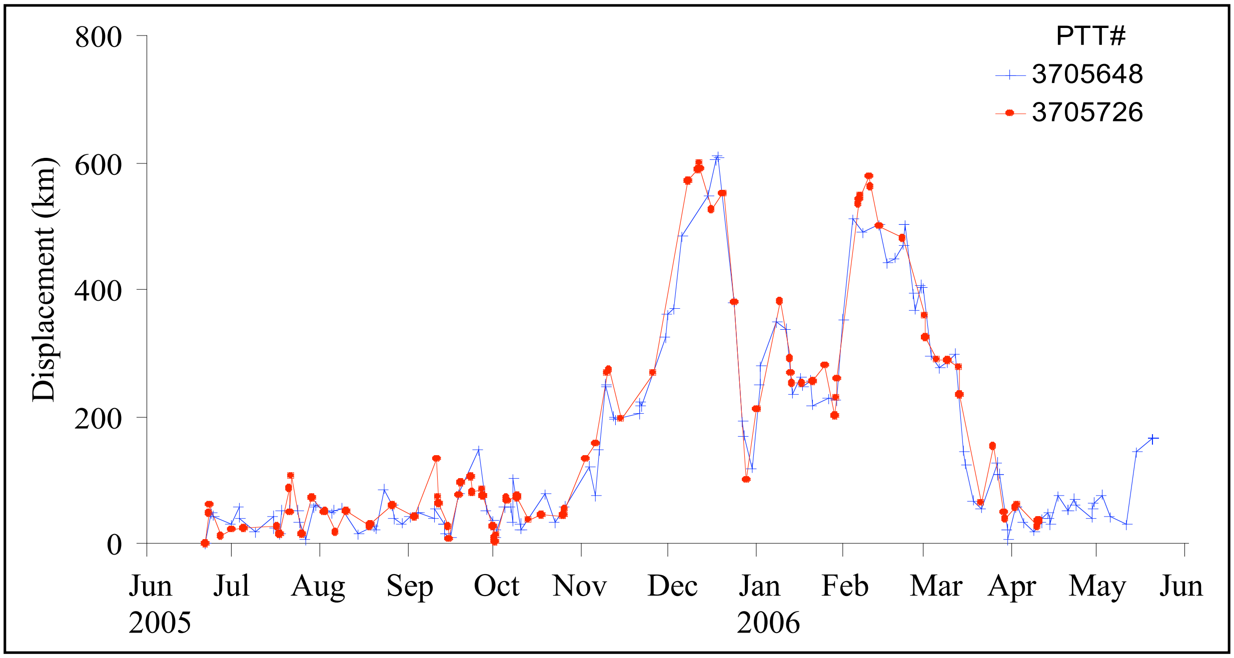

Figure 4.5.6. Displacement of social unit ***"D"*** away from tagging location.

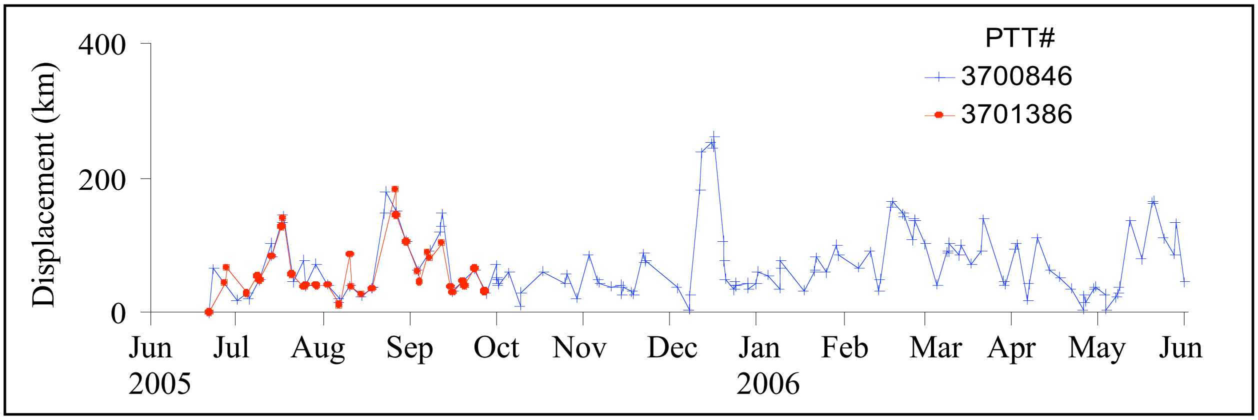

Figure 4.5.7. Displacement of social unit ***"E"*** away from tagging location.

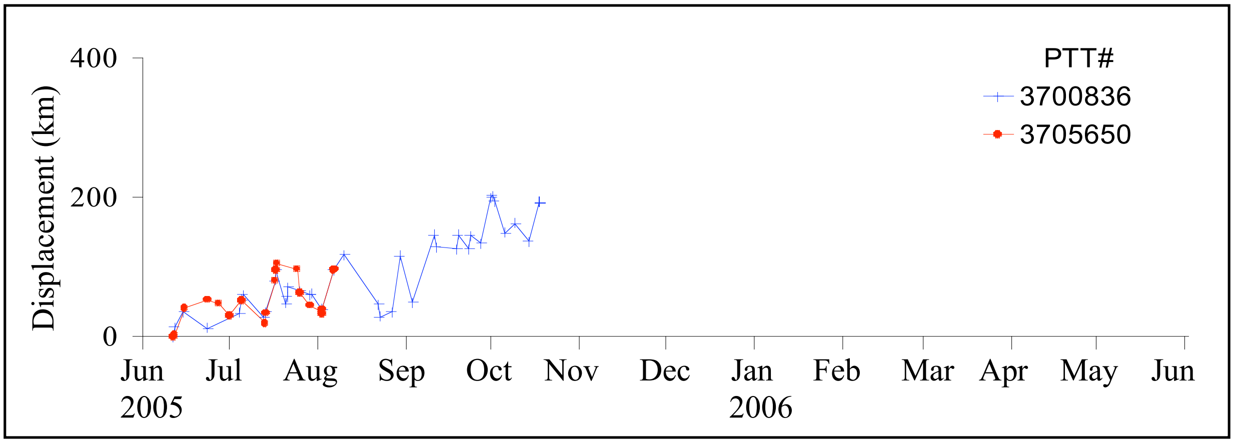

Figure 4.5.8. Displacement of whales with tag numbers 3700836 and 3705650.

Social structure and genetic relatedness of whales tagged in 2002, 2003, and 2005 are graphically displayed as sociograms in Figures 4.5.9, 4.5.10, and 4.5.11, respectively. In those figures, individuals are represented by yellow dots, and the thickness of lines connecting individuals is proportional to the magnitude of CoA (top panel) or relatedness (bottom panel). For example, social unit ***"A"*** can be identified on the top right side of the sociogram in Figure 4.5.9a as a cluster of individuals with lines connecting most of them. An example of a first order related pair can be seen in Figure 4.5.11b where a thick line connects the points representing females with tags number 3700846 and 3701386. The position of individuals is consistent between the association and relatedness sociograms for each year to allow a visual comparison between social structure and genetic relatedness.

No significant correlation was observed between genetic relatedness and association between whales tagged in 2002 (Table 4.5.2, Figure 4.5.3). Correlation between genetic relatedness and association was significant for whales tagged in 2003 (Figure 4.5.10) and 2005 (Figure 4.5.11) but only this last year remained significant after permutation tests.

4.5.4 Discussion

This study demonstrates that satellite-tracking (S-tag) data can be used for social structure analysis of sperm whales. The association analysis presented here is, obviously, limited to tagged individuals. Moreover, the transmission duty cycle we chose (4-hour transmission periods, 1 day on 3 days off) does not allow investigating short-term social structures, such as "clusters" and "aggregations". Nevertheless, S-tag location data provided good temporal coverage, on a timescale from days up to 20 months, and was not limited in space except for the accuracy of the locations. S-tag data allowed identification of social relationships, over time scales of months, between whales tagged in the same year.

Results from previous studies indicate that sperm whales form aggregations that span from 2-20 km (Jaquet 1996; Whitehead 2003). Although sperm whale aggregations are not cohesive and stable over time, it has been suggested that they are socially important, because individuals within the aggregation can likely hear one another (Whitehead 2003). The maximum distance between individuals criterion (8.3 km) that we used to identify association events is well within the range of aggregations mentioned above.

Based on the coefficient of association, 18 female whales were assigned to six social units. We are confident of the assignation of eleven individuals to four social units. Although we cannot make definitive conclusions on the other seven individuals and two of the social units, we consider the coefficient of association estimates as good indicators of their membership to the social units. It is possible that the S-tag data underestimate the coefficient of association between individuals due to the requirement of contemporary locations. Examination of tagged whale movement paths across space and time showed individuals who traveled together for several months, across the northern Gulf of Mexico. For example, dyad 2505669-2505670, tagged in 2002, traveled together for at least nine months. A total of 89 locations were retained and 60 contemporary locations were identified for individual 2505669 while individual 2505670 had 46 retained locations and 37 contemporary locations. Only 15 association events for this dyad were identified during the nine month period when, together with other members of social unit "***A***", they went from Mississippi Canyon to the Rio Grande Slope and back (Figure 4.5.3).

Table 4.5.2

Results of Mantel's Test for Correlation Between Association and Genetic Relatedness of Tagged Sperm Whales (Grouped by Tagging Year)

	Tagging year			
	2002	**2002 Females only**	**2003**	**2005**
Total number of individuals	12	7	11	9
Number of females	7	7	10	9
Number of males	5	0	1	0
Matrices Correlation	0.0899	0.1380	0.2482	0.6245
Mantel *Z*	-0.0462	-0.0383	0.2799	0.3938
t	0.7670	0.5894	1.8190	3.7014
p (t)	0.7783	0.7222	0.9656*	0.9998*
p after 10000 permutations:				
SOCPROG	0.7781	0.7181	0.9460	0.9976*
MatrixTester	0.7737	0.6980	0.9475	0.9979*

* Statistically significant values.

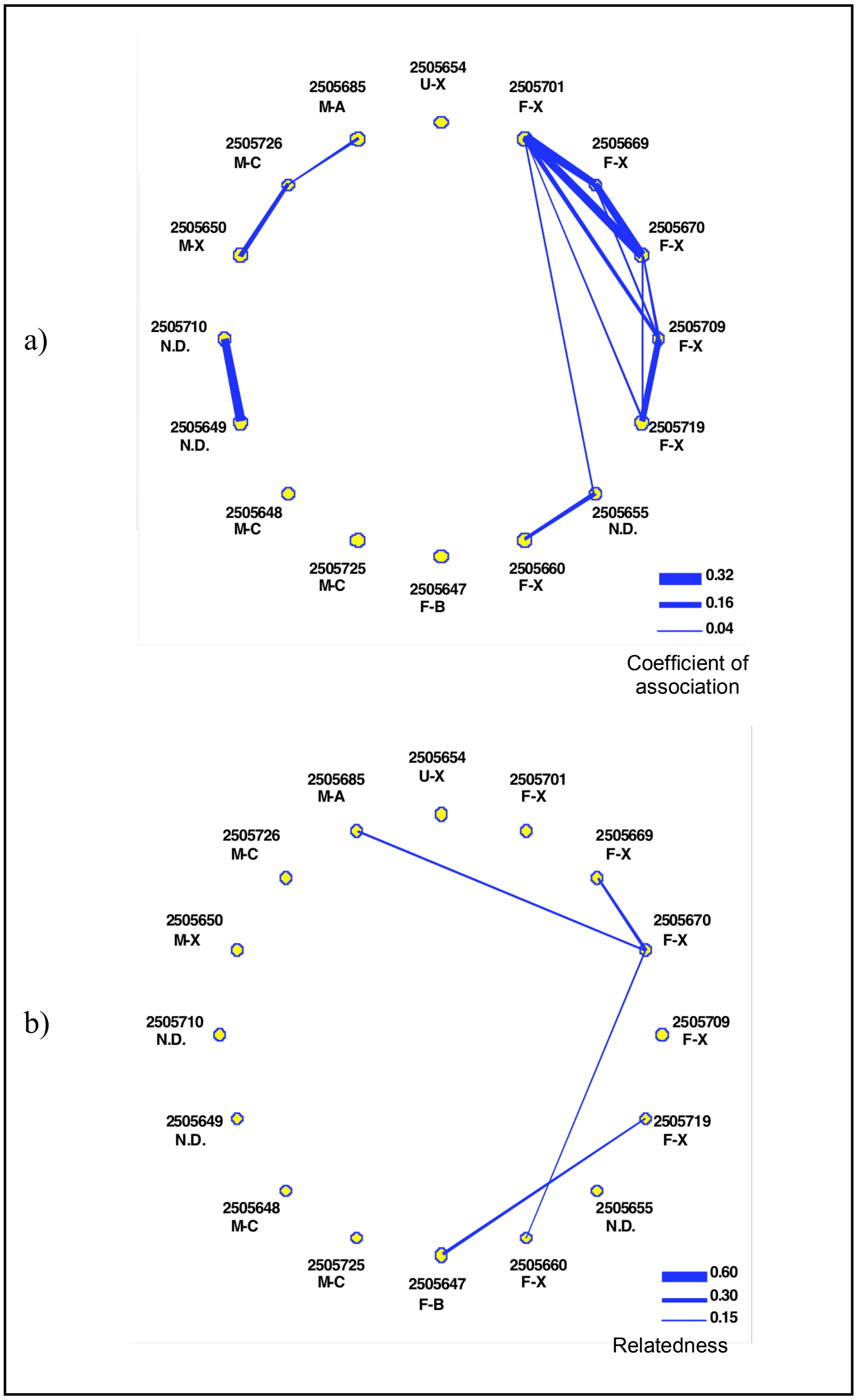

Figure 4.5.9. Sociograms representing coefficient of association (a) and genetic relatedness (b) between sperm whales tagged in 2002. Each point represents an individual whale and shows the tag number, sex (M = male, F = female), and haplotype (A, B, C, X, and Y). N.D. indicates no data. Thickness of lines connecting individuals correspond to the magnitude of the association or relatedness between them.

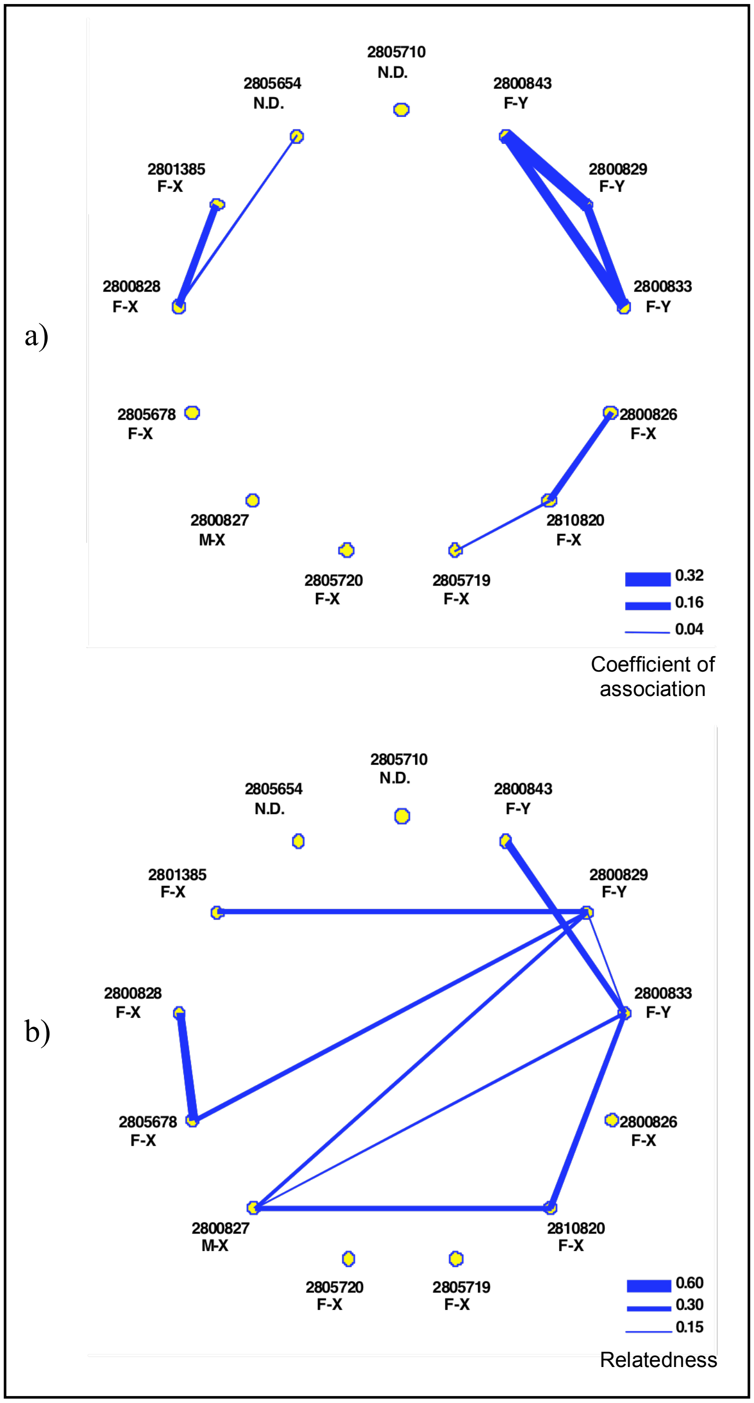

Figure 4.5.10. Sociograms representing coefficient of association (a) and genetic relatedness (b) between sperm whales tagged in 2003. Each point represents an individual whale and shows the tag number, sex (M = male, F = female), and haplotype (A, B, C, X, and Y). N.D. indicates no data. Thickness of lines connecting individuals correspond to the magnitude of the association or relatedness between them.

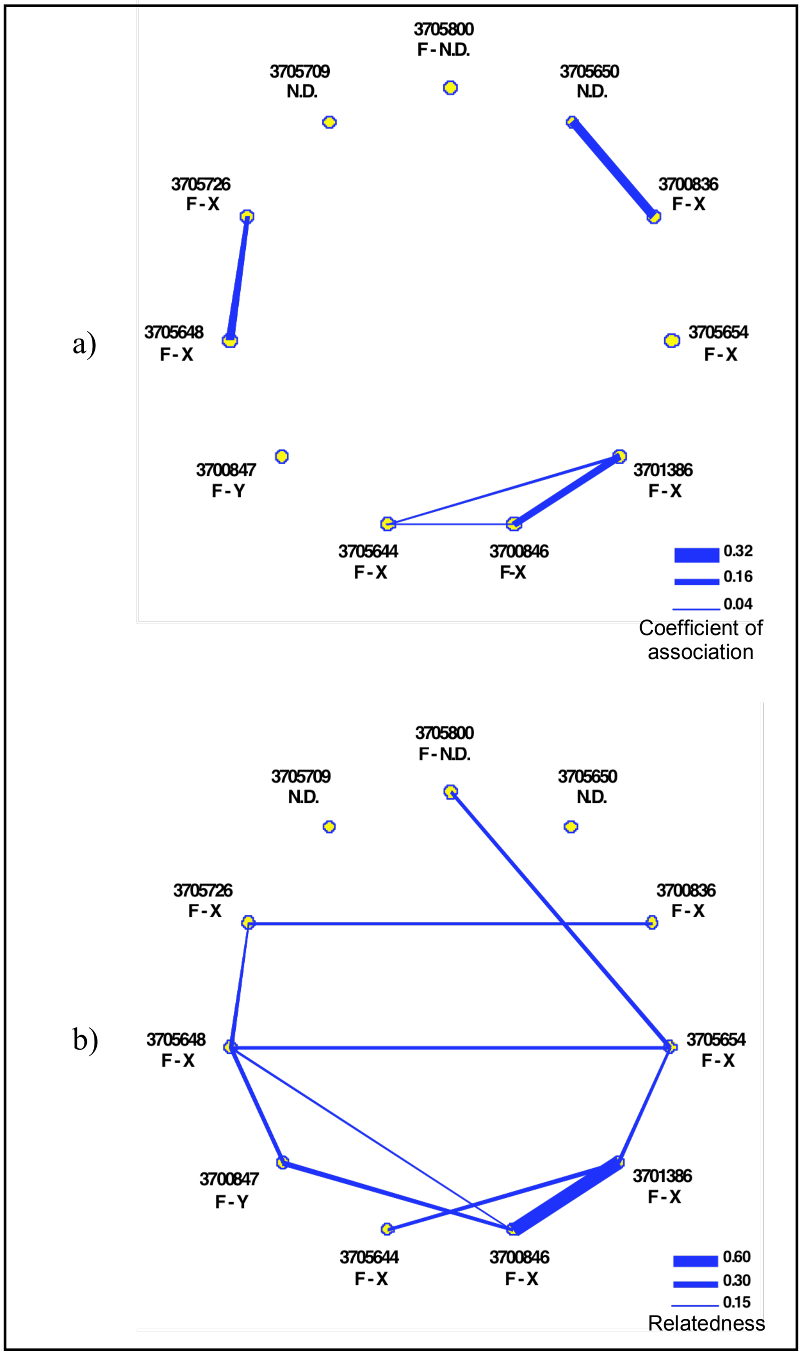

Figure 4.5.11. Sociograms representing coefficient of association (a) and genetic relatedness (b) between sperm whales tagged in 2004. Each point represents an individual whale and shows the tag number, sex (M = male, F = female), and haplotype (A, B, C, X, and Y). N.D. indicates no data. Thickness of lines connecting individuals correspond to the magnitude of the association or relatedness between them.

Although in several instances more than one individual from the same group was tagged and association analysis results indicated that we tagged individuals from the same social unit, very few of the tagged whales were first order relatives. This result is similar to what the genetic analysis of biopsies showed for social 'groups' (see Section 4.2). None of the whales in social unit **"*A*"** had a first order relationship (mother/daughter) with another tagged individual from the unit. The social structure of whales tagged in the Gulf of Mexico coincides with reports from other areas: long term (months) associations between females but no significant long term association between males (Whitehead and Weilgart 2000; Lettevall et al. 2002; Whitehead 2003). It is also consistent with previous studies which indicate that sperm whales do not form strictly matrilineal societies (Richard et al. 1996; Christal et al. 1998; Lyrholm and Gyllensten 1998).

4.6 Social Structure of Sperm Whales in the Northern Gulf of Mexico

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4.6.1 Introduction

One crucial aspect of the general biology of a species is its behavior towards conspecifics. Social behavior influences how individuals gain access to or compete for mates and resources, how they defend themselves against predators, and how they obtain information (Dugatkin 2005). In turn, social structure is closely related to population parameters and is consequently of crucial importance for management decisions.

Sperm whales have been recognized as a social species from earliest whaling days (Clark 1887; Melville 1851). Indeed, their group cohesion was used by whalers to catch as many members of a group as possible. However, our picture of the structure of these sperm whale groups has changed immensely since those early whaling days. While whalers described groups of sperm whales as male-dominated harems, we now know that small social units consist of adult females and their immature offspring, and remain together for years to decades. Such units often form larger groups with one or several other social units, staying together for periods of days (Whitehead 2003). because of their size, it is these larger groups that are most commonly encountered in the field.

Most of this modern perception of sperm whale social behavior is based on studies using benign research methods (Whitehead and Gordon 1986), and mainly Pacific sperm whale populations (Coakes and Whitehead 2004). Whitehead (2003) argued that the evolution of the social system of sperm whales was shaped chiefly by life history traits, morphology, ecology and their interactions. Thus, it could be argued that differences in ecological conditions in which various sperm whale populations live are reflected in the parameters of their social behavior, such as group size and association rate. Here, we describe the social behavior of sperm whales in the Gulf of Mexico with the aim to provide comparative data for sperm whale populations in the

Pacific and elsewhere. In concert with papers on the spatial behavior of Gulf of Mexico sperm whales (Section 4.4), the genetic population structure in the same area (Section 4.2), and large scale movement patterns (Section 4.3), this will allow us to better assess differences in population parameters between sperm whales in various parts of the oceans and thus shed light on the potential reasons for such differences.

In addition to helping elucidate the role of environmental conditions in the evolution of sperm whale society, we are also arguing that knowledge of the social structure of sperm whales in the Gulf of Mexico is a necessary consideration in management decisions regarding ongoing and planned oil exploration and production activities in the deepwater areas of the Gulf. Since the beginning of deepwater exploration and production in the Gulf in 1995, production of oil and gas has increased by 535 and 620 percent, respectively, and there are no signs of this trend slowing down (Richardson et al. 2004). If we want to ensure that current and future anthropogenic activities have no significant impact on sperm whales, as has been recommended by the National Research Council (NRC 2005), or that activities at least are managed to minimize such impacts, then we require knowledge of the residency and social structure of the sperm whales frequenting the Gulf. For example, cultural transmission of information between sperm whales (Whitehead 2003) could include knowledge on responses to anthropogenic activities, which in turn could cause groups of whales to be sensitized or desensitized to sounds.

4.6.2 Methods

Data for this paper were collected between 1994 and 2005. GulfCet data were collected between 1994 and 1996 (Section 3.1). The period between 2001 and 2004 was covered by NOAA information (Section 3.1). Dedicated Sperm Whale Seismic Study (SWSS) cruises were carried out between 2002 and 2005. In 2002 and 2003, research was carried out from a 60-m oceanographic research vessel (R/V *Gyre)*. Sperm whales were detected visually from the flying bridge equipped with BigEye binoculars (25x150), or acoustically through towed stereo passive hydrophones. Once groups of whales were encountered, small rigid-hulled inflatable boats (RHIBs) were launched to obtain identification photographs (see below), biopsy samples, and behavioral observations. RHIBs were able to follow submerged whales using directional hydrophones.

In 2004 and 2005, surveys were carried out from a 46’ motor sailor. Sperm whales were located mainly by acoustic detection since this smaller vessel did not offer raised observation platforms or the use of high-powered binoculars. However, the much lower noise level produced by the sailing boat made acoustic detection and following much more efficient. As explained in Section 4.4.2, photo-identification and all behavioral observations were carried out from the sailing boat. In all years, groups were followed as long as possible (given weather and/or time of day, and whale behavior), or until we felt confident that all individuals in the group were identified.

Sperm whales can be individually identified by photographs of the trailing edges of their flukes. We used a Canon EOS 1D with a SIGMA 70-300 mm f4 lens to obtain ID photographs. Every photograph was linked to date, time of day, and position (from handheld GPS in 2002 and 2003, and from ship’s GPS in 2004 and 2005) in a database on a HP200LX computer running custom-written software (2002 and 2003), or on a central computer running *Logger* (IFAW).

Fluke photographs were scored based on the extent of markings on the fluke (0 = no marks; 5 = easily visible, permanent marks) and on the quality of the photographs based on the markings recognizable on the photo (see Section 4.7 for details). Matching of photos was done visually and using the Phlex matching tool (available from *http://homepages.cwi.nl/~adri/europhlukes/flukes/index.html*).

Group sizes were calculated using a Peterson mark-recapture method following Coakes and Whitehead (2004). Periods during which we were following groups of sperm whales were divided into two equal time periods. For each of these periods, we counted the number of individual whales identified, as well as the number of whales identified during both periods. Using the formulas provided in Whitehead (2003) and Coakes and Whitehead (2004), we calculated estimated group sizes and associated CVs. These group sizes reflect what an observer outside of the actual group of whales can see. Animals within that group, however, experience a larger group size (Jarman 1974). This is termed "typical group size" and was estimated using the formula in Coakes and Whitehead (2004). In order to examine the social structure of the groups we encountered we calculated standardized lagged association rates. These rates give the probability of seeing two whales being associated again after a certain time period (lag), assuming animals associate at random (Whitehead 1995). Models including various parameters relating to group sizes and temporary stability were fitted to the lagged association rates. Best models were chosen based on their relative quasi Akaike Information Criterion (QAIC) value. This value indicates how much of the variability in the data is explained by that particular model while at the same time penalizing model complexity (Burnham and Anderson 2002). The model with the lowest QAIC value was chosen since it explains the most variability with the least number of variables. Lagged association rate analyses were carried out in SOCPROG 2.3 (*http://myweb.dal.ca/hwhitehe/ social.htm*).

4.6.3 Results

Between 1994 and 2005, we obtained 1052 identification photographs. Of these, 717 photos fulfilled our requirements for photographic quality and marking of the flukes (see Methods), and these were used for identification of individual animals through time. Overall, we identified 285 different individuals (Table 4.6.1). Putative sex was assigned to individuals within groups as explained in Section 4.4.3.

Due to different field protocols, only photo-identification data from 2002–2005 could be used for group size estimation. During these years, we usually followed only one group per day and thus can use photo-identification data to estimate the size of these groups, by employing a mark-recapture method. We divided the set of identifications from mixed groups (excluding males) per day into two equal sets and used a Peterson mark-recapture equation to estimate group size (Coakes and Whitehead 2004). Groups in 2005 may have been larger than in the two previous seasons (Table 4.6.2), but were not significantly so (ANOVA, $F_{2,31} = 0.86$, $P = 0.43$).

Given the differences in distribution of mixed groups and male whales we observed in 2005, we excluded 2005 data from the analysis of lagged association rates. This analysis (Figure 4.6.1) showed clear support for a social structure including long-term associates and short-term acquaintances (Table 4.6.3).

Table 4.6.1

Number of ID Photos and Whales Identified for Each Survey Season

Year	Number of photo IDs	Number of individuals identified	Number of new individuals identified
1994	8	8	8
1996	16	15	11
2000	39	26	25
2001	67	37	30
2002	72	48	38
2003	173	95	66
2004	204	73	50
2005	138	67	57
Totals	717	369	285

Table 4.6.2

Estimated Group Sizes for 2003-2005
(No appropriate data were available for 2002. Group size reflects group size as estimated by an observer external to group, whereas mean typical group size is that experienced by members of the group.)

Year	Group size (SD)	Mean typical group size
2003	6.9 (4.54)	9.2
2004	5.0 (2.47)	6.1
2005	7.6 (7.85)	14.7
Combined	6.1 (4.83)	9.77

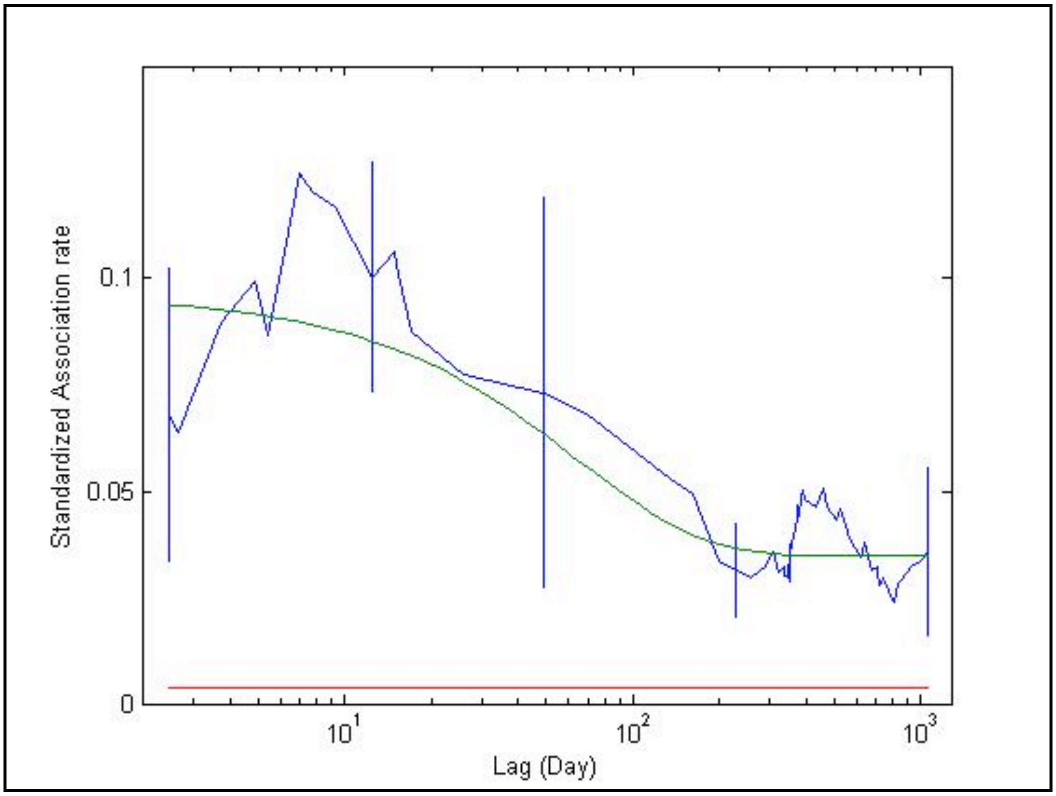

Figure 4.6.1. Standardized lagged association rate for female and immature sperm whales in the Gulf of Mexico, 1994-2004 (blue line). Error bars display ± 1 estimated standard error from Jackknife procedure. Best fitting model is shown in green. For comparison, the null association rate (red line) would result from individuals that do not associate over any time period.

Table 4.6.3

Parameters for Social Structure from Lagged Association Rate Analysis
(Units comprise long-term associates, groups also include short-term acquaintances. Differences in QAIC values less than two indicate little support for a single model. Larger differences indicate considerably less support for the model with the larger QAIC value; see Burnham and Anderson 2002. Data on potential males were too few to calculate association rates.)

Parameters	1994 – 2004 (SE)
Unit size	4.76 (0.156)
Group size	11.41 (0.078)
Disassociation rate	0.016 (0.021)
Difference in QAIC to next best model	3.33

In order to determine whether we encountered the same groups on different days, we used the criteria used by Weilgart and Whitehead (1997) and Coakes and Whitehead (2004). Two groups were considered the same when $m_{XY} > 0.25$ * minimum, where n_X and n_Y are the number of whales identified during day X and Y, respectively, and m_{XY} is the number of whales identified during both days. To avoid sightings of single whales to bias this analysis, we used only encounters during which at least two whales were identified. Table 4.6.4 lists all resightings during the SWSS project. Of the 19 resightings, five included single-animal encounters. One of those involved an animal seen twice in 2002 and then again 2005. The remaining 14 instances include five sets of resightings across years. All of these groups were most likely females and their immature offspring. The only resightings of groups containing potential males were in 2005.

Table 4.6.4

Pairs of Days (X and Y) from SWSS During Both of Which at Least One Identified Whale (Mark Quality ≥ 3, Photo Quality ≤ 3) was the Same
(Date, number of identified individuals in each period (n_X, n_Y), and ID of whale seen in X and Y are provided. When number of animals seen on both days is > ¼ of the smaller of n_X or n_Y, a group can be considered the same; see Weilgart and Whitehead 1997. Only groups with at least 2 identified individuals are used for analysis. IDs of potential males are indicated by an asterisk.)

Date	n_X	Date	n_Y	Seen in X and Y	Same group?
7/3/2002	1	6/26/2004	5	50062	–
7/6/2002	1	7/7/2002	3	50039	–
7/7/2002	3	6/26/2005	3	50039	Yes
7/7/2002	3	7/25/2004	2	50081	Yes
6/11/2003	2	6/18/2003	5	50051	Yes
6/17/2003	2	7/5/2004	4	50026	Yes
6/18/2003	5	6/26/2004	5	5004, 50051	Yes
6/26/2004	5	7/12/2004	1	50503	–
7/4/2004	2	7/7/2004	7	50040	Yes
7/5/2004	4	7/20/2004	3	50101, 50161	Yes
7/5/2004	4	7/6/2004	1	50101	–
7/11/2004	3	7/21/2004	3	50112, 50131	Yes
7/11/2004	3	7/23/2004	2	50112	Yes
7/20/2004	3	7/6/2004	1	50112	—
7/20/2004	3	7/21/2004	1	50106	Yes
7/21/2004	3	7/23/2004	2	50112	Yes
7/28/2004	5	8/3/2004	2	50102	Yes
7/3/2005	8	8/1/2005	6	50226*, 50231*	No
7/3/2005	8	8/2/2005	6	50231*	No

The number of whales identified as potential males increased during the last two field seasons, regardless of whether we limit photo-IDs to high quality only or not (Table 4.6.5).

Table 4.6.5

Number of Whales Identified as Possible Males by Their Size
(High quality photos show clear and obvious marks on good quality photos,
mark quality ≥ 3, photo quality ≤ 3.)

Year	All IDs	Only high quality IDs
2000	2	2
2001	1	1
2002	1	1
2003	1	0
2004	7	3
2005	12	11

4.6.4 Discussion

From daily estimates, we obtained an average typical group size of approximately 10 whales. Estimated group sizes may have been larger in 2005, but were not statistically so. This agrees reasonably well with the comparable estimates for typical group size from the lagged association rate analysis (this analysis excluded data from 2005 for the reasons stated above).

Nevertheless, changes in group size could be caused by the same factors as annual changes in other parameters that we observed in 2005, such as the more westerly distribution. For example, altered prey distribution and abundance could conceivably influence both sperm whale distribution and group size.

While the currently available data set is too small and short-term to delineate social units in the groups we observed, it still provides information on the social structure exhibited by sperm whales in the Gulf of Mexico. As in other areas, sperm whale groups seem to be made up of smaller units, which remain together for extended periods of time. This also matches our observations of repeated sightings of animals in the same company after time periods from weeks to years. For example, in 2004, we resighted two animals still together after 10 days; and two other individuals were seen in the same group in 2003 and 2004. Similarly, a group of five individuals sighted on 26 June 2004 contained an animal sighted first in 2002, two sighted together in 2003, and another individual sighted again two weeks later in July 2004 (Table 4.6.4).

Group sizes in the Gulf of Mexico were considerably smaller than off Chile or the Galápagos Islands, where group sizes range between 24 and 31 individuals (Coakes and Whitehead 2004), compared to the typical group size of approximately 10 individuals reported here. Typical group size in our study area is about one-third of those reported in Coakes and Whitehead (2004). This is the first time that such small groups have been reported for mixed sperm whale groups (compare also Whitehead 2003). Interestingly, Gulf of Mexico sperm whales also differ in other characteristics from those studied in the Pacific. Jaquet (2006) reported that sperm whales in the Gulf of Mexico are significantly smaller in individual size than those in the Pacific. Such population-wide differences could reflect different environmental conditions, ecological adaptations, or population dynamics. For example, Brodie (1975) argued that cetacean populations that occupy a small geographic range should be of smaller individual size, because they do not migrate over large distances and thus large body size is not favored. This point is that, unless there is a real advantage to large body size, small animals will outcompete larger animals because they have higher reproductive rates based on body size alone. A further interpretation is that large body size is preferred when resources are patchily distributed in space and time. This is because it takes time to find and locate prey patches of sufficient value to forage on. In this situation the animals must fast while transiting between prey patches. Large body size provides an animal with greater, faster endurance and the ability to efficiently swim between periodic shortages in prey. Further, if an animal has to swim great distances, larger animals are more efficient and can cover large distances faster and more efficiently. However, large body size also requires absolutely more prey resources or larger patches of prey. Large body size is favored when prey patches are scattered but of high abundance. In contrast, smaller size is favored when resources are more evenly distributed in space and time, and of possible of lower absolute abundance. In this situation, the advantage of fasting endurance and greater locomotor ability is not as important (Costa 1993a; Costa 2001).

Although Brodie and Costa make valid arguments, we caution that our dataset from the Gulf of Mexico is still small compared to those from other areas, and given the large interannual variability we observed, it remains to be seen how well our estimates approximate long-term values. Our observations nevertheless point to an opportunity to investigate the way in which sperm whales may adapt their social behavior to suit local conditions.

These differences are not only interesting for evolutionary analyses. They are also important for management purposes, since they may indicate that whales in the Gulf comprise an evolutionary significant unit. Such a unit would not only be based on genetic markers but also include ecological and behavioral characteristics (Mills 2007). Irrespective of whether whales are already impacted by current anthropogenic activities, the population and its environment should be monitored regularly to enable early detection of population changes and link them to possible causes.

No individuals larger in size than 12 m were encountered during the MPS surveys for this project. However, animals that we considered too large to be females, but not large enough to be mature bulls, were seen in our study area. On one occasion, two potential males were seen in a group of at least 8 individuals. Most likely, this association did not last for long, since the two potential males were identified less than a month later, in a probable all-male group. One male was seen first during NOAA projects in July 2000 and July and October 2001. We sighted him again during SWSS in August 2004.

Overall, we saw many more possible males during 2004 and 2005 compared to the previous years. This can be explained by the different methods used in these periods: whales were observed from a large vessel or small inflatable boats in 2000 – 2003. Neither of these platforms allow for reliable assessment of size of animals. Large vessels commonly are too far away from whales to estimate their size in a reliable manner, and small RHIBs are too low in the water. In contrast, working from a sailing vessel in 2004 and 2005 allowed us to approach whales close enough to assess sizes, and the higher vantage point increased the reliability of these estimates. In addition, we paid increased attention to identifying males in 2004 and 2005. However, the difference between 2004 and 2005 (when we used the same sailing vessel and techniques of observation) likely reflects a real increase in the number of possible males in our survey area. This increase was paralleled by the lack of mixed groups in the traditional areas where we had seen them in previous years and where the males were now in 2005. A similar situation was described by Christal and Whitehead (1997) for the Galápagos Islands, where female groups disappeared in the 1990s, to be replaced by male groups. Whitehead (2003) argues that such switches are due to better-adapted females usually occupying good foraging areas and only once they leave can male groups move into these locations. Our observations in the Gulf seem to support this scramble competition hypothesis, but since we have no data after 2005 to show whether females returned again or the distribution remained as in 2005, it is too early to conclude whether the changes in the Gulf are comparable to those off the Galápagos Islands.

4.7 Population Size and Other Parameters of Sperm Whales in the Northern Gulf of Mexico

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4.7.1 Introduction

The northern Gulf of Mexico has been known as a sighting area for sperm whales since its days as a "Yankee" whaling ground from the 18th to the early 20th centuries (Townsend 1935). The GulfCet cruises conducted in 1994-1996 identified areas along the northern shelf edge as being particularly important habitat for sperm whales and provided some of the first photo-identification images for the area (Jefferson and Schiro 1997; Weller et al. 2000). Population abundance estimates for sperm whales in the northern Gulf of Mexico have been made from data using both aerial and ship-board visual survey methods. Results from a series of ship board surveys conducted over a period of five years (1996-2001) in the US oceanic Exclusive Economic Zone (EEZ) of the northern Gulf of Mexico (from the 200-m depth contour to the 200 mile limit) are reported in Mullin and Fulling (2000). The estimated abundance of sperm whales in the entire area was 1349 (95% confidence intervals 869-2093). They also calculated abundance by sub-areas. Water depths between 200 and 2000 m were classified as slope areas and eastern and western slope areas were defined with a boundary at 88.5°W. Abundance and 95% confidence intervals were 99 (42-236) and 558 (275-1131) for eastern and western slopes respectively. The core study area for the study presented here is almost completely contained within Mullin and Fulling's slope survey blocks. Mullin et al. (2004) present results from aerial surveys conducted between 1992 and 1994. These covered the outer continental shelf and upper slope waters (100-1000 m) along the US continental shelf from the Mexican border to the border between Alabama and Florida and, in addition, the slope waters (1000-2000 m) for the region off the Mississippi River Delta region, which provided a high degree of overlap of the core study area for this study off the Mississippi River Delta. The sperm whale abundance for the entire area was calculated to be 1046 (95% confidence interval 488-2108).

Technological developments have allowed oil and gas exploration and production to extend into the deep offshore waters of the Gulf of Mexico in excess of 1000 m; these waters are also sperm whale habitat. Concerns surrounding the potential effects of these activities on endangered sperm whale populations were the motivation behind dedicated sperm whale studies in the northern Gulf of Mexico, the Sperm Whale Acoustic Monitoring Program (SWAMP) from 2000-2001 and the Sperm Whale Seismic Study (SWSS) from 2002-2006. These programs, especially SWSS, were multi-disciplinary undertakings including fine scale telemetry to investigate responses to exploration noise (Miller et al. 2004a; Miller et al. 2004b; Watwood et al. 2006), satellite telemetry to track long term movements (Section 4.3), passive acoustic monitoring for population survey and assessment of cultural population structure (Sections 4.4., 4.6, 4.7, and 4.8), genetic analysis to determine gender and population structure (Sections 4.2 and 4.5) and the collection of photo-identification data. Photo-identification (photo-ID) data have been analyzed as part of SWSS to investigate many aspects of the biology of sperm whales including movements, site fidelity and social organization. Here we present mark-recapture analysis of photo-ID data to estimate population size for the study area.

Individual sperm whales can be identified reliably from images of their flukes taken when the whales fluke up to initiate their long deep feeding dives (Arnbom 1987; Gordon 1987a). Photo-ID has provided useful data for studying many aspects of sperm whale biology (Whitehead 2003; Whitehead and Gordon 1986). Several authors have used mark-recapture methods to estimate the size of sperm whale populations in different parts of the world, for example, in the Galapagos Islands (Whitehead et al. 1997), off Kaikoura in New Zealand (Childerhouse et al. 1995) and in the Azores Archipelago (Matthews et al. 2001). Use of photographic images for mark-recapture requires that flukes are sufficiently well marked and marks are sufficiently stable to allow animals to be reliably reidentified over the time periods being considered. Several researchers have explored the stability and longevity of marks of different types on sperm whale flukes (Childerhouse et al. 1996; Dufault 1998; Dufault and Whitehead 1995b). Well-marked whales were shown to remain reliably identifiable over periods of several years validating the use of fluke photo-ID for mark-recapture studies of sperm whales. It is also important to assess the quality of any images used in a photo-identification analysis. Arnbom (1987) provides a scheme for this that has been used widely, although we use a somewhat adapted version here.

Sperm whales have the most complicated social organization known of any of the great whales. One consequence of is the way in which different animals within the population become available for "marking" and "recapture" in a mark-recapture photo-identification study. Whitehead (2003) provides a recent review of current understanding of sperm whale social organization. The core social grouping in sperm whales is the "mixed group" of females and immature males which are confined to tropical and temperate waters. Membership of the female component of mixed groups can remain stable for many years, in some cases it is likely that females remain within the groups in which they were born. In regions where the most complete photo-ID data on associations has been analyzed in conjunction with genetic information on relatedness, mixed groups have been shown to be matrilines, though this may not be the case in all areas, including the northern Gulf as indicated in Sectin 4.2. Males leave these groups as they begin to reach sexual maturity, between 3 and 15 years (Whitehead 2003), and they may then form all male groupings. As males get older and grow larger, they extend their distribution into colder waters, outside the range of the females and are found in smaller groups. Physically and socially mature males return to visit mixed groups to breed, though the details of the breeding system are not well understood in this species. Groups of immature sperm whales of both sexes have also been reported from whaling data. Whether these immature groups are a consequence of whaling, how long they persist and whether females from these groups return to their natal groups or join or even found new ones is not clear. In the Gulf of Mexico therefore we would expect to find both mixed groups which will remain in warm waters, groups of maturing males which ultimately will move into colder waters, occasional mature males joining female groups for short periods, predominantly for reproductive purposes. Results from satellite tagging (Section 4.3) and from photo-ID studies (Section 4.4) are generally consistent with this structure.

Hammond (1986) provides an accessible review of the application of some standard mark-recapture methods using photo-identification data from cetaceans. Hammond emphasises mark-recapture techniques rely on a series of assumptions, and biases can result if these are violated.

As with any assessment of population it is important to define what constitutes the population being assessed in any particular case. Sightings surveys generally provide a snapshot of animal densities over the surveyed area during the relatively short period of the survey. Mark-recapture provides an estimate of the total number of animals available to be captured within the study area between two or more sampling periods. Different components of a population may vary in their availability for capture resulting in heterogeneity of capture probabilities. It can be useful therefore to use other information on the structure of the population and the behavior of individuals in the population in determining the most appropriate analysis to apply. In this case we have used information, especially photo-ID and telemetry data from the SWSS project, to inform our mark-recapture analysis. The satellite tracking data collected as part of SWSS are particularly useful in providing independent information on the likely geographical range of the “population” being assessed using photo-identification. These data provide strong evidence for the existence of a discrete core population of mixed groups with a distribution mainly confined close to the shelf edge along the northern Gulf of Mexico. In the analysis that follows we have attempted to distinguish members of this core population to allow the size of this discrete population to be calculated.

4.7.2 Methods

Photo-ID data have been collected in the Gulf of Mexico in the course of a number of projects. Data available for this analysis are summarized in Table 4.7.1. Not all data were used for all analyses. The majority of data were collected during dedicated cruises as part of the SWSS program. As these formed the backbone for most of the analysis attempted, we describe their collection and processing in greatest detail.

Table 4.7.1

Quality of Photo-ID Data Used in Mark-Recapture Analysis
(Summary of number and proportions of image sequences based on the markedness of the flukes (MI: markedness index) and the quality of the photographs (QI: quality index), for all whales and for whales in the core population only (see Section 4.3 and 4.4 for definition of core population))

	All Whales				**"Core Population"**			
MI	**QI = 2 or better**		**QI = 1 or better**		**QI = 2 or better**		**QI = 1 or better**	
	Count	Proportion marked	Count	Proportion marked	Count	Proportion marked	Count	Proportion marked
1			25				19	
2	83		23	0.88	65		19	0.88
3	99	0.81	50	0.77	62	0.76	30	0.76
4	89	0.58	37	0.54	17	0.53	30	0.58
5	129	0.38	55	0.36	97	0.47	43	0.39
6	35		22		31		19	
Total	**435**		**212**		**272**		**160**	

Finding Sperm Whales and Survey Coverage

The locations at which images available for this analysis were taken are shown in Figure 4.7.1. Dedicated photo-ID surveys were conducted in 2003, 2004, and 2005 in a study area that extended along the mid-continental slope (500-1500 m) of the northern Gulf of Mexico between ~95°W and 87°W and southwards along the slope of the northeastern Gulf of Mexico as far south as 26° 30'N. For these dedicated surveys the area was divided into four survey blocks with the core survey blocks, in the Mississippi Canyon/Delta region, receiving most effort. Survey tracks were planned to provide good coverage in each survey block. Most effort was expended between the Mississippi and DeSoto canyons. However, a significant amount of effort was directed to the west of 95°W in the summer of 2005 during the satellite tagging (S-tag) cruise, and some images were collected in offshore waters and off Dry Tortugas by NOAA in the spring of 2001. During dedicated photo-ID surveys, predetermined survey tracks were laid out within each survey block using Distance software (Thomas 1999) to provide consistent coverage. However, as photo-ID research is much less sensitive to the requirement for equal survey coverage than methods such as line transect, alternative tracks would often be adopted to allow for contingencies such as poor weather, mechanical breakdown, and the need to make passages to harbour. On rare occasions tracks were directed towards areas for which we had information on whale presence, for example from telemetry data or from previous sightings patterns. Such survey effort was marked as being "directed" in the database. The International Fund for Animal Welfare (IFAW) "Logger" data collection program was run at all times when the vessel was collecting data.

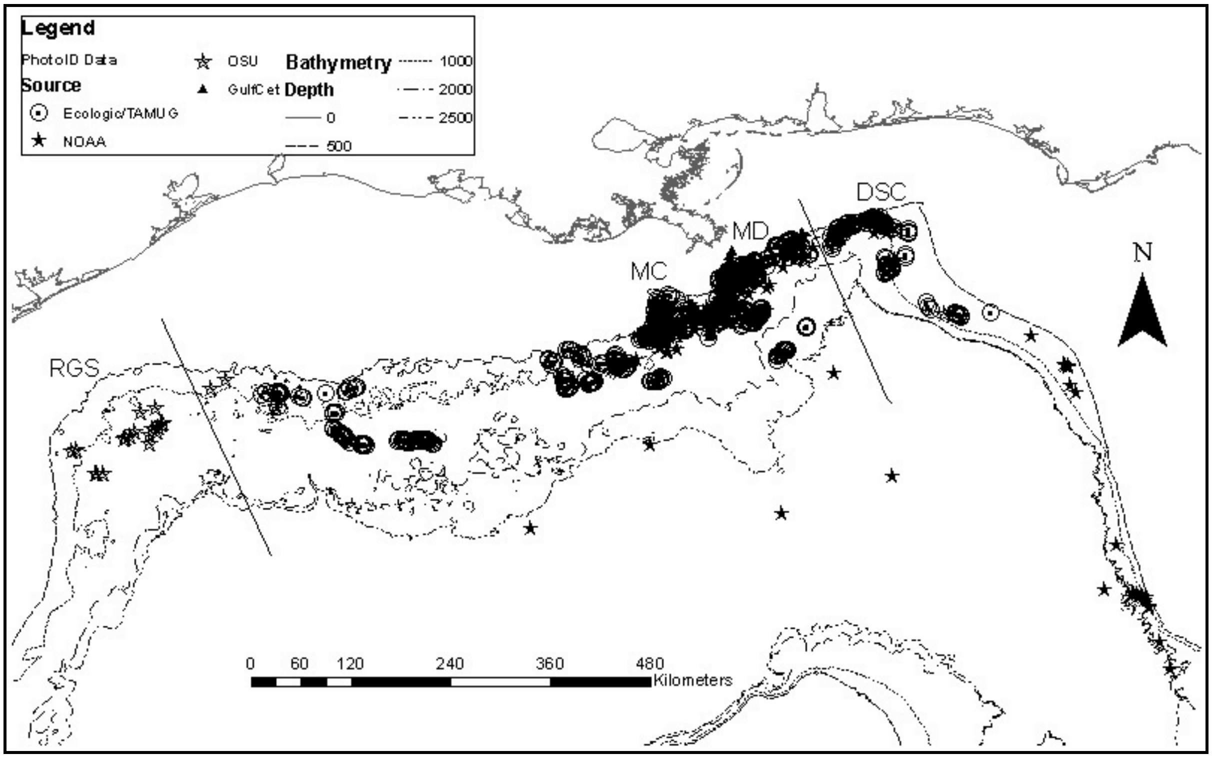

Figure 4.7.1. Location of photo-identification images taken in the northern Gulf of Mexico between 1994 and 2005 and available for this analysis. Symbol type indicates the organizations that collected the images. Locations of main study areas are indicated: RGS Rio Grande Slope, MC Mississippi Canyon, MD Mississippi River Delta, DSC DeSoto Canyon. Lines show demarcation used to determine the core area for some analyses.

Dedicated photo-ID cruises utilized two quite different types of vessels. In 2002 and 2003 the main survey vessel was the R/V *Gyre* (60-m oceanographic research vessel owned and run by Texas A&M University). On this platform teams of visual observers equipped with BigEye (25x150 mm) binoculars and stationed on the vessel's flying bridge worked in conjunction with acoustic teams monitoring towed stereo hydrophone arrays to detect and track groups of whales. Towed hydrophone systems utilized streamers, consisting of a pair of Benthos AQ4 hydrophones with Magrec HP02 wide band preamplifers separated 3 m apart within a 10-m long 4-cm diameter oil-filled polyurethane tube, which were towed on 400 m of strengthened cable. Each streamer typically included a depth sensor. On some cruises a matched pair of hydrophone streamers were towed on equal length cables off each quarter of the vessel so that the hydrophone elements formed an approximately rectangular array 400 m behind the vessel. Hydrophones were monitored consistently by acoustic monitors and standard sessions and recordings were taken every 15 minutes. When sperm whale clicks were heard the Rainbow Click[*] program was used to determine a bearing with left/right ambiguity. If a matched pair of hydrophones was deployed then Rainbow Click could be used to compare time of arrival for click trains for matching hydrophones in the left and right array to resolve the ambiguity. Alternatively, bearing ambiguities were solved by maneuvering the vessel.

Sperm whale groups were located and tracked by a combination of acoustics and visual surveillance and location. Once groups were within a few kilometers, rigid-hulled inflatable boats (RHIBs) were launched to allow sperm whales at the surface to be approached close enough for photo-ID images and other data to be collected. The RHIBs used directional hydrophones to track submerged whales and were guided to clusters of whales at the surface by visual observers on the larger vessel using VHF radio. Although the *Gyre* had a large, well equipped visual team and the vessel was quite noisy which would reduce acoustic range, detections were usually first made acoustically. Towing of the 400-m hydrophone arrays behind *Gyre*, hoewever, made rapid turningmaneuverability difficult, particularly when obstacles such as platforms and ships were in the area; in turn this made it hard to track groups overnight.

In 2004 and 2005, a 14-meter motor sailing vessel, *Summer Breeze*, was used as the sole research vessel for dedicated photo-ID cruises. This was provided with similar towed hydrophone systems, with shorter cable lengths (100-200 m) and proved a much more effective acoustic monitoring and tracking vessel. Groups were routinely tracked overnight. However it was not a good platform for long range visual searching or localization. This vessel proved to be significantly better as a platform for making careful observations and taking clear photographs than the RHIBs used from the *Gyre*.

All survey vessels ran data logging software on a computer linked to a GPS navigator. This system collected a variety of data both automatically and through user input including the locations of the vessel and of whale observations and fluke-up positions. The *Gyre* and the 46' motor sailor ran the "Logger" program on PCs while the RHIBs collected data on "hand held" HP200LX computers with a custom-written program (provided by Steve Dawson, University of Otago, New Zealand).

Of the other survey effort, the SWSS satellite tag and digital tag data and the GulfCet data were collected using a combination of a large survey vessel and RHIBs. NOAA data were collected using both this approach and an adapted shrimp trawler, *Caretta*, which was used as both the tracking and photographic platform.

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[*] Logger and Rainbow Click are programs written by Douglas Gillespie with support from the International Fund for Animal Welfare made freely available to assist projects to promote marine mammal conservation and welfare.

Collection of Images

Images of sperm whale flukes can normally be collected most effectively when the animals are foraging. In this behavioral mode sperm whales behave rather predictably making long dives of around 40-45 minutes interspersed with periods of around 8-12 minutes recovering and blowing strongly at the surface (Gordon and Steiner 1992; Watwood et al. 2006). In tropical/temperate waters sperm whales often feed in groupings that coordinate their movements but are dispersed over several miles. At the surface they are typically found alone or in small clusters swimming slowly and maintaining a steady course. Images of flukes for photo-ID can be most effectively collected by approaching such whales carefully and quietly from behind to a range of 30-50 m and keeping the vessel directly behind the whale until it raises its flukes to initiate a deep dive.

A variety of photographic equipment was used to collect the images used here. However, all the images from the dedicated photo-ID cruises were taken using Canon EOS1D digital camera and a Sigma 100-300 mm f4 lens. This camera will collect bursts of images at a rate of 8 frames per second and we found it useful to collect images through the whole of the latter part of a fluke sequence at this speed. It was rare to find that more than one image in a sequence were equally good, indicating the desirability of collecting sequences of images at this frame rate. Digital images were saved to hard drives at least once a day and image databases were maintained using a combination of the ACDSee image manipulation program and Microsoft Access. Exifer, a freeware program available at *http://www.friedemann-schmidt.com/software/exifer/*, was used to extract Exchangeable Image File (EXIF) data from images which were stored in a linked table in the image database. Images were cropped and exposure and contrast were optimized in most cases; however, unprocessed versions of the original image were also archived for reference.

In quantitative photo-ID studies it is important to assess individual whales for the type and extent of marking that they show. In effect what is being assessed is how reliably an animal can be identified again after a certain time period based on the pattern and longevity of its markings. Fortunately, the pattern and longevity marks on sperm whale flukes are well correlated (Childerhouse et al. 1996; Dufault 1998; Dufault and Whitehead 1995b). It is also important to assess the quality of each image sequence. Here what is being assessed is an image's ability to show markings of a particular type if they were present. We have adapted the scheme proposed by Arnbom (1987) to better align the types of fluke markings and photographic quality of image sequences. In the scheme used here the type and longevity of marks on flukes were summarized in a Markedness Index (MI). Flukes without any visible marks were scored as MI=0, those with slight marks as MI=1, small distinct marks as MI=2, clearly distinct marks as MI=3, major marks as MI=4, and gross marks as MI=5. Our assessment was that flukes with an MI of 2 and above might be recognized within a field season while flukes with an MI of 3 and greater would be reliably recognized between years. This reflects the fact that small fluke marks (MI = 0 to 2), such as small nicks and dents, can disappear or change shape more rapidly and frequently than larger marks, such as missing tips or large holes (MI = 3 to 5) (Dufault and Whitehead 1995b).

The image quality score (IQ) we adopted reflected the markedness index by being based on an assessment of the ability of an image to reveal particular marks if they had been present. Many factors contribute to this assessment, including intrinsic factors such as apparent size of a fluke on an image, resolution, focus, movement and blur; and extrinsic factors such as the orientation of the fluke, glare and obstruction by spray. Thus the best quality images with an IQ=0 were judged capable of showing the smallest markings (i.e., MI=0), while with an image of IQ=3, one would only be confident of identifying flukes with an MI=3 and above.

Two points are worth noting: First, IQ values *decrease* with *increasing* photo quality. Second, MI values assigned to a fluke on an image can never be smaller than the IQ score for that particular photograph. For example, it is possible to have an ID image showing a fluke with an MI=5 (e.g., a missing tip), but image quality scored as IQ=0, since the quality of the photograph would allow recognition of even the smallest marks were such marks present. On the other hand, it is not possible to score a fluke as MI=0 when the image showing this particular fluke has only an IQ=5, since such a poor quality photograph would not allow for identification of small markings.

For analyses related to population parameters it is important to use animals and photographs that allow reliable identification over at least the course of the study. Thus, only images with an IQ score of 3 or better were included in these analyses.

Images from each fluke up sequence were scored for quality and assigned an IQ score. Typically, images within a tracking period were matched by eye and assigned temporary ID numbers. The Phlex and Match programs developed as part of the Europhlukes project were then used to process and match the best image (or images) from each of these temporary IDs. Phlex extracts the contour of the trailing edge of the fluke while Match matches these to all other extracted contours in the database. These programs were written by A.G. Steenbeek using an approach similar to that described in Huele et al. (2000); see *http://homepages.cwi.nl/~adri/europhlukes/flukes/index.html*. The Match program ranks potential matches based on the value of a similarity coefficient and putative matches can be compared to the new image by eye. On the basis of this matching process new images were assigned to existing or new "individuals." A unified catalogue of individuals based on all available photo-ID data was complied and used to coordinate information collected from individuals during different encounters and in some cases by different research groups. Photo-ID images were also contributed to the North Atlantic and Mediterranean Sperm Whale Catalogue (NAMSC; *http://homepages.cwi.nl/~adri/europhlukes/flukes/index.html*), and this was searched using Phlex and Match for matches outside the Gulf of Mexico.

Data Sets Available

Given the complex and heterogeneous nature of the sperm whale populations generally and in the Gulf of Mexico in particular (discussed above), it was clear that it would be useful to apply some analyses differently to components of the population. SWSS photo-ID and telemetry data (Sections 4.3 and 4.4) suggest that there is a "core" population of animals centered on the Mississippi River Delta/Canyon, that seems to be comprised of mixed groups. Groups of maturing males are mainly found to the east and along the slope adjacent to Florida. Satellite tag data indicates that males roam more widely than females and S-tag and photo-ID data indicate that members of the core population remain within this home range across years with some individuals that were first marked during the GulfCet cruises in 1994 being seen in the same area ten years later in 2004. Whether or not an animal was a maturing male could be reliably determined in the field on the basis of the animal's size, lack of dorsal fin calluses, which are indicative of maturing females (Kasuya and Ohsumi 1966), and their more pronounced foreheads. Whether a whale was a maturing male was noted both in the field and during later analysis of images. However, there were too few reliably identified maturing males to analyze that population segment separately. We identified animals as probable members of the "core" population if they were not maturing males and were sighted west of 88°W and east of 94° 30'W.

Relatively few high quality images were available from the GulfCet cruises in 1994 and 1996 and these were excluded from the dataset for population assessment. The distribution and composition of sperm whale groups encountered in 2005 was unusual in that there were few encounters with members of the core population, and the core population members observed were not encountered in the Mississippi River Delta/Canyon region which had previously been hot spots. Instead maturing males were mainly found in these areas, including some that had been seen in the DeSoto Canyon region in other years. Thus, indications were that the whales photo-identified in 2005 were rather different than those encountered in other years. It is important to recognize that these observations may reflect natural variation in the distributions of different population segments. In 2005 the SWSS S-tag team collected photo-ID images of whales in the far west of the northern Gulf, but none of these matched existing catalogue images., The satellite tracking data from these whales (see Section 4.3) showed that only two of 12 animals ventured eastward, briefly reaching the Mississippi Canyon before returning west. Including images from a different "sub-population" would invalidate a mark-recapture analysis and for this reason images from 2005 were excluded from most analyses conducted here.

4.7.3 Mark-Recapture Population Analysis

Investigations of population size and trends were carried out using the population analysis models available in SOCPROG 2.3. SOCPROG is a suite of programs for analyzing mark-recapture data to investigate social organization, movement and population parameters written by Hal Whitehead in MATLAB and available from *http://myweb.dal.ca/hwhitehe/social.htm*. While the programs are suitable for use with many different types of mark-recapture data with a range of species it is interesting to note that Whitehead wrote them while analyzing photo-ID data from sperm whales.

SOCPROG provides five different models that use maximum-likelihood methods, conditioned on the first capture of each individual, to estimate population parameters. The Akaike Information Criterion (AIC) was used to determine which model provided the best fit to the data.

The models tested were
1. "Closed" (Schnabel) - population is assumed to be closed with no mortality, birth, immigration or emigration.
2. "Mortality" - population size remains constant with births and mortality balancing each other.
3. "Mortaltiy and Trend" - population is allowed to increase or decrease at a constant rate.
4. "Reimmigration" - In this model individuals are allowed to move out of and return to a study area which is within a much larger population. The procedure estimates the size of the local population and the total population as well as the emigration and reimmigration rates.

5. "Reimmigration and Mortality" - This model is as 4 but includes balanced mortality and births.

In mark-recapture studies the gaining of marks to make animals identifiable and permanent immigration are all equivalent to births while death, permanent emigration and the loss of marks so that an identified animal is no longer recognisable would be equivalent to mortality.

Confidence intervals were estimated using both the likelihood support function and by bootstrap with 1000 iterations. Support function plots and residual plots are also produced by the procedures.

SOCPROG can also calculate the Peterson Index for simple closed populations. To allow calculation of the Peterson Index for each season, survey effort within years with significant effort was divided into two sets. The division points were roughly halfway through each season but adjusted to avoid making a cut during a tracking period.

Assessment of Proportion of Population Marked

In photographic mark-recapture an animal is only effectively "sampled" if it is sufficiently well marked for it to be distinguishable as an individual. Thus, the population that is being assessed with a mark-recapture analysis is not the total population but that part of the population with a particular level of marking. To determine the total population size it is necessary to calculate the proportion of animals in the population with marks above this threshold. To achieve this we used only data collected during the dedicated photo-ID cruises and considered all fluke sequences taken (including those which were known to be repeat sequences from the same well marked individuals) and analyzed only images that were of sufficient quality to show the level of marks being scored. Coefficients of variation (CV) for these proportions were calculated by determining these marked proportions separately for each year of dedicated photo-ID data and weighting these by the number of sequences used in the calculation for each year (Wimmer and Whitehead 2004). Wimmer and Whitehead (2004) provide an equation (their equation 1) for calculating the 95% confidence intervals for the whole population based on the confidence intervals of the marked population and the CV for the proportion marked.

Calves

Calf production is an important population parameter that could also serve as a useful indicator of population well-being during a population monitoring scheme. Calf production in sperm whale populations is quite low. Mature females typically produce a single calf every 4-6 years (Whitehead 2003). Gestation is extended (15 months) and calves remain dependent for several years. They wean at an age of around 2 years though they may begin to take solid food after the first year of life. However, indications of milk ingestion have been found in the stomachs of sperm whales whose age was estimated to be 13 years, though suckling at this age may have more of a social than a nutritional significance (Best 1984).

Breeding and calving seasons in sperm whales typically extend over many months. However, the seasonality of breeding in sperm whales in the Gulf of Mexico is not known. No males large enough to be socially mature were encountered during field seasons in the summer months during the MPS study, though some recently born calves were observed. Calves are typically poorly marked and do not fluke up making most of them impossible to photo-identify.

One consequence of this lengthy period of dependency in combination with a lengthy but as yet unknown breeding season is that it can be far from straight forward to classify calves in the field. In this study, an animal was classed as a calf if it was obviously small and/or if it made repeated short submergences below the tail stock of an adult animal (a behavior that is characteristic of suckling behavior in sperm whales), and it did not fluke up at the end of the encounter. On some occasions animals that were initially assessed to be immature were reclassified as calves after they were seen performing bouts of apparent suckling.

We have calculated two indices of proportion of calves from the datasets collected on the dedicated photo-ID cruises. The first is a measure of the proportion of tracked groups that contained any calves; the second is the ratio between the number of adults and calves in a group. The number of adults was either based on the number of different animals identified photographically or on the estimated number based on spatial and temporal patterns of sightings and reflected in the maximum group size in the sightings record. The larger of these two values was taken as our best estimate of adult numbers reflecting that we did not always obtain photo-IDs of all adults. Our assessment of the number of calves in particular tracked groups was based on a variety of cues, including markings, body size, shape of dorsal fin, and spatial and temporal patterns of sightings.

4.7.4 Results

Proportion of Animals Marked

For any particular analysis it is necessary to determine the lowest degree of distinctiveness that is necessary to provide reliable identifications over the time period being considered. This threshold also determines the images that can be included in the dataset for that analysis, since only images of sufficient quality to show those marks can be included. Thus there is a trade off between the number of individuals that can be included because of their degree of marking and the number of image sequences that can be included: the lower the smallest accepted MI, the more animals can be included in the analysis based on their markings. At the same time, however, lowering the acceptable MI will reduce the number of available ID images, because less obvious marks (i.e., small MI values) require higher quality images (i.e., smaller IQ scores). Thus, including animals with smaller marks in an analysis may not necessarily increase sample size because acceptable image quality will need to increase, resulting in fewer sequences available for analysis.

We explored this with data collected on the dedicated photo-ID cruises. If we are willing to include flukes with small, distinct marks (MI=2), then 438 sequences with corresponding IQ scores of two or better would be available. Of these sequences, 80.2% (n=352) showed flukes with MI values of two or larger. If we wish to include only flukes with clearly distinct marks (MI=3), then 548 sequences with corresponding IQ scores of three or better would be available. Of these, 56.2% (n=308) showed flukes with MI values of three or larger. Restricting analysis to flukes with only major marks (MI=4), then 642 sequences with corresponding IQ scores of four or better would be available. Of these, 34.5% (n=222) showed flukes with MI values of four or better. As expected with this dataset, the available data increase as the MI threshold is raised, since poorer quality photographs can be included. The MI threshold should be set at the lowest level required for error free re-identification.

Table 4.7.1 summarizes the proportion of images from dedicated cruises showing different levels of fluke marking both for all whales and for whales considered to be from the core population. In general results are quite consistent. There are no substantial differences in the proportion of marked animals between the whole population and the whales encountered in the core area. The most consistent results came from the dataset that included only the clearest images with IQ scores of one and zero. These suggest that the proportion of whales in this population with MI values of two or higher is 88%, while 77% have MI values of three or higher. The standard deviation for the estimate for the proportion of flukes with MI of three or more was 0.058 with a CV of 0.075.

Figure 4.7.2 shows plots of the discovery curves (cumulative number of identified animals plotted against number of identifications made) restricted to reliably identified individuals and good quality images both for the full dataset and the "core" dataset. There is no indication of an asymptote. New individuals are continuing to be "marked" and we are some way from identifying the majority of the population.

A series of Petersen mark-recapture estimates comparing identifications made between sampling periods in the first and second halves of each research season from 2000-2005 are shown in Table 4.7.2 both for the whole population of reliably identified whales and for reliably identified individuals considered to be members of the core population. Results are highly variable. It should be noted that no attempts were made over this period to collect two repeat samples as the Peterson method requires.

Table 4.7.3 summarizes results from running the alternative models available within SOCPROG for both the core population and the whole population. In both cases the closed population models had the highest AIC score indicating this assumption was in poorest agreement with the data. They also gave the highest predicted population size; a positive bias would be expected when assumptions of closure are violated. Population predictions were reasonably consistent amongst the other models. For both the full population and the core population the "Mortality and Trend" model provided the best fit (lowest AIC value) and provided somewhat similar values for mortality and trend in both cases. Figures 4.7.3 and 4.7.4 show support functions for this model for the total and core population, respectively. Table 4.7.1 indicates that 77% of all high quality images showed reliable marks with a CV of 10.1%. Applying these values to the population sizes for the best fitting model results in mean population sizes of 281 animals (95% CI: 434-202) for the total population and 140 animals (95% CI: 200-103) for the core population.

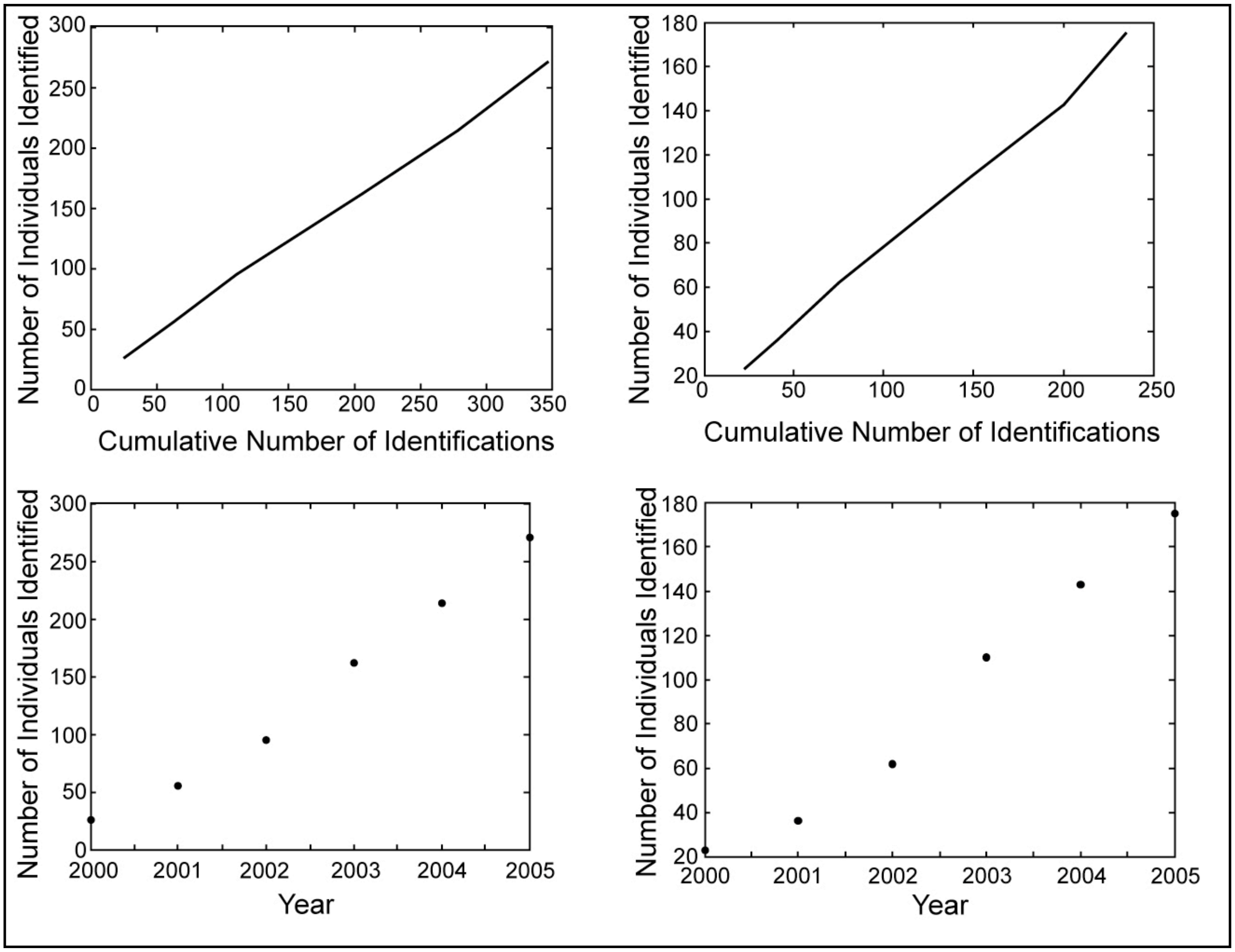

Figure 4.7.2. Discovery curves and cumulative number of identified individuals for the full and "core" sperm whale populations in the northern Gulf of Mexico.

Table 4.7.2

Summary of Petersen Closed Population Estimate for Reliably Marked Sperm Whales
(SE = Standard Error; CI = Confidence Interval)

	Whole Population		
Year	Population estimate	SE	95% CI
2000	89	43.2	17.9-150.1
2001	125	52.4	38.7-211.3
2002	95.3	22.4	58.5-132
2003	347.9	104.9	175.4-520.3
2004	136.1	23.9	96.8-175.5
2005	603.5	328.5	63.1-Inf

	Core Population		
Year	Population estimate	SE	95% CI
2000	15	7.2	3.1-26.9
2001	31	18.0	1.3-60.7
2002	23	13.1	1.4-44.6
2003	75.5	36.3	15.7-135.3
2004	68.3	27.2	23.6-113.1
2005	43	16.1	16.6-69.4

Table 4.7.3

Summary of Results from Fitting Models Within SOCPROG for the Total and Core Populations

Dataset	Model	Population Size	Mortality	Trend	Emigration/ reimmigration	AIC
Total Population 2000-2004	Closed	379 (307-478)				334.06
	Mortality	242 (159-339)	0.259 (0.813-0.574)			330.02
	Mortality and Trend	**217 (164-331)**	**0.179 (0.000-0.354)**	**0.356 (0.129-0.531)**		**324.06**
	Reimmigration	242			0.227 0.00	328.89
	Reimmigration and Mortality	243	0.136 (0.000-0.317)		0.106 (0.0-0.227) 3.83 e-014 (0-0.119)	334.02
Core Population 2000-2004	Closed	207 (179-264)				256.46
	Mortality	128 (96-184)	0.273 (0.104-0.477)			250.03
	Mortality and Trend	108 (84-152)	0.223 (0.030-0.400)	0.352 (0.123-0.576)		244.68
	Reimmigration	128 (93-163)			0.240 (0.117-0.387) 5.5 e-012 (0.0-0.0062)	252
	Reimmigration and Mortality	129 (96-183)	0.131 (0.065-0.254)		7.68 e-10 (0.0-0.226) 0.006 (0.0-0.0173)	254

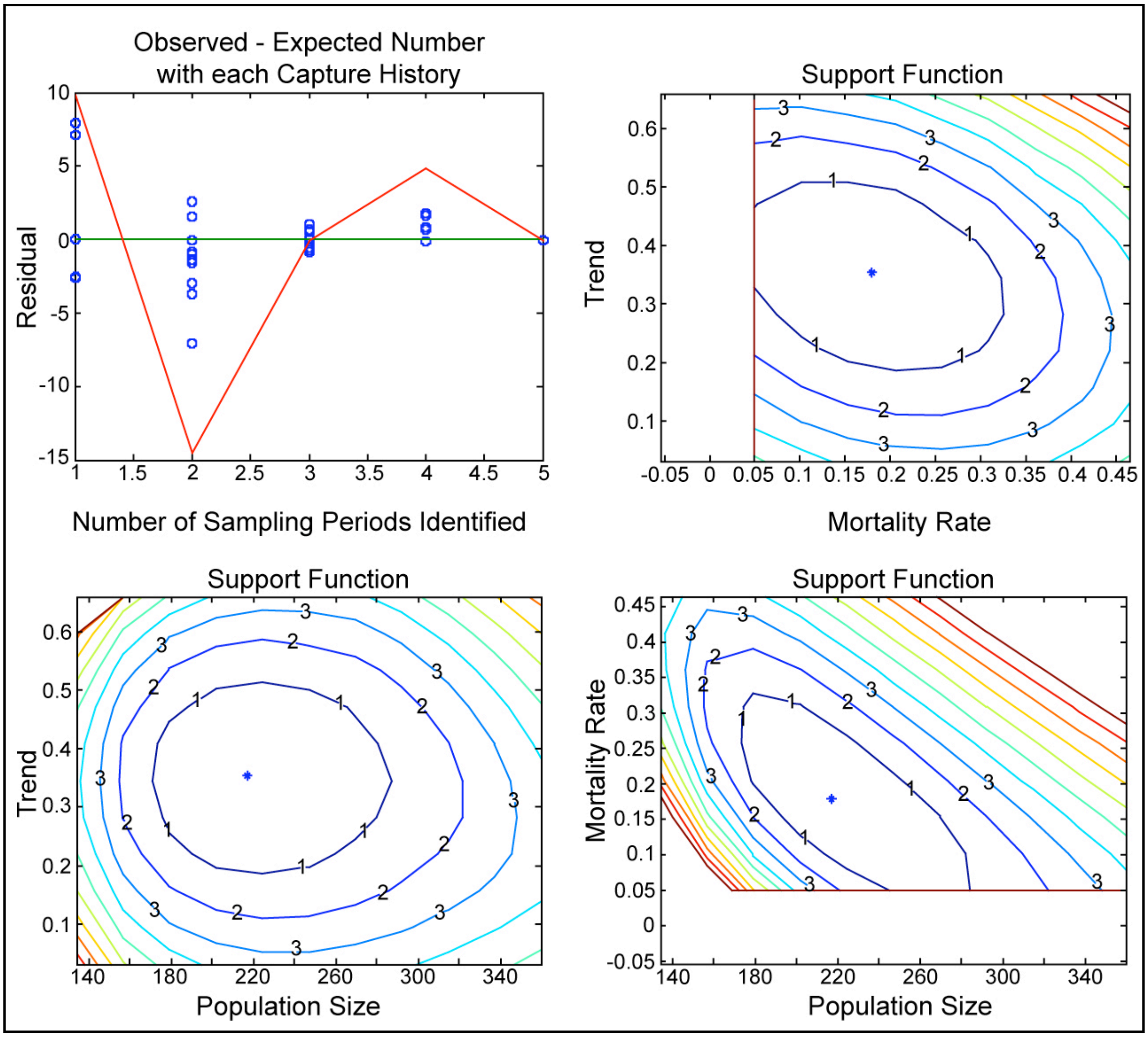

Figure 4.7.3. Residual differences between the expected and observed number of individuals plotted against the number of years and support surface contours of population size, mortality and trend for the entire dataset. Contours where the support is around two indicate the approximate boundaries of the 95% confidence region.

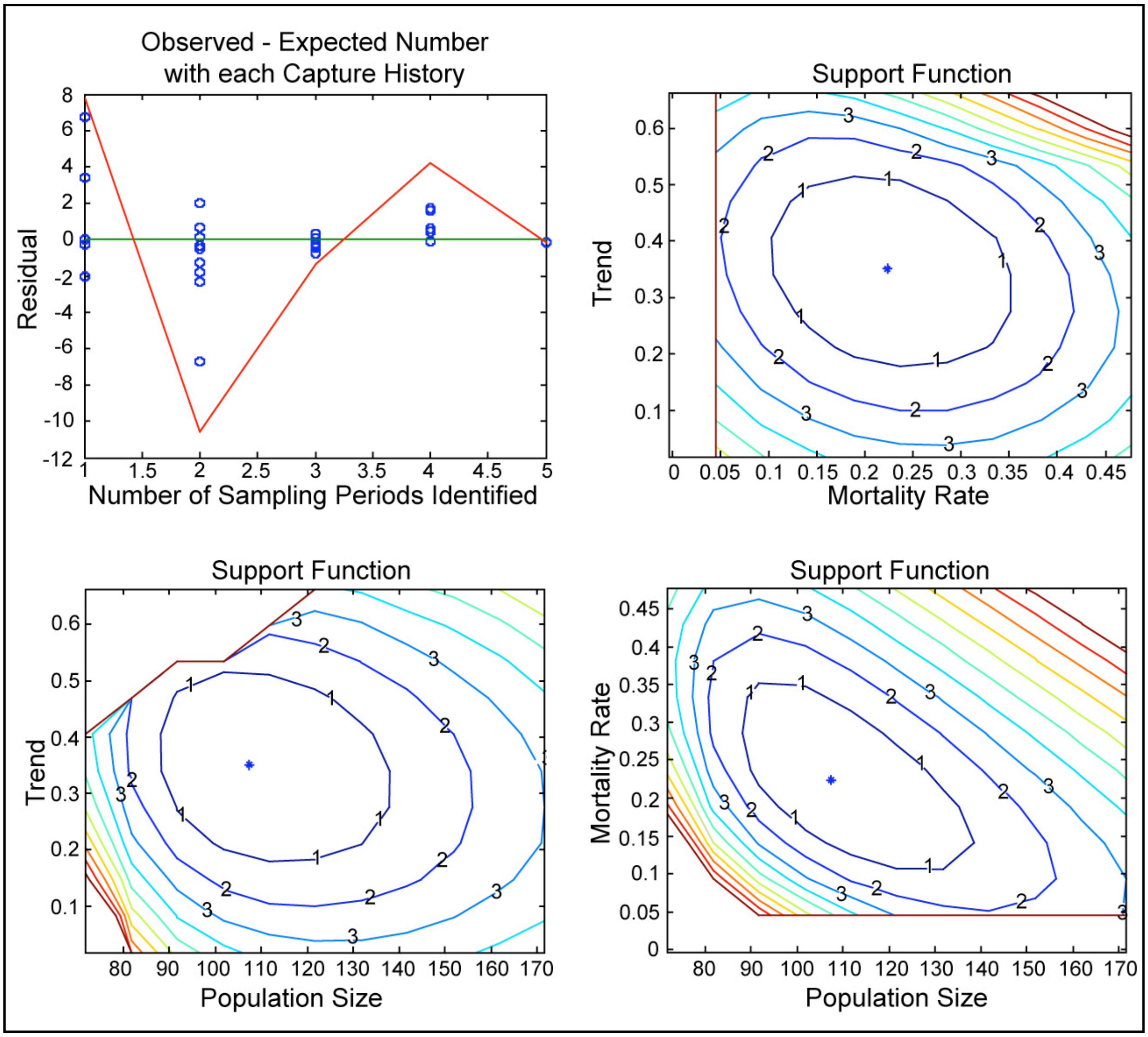

Figure 4.7.4. Residual differences between the expected and observed number of individuals plotted against the number of years and likelihood of support surface contours of population size, mortality and trend for animals considered to be part of the core population. Contours where the support is around two indicate the approximate boundaries of the 95% confidence region.

Calf Sightings

Table 4.7.4 summarizes data on calf sightings. Overall, 37% of groups (excluding medium sized male groups) tracked for extended periods contained at least one calf. Within these groups the overall proportion of adults to calves was 11%. The proportion of calves varied quite markedly between years, however the frequency of calves did not differ between years (Chi-square = 4.87, df = 3, P = 0.174).

4.7.5 Discussion

The widely differing values provided by the Peterson estimate and the poor fit of the Schnabel closed population model suggest that this population should not be treated as closed. The best fits of the open models suggest that the core population of mixed groups that have appeared to have a range focused around the Mississippi Canyon/Delta region for much of the study period number around 140 animals and the larger population, including medium size males might number around 281 animals.

Table 4.7.4

Summary of Calf Sightings by Year
(* Indicates that two calves were sighted in one of the tracking periods.)

		2002	2003	2004	2005
Tracking periods	Total number	14	17	30	18
	With calves (% of total)	4 (29)	7* (41)	14* (47)	3 (17)
	Overall % of tracking periods with calves		37%		
Number of whales	Total number of adult whales	47	36	118	70
	Number of calves (% of total)	4 (8.5)	7 (19.4)	15 (12.7)	4 (5.7)
	Overall % of calves		11.07%		

Best (1979) reviewed various sources of worldwide whaling data, including attempts to capture entire mixed groups, and these suggested that 78% of animals within mixed groups were females and that of these 75% were mature. Thus, 58% of animals in mixed groups would be expected to be mature females. If we apply this to our estimate of the "core population" and assume that these are all from mixed groups then we would expect there to be around 88 reproductively active females in the core population perhaps producing between 15 and 20 calves per year.

The best fitting population models suggests a "mortality" of around 20%. In this case mortality is the rate at which animals enter the population by becoming well enough marked to be recognised or by immigration and leave the population through emigration, death and becoming unrecognisable. In a stable population with no emigration, immigration or mark loss, mortality would indeed equal both the mortality rate and rate of survival to average age of becoming marked. Given the assumptions on population composition above and assuming a calving production of one every 4-6 years we would expect a calving rate as a proportion of total number of adults of between 10 and 15%, somewhat lower than the 20% mortality suggested by the model.

A positive population trend of some 35% is also indicated by the model. This is much too high to represent real population production. It is possible that animals are moving into the area increasing the local population density but a more likely explanation is that this is related to an expanding survey effort by a small team operating over a very extensive area. The fairly consistent population size estimates provided by the different models suggest an extended population of around 300 animals and a core population of some 150 or so. This is somewhat lower than the estimates provided by Mullin and Fulling (2004) for slope waters of the entire northern Gulf of 657 animals. However, their survey covered a wider area and the current population estimate, which excludes maturing males, is within Mullin and Fulling's 95% confidence limits.

Given the low level of photo-ID effort so far expended over a very large area these results should be treated as preliminary. However, these data do indicate that techniques based on mark-recapture will prove to be effective in assessing and monitoring the sperm whale population in this area. The indications from both photo-ID and telemetry are that this is a highly structured population and quite dynamic. The additional data that photo-ID provides allied with an ability to use models that reflect the population structure allows a better assessment of population size and population dynamics.

Approximately 1/3 of the tracked groups contained at least one calf. Group size varied, however, and in order to obtain an estimate of calf production, the ratio between adults and calves is more appropriate to consider. Whitehead et al. (1997) summarize ratios of calves to females and immature whales reported by studies using similar methods to the one used in this paper. Values were lowest for the Pacific (0.0037 for the Galapagos and 0.019 for mainland Ecuador). In the Indian Ocean values were higher, being 0.089 in the Seychelles (Kahn et al. 1993) and 0.126 in Sri Lanka (Gordon 1987b). Whitehead et al. (1997) speculated that the low reproductive rates in the Pacific could be an effect of recent intensive whaling reducing the number of breeding males in that population. The expected ratios based on population parameters in the International Whaling Commission (IWC) sperm whale model were 0.098 – 0.11 (Whitehead et al. 1997).

The overall ratio of 0.11 observed in the Gulf of Mexico is comparable to the non-Pacific field observations and values predicted by the IWC sperm whale model and is much higher than observations from the intensively exploited Pacific Ocean. This suggests that calf production in the Gulf population is in line with expectations for a healthy population.

One caveat that should be born in mind is that this assumes that all the animals that we classified as calves were indeed first year animals. If animals over one year of age are included in our "calf" category, which is likely given our behavioral and size-based categorization, then the proportion of calves would be lower than 0.11, and consequently lower than expected for a healthy population. Of course, this fact has also be kept in mind when comparing our results with those from other areas where only first-year calves are included.

Calving rate is a useful parameter to assess in any population monitoring program because it should provide an early warning of reduced reproductive rate which is certainly biologically significant enough to be of conservation concern. This work shows that such data can be collected with the appropriate techniques and temporal effort, and suggests that the observed calf proportion is in line with expectations, given the above caveat. However, it also highlights that data on calves are difficult to collect reliably. Assessment of number of calves and the number of year groups classified as calves could be improved by an increased effort to obtain short term identifications of calves (for example, see Gero and Whitehead 2007) and to measure their body lengths during all encounters that could then be used in conjunction with a model of seasonal reproduction.

4.8 Analysis of Codas from the Gulf of Mexico and Implications for Management

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4.8.1 Introduction

Sperm whale coda vocalizations consist of bursts of 3-20 broadband clicks, produced in stereotyped patterns. Each coda typically lasts for less than 3 seconds and they are often produced in repeated sequences. Codas were first described by Watkins and Schevill (1977), who reported that they often occurred at the end of sequences of regular clicks, hence their name. Most extended sequences of codas though are heard from members of mixed groups as they interact or "socialize" in large clusters at the surface. A typical pattern, reported from many regions, including the Gulf of Mexico, is for mixed groups to cease foraging and form large "socializing" clusters for an hour or so about once a day. An analysis of codas recorded in the Gulf of Mexico during GulfCet cruises between 1991 and 1997 identified 17 different types of codas and found no evidence of changes within coda types over this period (Apple 2002). Codas are thought to function as communication signals, and there is a rich field of fascinating research relating to the way in which sperm whales use codas to communicate. Here though, we focus on the important information that analysis of codas can provide for management and the insights this provides into population structure.

Within the Pacific Ocean, Weilgart and Whitehead (1997) found evidence of both group specific dialects and geographical variation in coda repertoires. Whitehead et al. (1998) showed that variation in coda repertoire was also correlated with differences in mtDNA suggesting that codas might be learned within matrilines. More recently, Rendell and Whitehead (2003b) have found that sperm whale social groups can themselves be organized into larger units called clans on the basis of their coda repertoires. Members of clans preferentially associate with groups in the same clan even though the spatial ranges of clans often overlap. It is clear that codas are learned behaviors, thus the existence of clans has been taken as evidence of culturally based organization in sperm whales. [Note: Here we use the word "culture" in the most straight forward sense, *sensu* Rendell and Whitehead (2001), namely "information or behavior – shared by a population or sub-population – which is acquired from conspecifics through some form of social learning".] Other types of behaviors, which may significantly affect the fitness of individuals, also seem to vary between clans. For example, Whitehead and Rendell (2004) showed that two clans encountered in the Galapagos appeared to differ in their foraging behavior and in the way that they adapted their foraging behavior to an El Niño event, while Marcoux et al. (2007) have found evidence of fitness differences between members of different clans. Thus, members of clans may vary in many ways that may be of greater biological significance than differences in vocal behavior. However, analysis of coda repertoires remains the most effective way of determining clan membership and structure. The significance of clans from the perspective of management may go far beyond the fact that they make similar vocalizations.

The realization that biological diversity within a species may be an important component of its evolutionary potential has led to an understanding that it is important to conserve population units at a lower level than that of the sub-species. The appropriate unit is often called the Evolutionary Significant Unit or ESU. However, there is, as yet, little consensus on a definition for an ESU. Fundamentally, it should be a subset of individuals which, if they were to be depleted, would result in the loss of a significant part of the species' overall biological diversity and evolutionary legacy. In most cases, biodiversity is thought of in terms of genetics and this is reflected in most definitions of ESU. For example, Waples (1995) suggested that it is a population or group of populations that is (a) substantially reproductively isolated and (b) represents an important component of the evolutionary legacy of the species. However, long-lived species with a complex social organization and overlapping generations may carry and pass on culturally some of their evolutionary legacy and information, which is important for the survival and wellbeing of individuals. For these species, cultural as well as genetic subdivisions may define ESUs. Weilgart et al. (1996) and Whitehead and Weilgart (2000) have drawn attention to the similarities in life history and social organization between sperm whales and elephants. They present sperm whales as extreme k selected animals living in an environment that is subject to large annual and decadal fluctuations. They suggest that information on how to best respond to particular rarely encountered situations (major oceanographic changes such as El Niño for example) may be held within social groups in the memories of older individuals and transferred culturally between generations within social units such as clans. In such a situation, maintaining diversity of knowledge and learned behavior should become an important goal for conservation. In the case of sperm whales it may then be argued that conservation management should be considered at the level of the clan, as a likely repository of biologically significant knowledge. As we have seen, clans can be most readily distinguished through analysis of coda repertories. The argument here is not that conserving codas is important per se but rather that codas are indicators of a level of diversity of other learned behaviors which are likely to have survival significance. These may also include a collective experience and learned responses to anthropogenic activities such as seismic surveys and other offshore activities.

Managers will usually have more immediate concerns in addition to those of conserving biological diversity. Often animals will be managed as "populations" but population structure is a broad and often poorly defined concept. In essence it is a description of differential association between a collection of individuals but the temporal and spatial scales over which this association occurs, and the nature of the association, for example whether it involves breeding or simply being in the same area, can vary from example to example. From a management perspective, animals should be considered in separate populations if management is improved by applying different management rules to each population group. Thus, the levels and scales at which populations should be defined should be determined by the management questions that need to be addressed. Animals that differentially associate to breed may, over many generations, develop genetic differences from other groups that can be measured as differences in genetic material (DNA), in proteins, or in morphological traits. In animals with long generation times, such as whales, such differences may take thousands of years to develop. Populations defined on this scale are relevant to management concerns relating to loss of genetic diversity (see above) and the extinction or recovery of populations over time periods of centuries. Typically, however, management concerns and goals are orders of magnitude more immediate than this. Thus, even in cases where no significant genetic differences are evident between them, it may be appropriate to manage groups as independent units. For example, western North Atlantic humpback whales share a common breeding ground in the Caribbean but sub-groups of the population are faithful to particular feeding grounds, which they come to know through following their mothers on migration as calves. In this case, management in feeding areas should be based on feeding populations not the larger breeding population indicated by genetics. Conversely, genetically distinct populations may share common feeding grounds where they may compete for food or be vulnerable to the same human impacts.

The conservation implications of cultural learning and organization in non-humans are discussed in a recent paper (Whitehead et al. 2004) that draws most of its examples from cetaceans. The authors point out that the existence and nature of cultural organization can affect the way in which animals learn to adapt to, or to exploit, human activities. Where culture is horizontally structured newly learned traits can spread quickly through a population. Where cultural organization is vertical or oblique, i.e., across generations (as is the case in sperm whales), different cultural units may develop different strategies to new situations. Because it can tend to favor conformity, culture can also lead to the persistence of maladaptive behavior in a population.

Whitehead and Mesnick (2003) presented a comprehensive review of methods for determining population structure and movements in sperm whales. They considered the strengths and shortcomings of a number of methods including telemetry, photo-identification, various types of genetic analysis, contaminants, morphology, trace analysis and others. They emphasized that many of the methods were complimentary; each gave a different perspective on population structure often providing information at very different temporal scales. Telemetry can provide information at the most immediate scales of hours to months. Photo-identification can best provide data at scales of years, while genetic analysis gives information on population structure at temporal scales of 100s to millions of years. Analysis of coda repertoires provided information at the temporal level of generations (decades) and was the only characteristic that reliably showed geographical variation in sperm whales at spatial scales of less than an ocean basin (~5,000 km). In many cases, these will be the scales at which many sperm whale management issues in the Gulf of Mexico will need to be addressed.

4.8.2 Methods

Data for this study have come both from cruises in the Gulf of Mexico as part of SWSS and SWAMP and from recordings made during cruises in the Azores and the Caribbean (collected by IFAW and Luke Rendell).

Coda Recordings and Acoustic Analysis: Most recordings were made close to socializing groups of sperm whales, and in most cases we had information from photo-id on the time and location at which particular individual whales had been photographically identified within a day or so of the recording. Field recordings were made on a variety of media including analogue tape, DAT digital tape and directly to computer hard drives. Usually recordings were made using stereo towed hydrophones with 3-m separation between elements. Recording systems had a fairly flat response between 0.1 and 15 kHz. In the analysis applied here we are only concerned with the relative time of individual clicks within codas, and for this, slight differences in the sensitivity and bandwidth of the recordings systems are not relevant.

Analogue field recordings were digitized at 48 kHz and stored as wav files while DAT tape recordings were transferred directly to computer sound files. These files and files recorded directly to hard disks in the field then were edited into a series of shorter files of more manageable size (< 2 mins) containing coda sequences. A personal computer and appropriate software, usually Cool Edit (Syntrillium Software), was used for editing.

Codas within these files were characterized using the computer program Rainbow Click (Gillespie and Leaper 1996). Rainbow Click identifies transient “click like” sounds and displays these on a time-bearing display. With user supervision, clicks produced by particular individuals were labeled on the basis of their bearing, their spectral content and how they “sounded” when played back at full or reduced speed. Sequences of clicks that made up a single coda were identified and linked. At this stage of the analysis the clicks within all of the codas for a recording had been allocated to individual whales where possible and been assigned a coda number. Rainbow Click’s Export function was then used to export the time and identity of all clicks for all codas within the file for further analysis.

Photo-identified whales were assigned to groups based on rules used in previous studies (Weilgart and Whitehead 1997; Rendell and Whitehead 2003a). Group repertoires were compared between all groups from which more than 25 codas were recorded and analyzed.

Methods for comparing repertoires followed the techniques described by Rendell and Whitehead (2003a) using code written in Matlab. Readers are referred to that paper for methodological details.

Entire repertories of codas recorded from the groups identified using photo-id were compared using an average multivariate similarity method that compared sets of codas based on the infinity-norm distance between two coda vectors:

$$s_{\mathrm{AB}} = \frac{\displaystyle\sum_{i=1}^{n_{\mathrm{A}}} \sum_{\substack{j=1 \\ l_j = l_i}}^{n_{\mathrm{B}}} \frac{0.001}{0.001 + d_{ij}}}{n_{\mathrm{A}}.n_{\mathrm{B}}},$$

where S_{AB} denotes the similarity between coda sets A and B, l_i is the number of clicks in coda i of set A, l_j is the number of clicks in coda j of set B, and d_{ij} is the maximum absolute distance between the vectors containing the standardized inter-click intervals of the codas. Codas having different numbers of clicks were assumed to have no similarity.

Repertoire similarity scores were displayed using dendrograms with a boot-strap analysis being performed to calculate the level of support for different branch structures.

4.8.3 Results and Discussion

Repertoire Similarities between groups in the Gulf of Mexico: A total of 8405 codas recorded from 21 different photo-identified groups in the Gulf of Mexico were extracted and measured. The similarity indices between the repertoires of these groups are displayed as a dendrogram in Figure 4.8.1. Most comparisons between groups gave similarity values close to the mean *within* clan similarity reported from the Pacific, which is a region for which there are published data (Rendell and Whitehead 2003b). However, two groups stand out as being different. The first (code 22) represents a repertoire recorded from a group encountered in 2005 which was noted as being made up entirely as maturing males. This group made a repertoire that clearly separates well from the rest of the groups, with a high bootstrap confidence on the dendrogram branch that excludes it. The second group (code 104) represents recordings made in the western Gulf of Mexico in 2005. Although group 104 does not separate as strongly as group 22, it is still rather dissimilar from the other groups, indicating that there may be further repertoire diversity in that geographic region.

Two other groups (codes 19 and 23) cluster out with low similarity to the rest; these were groups recorded on 20 July 2004 and 25 July 2005, respectively. The high bootstrap support for their paired branch indicates a robust separation. Finally, group code 2 (1 July 2002) also separates out from the main cluster with 61% support for its separation. After this branch, bootstraps became highly variable, and the regular, closely spaced branching of the dendrogram indicates little variation at this level.

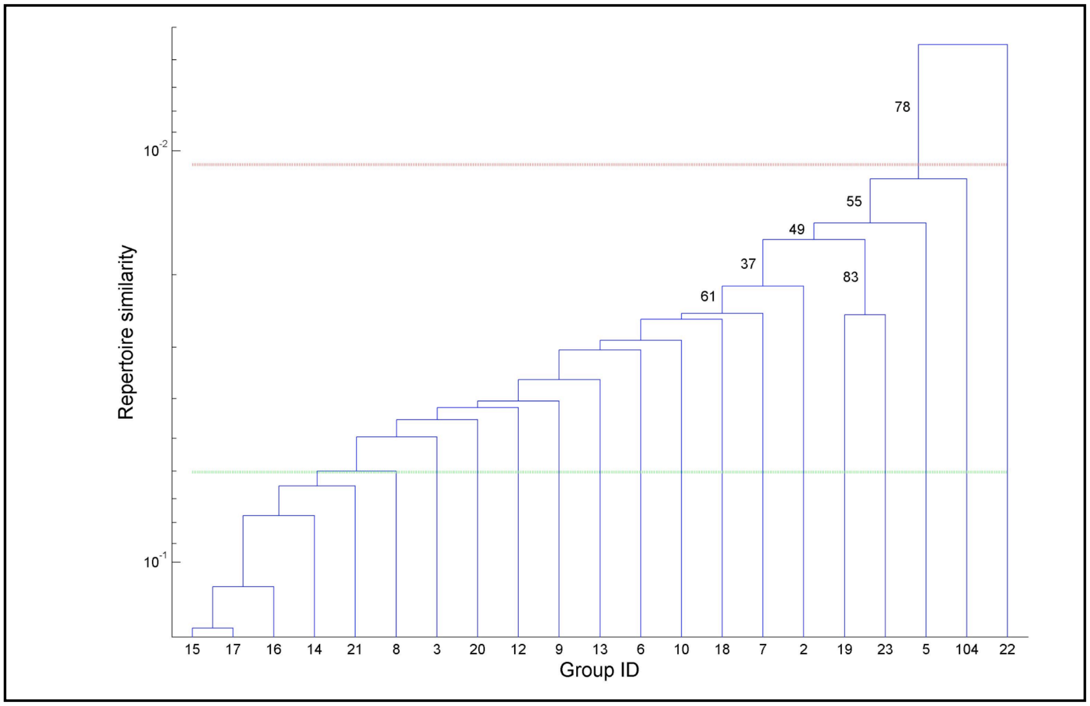

Figure 4.8.1. Repertoire similarities between groups from which at least 25 codas were recorded in the Gulf of Mexico. Red line shows the value of the average *between* clan similarity in the Pacific, green shows average *within* clan similarity. Numbers next to branches represent the number of times that that branch was reproduced in 100 bootstrap samples.

Comparison of Gulf of Mexico repertoires and those from groups from the Azores and Caribbean: The repertoires of the groups recorded in the Gulf of Mexico, described in the earlier section, were compared with repertoires recorded from groups encountered in other parts of the wider North Atlantic, specifically the Caribbean Sea, Windward Islands and Azores archipelago. This dataset consisted of 1459 codas from 13 groups (Azores 10 groups; Caribbean, 2 groups; Windward Islands, 1 group). Not all groups were photo-identified, but recordings were generally separated by extended time periods so it is likely that they represent different groups.

A dendrogram of similarity indices for group repertories is shown in Figure 4.8.2. In this figure, 200 has been added to the codes from Figure 4.8.1, so that codes greater than 200 represent Gulf of Mexico groups (e.g., 201 represents Gulf of Mexico group 1 in Figure 4.8.1, 202 is group 2, and so on). Group codes less than 100 represent recordings from the Azores, and group codes between 100 and 200 represent groups recorded in the Caribbean Sea (103, 104) and Windward Islands (101).

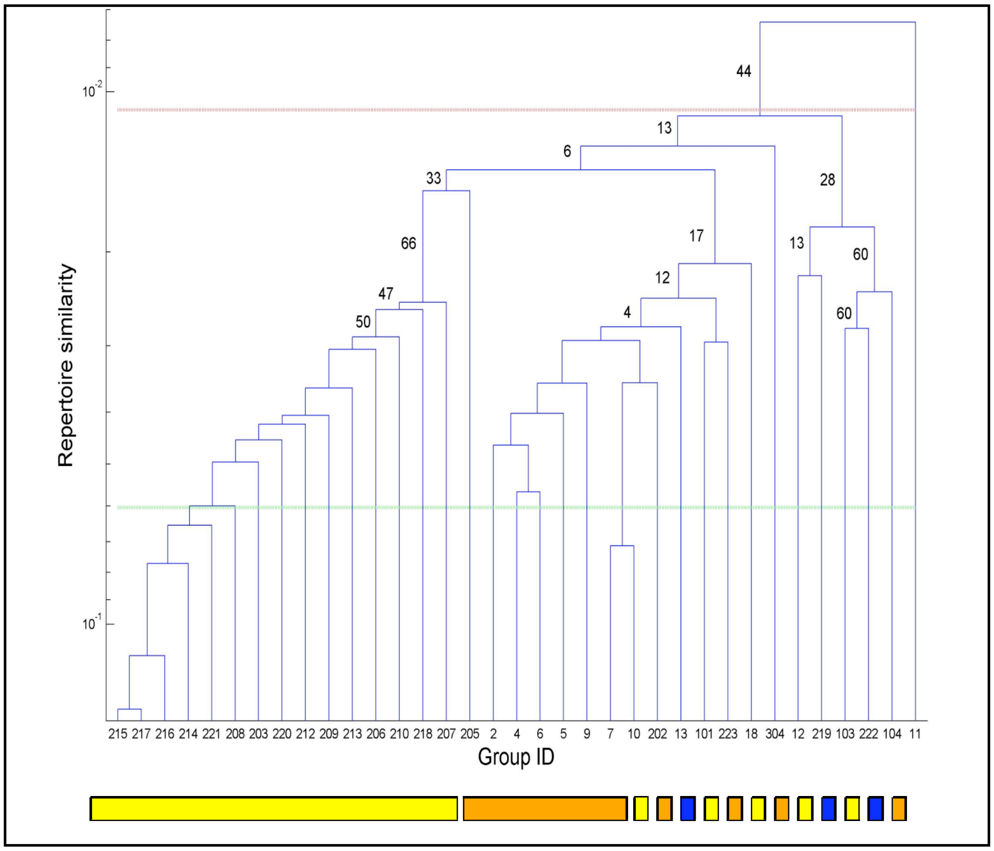

Figure 4.8.2. Repertoire similarities between groups recorded in the Gulf of Mexico (yellow), Azores (orange) and the wider Caribbean (blue). Red line shows the value of the average *between* clan similarity and green shows average *within* clan similarity in the Pacific. Numbers next to branches represent the number of times that branch was reproduced in 100 bootstrap samples.

Most of the Gulf of Mexico groups cluster out together on the left of the dendrogram in Figure 4.8.2. This grouping, with 66% bootstrap support, is virtually identical to the main branch in the dendrogram in Figure 4.8.1 that received 61% support. This appears to be a distinctive grouping similar in discreteness to the clans identified in the Pacific. Those groups highlighted in the first analysis as being distinctive from the main Gulf of Mexico cluster, now separate out variously with groups from the Azores and Caribbean. However, low bootstrap support for branches in this cluster indicates that the clustering in Figure 4.8.2 might not be very robust; in particular, group code 205, which clustered out in the previous analysis, here clusters with the main Gulf of Mexico grouping but at a much lower similarity level. It is likely that in bootstrap resampling this group is switching between this and the primarily Azores cluster to its right. The group code 304 (the same as code 104 in Figure 4.8.1), the only group recorded from the western Gulf, does not cluster convincingly with any of the other groupings here, suggesting a rather unique repertoire meriting further investigation. It is also interesting to note that the group highlighted as immature males (22 in Figure 4.8.1, 222 in Figure 4.8.2) clusters, with good bootstrap support, with two groups recorded in the wider Caribbean Sea just south of the Gulf of Mexico. Codes 103 and 104 represent groups recorded off the north-west coast of Cuba and in the waters north of Panama, previously reported in Rendell and Whitehead (2003b).

We have explored the characteristics of some of the specific coda types which contribute most to the differences in repertoires using plots summarizing inter click intervals (ICIs) for codas with specific numbers of clicks. Figure 4.8.3 summarizes data on standardized interclick intervals for codas with between 3 and 10 clicks. In each plot, Gulf of Mexico codas are plotted in black and those from the wider Atlantic are red.

The first panel in Figure 4.8.3 is a histogram of the first standardized ICI for three click codas. This shows that Gulf of Mexico groups made large numbers of 3 click codas, in contrast to groups from other areas. The first ICI is also relatively long in the Gulf of Mexico codas compared to those from the wider Atlantic. This preponderance of three click codas is one factor driving the differences in repertoire similarity indices, as similarities between codas of different click number are scored as zero. From analyses for codas with greater number of clicks, it is clear that there are also distinctive clusters of Gulf of Mexico codas in the plots for 4 click, 7 click and 8 click codas. These represent characteristic coda types produced almost exclusively by Gulf of Mexico groups and they are described below.

The first and second ICIs for four click codas are plotted against each other in Figure 4.8.4. This shows a distinct cluster in the Gulf of Mexico data representing a coda type with a much reduced first ICI; this could be described as a ‘2+’ coda, in this case a ‘2+2’ type (following the nomenclature of Weilgart and Whitehead 1997). This contrasts with the codas made by groups outside the Gulf (red crosses) that were nearly all of the ‘regular’ type, containing four regularly spaced clicks.

Figure 4.8.5 shows a plot of the first two principal components for ICIs from 7 click codas. Again, a coda type made almost exclusively by Gulf groups can be identified, in this case characterized by an extended first click interval; these may be described as ‘1+’ codas, in this case the ‘1+6’ type. Both Gulf and non-Gulf groups make the ‘7-regular’ type highlighted in the centre of the plot. There is also a cluster of red crosses in the top left of the plot indicating a type made outside the Gulf but not in it.

Figure 4.8.6 is a plot of the first two principal components for 8 click codas. In this case the coda type made almost exclusively by the Gulf groups is complex, containing a much reduced *second* click interval, producing a pattern that might be characterized as ‘1+2+5’. Again, groups from the Gulf and from the wider Atlantic made some of the ‘8-regular’ type highlighted in the centre of the plot. There is another type shown to the right by a cluster of red crossed made predominantly in the wider Atlantic but not the Gulf.

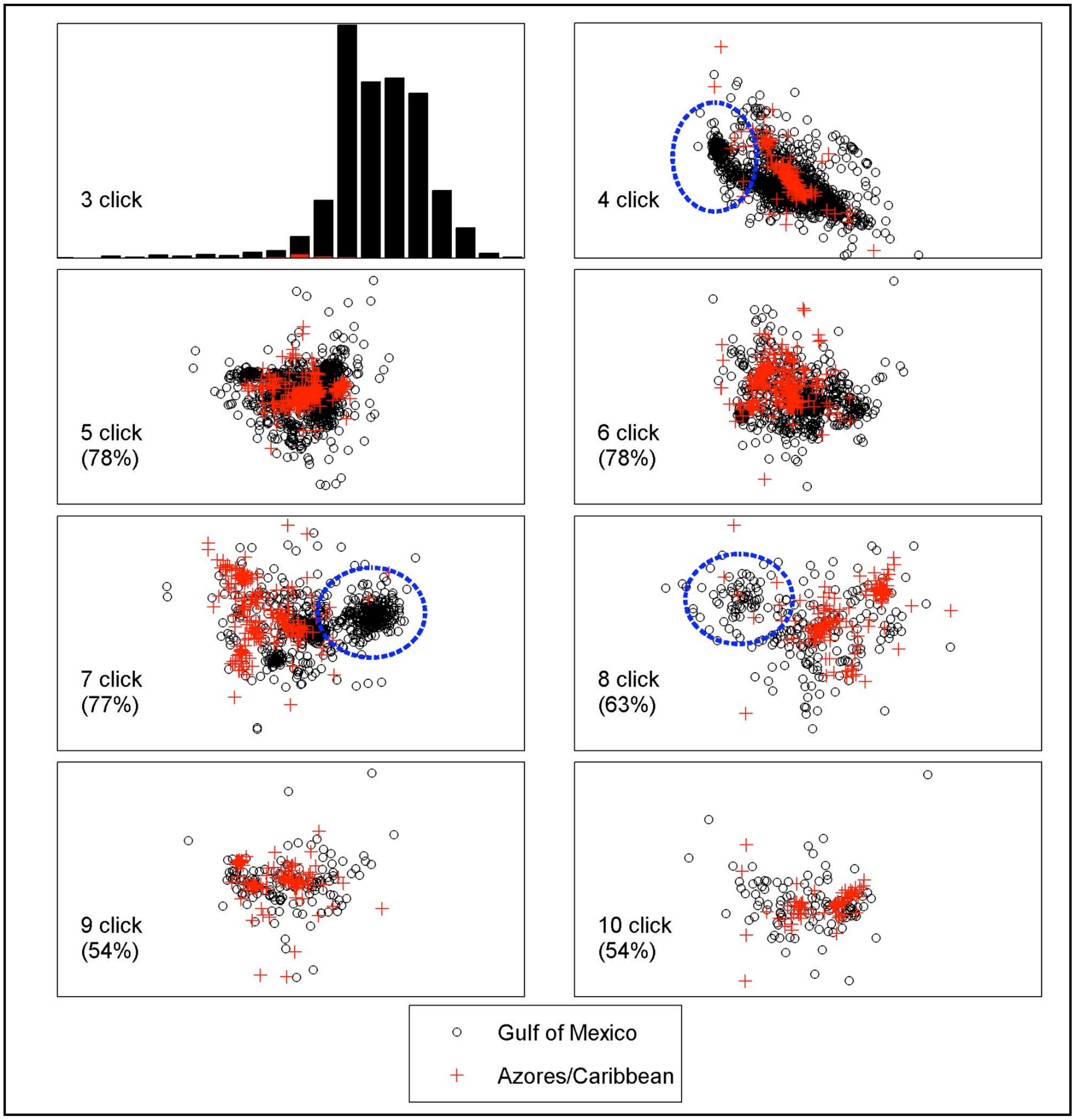

Figure 4.8.3. Characteristics of codas recorded in the Gulf of Mexico and other Atlantic areas. Three click codas are represented by a histogram of the first standardized inter-click interval, 4 click codas by a plot of the first and second intervals, and other coda lengths by the first two components of a principal components analysis of the standardized ICI values (number in brackets are the percent variance explained by these first two components). Blue dashed circles highlight clusters representing coda types produced almost exclusively by Gulf of Mexico groups.

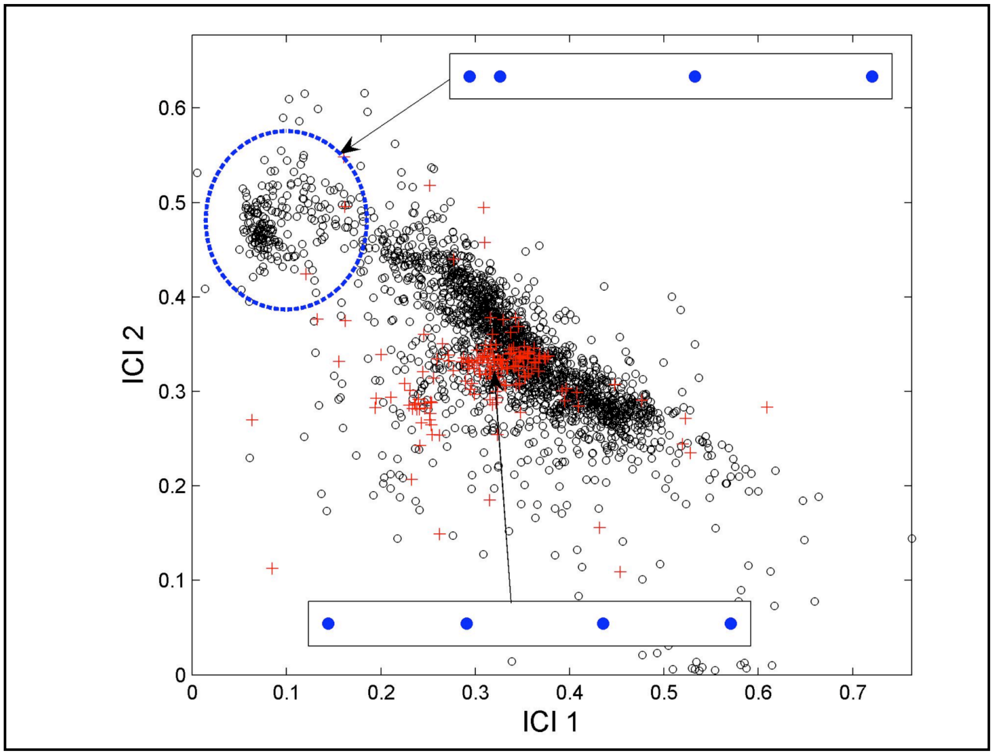

Figure 4.8.4. First and second standardized ICI from 4 click codas (same data as 4 click panel above). Blue ellipse highlights a coda type made nearly exclusively by Gulf groups, shown by the upper blue dots. Lower blue dots show a coda pattern typical of the non-Gulf groups.

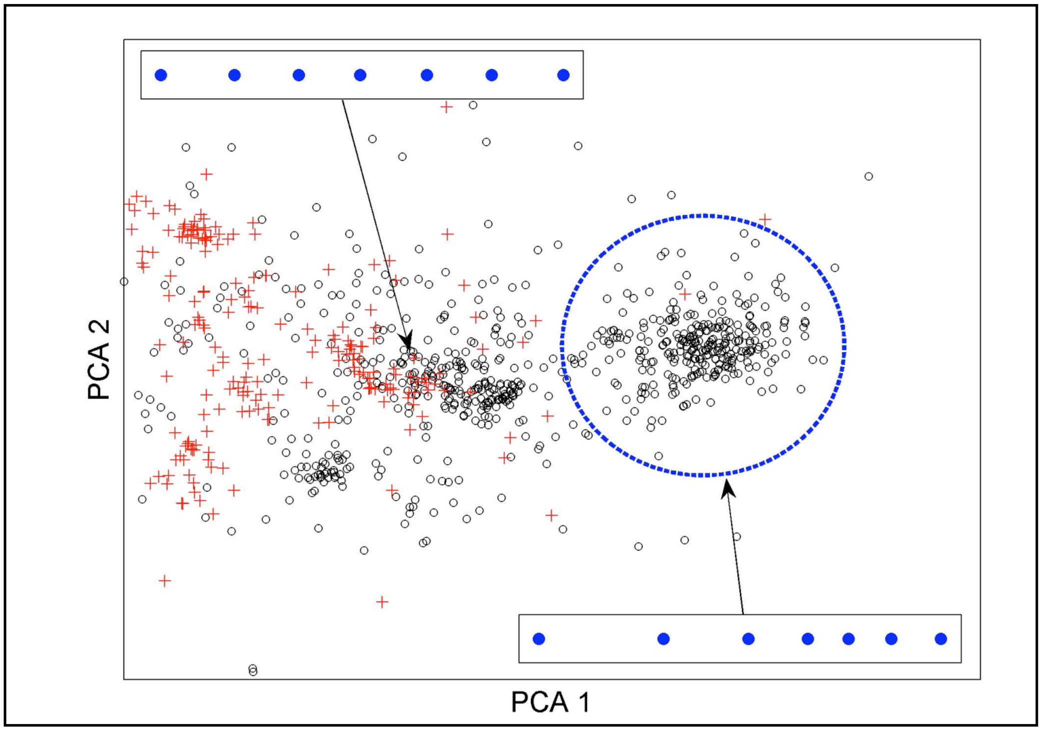

Figure 4.8.5. Seven click codas represented by their first two principal components. The blue ellipse highlights a coda type made almost exclusively by Gulf of Mexico groups.

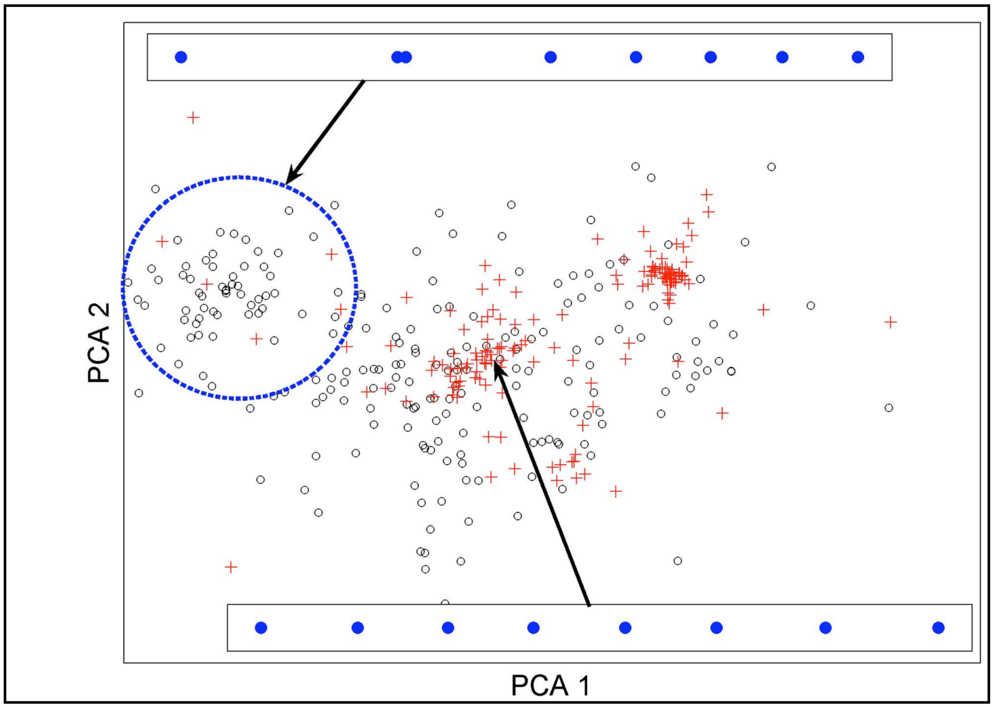

Figure 4.8.6. Eight click codas represented by their first two principal components. The blue ellipse highlights a coda type made almost exclusively by Gulf of Mexico groups.

4.8.4 Conclusions

The vocal repertories of most groups recorded in the Gulf of Mexico form a single coherent cluster. These groups could be described as members of a distinct 'clan', characterized by the production of '2+2', '1+6' and '1+2+5' coda types (as well as several coda types also heard elsewhere). However, some repertoires from Gulf of Mexico groups did not fall into this cluster. Of these, some appeared to cluster with repertories from groups recorded in the Azores; this may suggest a widely distributed North Atlantic clan (similar perhaps to the 'short' clan in the South Pacific that had a distribution from South America to New Zealand (Rendell and Whitehead 2003b)) whose members are occasionally encountered in the Gulf of Mexico. One repertoire (304) did not cluster reliably with any others. This was extracted from the only recordings analyzed from the western Gulf of Mexico. This finding is intriguing. It suggests that there may be further vocal (and thus cultural) diversity to be investigated in the western region of the Gulf (an area from which very few recordings have been collected so far). If this distinction is supported by additional data, it may indicate a degree of segregation between groups from the western and eastern portions of the Northern Gulf of Mexico. Results from satellite telemetry and from photo-identification also suggest movement between the western Gulf of Mexico and the rest of the northern Gulf is limited for at least some animals.

Another repertoire from the Gulf of Mexico that was distinctive (222) was collected from a group made up entirely of maturing males. This repertoire was similar to those from groups recorded in the wider Caribbean south of the Gulf of Mexico. It is interesting to note that data from satellite tracking of sperm whales in the Gulf of Mexico also indicates that males range far more widely than female members of mixed groups (Section 4.3).

The existence of a distinct Northern Gulf of Mexico coda repertoire suggests a discrete population that is behaviorally distinct from that of the north Atlantic, at least in terms of vocal behavior, but likely also in other behavioral characteristics, given the observations made in the Pacific (Whitehead and Rendell 2004). Members of these units may therefore share other biologically significant behavioral traits which are important for their survival, as well as a unique, culturally inherited knowledge of the Gulf of Mexico habitat. They may also have a shared experience of anthropogenic activities, which may be different to that of whales from other clans.

These results, though still preliminary, agree well with those provided by many other lines of evidence from the SWSS project (e.g. photo-id, telemetry, genetics and body length comparisons). All of them indicate that the Northern Gulf of Mexico sperm whale population is reasonably discrete and should be managed as a unique stock. In addition, the suggestion that whales from the western Gulf may be segregated to some extent could have important management implications as offshore activities in this region increase. Further research is needed to elucidate this.

5 HABITAT USE IN THE SWSS STUDY AREA

5.1 Synopsis of Habitat Use in the SWSS Study Area

The SWSS habitat characterization effort merged biological oceanography, physical oceanography, and remote sensing data to provide an interdisciplinary description of the oceanographic habitat in which sperm whales are encountered. Correlations between oceanographic surface conditions and the locations of whale encounters during survey cruises were reviewed by Biggs et al. (2005) for SWAMP fieldwork in summers 2000 and 2001 and for the first two summers 2002 and 2003 of SWSS fieldwork. In that review, we concluded that summer-to-summer variability in the intensity and geographic location of Loop Current eddies, warm slope eddies, and areas of cyclonic circulation over the middle slope region of the northern Gulf forced striking year-to-year differences in the locations along the 1000-m isobath where there was on-margin and off-margin flow, and in locations where sperm whales were encountered along the 1000-m isobath. We showed that most sperm whales were encountered in divergence regions of negative SSH and/or higher-than-average surface chlorophyll.

In our overview of the physical and biological oceanographic habitat of the northern Gulf in Section 3.2, we have continued and extended these analyses. We describe there how eddy-forced variations in off-margin flow, in combination with summer-to-summer variations in volume discharge of the Mississippi River, begin to explain some of the summer-to-summer differences in where sperm whales were encountered by SWSS cruises. For example, when there was on-margin flow into the Mississippi Canyon region in early summer 2003, sperm whales were rarely seen or heard there. In contrast, later that summer and during other summers when flow was along-margin or off-margin there, sperm whales were locally abundant. As a corollary, during summer 2005 when Mississippi River outflow was more than one standard deviation lower than the ensemble mean discharge for the 26-year period 1980-2005, sperm whales were much less abundant off the Mississippi River Delta and in Mississippi Canyon and De Soto Canyon than in the previous summers of 2002, 2003, and 2004.

In Section 5.5, we extend this analysis of summer-to-summer variability in Mississippi River discharge to speculate on its control by far-field climatic factors. We report both positive and negative correlations between Mississippi River (MR) discharge and climate teleconnection indices. Specifically, we find a positive cross-correlation between monthly MR discharge and monthly Pacific Decadal Oscillation (PDO) anomaly, with PDO leading the discharge by 5-8 months, and a negative cross-correlation with Atlantic Multidecadal Oscillation (AMO) anomaly, with AMO leading the discharge by 7-12 months. Such cross-correlations between climate teleconnection indices and MR discharge are encouraging, for they suggest that up to 40% of the monthly variation in MR discharge can perhaps be predicted 5-12 months in advance. Because most of the sperm whales seen or heard on S-tag cruises, D-tag cruises, or Mesoscale Population Study (MPS) surveys in summers 2002-2005 were encountered within just tens of kilometers of areas of off-margin surface flow of green water, there are in turn positive correlations between MR discharge and off-margin surface flow.

In Section 5.2, we explore in greater detail the spatial correlation between locations where whales were encountered on D-tag cruises and the local areas of off-margin surface flow. On average, animals D-tagged in summer 2003 were found within 150-200 km of the shifting core location of area(s) of off-margin flow. Eleven additional whales D-tagged in summers 2001 and 19 other whales D-tagged 2002 were located on average 66-87 km and 51-92 km, respectively, from the core locations of off-margin flows of high sea surface chlorophyll (SSC) in summers 2001 and 2002. But because weekly and biweekly composites of ocean color data tell us that eddy geometry that sets up these flows changes on a week-to-week time scale, our attempts to link whale encounters with off-margin flows certainly have that temporal limitation. We also think, based on S-tag trajectory data from periods of the high-resolution (4 times a day) reporting in summer 2002, that most whales are moving around from kilometers to tens of kilometers a day as they forage. Photo-ID follows of groups of animals during MPS fieldwork in summers 2004 and 2005 lead to the same conclusion. So we're not surprised that whales do not stay exclusively within the footprint that one-week composites of color data tell us were where off-margin flows of locally higher SSC were located. But we hypothesize that there may be more prey for sperm whales to find in the deep midwater below these off-margin flows, because these off-margin flows are regions of locally higher export production out of surface waters.

Results from a Deep Gulf of Mexico Benthic Habitat (DGoMB) companion study that was funded by MMS (with the Final Report expected in 2008) offer the supporting evidence. As a paper in press details, weekly composite averages of the standing stock of SSC were derived from SeaWiFS satellite ocean color data at 44 benthic sampling stations occupied along the continental slope and rise by the program (Biggs et al., in press). At 22 DGoMB sites north of 26°N and west of 91°W in the northwest Gulf of Mexico, annual average SSC was 0.19 $mg \cdot m^{-3}$, ranging at most locations from annual highs of about 0.3 $mg \cdot m^{-3}$ in November-February to lows of about 0.1 $mg \cdot m^{-3}$ in May-August. Comparison of three years of SeaWiFS data (January 1998-December 2000) showed little inter-annual variation at these northwest Gulf stations. In contrast, at the 22 northeast Gulf sites north of 26°N and east of 91°W, SSC averaged 2.8 times higher than in the northwest Gulf, showing also strong inter-annual variation. Maxima in the northeast region occurred in November-February and also during summers. The summer maxima were associated with Mississippi River water transported offshore to the east and southward by anticyclonic eddies in the northeast Gulf. The apparent increased in SSC in June-August at northeast Gulf stations reached average monthly concentrations more than 50% greater than in November-February. Based on a primary productivity model and a vertical flux model, the calculated export of particulate organic carbon (POC flux reaching the seafloor) was estimated as ~18 mg C m^{-2} day^{-1} at the 22 northeast Gulf stations, and ~9 mg C m^{-2} day^{-1} at the 22 northwest Gulf stations. The locally highest calculated export for any of the 44 stations was over the upper slope in Mississippi Canyon, and at a location called "HiPro" over the middle slope to the west of the head of De Soto Canyon. These export estimates were comparable to fluxes measured by benthic lander by others in the DGoMB program, and may drive the differences in west versus east bathymetric zonation and community structure of macrobenthos that were sampled with large box corers by others in the DGoMB program.

Preliminary findings of the acoustic assessment of sperm whale distribution, habitat, and habitat use by Benoit-Bird and Ortega-Ortiz (Section 5.3) also support the paradigm that where there is higher export production there should be higher biological production at all trophic levels, since they report that fishery echosounder volume scattering in the water column was significantly higher when whales were locally abundant. It was in fact possible for them to identify sperm whales within the fishery echosounder data as extremely large, strong scatterers. Looking at the overall pattern in the relationship between where submerged whales were detected and volume backscattering revealed significant relationships at 5, 10, and 25 km spatial scales, but fewer relationships at 1 km and 50 km and even fewer at the 100 km scale. In other words, the fishery echosounder data suggest that sperm whales are detecting changes in the habitat at horizontal scales of 10 kilometers, rather than at 1 or 100 kilometers.

Working with the D-tag data, Watwood et al. (2006) reported that foraging dives by sperm whales in the northern Gulf took them to average maximum depths of 644 m. They noted that sperm whales produce buzz (creak) sounds during the deeper parts of their dives, and that they increase their maneuvering during buzzes. From an examination of the depths at which diving whales produced buzz sounds, they reported that animals descended to a mean depth of 392 m from the start of regular clicking to the first buzz, and that diving animals made most of the buzz sounds in the depth range 350-600 m. While buzz sounds do not reveal the size of a prey target, nor whether a presumed capture attempt was successful, buzz production is a useful proxy for where and how often sperm whales attempt to catch prey (see also Miller et al. 2004a). Irvine and Mate (in preparation), who analyzed 17 days of dive depth data from an animal that was tagged in summer 2005 with an S-tag that had been enhanced with addition of a pressure transducer, likewise reported that most of the dives this animal made were to the 400-700 m depth range.

In Section 5.3, Benoit-Bird and Ortega report that sperm whales they observed in the fishery echosounder data collected in summer 2005 between 400 and 600 m were observed at this dive depth approximately 50% of dive time, so they suggest that this depth range is a biologically significant depth for these animals. However, they also point out that whales detected at depth in the fishery echosounder data were found to correlate with very small scales (1 m) of volume scattering in the vertical dimension, which implies these diving animals have the ability to key in to highly local patches of potential prey. Echosounder diving results were compared to results from a new technique for passive acoustic tracking (Section 5.4), with the conclusion that both techniques were observing a diving sperm whale.

In Section 5.2, Miller et al. summarize a re-examination of the D-tag data from summers 2001, 2002 and 2003 to determine how the average depths at which diving whales produced buzz foraging sounds may vary with time of day. By comparing buzz depth with volume scattering determined using a 38-kHz hull-mounted ADCP (no fishery echosounder was available on SWSS cruises before summer 2005), they report that some whales foraged at the 400-600 m depth of the main deep-scattering layer (DSL), both day and night. Other animals foraged both day and night just below this main DSL, in the 600-750 m depth range where substantial but patchy backscatter returns deeper than the main DSL were detected by the ADCP. Interestingly, the shallowest foraging dives of whales moved upwards in the water column just prior to sunset, suggesting that the animals were tracking the diel movements of the DSL. After sunset, most of the foraging occurred deeper than the main DSL.

To conclude, using data from a variety of sources, SWSS researchers believe that sperm whales diving and foraging in the northern Gulf of Mexico apparently target prey at various depth layers. We hypothesize from volume backscatter data that these depth layers contain local aggregations of squid, prey of squid, or other sperm whale prey. The trophic cascade through which surface productivity reaches the deep-living prey of sperm whales is unclear, and likely quite complex. Moreover, the choice by sperm whales of which depth to exploit is likely to be dynamic, depending on a diving whale's real-time assessment of the prey field. While we have not found any direct effect of surface oceanographic conditions on the diving depth of sperm whales in our data sets, we realize that whales we encountered on SWSS cruises had already "chosen" their location, likely based on trophic cascade conditions, which might be predicted from surface oceanography. Although we will continue our analysis of existing data, we recommend additional research to obtain real-time information on prey at depth during future tag deployments.

5.2 Foraging Behavior of Sperm Whales in Relation to Oceanographic Characteristics in the Northern Gulf of Mexico

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5.2.1 Introduction

Based on behavioral ecology theory, it is expected that movements and foraging behaviors of top predators should be shaped by the physical and biological processes that generate their prey. In the case of marine foragers, it is challenging both to observe the forager and their environment (Costa 1993b), so our understanding of the behavioral ecology of most marine foragers is incomplete at best. Croll et al. (1998) presented a breakthrough approach to integrate multiple data sets of measurements of the marine environment and predators living within the environment to describe the relationship between them. They used a two-pronged approach to describe (1) the horizontal and vertical movements of a top predator (the blue whale) in relation to the distribution of its prey, and (2) the fine-scale foraging behavior of predators in relation to fine-scale measurements of their prey. In the case of their blue whale study, krill prey was tracked horizontally and vertically, and formed dense aggregations that could be predicted from oceanographic features. Instrumented whales were found to concentrate their diving effort to the depth where prey occurred (Croll et al. 1998; see also Croll et al. 2005), and dive depths of one instrumented whale that foraged from 2 PM until 9 PM local time tracked diurnal movements of the prey toward the surface at sunset (Figure 5 in Croll et al. 1998).

Even further challenges are faced when attempting to apply this methodology to deep-diving marine predators such as the sperm whale, although perhaps surprisingly, it has been easier to study the predator than the prey. Recent research has been effective at sighting and tracking sperm whales and in recording the detailed foraging behavior of individuals while an instrument (D-tag) has been attached to them using suction cups. These high-resolution archival tags record diving, movement, and other behaviors including sound production which is important for odontocete cetaceans (Miller et al. 2004a; Johnson et al. 2004). Though certain whale behavior can now be measured, challenges to place those behavioral measurements into the ecological context of the predator include: (1) difficulty in determining the specific prey species, particularly during fine-scale measurements of predator behavior that can be made using short-duration suction-cup tags; (2) general inability to effectively sample deep prey fields, particularly mobile cephalopod prey which are noted for their escape behavior from trawl nets; and (3) because cephalopod prey are difficult to sample, it is likewise difficult to measure the vertical or horizontal distribution and movements of the prey. These challenges certainly exist for the study of the behavioral ecology of sperm whales in the Gulf of Mexico, as we have little published information about their prey species, or the distribution and movements of the prey.

Because of the lack of direct information about sperm whale prey, some studies have used an indirect approach which links sightings of sperm whales to measurable oceanographic variables. For example, Baumgartner et al. (2001) found that sperm whales were sighted significantly less in on-shelf waters and in locations where the 15° thermocline was deeper than 200 m, which is a feature of warm-core anticyclonic eddies. In contrast, surface temperature, depth (within off-shelf waters), surface chlorophyll, and zooplankton biomass from oblique bongo tows to depths <200 m did not have a significant effect. The influence of meso-scale anticyclone-cyclone eddy systems which form off the Loop Current in the northern Gulf of Mexico was explored in more detail and were shown to entrain nutrient-rich Mississippi River plume water offshore. This interaction between eddies and river water was found to explain some interannual variations in sperm whale sightings (Biggs et al. 2005). In locations which apex predators use primarily for foraging, it is likely that such oceanographic variables influence sperm whale distribution because they more directly influence prey distribution and behavior (Biggs et al. 2005). However, the links between oceanographic processes and sperm whale prey are likely complex.

Here we use an indirect approach to study sperm whale foraging ecology by relating oceanographic measurements to fine-scale diving and presumed feeding behavior of sperm whales recorded using archival suction cup tags (D-tag). The D-tag records animal depth to an accuracy of <1 m, and the D-tag acoustic recording can be used to identify likely encounters with prey because sperm whales appear to produce buzz (aka “creak”) vocalizations during prey capture attempts (Johnson and Tyack 2003; Miller et al. 2004a). We describe diel vertical biological oceanographic patterns in the northern Gulf of Mexico using volume backscatter from a 38-kHz acoustic Doppler current profiler, and relate those biological patterns to diving behaviors of sperm whales. Then we consider whether diving behavior of sperm whales might vary depending on oceanographic variables related to the eddy cycles thought to be important in the horizontal distribution of sperm whales. These oceanographic features vary over tens-hundreds of kilometers within the northern Gulf of Mexico. Our findings reveal that the diving behavior of sperm whales is related to vertical biological processes, including diel movements near sunset, and increased prey encounter rates at depths below the primary deep scattering layer. In contrast, sperm whale foraging behavior does not appear to systematically vary with near-surface oceanographic features including sea surface height, surface chlorophyll, and distance to offshore flow.

5.2.2 Methods

Archival sound and depth-recording tags were attached to sperm whales using a 12 m cantilevered pole from a small boat (see Miller et al. 2004b for details). Reactions to tagging were minor and short term. We found that the depth of the first recorded dive does not differ from that of subsequent dives, although the duration of the first dive is somewhat shorter than subsequent dives. After the D-tag detaches from each whale, it is recovered using VHF radio signals from its antenna. The archived data are then downloaded for analysis. The D-tag has multiple sensors, but for this presentation our focus is on dive depth and on the click and "creak" (buzz) sounds that are produced by diving whales (Miller et al. 2004a). At least one entire dive was recorded from 26 sperm whales using D-tags, with a total of 144 deep foraging dives recorded. We analyzed in detail a total of 26 D-tag attachments on diving sperm whales during summers 2001 (4 whales, 20 dives), 2002 (14 whales, 72 dives), and 2003 (8 whales, 52 dives). For each of these records, the depth of dives and buzz production were tracked versus time of day. The bottom-phase of each dive was specified using the vertical pitch of the whale to ascertain the end of descent and start of ascent (Miller et al. 2004b). The mean depth and mean buzz-rate were calculated for each bottom phase for the tagged whales.

During each of the three years, surface oceanographic features were measured from ship-based and satellite-based platforms. In addition, subsurface biological stocks were imaged during summers 2002 and 2003 using relative acoustic backscatter intensity (RABI) and are reported in units of raw acoustic counts from a 38-kHz acoustic Doppler current profiler (ADCP). A daily average RABI was calculated for the data collected in 2003, and is presented in Figure 5.2.1 (left). For each D-tag deployed, we obtained the sea-surface height at that location. When available, surface chlorophyll was calculated using SeaWiFS data. The general pattern of eddies in the northern Gulf of Mexico during SWSS fieldwork was described by integrating ship-based and satellite-based measurements (see Biggs et al. 2005; see also Table 5.5.2 in Section 5.5 of this report; a full description of the patterns from year to year is given in the Appendix). For each D-tag deployed, we then calculated the distance from the tagged whale to the predominant offshore flow of chlorophyll-rich water. Dive depth and buzz rates were then related to the vertical and horizontal oceanographic measurements.

5.2.3 Results

Vertical Biological Oceanographic Processes and Sperm Whale Foraging

The RABI data from the 38-kHz ADCP revealed two predominant features in water column signal strength in the upper kilometer of the northern Gulf of Mexico. The first is the presence of a zone or layer of deep-scattering between 350 and 550-m depth (Figure 5.2.1, left). This deep-scattering layer is likely composed of a diverse array of zooplankton and nekton, at least some of which show a clear diel migration which occurs at local sunrise and sunset. A second feature revealed in many of the daily backscatter intensity data sets was the presence of secondary but patchy returns at depths greater than that of the depth of the deep scattering layer (Figure 5.2.1, right). We found no correlations between when and where these patches of locally high backscatter occurred and either day of month or local time of day. Rather, one or more such higher-than-average backscatter patches that persisted at least one hour can be found every day of the 20 days at sea. While we do not know what biological assemblages might form these deeper patches of backscatter targets, we feel it is likely to include nekton which can move into and then out of biological assemblages within the deep-scattering layer.

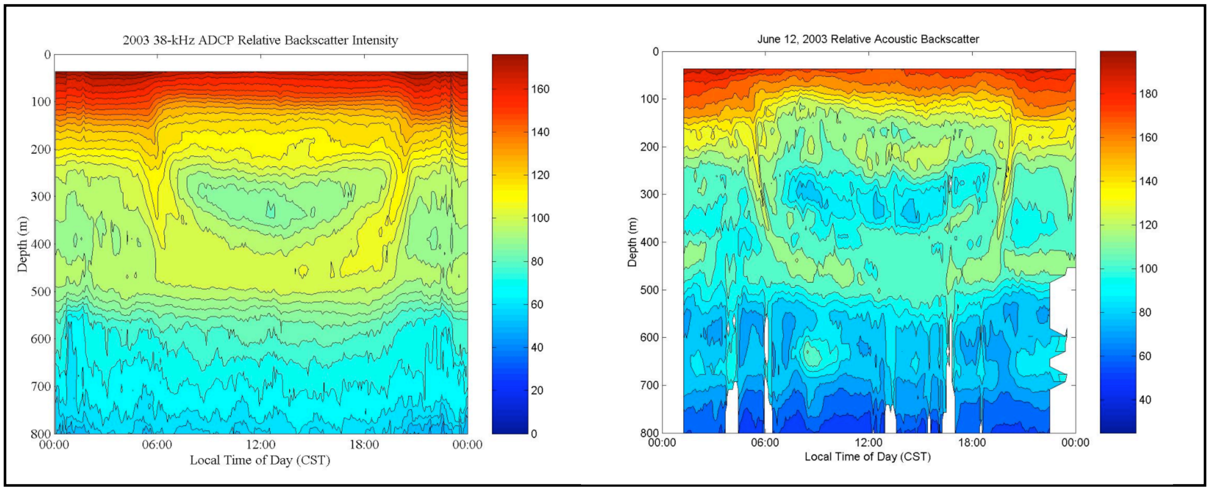

Figure 5.2.1. Relative acoustic backscatter intensity in 2003. (Left) Average relative acoustic backscatter intensity (proxy for nekton and micronekton biomass) was measured by a hull-mounted acoustic Doppler current profiler concurrent with D-tag fieldwork in summer 2003. Note the clear presence of a deep-scattering layer which includes migratory and non-migratory elements. (Right) A single day of relative acoustic backscatter data revealing substantial but patchy assemblages at depths greater than the deep scattering layer. After Kaltenberg (2004).

Prey encounters of sperm whales, scored as buzzes produced by the tagged whale, occurred in three distinct depth layers (Figure 5.2.2). In all three years 2001-2003, some whales foraged at depths from 350-550-m depth, which corresponds to the depth of the main deep scattering layer (Figure 5.2.1, left). The shallowest prey-encounter depth of whales moved upwards in the water column just prior to sunset, suggesting that the whales foraging within the deep-scattering layer track the diel movements of some migrating organisms. Foraging after sunset occurred mostly at depths greater than the main deep-scattering layer. This diel pattern was observed for whales in other years, though no tagged whales dove just prior to or just after sunset in 2001.

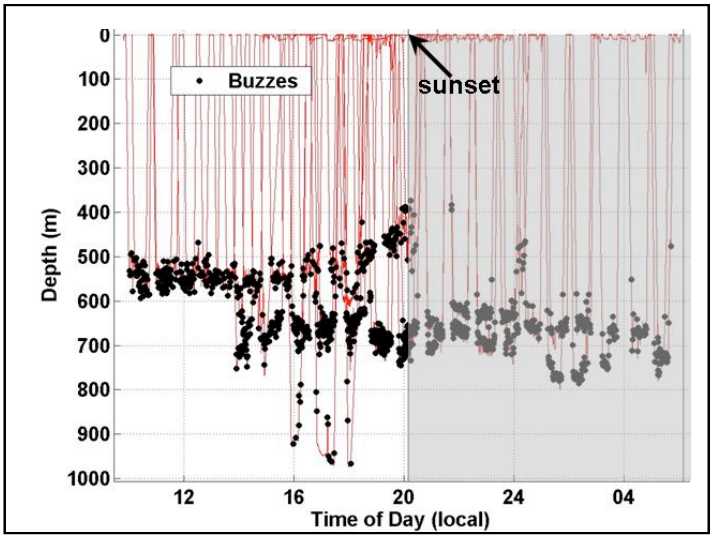

Figure 5.2.2. Dive profiles (red) and depth of buzz production (black) versus local time of day for 8 sperm whales tagged during the 2003 D-tag cruise. A total of 52 dives are shown. Sunset is shown as the transition between light and dark backgrounds.

Both day and night with little apparent diel pattern, sperm whales also foraged at depths just below the main deep-scattering layer, primarily in the 600-750-m depth range where patchy acoustic backscatter returns were found (Figure 5.2.1, right). Foraging at depths below the deep-scattering layer was observed in all three study years. Foraging at these depths was typically within the water column, although rarely some whales at these depths approached the seafloor for brief intervals. One whale in 2002 appeared to actively search along the sea floor at depth of ~600 m, rising off the sea floor during buzz production. Lastly, we observed two cases of primarily benthic foraging at greater depths than typically utilized for water-column foraging. These deep benthic dives were made by the only two large males that we D-tagged during the study, one in 2001 and the other in 2003. These two whales also produced buzzes in the mid-water column during dive transit to and from the seafloor, but spent a majority of the recorded bottom-phase of dives along the sea floor.

Prey capture attempt rates, scored as buzz rates, were higher in tag records when foraging occurred at great depths (Figure 5.2.3). This pattern of increased buzz rates with depth suggests that prey fields accessed by sperm whales deeper than the main deep-scattering layer had denser or higher quality types of prey aggregations (see discussion in Section 5.2.4).

Near-surface Biological Oceanographic Processes and Sperm Whale Foraging

Consistent with previous reports, sperm whales were generally found and tagged in areas with low sea-surface height although some variation was observed from location to location (Figure 5.2.4, left). In summer 2003, a dynamic squirt of primary production into deepwater was observed (shown for the second week of the cruise by the black "+" symbol in Figure 5.2.4, right panel). On average, animals D-tagged in summer 2003 were found within 150-200 km of the shifting core location of this off-margin flow. Eleven additional whales D-tagged in summers 2001 and 19 other whales D-tagged 2002 were located on average 66-87 km and 51-92 km, respectively, from the core locations of off-margin flows of high primary production in summers 2001 and 2002. Whales encountered in water depths of 800-1200 m over the continental slope were seldom encountered at distances of > 250 km from such off-margin flows (Biggs et al. 2005). Surface chlorophyll was not available for all tag deployments due to cloud cover, but most of the whales were tagged in locations with relatively low surface chlorophyll (see Appendix for more details on the surface oceanography at D-tag deployment locations).

The mean foraging depths of the tagged sperm whales were not consistently related to any of the snapshot surface oceanographic measures scored (Figure 5.2.5). Because foraging depth and buzz rate are so strongly correlated (Figure 5.2.3), this result also indicates that prey encounter rates did not vary in a consistent fashion with the surface oceanographic descriptors scored in this study.

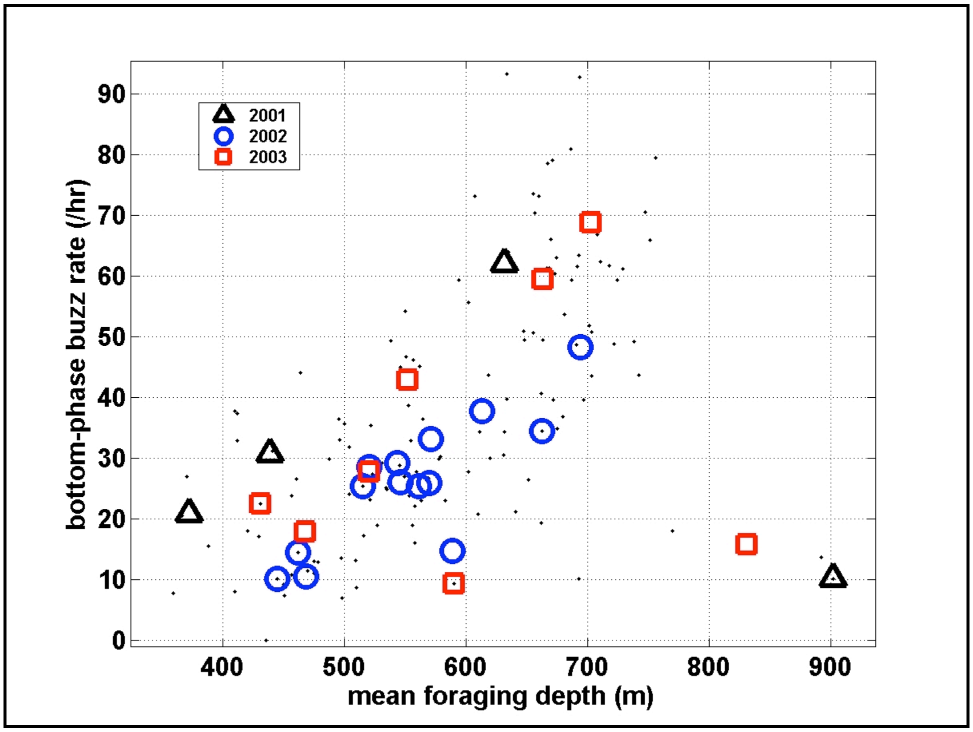

Figure 5.2.3. Mean rate of buzz production during dive bottom-phase versus the mean depth of the bottom phase for the 26 whales tagged in this study. Small dots are individual dives, while colored symbols are the mean for each whale coded by year. The two whales that foraged deeper than 800 m were the benthic foraging large males. Excluding these two whales, there is a clear increase in buzz-rates for the primarily mid-water foragers at greater foraging depth, a pattern which was consistent across all three years.

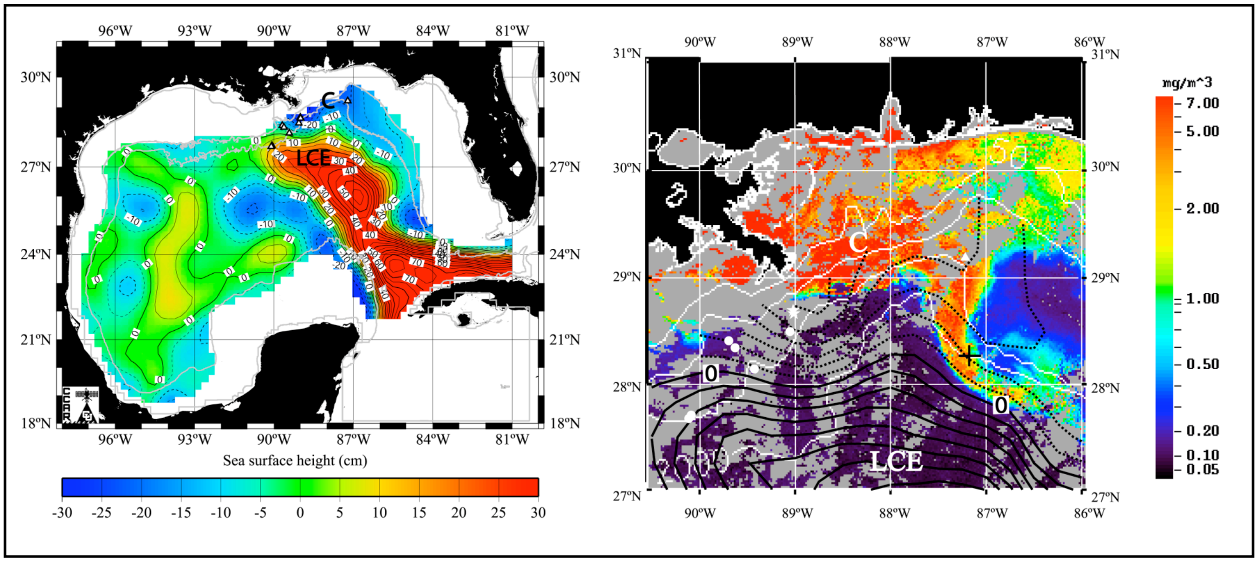

Figure 5.2.4. Surface oceanographic features measured in this study. (Left) Sea surface height field for 14 June 2003, the mid point in time of the 2003 D-tag cruise (June 5-22). Triangles show locations of sperm whales tagged with the D-tag during the cruise. LCE refers to Loop Current Eddy. C refers to Cyclone. (Right) SeaWiFS 7-day composite of ocean color imagery centered on 14 June 2003. The contours of sea surface height for 14 June 2003 are shown in dark black lines. The contour intervals are every 5 cm; solid lines are positive SSH and dashed lines are negative SSH. The white triangle shows the location of a sperm whale tagged on the 2003 D-tag cruise during the time period of 4-10 June 2003. The white circles show the locations of sperm whales tagged during the time period 11-17 June 2003. The white stars show the locations of sperm whales tagged during the time period 18-24 June 2003. The black cross indicates the location of the strong offshore flow of nutrient rich river water, and the distance of each sperm whale to this feature was measured. LCE denotes Loop Current Eddy. C denotes Cyclone. The 10-, 200- and 1000- isobaths are shown.

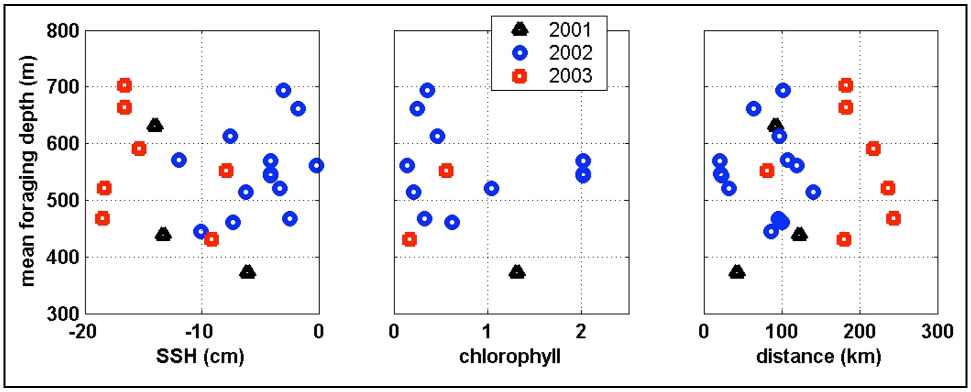

Figure 5.2.5. Mean foraging depth of sperm whales tagged in the Gulf of Mexico in relation to sea-surface height (left), surface chlorophyll (center), and distance from the primary squirt of productive water into deeper waters explained in Figure 5.2.4 (right). While there are differences from year-to-year in the surface features measured, these do not correspond to the foraging depths exploited by the tagged sperm whales.

5.2.4 Discussion

Our results indicate the foraging behavior of sperm whales in the Gulf of Mexico appears to be strongly related to vertical biological assemblages that can be tracked using acoustic techniques, despite the fact that we do not know which acoustic targets might actually be sperm whale prey. The "shallowest" foraging occurred at a depth consistent with the daytime depth of the deep-scattering layer – and we did observe diel patterns in foraging depths of sperm whales in 2002 and 2003 just before sunset. None of the sperm whales tagged in 2001 conducted deep foraging dives just before or just after sunset. Rather, these summer 2001 whales usually engaged in social interactions at or near surface, from late afternoon to early evening. Prey layers below the typical deep-scattering layer depth were also exploited by tagged whales. We found that buzz rates increased as whales dove to deeper depths, suggesting that these deeper patches provide higher quality foraging. If so, the presence of these deeper patches may be a useful predictor of sperm whale presence. Finally, some whales foraged directly along the seafloor, including the only 2 adult males that we tagged. These whales also foraged in the mid-water column during dive transit to and from the seafloor.

The choice by sperm whales of which depth to exploit is likely to be dynamic, depending on their real-time assessment of the prey field. Sperm whales produce some of the most powerful sounds in the animal kingdom, including highly directional regular clicks with source levels in excess of 230 dB re. 1µPa (rms) (Møhl et al. 2003) at frequencies low enough for efficient long range detection (Madsen et al. 2002b). By acoustically searching the water column during descent, sperm whales appear to have a mechanism to locate profitable prey patches or perhaps individual items of prey from a distance, which we hypothesize they employ to select the most promising foraging depth. We believe the dive profiles and buzz production, which are summarized in Figure 5.2.2, indicate that sperm whales in the northern Gulf of Mexico have the capability to detect preferred patches of prey both within and below the main deep-scattering layer. When diving whales detect deep-living prey or patches of prey below the main scattering layer, it may be worthwhile for them to dive to greater depth to access these deeperr prey resources. Otherwise, sperm whales may "decide" to forage within the deep-scattering layer. In some D-tag records, particularly in 2002, whales produced buzzes over a range of depths, some at the depth of the deep-scattering layer and others deeper – this reflects the dynamic nature of sperm whale foraging and information gathering using relatively long-range echolocation.

Interestingly, sperm whale dive depths (and by extension buzz rates) did not appear to be predicted by typical surface oceanographic variables, including sea-surface height, surface chlorophyll, and distance from surface blooms related to offshore flow. Sperm whales were observed to dive deeper than the depth of the main deep scattering layer to access what we hypothesize were deeper-living prey or patches of prey (Figure 5.2.3). Therefore, the lack of correlation between sperm whale dive depth and surface oceanographic data indicates that variations in those oceanographic variables within the northern Gulf of Mexico did not reliably correspond to presence or absence of deep prey or patches of prey. However, the D-tagged whales had already "chosen" their location, likely based on prey conditions, which might be predicted by surface oceanography over a wider spatial scale (Biggs et al. 2005). If so, then sperm whale movements over periods of days to weeks might be more closely linked to surface oceanography than movements over hours to days (e.g., Rendell et al. 2004). As a corollary, the factors which determine the location of specific prey patches within a feeding ground are better studied with higher vertical resolution fishery echosounders than with the ADCPs available to us in 2002 and 2003, which averaged over 16 m vertical bins. As discussed by Benoit-Bird and Ortega (Section 5.3), the Simrad fishery echosounder that was first available for SWSS use in summer 2005 often found high backscatter below the main scattering layer to be compressed into vertical ranges of only meters to tens of meters. Such vertically-compressed patches would be averaged with much less signal-to-noise by the 16-m vertical bin size of the 38-kHz ADCP.

Buzz rates were dramatically higher when sperm whales in the northern Gulf of Mexico foraged at depths below the main deep-scattering layer, but some whales had lower buzz rates at depths within the deep-scattering layer (Figure 5.2.3). Relative acoustic backscatter intensity data from the 38-kHz ADCP in summers 2002 and 2003 revealed patchy biological aggregations at depths below the deep-scattering layer. These observations appear to correspond, and we hypothesize that the backscatter data reveal patches which include dense aggregations of sperm whale prey, and may therefore be useful predictors of sperm whale presence or absence. However, we must emphasize that we did not systematically collect 38-kHz backscatter data during D-tag deployments. We suggest that a critical next step is to use acoustic methodologies to track variations in the vertical distribution of prey simultaneous with a technique to observe foraging by diving whales, such as the D-tag, to test whether deeper patches which can be detected acoustically (Figure 5.2.1, right) are actually those being exploited by sperm whales when they forage at depths greater than the deep-scattering layer.

On a broader scale, it is important to identify more fully what factors drive the occurrence and location of the deeper prey patches of sperm whales, and to identify what potential prey species occur in the patches. Kaltenberg (2004) found indications that deep patches were more common in slope waters than in the deeper basin of the Gulf of Mexico, but found no strong correspondence between presence of deep patches and sea surface height. Though prey patches appear to be more common when sperm whales forage at greater depths, variations in prey size and species are also critical factors which influence the foraging ecology of diving sperm whales. Wormuth (2005) reported on results from trawls made in midwater in and below the main DSL in summer 2003 (see also Section 3.2 of the SWSS Summary Report), but it is evident that more research is needed to identify the potential prey items of sperm whales that live within these depth layers.

In conclusion, though we are still not able to use the technique of Croll et al. (1998) to directly describe foraging behavior of sperm whales in relation to their prey, some indirect measures of prey distribution appear to relate to sperm whale foraging behavior in the northern Gulf of Mexico. The vertical distribution of biological assemblages appears to relate quite strongly to dive and foraging depths of sperm whales, and acoustic technologies appear to have the potential to identify sperm whale prey patches. More work is needed to describe what environmental conditions drive the location of prey patches, particularly over scales of 10s-100s of km within foraging grounds, and to identify what prey species occur within those patches.

5.3 Active Acoustic Assessment of Sperm Whale Distribution, Habitat, and Habitat Use

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5.3.1 Introduction

Sperm whales (*Physeter macrocephalus*), the largest of the toothed whales, are listed as an endangered species under the U.S. Endangered Species Act (see the URL at http://www.nmfs.noaa.gov/pr/species/esa/mammals.htm) and classified as a “vulnerable” species by the International Union for the Conservation of Nature and Natural Resources (IUCN). A significant concern for the health of these animals is the increasing anthropogenic noise in the marine environment (Richardson et al. 1995). A series of research cruises in the Gulf of Mexico has been sponsored by the Minerals Management Service and the oil and gas industry to study the potential impacts of offshore exploration with seismic techniques on sperm whales as well as to characterize the habitat and behavior of the whales. This collaborative effort has involved large teams of researchers with a wide range of expertise. Scientists have successfully satellite-tracked radio-tagged sperm whales to determine annual movement and home range (Section 4.3; Mate et al., submitted), placed acoustic recorders on the animals to study diving behavior (Watwood et al. 2006) and the sounds they produce and receive (Zimmer et al., submitted), tracked animals passively from the sounds they produce (Thode et al. 2002), and looked at the physical and biological oceanography surrounding the whales to assess their habitat (Biggs et al. 2005; Biggs et al. 2000; Davis et al. 2002). Studies of whale habitat have included looking at the circulation features of the water while measuring the primary productivity (phytoplankton or plant life) and preliminarily assessing the zooplankton (small animal) abundance.

Sperm whales, unlike many other large whales, are high trophic level predators rather than filter-feeding zooplanktivores. A review of stomach contents from sperm whales when commmercial whaling was allowed shows they feed primarily on mesopelagic (200 to 2000 m deep) and bathypelagic (>1000 m deep) fish and cephalopods (squids and octopuses) (Kawakami 1980). Dive profile records indicate that sperm whale the Gulf of Mexico forage near 520 m depth in the water column (Watwood et al. 2006). They may consume several thousand kilograms of prey a day (Best 1979) comprised of about 1000 individuals (Clarke et al. 1993). Given their food consumption needs, their prey resources are likely to be a critical factor driving their distribution and foraging behavior in the Gulf of Mexico. While their food is undoubtedly linked to physical processes and the distribution of plankton, the trophic levels between whales and plankton are expected to introduce temporal and spatial lags between any correlations of whale distribution and the features that have been measured (Jaquet 1996). To describe sperm whale habitat, the distribution of fish and cephalopods in the mesopelagic and bathypelagic zones must be characterized.

Estimating the distribution of potential prey within the 1000-meter depth range of regular sperm whale dives, however, is not easy, particularly when the prey are highly mobile animals. Traditional techniques like trawling with nets have significant limitations. Trawling studies are relatively localized and can assess only one depth at a time, making a description of distribution in a large area with animals that move quickly difficult. There is also an inherent bias associated with ‘net avoidance’ (see, for example Holliday and Pieper 1995; Medwin and Clay 1997), preventing quantitative assessment of abundance. Sampling with nets yields a highly biased assessment of overall biomass of marine pelagic communities (Kenchington 1989). While not providing taxonomic information, acoustic techniques have the potential to provide considerable information on the distribution of the mobile organisms, permitting rapid coverage of the habitat while surveying a large portion of the water column simultaneously (Benoit-Bird and Au 2003).

The objective of this work was to assess the distribution in space and time as well as the availability of potential prey for sperm whales in the Gulf of Mexico. Prey assessment was done in conjunction with sperm whale visual and acoustic surveys, tagging and passive acoustic tracking, as well as oceanographic sampling (temperature, salinity, fluorescence, acoustic Doppler current profiler).

5.3.2 Methods

Acoustic Surveys

A two frequency split-beam echosounder (Simrad EK60 at 38 and 70 kHz) aboard the R/V *Gyre* was used to measure the distribution of midwater sound-scatterers in the Gulf of Mexico during June 3-29, 2005. The 38 kHz echosounder used a 1024 μs long pulse, had a 12° conical split-beam, and a maximum depth range of approximately 1200 m. The 70 kHz echosounder used a 512 μs pulse, had a 7° conical split-beam, and a maximum depth range of 600 m. Surveys using the 70 kHz echosounders were conducted continuously throughout the cruise in conjunction with other field efforts. The 38 kHz echosounder was utilized when other operations permitted, approximately one third of the cruise. Raw echo data from each frequency was simultaneously saved to a laptop computer along with location information from the ship’s global positioning system (GPS). The system was calibrated using an indirect procedure incorporating a 38.1 tungsten carbide reference target prior to and following the cruise according to the procedure laid out by Foote et al. (1987).

Visual Surveys

A visual observation station was established on the flying bridge consisting of three mounted 25x150 BigEye binoculars and a data entry station. At least three observers maintained a continuous watch during daylight hours (07:00 - 20:00 CDT; weather permitting) while the R/V *Gyre* surveyed in water depths of 800 - 2200 m. Two observers scanned with big-eye binoculars while the third person entered data into the data acquisition software program (Whale Track II) on a laptop computer. During surveys, each observer on the big-eye binoculars searched from 10 degrees on the opposite side of the ship to 90 degrees on their side while the third person (data recorder) concentrated on data input and supported visual observations in the near field using only naked eye and Fujinon 7x50 binoculars. The visual team operated in concert with the acoustic team to maximize sperm whale detection, following predetermined survey tracks. Survey tracks were determined each preceding evening. However, after a group of sperm whales was encountered the planned trackline was interrupted to follow the whales and deploy the tagging vessel if weather conditions were favorable. Moreover, when sperm whales were followed the visual survey team switched from “survey” into “tracking” mode. While on tracking mode, observers on the big-eye binoculars stopped scan swaths and focused their observations to the areas where sperm whales were at the surface.

5.3.3 Data Analysis

Acoustic Data

Echosounder surveys were used to characterize the vertical extent, density, and horizontal distribution of scattering layers. For animals acoustically detected in groups, data were simply interpreted as volume scattering (Sv) in dB per m^3. This allows direct comparison between scattering at various depths as well as between the two frequencies. The Webster method (Webster 1973) was used to determine the edges of layers in the group.

In situ measurements of target strengths of individually ensonified animals were made using the split-beam echosounder whenever target density and separation permitted. The number of targets per acoustic reverberation volume for each frequency was determined for each pulse and any values that excluded 1 were not included in the analysis (Sawada et al. 1993).

Volume Scattering and Visual Surveys

To examine the relationship between whales and acoustical scattering, visual survey results were compared with average volume scattering. A total of 29 visual survey legs ranging from 3 to 108 km in length (mean=57 km) were analyzed. This included all visual surveys transects greater than 10 minutes in duration. A one-way ANOVA was used to determine if there were significant differences in survey length when whales were detected versus when they were not. The average volume backscattering (S_v) and standard deviation for S_v at 70 kHz was calculated in 100-meter depth bins from the surface to 600 m for each transect. The relationship between visual sightings per kilometer surveyed and average volume scattering for the transect was examined with a Pearson correlation analysis.

Sonar Whale Detections

Extremely large, individual targets were detected in the data set. Often these targets saturated the echosounder, appearing stronger than bottom reflections. These targets consistently had the stronger echoes near one end of the multiple echoes. These echo characteristics are consistent with a marine mammal the size of a sperm whale (Benoit-Bird and Au 2003). Active-acoustic detections of diving targets meeting these criteria were characterized as likely sperm whales. To calculate whale detection rates, the number of whales was corrected for search area differences as a function of depth (caused by the conical shape of the transducer's beam) by dividing the number of animals located at a particular depth by the diameter of the beam at that depth as in Benoit-Bird and Au (2003). Diameter, not area of the beam, was used because the second dimension of the beam is covered by the direction of the transect. The depth of whales was calculated as the maximum depth of any single target in each observation. Dive depth of detected whales was only characterized when the animal was observed both descending and ascending in the water column within a single observation.

Visual Surveys and Sonar Whale Detections

For each transect surveyed by visual observers, the number of sperm whale locations recorded per distance surveyed was compared to the sonar detection rate for sperm whales using a Pearson correlation analysis. With both whale detection approaches, the results are not to be considered a direct measure of the number of whales in the area because the data includes effort on systematic surveys as well as effort in whale tracking mode. The probability of detecting the presence and abundance of whales in the area is different in these two modes but is likely similarly affected by the changes in effort, allowing for a direct comparison between the two data sets.

Whale Detections and Volume Scattering

The whale dive depth, that is the depth of a single target detected both descending and ascending, was compared with the volume scattering in 1 m vertical depth bins. First, the volume scattering was compared with the volume scattering at all depths using an ANOVA. Second, the scattering at the whale's dive depth was compared with the scattering in the 25 m surrounding the whale and the 100 m surrounding the whale.

To determine how sperm whales were related to volume scattering at a range of scales along acoustic transects, the mean volume backscatter in 100 m depth bins was calculated for 1 km, 5 km, 10 km, 25 km, 50 km, and 100 km long segments. Transect segments in which whales were detected in the echosounder data were compared to segments in which whales were not detected using an ANOVA.

5.3.4 Results

Scattering Layers

Diurnal variation in scattering was apparent as shown in Figure 5.3.1. Diel vertical migrations were evident within scattering layers (Figure 5.3.2). These migrations typically covered 200 m within 30 minutes on both the descent at sunrise and ascent at sunset.

Scattering was found in layers that typically had scales of at least hundreds of meters horizontally. Analysis for scale was restricted to vertical structure because of the sampling design and the horizontal scale of observed layers. Vertical layers identified using the Webster method ranged in scale from 1 m (the smallest size observable with the approach used) to 121 m. The mode was 4 m.

Volume Scattering and Visual Surveys

A one-way ANOVA comparing the length (km) of transects in which whales were visually detected and those in which no whales were detected showed no significant difference ($F=0.006$, $p>0.05$). A Pearson correlation analysis revealed that only scattering in the upper 100 m of the water column was significantly correlated with the rate of sperm whale locations per survey distance ($R=0.80$, $p<0.001$, all other relationships $p>0.05$). The relationship between whale sightings and mean volume scattering in the upper 100 m of the water column is shown in Figure 5.3.3. Mean volume scattering from 300-400 m, 400-500 m, and 500-600 m were all significantly correlated with each other ($p<0.05$). Scattering in the upper 100 m and 100-200 m was not significantly correlated with scattering in any other depth range. There were no correlations between whale locations/distance rate and the standard deviation in acoustical scattering, a simple measure of variability ($p>0.05$ for all relationships).

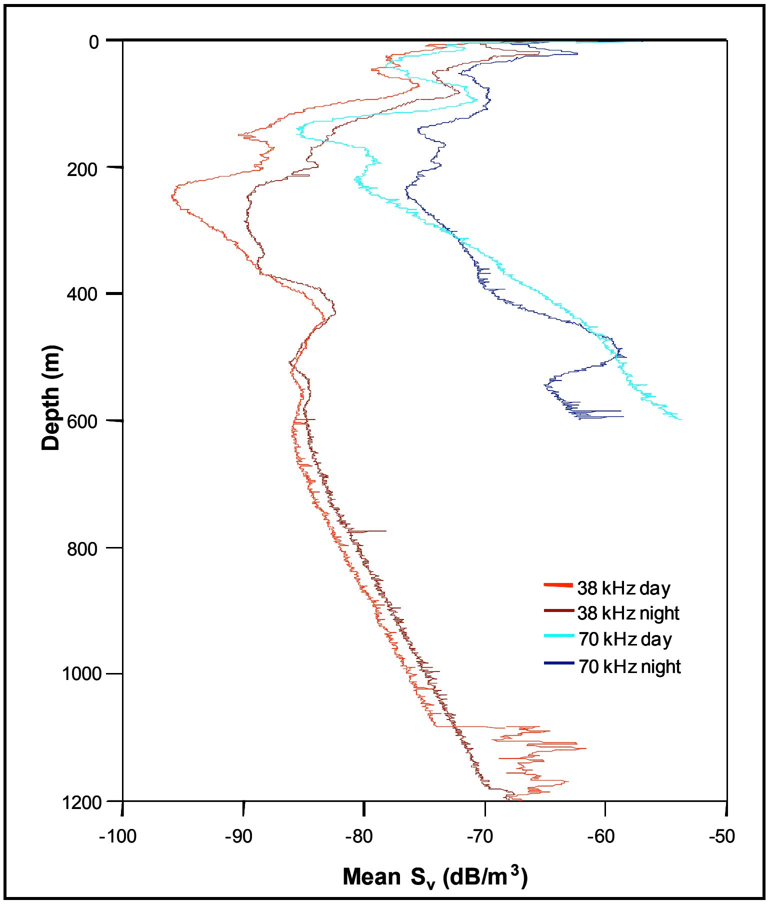

Figure 5.3.1. Diurnal differences in mean volume scattering at 38 and 70 kHz as a function of depth. The mean in 1-m depth bins was calculated for all daytime and all nighttime sampling during the field effort, ignoring the one hour surrounding dusk and the one hour surrounding dawn.

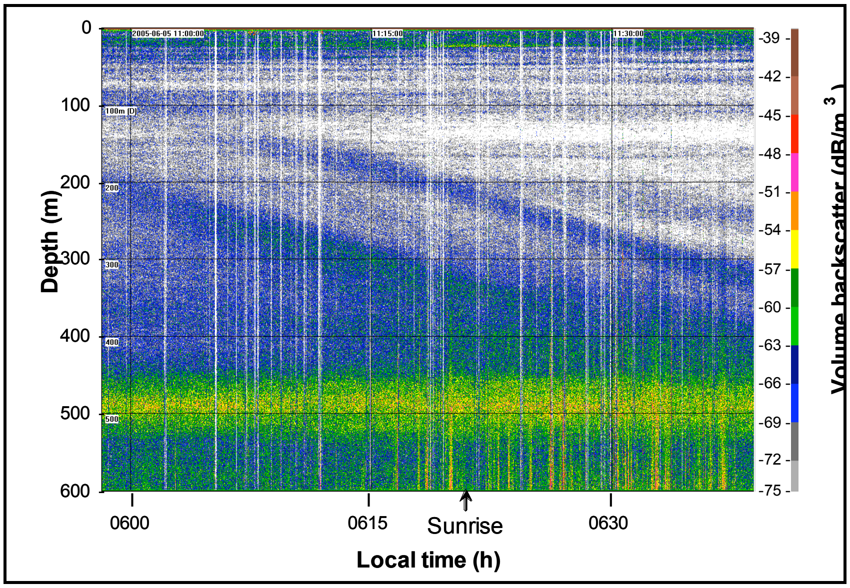

Figure 5.3.2. Volume backscatter at 70 kHz as a function of depth and time shows a representative downward vertical migration of -63 to -69 dB scattering observed shortly before local sunrise.

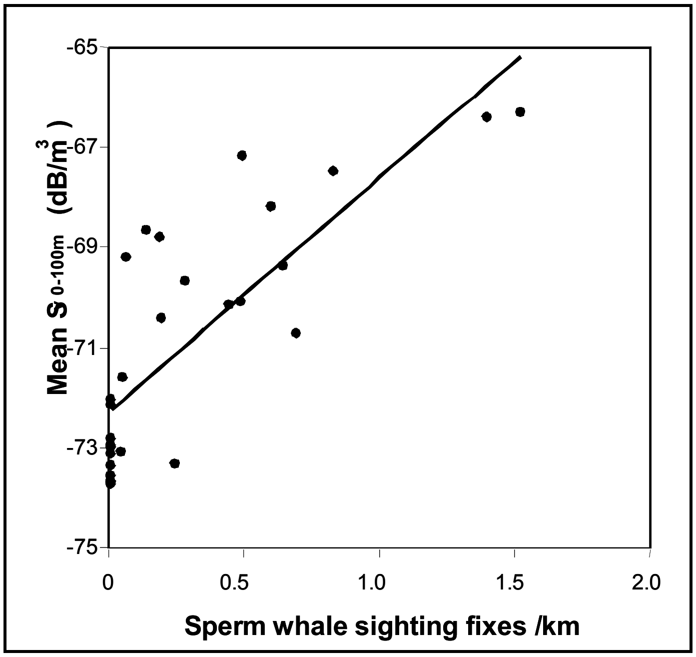

Figure 5.3.3. Mean volume backscatter in the upper 100 m of the water column is shown as a function of the visual sighting rate along the same transect. There was a significant correlation between sighting rate and volume backscatter only in the upper 100 m.

Sonar Whale Detections

Targets consistent with sperm whales (Figure 5.3.4) were detected using the 70 kHz echosounder (600 m depth range) a total of 2781 times, for an average detection rate of 0.36 whales/km surveyed. Using the 38 kHz echosounder (1000 m depth range), a total of 2112 sperm whales were detected for an average detection rate of 0.45 whales/km surveyed.

Visual Surveys and Sonar Whale Detections

There was a strong correlation between the number of whale sighting locations recorded along a transect and those detected with the echosounder (Figure 5.3.5, Pearson correlation coefficient = 0.955, $p<0.01$ (two-tailed)). However, a two-tailed paired t-test revealed that the recorded visual locations/distance rate was consistently significantly lower than the sounding rate (paired differences mean=-0.75, 95% confidence interval of the difference $-1.18<x<-0.33$, $p<0.001$). Mean visual locations/distance rate was 1.09 whales/km while mean sounding rate was 1.82 whales/km. When both echosounders were running, whales in the upper 600 m of the water column were always detected at both frequencies so differences in detection rates between the two frequencies can be accounted for by whales detected between 600 and 1200 m.

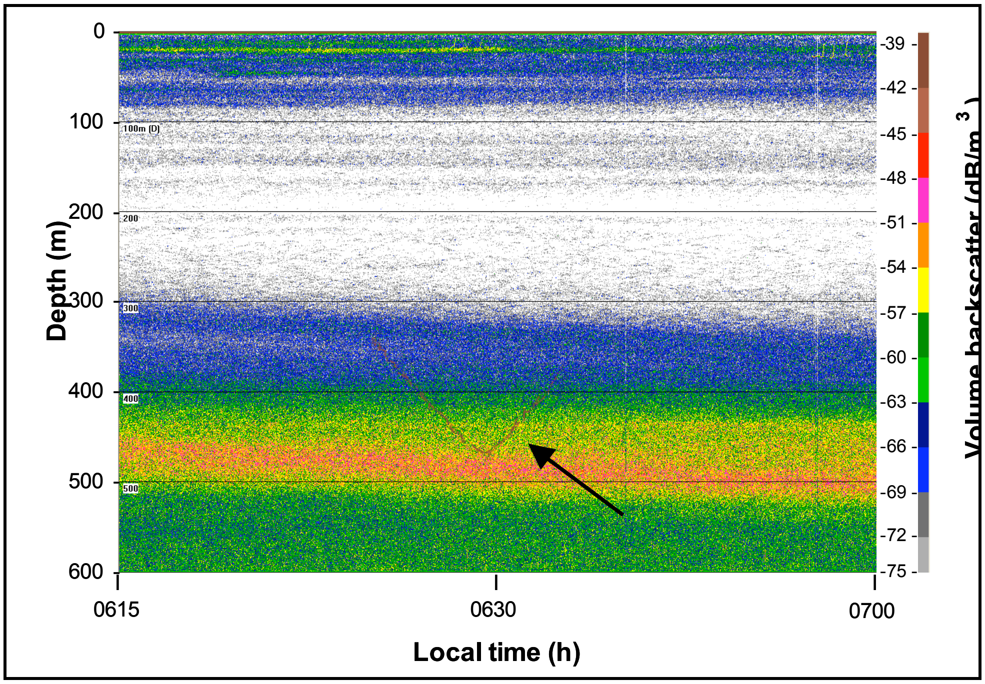

Figure 5.3.4. Volume backscatter at 70 kHz as a function of depth and time shows a large target, consistent with a sperm whale diving to a depth of about 630 m at 0630 local time. The arrow points to the target dive profile. This animal was observed both descending and ascending and thus a dive depth could be determined.

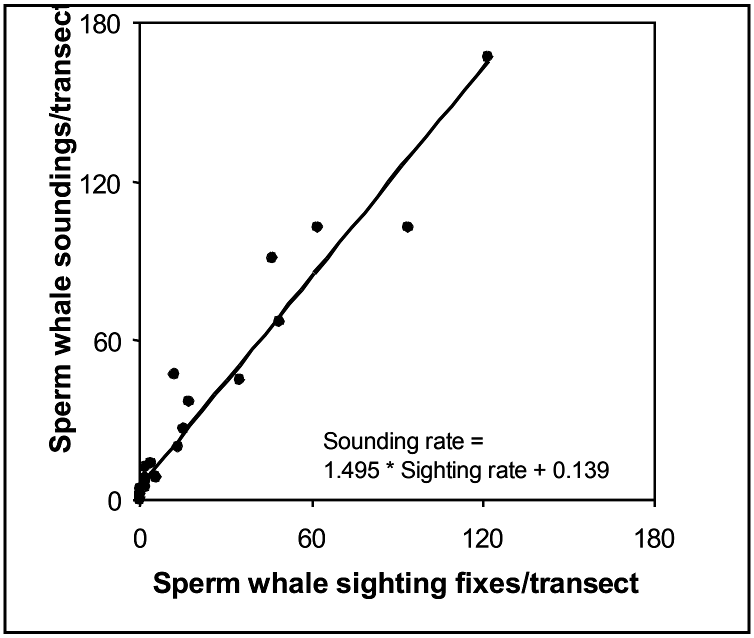

Figure 5.3.5. Sperm whale detection rate made with the echosounders is shown as a function of visual sighting rate along the same transect. There was a very strong correlation between the two whale detection rates although sighting rate was consistently lower than the sounding rate.

Whale Detections and Volume Scattering

The depths of all whales detected with the sonar are shown in Figure 5.3.6. The depths of whales in the upper 600 m is shown separately for daytime and nighttime hours, ignoring the hour surrounding dusk and the hour surrounding dawn in Figure 5.3.7. Because of limited sampling with the 38 kHz during the day, the 600-1200 m depths are not shown in the diurnal comparison. Whales were detected slightly more frequently at night than during the day.

An ANOVA comparing volume scattering from the dive depth of whales (N=1973) to the volume scattering at all other depths showed no significant difference (F=0.34, p>0.05). Scattering at the whale's dive depth was significantly different from scattering in the 25 m and 100 m surrounding the whale (F_{25m}=57.98, p<0.01; F_{100m}=36.23, p<0.01).

The results of the ANOVA on whale presence and mean volume scattering are shown in Table 5.3.1. Whales were significantly related to mean volume scattering at several depth intervals though these relationships changed with scale.

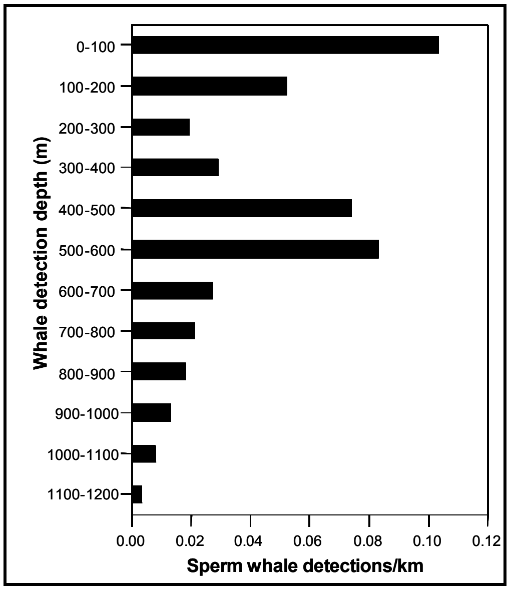

Figure 5.3.6. Rates of detection of sperm whales using the echosounders as a function of depth.

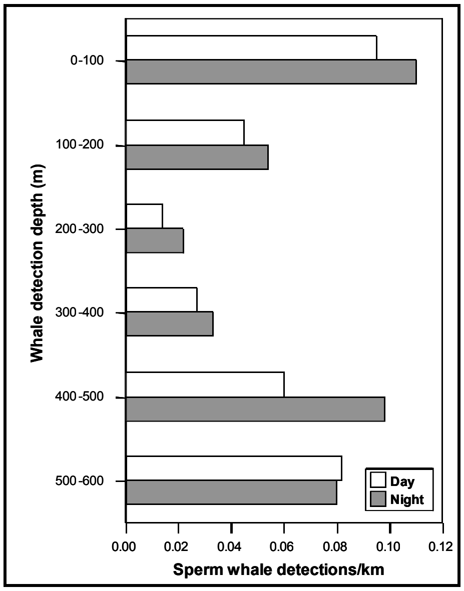

Figure 5.3.7. Rates of detection of sperm whales using the 70 kHz echosounder as a function of depth separated into daytime and nighttime hours ignoring the hour surrounding dusk and the hour surrounding dawn. Only whales in the upper 600 m are shown because of limited sampling with the 38 kHz during the day.

Table 5.3.1

ANOVA Results Comparing Volume Scattering from Each Frequency Echosounder Where Whales Were Detected with Areas in Which No Whales Were Detected at a Range of Spatial Scales

70 kHz	100 km		50 km		25 km		10 km		5 km		1 km	
n whales/total n	36/76		70/153		132/307		302/767.5		553/1536		2535/7682	
	F	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
0-100 m	38.71	<0.05	54.32	<0.01	69.81	<0.01	44.65	<0.01	100.70	<0.01	65.99	<0.01
100-200 m	0.99	ns	0.50	ns	0.97	ns	2.70	ns	2.94	ns	1.76	ns
200-300 m	0.68	ns	1.15	ns	0.22	ns	1.17	ns	1.48	ns	0.18	ns
300-400 m	1.87	ns	2.91	ns	1.32	ns	0.67	ns	1.28	ns	2.11	ns
400-500 m	0.52	ns	0.25	ns	0.81	ns	56.82	<0.01	73.87	<0.01	36.94	<0.05
500-600 m	0.24	ns	0.05	ns	27.69	<0.05	29.84	<0.05	18.65	<0.05	2.08	ns

38 kHz	100 km		50 km		25 km		10 km		5 km		1 km	
n whales/total n	24/46		47/94		88/187		203/468		375/937		1781/4687	
	F	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**	**F**	**p**
0-100 m	51.10	<0.01	87.38	<0.01	13.87	<0.05	28.80	<0.01	11.46	<0.05	77.23	<0.01
100-200 m	1.32	ns	0.57	ns	1.65	ns	0.71	ns	1.36	ns	1.44	ns
200-300 m	0.81	ns	0.80	ns	0.54	ns	0.32	ns	0.52	ns	0.94	ns
300-400 m	0.04	ns	56.11	<0.01	33.52	<0.01	19.18	<0.05	40.02	<0.01	39.28	<0.01
400-500 m	32.22	<0.01	40.22	<0.01	71.28	<0.01	86.53	<0.01	28.85	<0.01	89.22	<0.01
500-600 m	1.05	ns	34.78	<0.01	40.98	<0.01	37.36	<0.01	71.81	<0.01	0.90	ns
600-700 m	2.58	ns	0.69	ns	55.14	<0.01	51.37	<0.01	23.39	<0.01	1.53	ns
700-800 m	0.93	ns	1.28	ns	69.36	<0.01	40.28	<0.01	45.22	<0.01	0.71	ns
800-900 m	1.24	ns	12.82	<0.05	67.78	<0.01	64.87	<0.01	12.63	<0.05	1.04	ns
900-1000 m	0.07	ns	0.03	ns	0.30	ns	43.43	<0.01	46.22	<0.01	0.35	ns
1000-1100 m	0.87	ns	2.73	ns	2.43	ns	1.09	ns	2.76	ns	2.11	ns
1100-1200 m	1.80	ns	1.22	ns	2.10	ns	3.02	ns	1.89	ns	1.87	ns

5.3.5 Discussion

Scattering Layers

Scattering layers in the Gulf of Mexico during the study period were extensive. Even averaging over the entire study period, distinct layers in volume scattering are evident. Layers ranged in vertical extent from 1 m to over 100 m. Layers were most often less than 5 m in vertical extent. This necessitates sampling at smaller vertical scales than has been permitted by previous approaches using an acoustic Doppler current profiler (ADCP) to measure backscatter. Many layers showed distinct scattering patterns between the two frequencies used, with some layers appearing only at 38 kHz and others only at 70 kHz. The vertical scale of scattering layers and their strong frequency dependence raises important questions about how to best interpret existing ADCP backscatter data sets.

Diel vertical migration in the scattering layers was apparent throughout the study. Layers moved up to 200 m in 30 minutes or less. These migrations changed the distribution of scattering within the water column; however, they rarely eliminated layers or added new ones when comparing pre- and post-migration scattering. This indicates that only some of the animals within layers are migrating while others remain at a constant depth across the dusk and dawn time intervals.

Active Acoustic Detection of Sperm Whales

The echosounders used in this study permitted the observation of individual targets rather than simply volume backscatter. Extremely large, strong scatterers that were consistent with the backscatter characteristics expected from sperm whales were observed often within the data. Both the 38-kHz and 70-kHz echosounders detected targets with these characteristics though the 38-kHz echosounder provided a much greater detection range. A comparison of the detection rate of whales from the echosounder and the detection rate of whales made by the visual observers showed a strong, linear correlation. This supports the conclusion that these targets are sperm whales. The detection rate with the echosounder was consistently higher than the visual sighting rate. This is not surprising given the ability to sample the water column down to 600 or 1200 m, depending on the frequency compared with sightings only being possible at the surface. Also, the survey area covered by the echosounder was constant, while the visual observers often focused their observations on specific individual whales (for tracking purposes) and stopped scanning the entire visual field. The ability to actively detect whales at depth while potentially foraging provides a great advantage in looking for correlations of backscatter with their distribution.

Sperm whales were detected by the sonar at all depth ranges in the water column. Whales were most often detected in two depth ranges – the upper 200 m and 400-600 m. Individual whales in the upper 200 m were only rarely observed to both descend and ascend, suggesting that these animals were observed diving down to or coming up from a deeper dive. Animals observed between 400 and 600 m were observed at dive depth approximately 50 percent of the time, suggesting that this depth range represents a biologically significant depth for these animals. This correlates well with the observations of Watwood et al. (2006) in the Gulf of Mexico who saw evidence of sperm whales foraging around 520 m.

Prey Abundance and Presence of Sperm Whales

Comparing the acoustic backscatter data from the echosounders with the visual observations for sperm whales provides enticing information on the correlation between sperm whales and potential prey. While transects along which whales were sighted and those along which whales were not sighted did not vary in length, they did vary significantly in the volume scattering in the upper 100 m of the water column. These data only represent a correlation at a horizontal scale of around 25 m. To understand the relationship between whales and their prey, it is critical that we look at the relationship between whale distribution and the distribution of acoustic scattering at smaller horizontal scales.

There was a consistent and rather intense series of scattering layers within the depth range (400-600 m) in which sperm whales were detected. The layers within this range had distinct scattering characteristics with a shallower layer more intensely scattering at 38 kHz and a deeper layer having stronger scattering at 70 kHz. This suggests differences in target size within each scattering layer with the deeper layer being composed of smaller animals than the shallower layer.

Within the 400-500 m depth range, whales were detected significantly more frequently at night than would be expected from the general increase in detection rate seen in nighttime versus daytime observations. This is in contrast to the finding of deeper dives at night reported in Section 5.2 (see Figure 5.2.2); however, the areas of sampling were in different parts of the Gulf (NW here, NE for D-tag) and nighttime data from the echosounder deeper than 600 m were sparse making direct comparisons problematical. The layers present within this depth range also showed diel differences. At night, the layer showed slightly stronger scattering at 38 kHz. At 70 kHz, the layer became much more pronounced and intense at night.

Scattering strength at 400-500 m and 500-600 m was also significantly related to overall whale detection rate at several spatial scales. Like the recorded visual locations/distance rate, acoustic backscatter whale detection rate was also related to scattering in the upper water column. In this case the relationship was significant at all the spatial scales analyzed for both frequencies.

Looking at the overall pattern in the relationship between whale detection rate and volume scattering, patterns with respect to horizontal scale emerge. First, while many depth bins showed significant relationships at 5, 10, and 25 km scales, fewer show relationships at 1 km and 50 km and even fewer at the 100 km scale. Whale detection rate is not correlated with prey at the smallest horizontal scales. This lack of small-scale correlation has often been observed in marine predators (see a review in Rose and Leggett 1990). The lack of a relationship at the largest scale suggests that sperm whales are detecting changes in the habitat at horizontal scales of tens of kilometers, not hundreds.

Whale dive depths were not at absolute maxima in volume scattering within the measured portion of the water column. However, when looking at smaller scales, 25 and 100 vertical m, the 1 m surrounding the whale was the maximum scattering depth. Whales were diving to local maxima in scattering within a layer. Whales were found to correlate with very small scales (1 m) of scattering in the vertical dimension

This study represents the first calibrated acoustic data of the distribution in space and time of animals that occupy trophic levels relevant as food resources to sperm whales in the Gulf of Mexico. This approach provides a powerful tool to obtain high-resolution information on the distribution of potential prey while simultaneously observing diving sperm whales. Collected in concert with a variety of other observations, these data give us insight into how prey resource distribution may impact the distribution of sperm whales in this habitat. It appears that whales are either directly or indirectly influenced by the distribution of acoustic scatterers. In particular, scatterers in the upper 100 m and those below 400 m are significant predictors of sperm whale presence. Whales appear to be selecting these stronger scattering areas at horizontal scales of tens of kilometers but at much smaller scales vertically. Further work to characterize the source of the scattering in these depth intervals as well as measurements that would allow the use inversion approaches to identify probable prey is likely to provide important information on sperm whale habitat use and feeding behavior.

5.4 Comparison of Sperm Whale Diving Depths Using Two Techniques

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5.4.1 Introduction

During the SWSS project, three techniques were used to measure the foraging depths of sperm whales in Gulf of Mexico waters: tagging, fishery echosounder returns, and passive acoustic tracking. Two different tags used in SWSS to measure dive depths are the Woods Hole Oceanographic Institution D-tag and a modified satellite-tag used by Oregon State University to collect histogram bins of animal depths. The results from these studies are summarized in Section 5.2 and in Irvine and Mate (in preparation). In Section 5.3, acoustic returns from a Simrad echosounder were used to measure depths of animals underneath the R/V *Gyre* during the 2005 season. In this section the third technique, passive acoustic tracking, will be described, and then depth estimates from selected acoustic tracks will be compared with the echosounder returns.

5.4.2 Background

Sperm whales are acoustically active animals, generally producing thousands of short impulsive sounds, or "clicks," per dive (Thode 2004a, b; Miller et al. 2004a). If these clicks are recorded on hydrophones that are sufficiently spatially separated, then by measuring the relative arrival times of a particular sound on the hydrophones information about the animal's location can be derived. Furthermore, if the hydrophones are deployed to a depth greater than 30 meters, the surface-reflected paths, or "ghosts," of the sounds can be distinguished in time from the direct arrivals, providing additional information about the animal's location if the depth of the hydrophone is known or accurately measured.

The SWSS project used a towed array cable to collect whale clicks across a large-aperture passive acoustic monitoring system (PAM) to estimate animal ranges and depths. The concept was first demonstrated off the R/V *Gyre* and R/V *Ewing* during SWSS cruises in 2002 and 2003 (Thode 2004a, b). If two small-aperture sub-arrays are towed behind a vessel, such that the horizontal offset between the sub-arrays is at least 200 m, range estimates of shallow animals out to 1 km can be obtained by triangulating bearings measured simultaneously by the sub-arrays (Figure 5.4.1). For cases where the slant range differs significantly from the true horizontal range, an animal's depth is estimated by using the surface-reflected path from one or both of the sub-arrays to create a virtual vertical array. The animal's depth can then be triangulated, provided that at least one of the sub-array tow depths are independently measured and the sub-array depth is deeper than 25-30 m.

In 2004 a prototype towed array system was assembled and tested with support from the MMS and the Industry Research Funders Coalition (IRFC). The total "tandem" array is comprised of six hydrophones on a single cable, arranged as two sub-arrays of three phones each, with the sub-arrays separated by 200m. Each sensor on the tandem array has between -165 to -170 dB re 1V sensitivity, with a flat frequency response between 100 Hz to over 24 kHz, although usable signal could be obtained past 30 kHz. The presence of a third sensor in each sub-array provides redundancy in case of a sensor failure. Each sub-array also has a pressure transducer that permits the depth of each sub-array to be logged independently.

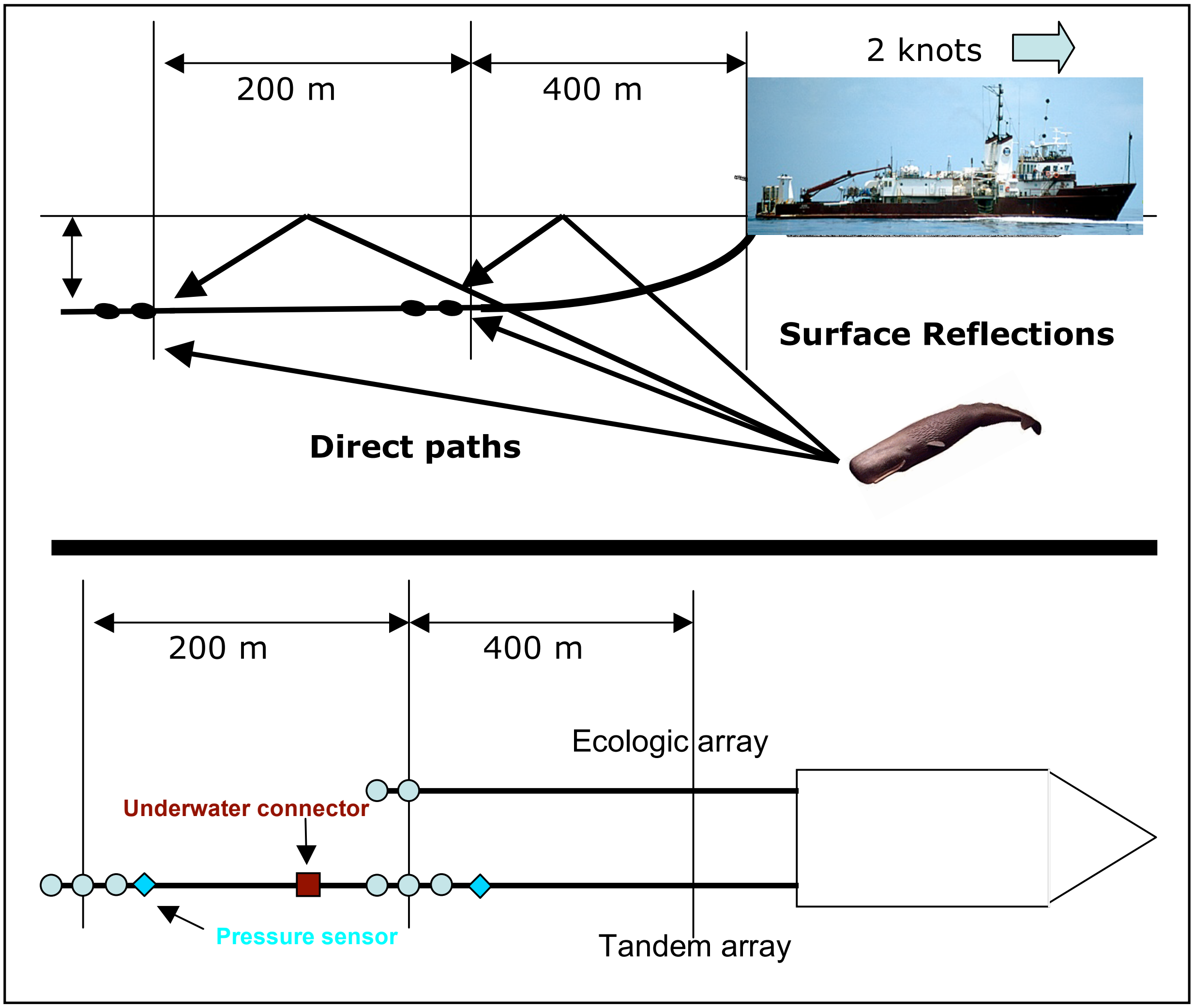

Figure 5.4.1. Illustration of 2005 3-D deployment off R/V *Gyre*, using a tandem array specifically built for SWSS. Top: side view of tandem array during S-tag deployment. Bottom: View of S-tag array deployment from above, showing how tandem and Ecologic array were deployed in parallel, which would permit bearings of sounds to be determined without a port/starboard ambiguity. This configuration permitted 3-D tracking data to be collected without interfering with S-tag requirements. Round circle: calibrated hydrophone; blue diamonds: pressure (depth) sensors; red square: underwater connector.

This new array was deployed off the starboard side of the R/V *Gyre* during the 2004 and 2005 SWSS S-tag cruises. At ship speeds less than 3 knots the array cable sank deep enough to record surface-reflected acoustic paths. During the 2004 cruise 200 m of cable separated the forward sub-array from the *Gyre*. In 2005, 200 m of additional cable were added to the lead-in cable, producing a 400 m separation between the towed array and the ship vessel (Figure 5.4.1). A detailed description of the towed hydrophone cable and tracking algorithms are provided in three peer-reviewed publications (Thode 2004a, 2004b, 2005).

5.4.3 Comparison of Active and Passive Tracking Data

A spreadsheet of times and whale depths obtained by the Simrad fishery echosounder were provided by Kelly Benoit-Bird of OSU to SIO on two selected days, June 7 and 12, 2005. This information was then overlaid on 3-D plots of animals' positions as derived by the towed array.

Figure 5.4.2 shows the first match between Simrad and towed array data, starting at 19:25 on June 7, 2005. Three Simrad depths have been located, marked by squares in the plot. The depth uncertainty of the Simrad data is ±10 m. The greatest uncertainty in the passive acoustic data is the bearing of the sound relative to the array (0.4 degrees), which translates into a ±30 m uncertainty. One can see from the top subplot that the 200-m Simrad measurement depth overlaps well with this passive acoustic tracking depth profile. Furthermore, the range of the whale, as measured from the rear towed array, lies between 600-800 meters and an azimuth of less than 20 degrees. As the *Gyre* is 600 meters forward of the rear subarray, the range and azimuth is consistent with that of an animal underneath the *Gyre*, and thus presumably detectable by the active sonar. Additional cases for comparison are under development. However, the results of this one match provide additional evidence that the Simrad fisheries echosounder was detecting sperm whales as discussed in Section 5.3.

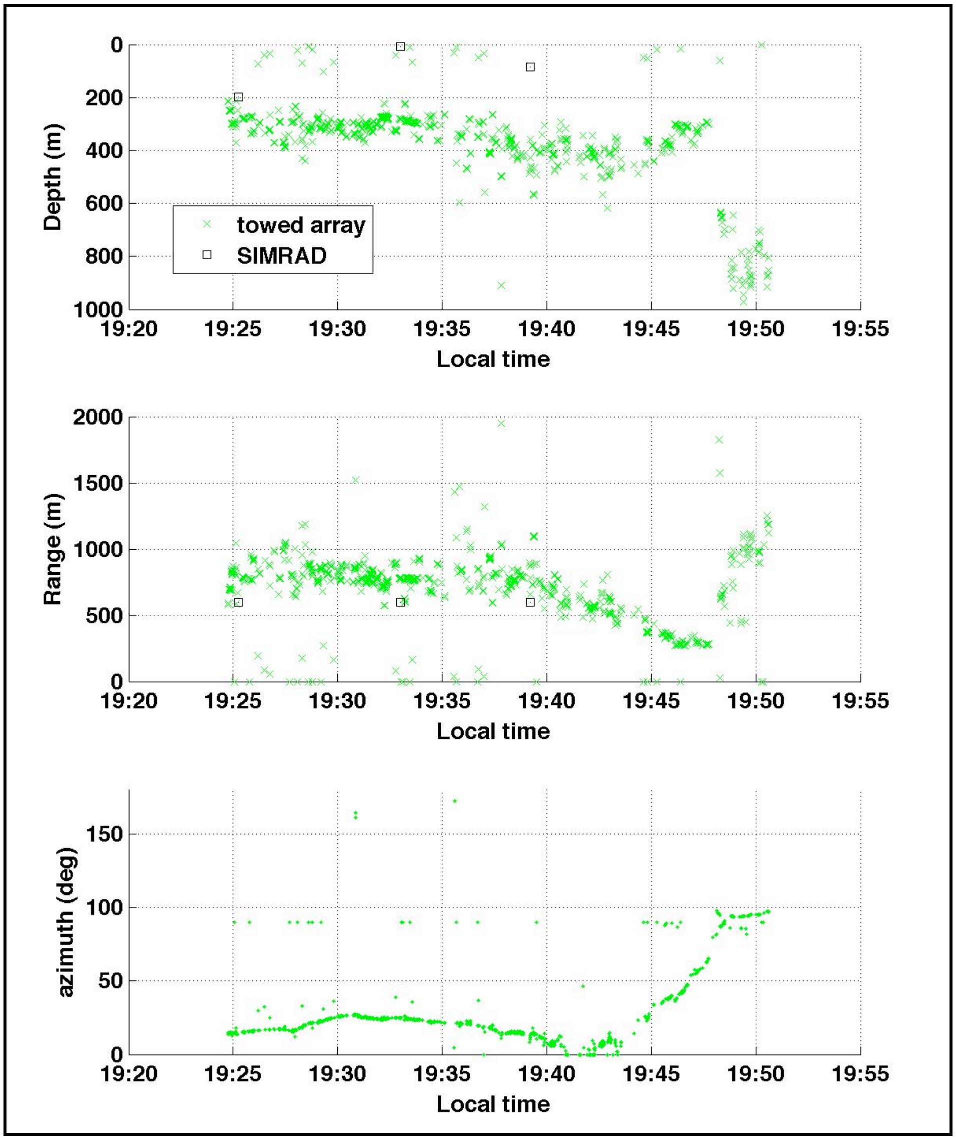

Figure 5.4.2. Comparison between active sonar detection and passive acoustic location. Top subplot: estimated depth of animal, with cross ('x') indicating an acoustic detection, and a square indicating the depth measured from an echosounder return. Middle subplot: range to source from rear towed subarray, which is 600 m behind the R/V Gyre. Bottom subplot: azimuth of acoustic detection, with '0' indicating the direction toward the Gyre's stern.

5.5 Speculations on the Physical Forcing of Interannual Variations in Encounters with Sperm Whales in the Northern Gulf of Mexico

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5.5.1 Introduction

Chapter 3.2 in the SWSS Summary Report to MMS for SWSS fieldwork 2002-2004 discussed the oceanographic conditions where sperm whales were encountered during three summers of visual and passive acoustic ship surveys along the continental margin of the northern Gulf of Mexico (Jochens et al. 2006). A companion paper by Biggs et al. (2005) added data for habitat where sperm whales were encountered during summers 2000 and 2001, during pre-SWSS fieldwork that was carried out in cooperation with NOAA. A manuscript prepared by Jochens and Biggs (2006) adds data for summer 2005. That summary report to MMS and the two companion reports concluded that summer-to-summer variability in the intensity and geographic location of Loop Current eddies (LCEs), warm slope eddies (WSEs), and areas of cyclonic circulation (upwelling) forced striking year-to-year differences in the locations along the 1000-m isobath where there was on-margin and off-margin flow and in locations where sperm whales were encountered along the 1000-m isobath. The three reports documented that most sperm whales were encountered in regions of off-margin flow or other areas of higher-than-average sea surface chlorophyll (SSC).

In these reports we noted that anomalous oceanographic conditions created eddy-forced on-margin flow of LCE water into the Mississippi Canyon region in early summer 2003. During R/V *Gyre* cruise 03G06, when the LCE called *Sargassum* was located close off the Mississippi River Delta, anticyclonic circulation around the northern perimeter of this very large LCE apparently flushed the Mississippi Canyon area with low nutrient, low chlorophyll water of Caribbean origin. We hypothesized that as a consequence, little or none of the usual prey for sperm whales remained in the Mississippi Canyon area, because we very rarely saw or heard sperm whales in this region during cruise 03G06. In contrast, after the LCE had retreated and the follow-on R/V *Gyre* cruise 03G07 resurveyed the Mississippi Canyon region, sperm whales were again seen and heard in Mississippi Canyon. After surface flow that had been on-margin during the flushing event in June 2003 had re-established to be along-margin or off-margin by July 2003, oceanographic conditions (and prey conditions for the sperm whales) there apparently returned to normal.

In Section 3.2, we carried such analyses one step further. We compared the cumulative monthly discharge of the Mississippi River (MR) in May in each of summers 2002-2005 with whether June-July surveys seemed to encounter sperm whales in “typical” abundance along the 1000-m isobath, or whether field teams thought that whales were uncommon there. We reported that, when MR discharge was within normal limits for the month of May for the 26-year record mean, as it was in summers 2002-2004, sperm whales were generally present, even if they were not uniformly distributed, along the 1000-m isobath from 86°W to 92°W. However, in May 2005 when MR discharge was more than one standard deviation below normal limits, SWSS field teams had judged that sperm whales were uncommon everywhere along the 1000-m isobath, from 86°W to 92°W. The post-cruise report of the Mesoscale Population Survey (MPS) fieldwork carried out in June-July 2005 by sailboat *Summer Breeze* makes it clear that sperm whales were seldom heard or seen along the 1000-m isobath near the Mississippi River Delta (O'Hern et al., in preparation). Instead, sperm whales were locally abundant only in the far western Gulf of Mexico, as documented by R/V *Gyre* cruise 05G09 (Jochens and Biggs 2006). Sightings of at least 18 groups of whales were made within a deepwater region of cyclonic (upwelling) circulation in the NW Gulf in June 2005, with very few of these sightings in low-chlorophyll environments to the south and east of the upwelling region.

Our purpose in writing this chapter is to examine the far-field teleconnection conditions that might in part explain why sperm whale encounters during the summer 2005 fieldwork were so very different from those in previous summers. We examine whether month-to-month variability in freshwater discharge of the MR may correlate to, and so be predicted from, variations in climate change teleconnections such as indices of Pacific Decadal Oscillation (PDO) and Atlantic MultiDecadal Oscillation (AMO). Both are cyclic variations in the large-scale atmospheric flow and ocean currents that combine to alternately increase and decrease sea surface temperature (SST). Both operate on a time scale of multiple decades, with a temperature difference of about 0.5°C (AMO) to 1.0°C (PDO) between the extremes of cool and warm phases. Published multi-decadal time series show instances in which variations in both indices are in phase, and other times when variations are out of phase. Our goal in writing this synthesis is to examine the month-to-month variability in both indices during the last 26 years, 1980-2005, and to evaluate by cross-correlation how much of the variability in either index correlates with the month-to-month variability in MR discharge.

The PDO index is the leading principal component of the monthly SST anomalies in the Pacific Ocean, north of 20°N (Mantua et al. 1997). Interannual changes in sign and intensity of this index reflect differences in SST conditions throughout the northern Pacific Ocean, as well as atmospheric pressure changes in the tropical Pacific Ocean. A positive PDO index generally correlates with warmer SST in the Eastern Pacific (Eastern Pacific Warm Phase) and with cooler SST in the western Pacific and in the Gulf of Mexico. A negative PDO index generally correlates with cooler SST in the Eastern Pacific (Eastern Pacific Cool Phase) and with warmer SST in the western Pacific and in the Gulf of Mexico. Chavez et al. (2003) linked these positive and negative phases of PDO with regional changes in Pacific Ocean fishery production. They argued that during the period 1950-2000, fishery production regimes shifted in 1975 and again in 1995. They speculated that the reversal in sign of the PDO index from positive to negative, which occurred during 1999-2002, likely marked the beginning of another regime shift from Warm Phase back to Cool Phase. However, the reversal in sign of the PDO index was apparently only temporary, for the monthly PDO index reverted to a positive sign again late in 2002 and it has varied between positive and negative since 2004.

The AMO index is the average of SSTs north of the Equator in the Atlantic Ocean, between 75°W and 7.5°W and south of 60°N. Enfield et al. (2001) reported that the AMO has been through about two complete cycles since detailed measurements of the Atlantic began in the mid-1880s. A cool phase lasted 25 years from 1901-1925, a 44-year long warm phase from 1926-1969, and a 25-year long cool phase from 1970-1994. A new warm phase began in 1995, and since 1995 many of the monthly AMO index values have been the highest on record.

5.5.2 Methods

Cumulative monthly Mississippi River discharge was calculated from on-line data that are summarized daily as average cubic feet per second discharge by the New Orleans District of the US Army Corps of Engineers for the Mississippi River at Tarbert Landing, MS (gauge 01100). The public-domain website is: *http://www.mvn.usace.army.mil/eng/edhd/Wcontrol/discharge.htm*.

Monthly PDO and AMO data were downloaded from NOAA's National Climatic Data Center (NCDC) research websites *http://www.ncdc.noaa.gov/pub/data/ersst-v2/pdo.1854/latest.ts* and *http://www.ncdc.noaa/gov/Timeseries/AMO/*, respectively. At NCDC, the PDO monthly data are computed from NOAA's extended reconstruction of sea-surface temperature for the North Pacific Ocean, as explained by Mantua (1999). The AMO time series are calculated from the Kaplan SST dataset (5x5) which is updated monthly, as explained by Enfield et al. (2001).

To investigate cross-correlations between PDO, AMO, and river discharge, we started with monthly averaged but otherwise unsmoothed NCDC data. NCDC had detrended the PDO and AMO data sets by removing the mean, so we removed the mean MR monthly discharge 1980-2005, prior to calculating the pairwise cross-correlations. Each of the indices was then low frequency filtered by computing the 24-month running average, and lagged by -36, -30, -24, -18, -12, -11, -10, -9, -8, -7, -6, -5, -4, -3, -2, -1, 0, +1, +2, +3, +4, +5, +6, +7, +8, +9, +10, +11, +12, +18, +24, +30, and +36 months to test for the amount of cross-correlation.

5.5.3 Results

Mississippi River Discharge

Table 5.5.1 summarizes cumulative MR discharge for the month of May for the last seven years, 2000-2006. In two of these years, the cumulative discharge in May was less than 60% of the mean for the 26-year record, 1980-2005 (more than one standard deviation less than the mean May discharge of 59.7 km^3). These anomalies occurred in May 2005 and in May 2000. Figures 5.5.1 and 5.5.2 show the month-to-month cumulative MR discharge in two different ways. Figure 5.5.1 shows running plots of monthly cumulative discharge and monthly discharge anomaly for the 26-year record, 1980-2005. Figure 5.5.2 zooms in for each of SWSS field years 2002-2005, to show cumulative monthly discharge in each of these years in relation to the mean monthly discharge (plus and minus one standard deviation) for the 26-year climatologic average for 1980-2005.

Loop Current Eddy Separation Events

Table 5.5.2 summarizes the year-to-year variability in LCE separation events for the same period 2000-2006. Large (or even bigger = huge) eddies, as measured by the surface area of their warm surface waters, separated in 2001, 2003, 2004, and 2005. As we emphasized in our introduction, one of these (LCE *Sargassum*) interacted vigorously with the continental slope south of the Mississippi River delta in May-June 2003. During that interaction, low chlorophyll water of Caribbean origin apparently flushed the margin, and sperm whales were rarely seen or heard in

Mississippi Canyon until the event had ended. While still attached to the Loop Current in early June 2005, another of these (LCE *Vortex*) also interacted vigorously with the continental slope between Mississippi Canyon and the apex of De Soto Canyon. Panels B and D in Figures 3.2.1 and 3.2.2 in our summary of basin wide conditions in Section 3.2 show these LCE interactions as modeled fields of SSH and SSS. The Mesoscale Population Study field teams on board the sailboat *Summer Breeze* rarely saw or heard sperm whales anywhere near LCE *Vortex* that summer.

Climate Change Teleconnections and Mississippi River Discharge

Figure 5.5.3 summarizes the month-to-month variability in PDO and AMO indices for two climate change teleconnections for the 26-year period 1980-2005. For this 26-year climatology, the monthly PDO is positively correlated with monthly MR discharge, while the monthly AMO is negatively correlated with monthly MR discharge. The highest cross-correlations between MR discharge (y) and PDO (x) are +0.40, and between MR discharge (y) and AMO (x) they are -0.41. These highest correlations occur with time lags of 5-8 months for PDO, and for lags of 7-12 months for AMO. In other words, increased MR discharge lagged positive monthly PDO index by 5-8 months, while decreased MR discharge lagged positive monthly AMO index by 7-12 months.

Table 5.5.1

Cumulative Mississippi River Discharge for the Month of May, 2000-2006

Year	Monthly discharge (km^3)	May discharge as % of 26 yr record mean
May, 2000	31.1	54
May, 2001	40.4	70
May, 2002	68.1	118
May, 2003	56.4	98
May, 2004	50.5	88
May, 2005	34.0	59
May, 2006	37.9	66

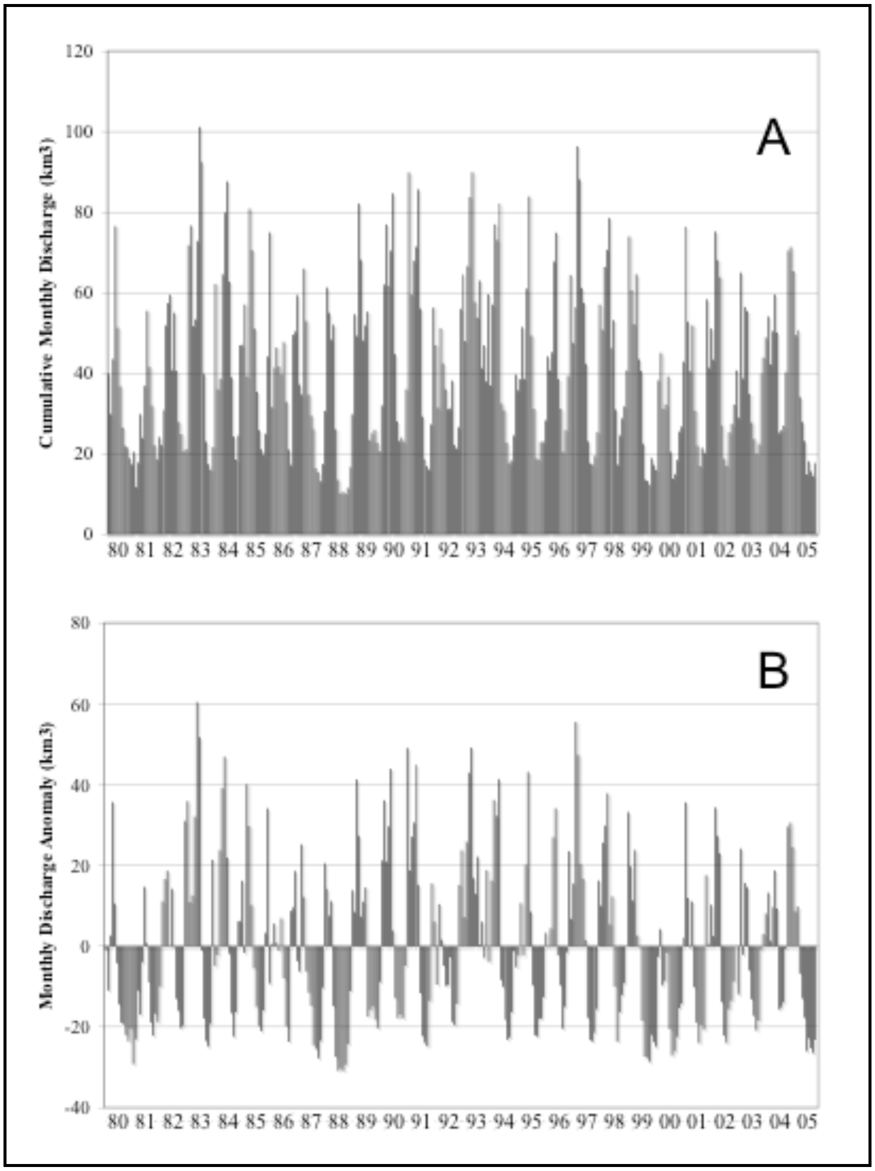

Figure 5.5.1. Mississippi River discharge for 1980-2005. Shown are: A) Monthly cumulative discharge (km^3) of the Mississippi River at Tarbert Landing, MS, for the period 1980-2005. B) Discharge as monthly anomaly greater or less than the mean discharge of 40.8 km^3 for the 26-year period.

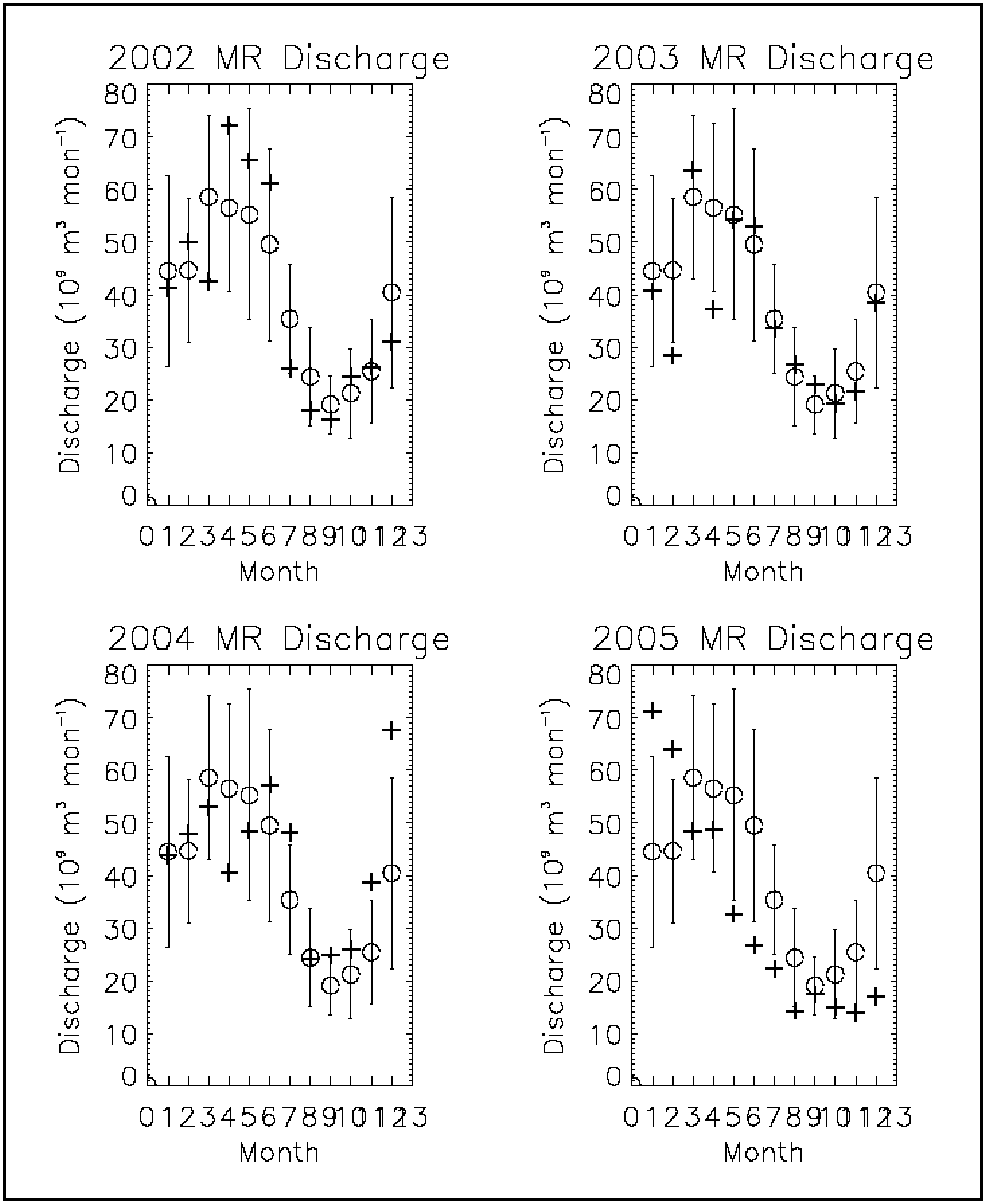

Figure 5.5.2. Monthly cumulative discharge (km^3) of the Mississippi River at Tarbert Landing, MS, for SWSS field years 2002-2005. The "+" symbols plot month-by-month data for each month of 2002-2005, relative to dot-and-whisker designation of monthly mean discharge (± one standard deviation) for the 26-year period of record, 1980-2005.

Table 5.5.2

Loop Current Eddy Separation Events, 2000-2006
(from Leben 2005, with additional information from Horizon Marine, Inc.)

Eddy Number	Eddy Name	Eddy Size	Year	Comments
1	Juggernaut	huge	1999-2000	separated Oct 99; dominated central Gulf in 2000; dissipated in SW Gulf
2	Kinetic	small	2000-2001	dissipated or merged with other old eddies in w Gulf
3	Lazy	small	2000	dissipated in n central Gulf
4	Millennium	huge	2001	separated Apr 01; reattached to Loop after 1 week
5	Nansen	medium	2001	separated Sep 01; merged w Odessa Nov 01; reabsorbed by Pelagic/Loop Current
6	Odessa	medium	2001	briefly attached to Nansen, reattached late Nov 01; reabsorbed by Loop
7	Pelagic	huge	2002	separated Feb 02; mostly western extension of Loop water; dissipated in w Gulf
8	Quick	huge	2002	separated Mar 02; shed QE-2 shortly thereafter; dissipated in w Gulf
9	QE-2	small	2002	shed from n front of Quick Eddy; dissipated in central Gulf
10	Rebel	small	2002	formed in e Gulf from LC outflow; dissipated in central Gulf
11	Sargassum	huge	2003	separated from & rejoined LC several times May-July 03; final separation Aug 03
12	Titanic	large	2003-2004	separated late Dec 03; dissipated in w Gulf
13	Ulysses	huge	2004-2005	separated Sep 04; shed U2 early in 2005
14	U2	small	2005	pinched off NE edge of Eddy U; later merged again with Eddy U
15	Vortex	large	2005	separated from & rejoined LC several times before final separation
16	Walker	medium	2005-2006	separated & rejoined several times with final separation (as small eddy) in Feb 06
17	Xtreme	medium	2006	separated Mar 06

5.5.4 Discussion

The average cumulative monthly Mississippi River discharge for May of the last 26 years 1980-2005 was 57.5 ± 20.9 km^3. Each year the highest monthly cumulative Mississippi River discharge generally occurs in March-April-May, and the lowest in August-September-October (see Figure 5.5.2). Because flow gauged by the US Army Corps of Engineers at the Tarbert Landing location takes about 1-2 weeks to enter the Gulf, we regard the cumulative May discharge as a proxy for the volume of freshwater on the continental shelf in the month of June. In Table 5.5.1 we have summarized the year-to-year variability in the May discharge of the Mississippi River for SWSS field years 2002-2005. Cumulative river discharge in May 2002, May 2003 and May 2004 ranged from 12% below to 18% above average, but cumulative discharge in May 2005 was only 59% of average. The May 2005 discharge was more than one standard deviation less than the average May discharge for the period 1980-2005. Table 5.5.1 also includes May discharge data for SWAMP field years 2000 and 2001, and for May 2006. We emphasize that May 2000 discharge was also more than one standard deviation less than the average May discharge for the period 1980-2005. Biggs et al. (2005), in their Plate 1, show that sperm whales were encountered only infrequently along the 1000-m isobath in the NE Gulf during SWAMP 2000 Leg 1 (late June to early July 2000). SeaWiFS ocean color for this period show that high SSC green water near the mouth of the MR was found close in, over continental shelf depths. As a result, most of the surface water along the 1000-m isobath was low SSC, blue water. It was not until SWAMP 2000 Leg 2 (mid to late July 2000), when a combination of LCE-K and a warm slope eddy interacted with the margin there to pull green water off-margin, that sperm whales were encountered in typical abundance there (Biggs et al. 2005).

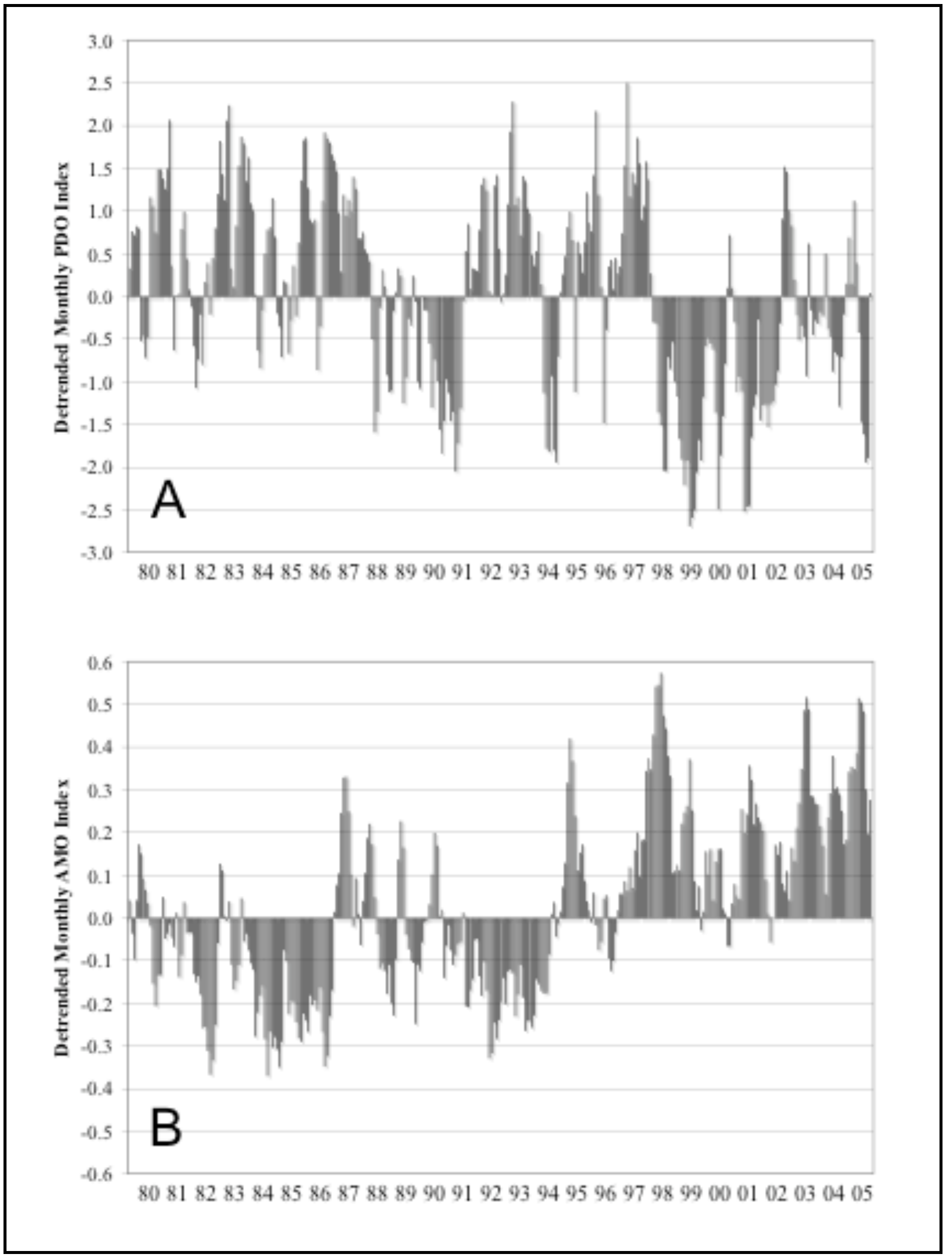

Figure 5.5.3. Monthly PDO and AMO indices for the period 1980-2005 (data from NOAA-NCDC).

Our qualitative perception from S-tag 2005 and sailboat *Summer Breeze* fieldwork is that the distribution and abundance of sperm whales in 2005 was also different than in previous years 2002-2004. The low volume of May 2005 discharge, coupled with the mostly on-margin flow of surface currents, resulted in a pattern of on-margin and off-margin flow that was strikingly different in 2005 than for that of previous years 2002, 2003, and 2004. The NGOMNFS numerical model outputs shown in Section 3.2 demonstrate that high salinity water extended well up onto the outer shelf between 93°W and 89°W in June 2005, whereas high salinity surface water seldom covered more than about a third of the 1000-m isobath in previous summers 2002, 2003, and 2004. The exception was June 2003, when LCE Sargassum flushed the 1000-m isobath with high salinity water of Caribbean origin, from about 92°W to 89°W. However, conditions had returned to "normal" along the 1000-m isobath by July 2003, and sperm whales were once again heard and seen in Mississippi Canyon on cruise 03G07 (SWSS 2003 Leg Two).

During episodes of strong on-margin flow (June 2003 and June 2005), the whales apparently moved east or west away from the disturbance. In June 2003, whales were seen and heard at the northern periphery of LCE *Sargassum*. In June 2005, whales were seen and heard in a deepwater region of upwelling in the NW Gulf, rather than where we expected to encounter them spaced out along the 1000-m isobath, between 93°W and 89°W. However, photo-ID data tell us that the whales in the upwelling area in 2005 were not the same individuals seen to the east in previous summers 2002-2004. Further, S-tag data from these animals show they generally stayed in the northwest Gulf (Section 4.3). So apparently these were not animals that had sought out or ended up in this cyclone, after the areas of the 1000-m isobath to the east were flushed with on-margin flow of low productivity, high salinity open ocean water. We do not know where the animals normally encountered in the northeast and north central Gulf went in summer 2005. It is possible they went further offshore, i.e. south of the region 27°N-28°N where we put the focus of our acoustic and visual search effort.

In summary, we hypothesize that summer-to-summer differences in the cumulative discharge of the Mississippi River are the primary physical forcing function for variations in when and where sperm whales are encountered along the 1000-m isobath of the northern Gulf. In this report, we have emphasized that when MR discharge was unusually low, during June-July 2000 and June-July 2005, encounters with whales along the 1000-m isobath of the NE Gulf were infrequent, except when and where the local eddy geometry either set up the off-margin transport of high SSC from the continental shelf to the continental slope, or when upwelling in cyclonic eddy(s) allowed locally higher SSC to grow in via new production. As a corollary, encounters with whales were more frequent in summers 2002, 2003, and 2004, except when and where the local eddy geometry flushed the margin with low-SSC, oligotrophic Caribbean water.

In general, most of the sperm whales seen or heard on S-tag cruises, D-tag cruises, or MPS surveys were encountered within tens of kilometers of areas of off-margin surface flow of green water. The ocean color dataset of weekly and biweekly composites (see the CDROM appendix to the paper by Biggs et al. 2005) tells us that eddy geometry that sets up these flows changes on a week-to-week time scale, so our attempts to link whale encounters with off-margin flows certainly have that temporal limitation. We also think, based on S-tag trajectory data from periods of the high-resolution (4 times a day) reporting in summer 2002 that most whales are moving around from kilometers to tens of kilometers a day as they forage. So we're not surprised that whales do not stay exclusively within the footprint that one-week composites of color data tell us were where these off-margin flows of locally higher SSC were located. But we hypothesize that there may be more prey for sperm whales to find in the deep midwater below these off-margin flows, because we hypothesize these off-margin flows are regions of locally higher export production out of surface waters. Preliminary findings of the acoustic assessment of sperm whale distribution, habitat, and habitat use by Benoit-Bird and Ortega-Ortiz support this hypothesis, since they reported that fishery echosounder volume scattering in the water column was significantly higher when whales were detected (Section 5.3; see also Section 5.2).

The cross-correlations reported here between climate teleconnection indices and MR discharge are encouraging, for they suggest that up to 40% of the monthly variation in MR discharge can perhaps be predicted 5-12 months in advance. The teleconnection link between the temperature conditions in the North Pacific and North Atlantic and the amount of physical oceanographic variability in the Gulf is the difference between local precipitation and evaporation averaged over the area of the Mississippi River drainage basin (McCabe et al. 2004). Enfield et al. (2001) reported there is a generally negative correlation between rainfall over the Mississippi River drainage basin and the sign of the AMO index. Given this, one would expect decreased river outflow into the Gulf during periods of positive AMO index. However, the high-frequency correlation is not that perfect, since the lowest river discharge of the 26-year period 1980-2005 took place in 1988, a year in which much of the monthly AMO index was negative. We have been unable to find any report(s) of a teleconnection link between MR discharge and the sign of the PDO index. However, Jim Tolan (personal communication 2006) is completing a manuscript in which he reports a 12-36 month lag between the PDO index and the salinity of some of the estuaries along the Texas coast. Tolan has determined that periods of positive PDO index correspond to conditions in which evaporation exceeds precipitation in Texas, so these periods are followed 1-3 years later by increased salinity in Texas estuaries. The opposite is apparently true for the Mississippi River drainage basin, for we found that periods of positive PDO index tended to be followed 5-8 months later by increased MR discharge.

Although SWSS did not field any surveys for sperm whales in the summer of 2006, Table 5.5.1 presents the MR discharge data for May 2006 and we have reviewed the eddy field. The cumulative MR discharge for May 2006 was one-third lower than average, and by July the LCE called *Xtreme* was interacting with the 1000-m isobath between Mississippi Canyon and the apex of De Soto Canyon. So from a physical oceanographic point of view, we expect that conditions along the 1000-m isobath of the northeast and north central continental margin should have been quite similar to those of summer 2005. The NGOMNFS model results for summer 2006 support this view (*http://www.7320.nrlssc.navy.mil/IASNFS_WWW/NGOMNFS_WWW/NGOMNFS_intro.html*). OSU's S-tag trajectory data indicate that two whales tagged in the far western Gulf in summer 2005 moved east to the Mississippi Canyon where they stayed for less than a week before moving slowly back west; the other ten whales stayed close by the area where they had been tagged (see Section 4.3). So we would predict for summer 2006 that whales were probably uncommon once again along the 1000-m isobath for most of the northern Gulf.

6 RESPONSES OF SPERM WHALES OF THE NORTHERN GULF TO ANTHROPOGENIC NOISE

With geophysical exploration moving into the deepwater Gulf of Mexico where the sperm whale population lives, a prime motivation for SWSS was to assess the possible response of the sperm whale population in the northern Gulf to the sound emitted by seismic airguns. This was the focus of SWSS objective 3. Two approaches were taken. The major study approach used D-tags to measure received sound levels and monitor behavior of sperm whales in Controlled Exposure Experiments (CEEs) of the whales to airgun sounds. A secondary, opportunistic approach used S-tag and other whale location data with temporally coincident locations of operational seismic surveys. Section 6.1 provides a synopsis of the CEE results and the opportunistic study results that were detailed previously in Sections 7 and 8, respectively, of the SWSS Summary Report (Jochens et al. 2006). Ongoing analyses by the D-tag and S-tag teams are summarized in Section 6.2 for CEEs and Section 6.3 for the S-tag opportunistic study.

6.1 Synopsis of Responses to Anthropogenic Noise

6.1.1 Controlled Exposure Experiments

Introduction

WHOI developed the D-tag to sample sounds and behavior of the tagged whale throughout its dive cycle. The tag was designed to measure acoustic exposures directly at the whale and to measure the orientation of the animal in three dimensions at a sampling speed and resolution that would observe individual fluke strokes (see Johnson and Tyack 2003 for tag details). These measures then could be used to assess behavioral responses of the whales throughout their dives, estimate functions and costs of behaviors that would allow inference of biological significance of behavioral disruption, and develop a dose:response function by measuring the received level of the sound at the whale while also measuring the animal's behavioral responses.

WHOI designed an experimental method, the controlled exposure experiment (CEE), that uses controlled exposures to sounds to develop an acoustic dose: behavioral response function for the whales studied (see Tyack et al. 2004 for additional discussion of this method). Many of the measurement properties of the D-tags were optimized for this kind of study. Because many potential impacts are very difficult to detect, no experiment or monitoring method can prove absolutely that there is no adverse impact to marine mammals. However, CEEs allow testing of specific hypotheses about potential impacts. To address the issue of likely biological significance to the population, WHOI designed the SWSS D-tag/CEEs to evaluate effects of airguns on avoidance, foraging, and communication of sperm whales in the northern Gulf of Mexico (see Section 7.1 in the SWSS Summary Report for details on the test design). The data collected on the two D-tag/CEE cruises conducted under SWSS in summers 2002 and 2003 were analyzed to study the potential effects of airgun sound exposure in terms of avoidance and changes in foraging effort during the course of several dive cycles.

Each CEE subject was followed after tagging and before exposure to provide a pre-exposure control. The seismic vessel was initially positioned approximately 7-13 km from the tagged animal and its associated group and then a ramp-up firing of the airguns began. The vessel then was directed to move in closer toward the animals with an exposure to a full-array firing of up to 2 hours (2 dive cycles). Care was taken to monitor the locations, not only of the tagged animal, but also other animals in the group in order to avoid excessive exposure to any of the animals in the group.

Data from the exposure period were compared to pre- and post-exposure data collected within 90 minutes of an airgun firing. Most animals carried the D-tag for long enough after exposure stopped that the post-exposure control period could be used in analysis. However, analysis of the pre-exposure data sets from 2002 showed that the first dive after tagging was affected by the response of the animal to the attachment of the tag itself, while the second dive was not statistically different from later ones. If the first dive is removed from the pre-exposure data of 2002, the duration is not long enough to use for a pre-exposure control period as only 1-2 dives were recorded after tag attachment. This problem was remedied in 2003 by modifications to the D-tag that allowed longer pre-exposure periods with 3-8 dives being made after tag attachment. However, to be able to include the 2002 data in the statistical analyses, only comparisons of post-exposure data were made to exposure data.

The NMFS (2003) defined the safety radius for cetaceans as the radius from a seismic sound source within which received levels are 180 dB re 1 μPa (rms) and the distance within which some cetaceans may be subject to behavioral disturbance as the radius from a seismic sound source within which received levels are 160 dB re 1 μPa (rms). NMFS also established 180 dB re 1 μPA (rms) as the maximum received level permissible under the D-tag/CEE permits. The primary goal of the SWSS D-tag/CEEs was to assess the effects of seismic airgun pulses on sperm whales with a target received level of 120 to 160 dB re 1 μPa (rms). Madsen et al. (2006; Table II) report that in 2002, two CEEs were conducted involving 4 subjects with maximum received levels of 135-144 dB re 1 μPa (rms). They report that in 2003, three CEEs were completed also with a total of 4 subjects with maximum received levels of 146-147 dB re 1 μPa (rms). Following the argument of Madsen (2005; see below) that a safety threshhold in terms of peak-to-peak measure of received level would be better than the RMS measure, the 8 whales for which these CEEs were conducted were exposed to maximum sound levels between 131 and 164 dBp-p re 1 μPa (111 – 147 dB re 1 μPa (rms)) at ranges of approximately 1.4-12.6 km from the sound source (Table II in Madsen et al. 2006).

The extensive discussion of D-tag/CEE results was reported on Section 7 of the SWSS Summary Report (2006) and in peer-reviewed journals. The D-tag/CEE work that examines technical sound propagation issues (RMS safety thresholds for transients, quantitative measures of airgun sounds at the tags, and acoustic propagation of airgun sounds) is summarized first below. This is then followed by summaries of the results on avoidance and foraging behaviors.

RMS Measures as Safety Thresholds

Madsen (2005) evaluated the SWSS D-tag/CEE data sets to consider the consequences of using the maximum root-mean-square (RMS for method, rms for units) sound pressures of 180 dB re 1 μPa (rms) for cetaceans as safety thresholds for transient sounds impinging on marine mammals (see also Section 7.3.3 in the SWSS Summary Report). He found three main possible problems with this approach. First, the RMS measure does not represent the total energy exposure of the noise pulse impinging at the animal. Second, different RMS measures can be derived for waveforms with identical peak pressure depending on the duration over which the squared pressure is averaged. Third, the RMS measure does not represent the exposure level of transients with high peak pressure and a slowly decaying tail as is common in reverberant underwater environments. Because of these limitations, Madsen (2005) concluded that RMS safety measures are unsuited as a stand alone mitigative measure for possible transient noise effects on marine mammals irrespective of what the absolute level is. He recommended that safety levels for noise transients include a maximum peak-peak received sound pressure level in concert with a maximum received energy flux density level.

Quantitative Measures of Airgun Pulses Impinging on D-tags

Sound energy can radiate both on and off the vertical axis of an airgun array, which emits a downward directed energy pulse. Radiated peak pressures off-axis can be an order of magnitude lower than those on-axis (Madsen et al. 2006), so many investigations into effects on marine mammals have focused on the peak pressures generated on the acoustic axis rather than on the off-axis. Considering that most marine mammals will receive acoustic energy from the off-axis levels, Madsen et al. (2006) used the SWSS D-tag/CEE data to investigate the actual sound field received by sperm whales during exposure to an airgun sound field (see also Section 7.3.4 of the SWSS Summary Report). Their analysis showed that each firing of the airgun array exposed sperm whales to several pulse arrivals, derived from the primary pulse traveling along different propagation paths, that had different spectral, energetic and temporal properties. It showed that some of the direct arrivals had dominant energy at higher frequencies than currently reported or modeled (0-1000 Hz) for airgun arrays. While the energy radiated off the axis of the array is considerably lower than on the axis, the absolute levels of these high frequency pulses may reach received levels of more than 160 dB re 1 μPa (p-p) at ranges of more than 10 km. Madsen et al. (2006) concluded that models based on simple geometric spreading laws were inadequate to obtain accurate predictions of received levels at diving sperm whales and that complex multipath acoustic propagation models were needed (see also DeRuiter et al. 2006, summarized below).

Modeling Acoustic Propagation of Airgun Sounds

DeRuiter et al. (2006) modeled acoustic propagation of airgun sounds for the environmental conditions present during SWSS D-tag/CEEs and compared the model results to the received levels recorded by the D-tags on sperm whales. They successfully explained the relative levels of multipath arrivals that were recorded, but could not model absolute received levels because of the lack of the airgun source signatures at all launch angles. They found that, under environmental conditions where surface-ducting was present, whales located near the surface may be exposed to measurable high-frequency sounds (above 500 Hz) derived from the airgun emissions. They noted that the surface duct and its effects on acoustic propagation and received levels were present during only one of the two SWSS cruises, thus demonstrating the importance of the variability of oceanographic conditions, both temporally and spatially, on the characteristics of acoustic propagation. DeRuiter et al. (2006) concluded that the received level at the whale depends on multiple factors that should be accounted for in any model. These factors include source-receiver range, on-axis source level, source beampattern, sound speed profile of the water column, bathymetry, and bottom properties of the specific locale. They recommended that the airgun array source signatures be characterized at a full range of angles and at frequencies up to several kilohertz.

Avoidance Behavior

The location data from the tagged whales and the airgun source vessel allowed each tagged animal to be tracked and its orientation and movement relative to the airgun source to be determined. Miller et al. (2005) determined a 3-dimensional pseudotrack of each subject whale's movement during the experiment. They checked the accuracy of the pseudotrack against the visual observations and found generally good agreement. They determined the direction of movement of each tagged whale over a series of 30-minute intervals during pre-exposure, ramp-up, and full-array firing. They then used circular statistics (Zar 1984) to compare the movements of each animal relative to the airgun source vessel and to that animal's previous direction of movement (see also Section 7.3.5 of the SWSS Summary Report). The results of this analysis showed no evidence for avoidance reactions during ramp-up relative to that before exposure to the airgun sounds and during full-array firing conditions relative to that before exposure; the range of exposures was between 1.4 and 12.6 km.

Miller et al. (2005) found that the direction of movement did not change for any of the eight exposed whales at the onset of gradual ramp-up at ranges of 7.3-12.5 km nor during full power exposures at ranges of 1.5-12.6 km. Acoustic exposure ranged from 111 to 147 dB re 1 μPa (rms)(131 to 164 dBp-p re 1 μPa; see Table II in Madsen et al. 2006). For seven of the eight animals, they found that the gross diving behavior did not change. Results were different for the whale that had the highest received levels of the 8 animals from the airgun source. This whale rested at the surface for an interval of over 4 hours, which was twice as long as the 10 other resting bouts of ≤ 2 hours that were observed for this animal in SWSS. It dove immediately following the final airgun transmission. This behavior suggests the possibility that the animal had responded to the airgun sounds by resting at the surface until airgun exposure ceased.

Foraging Behavior

Miller et al. (2005) assessed the effects of airgun emissions on the foraging behavior of sperm whales by using a model estimating costs and benefits of foraging (see also Section 7.3.5 of the SWSS Summary Report). They used the animal's pitching energy, which reflects fluking movements, to estimate locomotion cost and buzz-rates (creaks) to measure feeding rates (Miller et al. 2004a; see Section 7.2 of the SWSS Summary Report for a discussion of evidence that buzzes correspond to attempts to capture prey). Data from the 7 whales that made at least one dive in pre-exposure, exposure, and post-exposure conditions were used for this analysis. Data from the whale that rested at the surface during the exposure were not included. Further, pre-exposure conditions were not compared to exposure conditions because of the lack of sufficient data from 2002, and data from ramp-up periods were removed because of the mix of airgun acoustic transmission levels, from very low-levels at the start to full levels at the end, over the 25-30 minutes of the ramp-up period.

Using an ANOVA, Miller et al. (2005) compared foraging response measures between full-array exposure and post-exposure control periods for the 7 whales. The comparison included a range of full-array exposures at <120-147 dB re 1 μPa (rms) (Tyack 2005). Miller et al. (2005) found pitching movements generated by swimming motion were 11% lower during full-array exposure relative to the post-exposure ($F_{1,6} = 6.80$, $P < 0.05$). Buzz rates were 24% lower during the full-array exposure condition than the post-exposure condition, but this effect was not statistically significant at the 0.05 level ($F_{1,6} = 2.62$, $P = 0.16$). They concluded that the data indicate a reduced foraging effort during airgun emissions.

Given the low sample size of exposure subjects, a Bayesian analysis was conducted to quantify the odds-ratio for whether the data support models of increase, decrease, or no change in buzz rate (the proxy for foraging) and pitching movement (the proxy for locomotion costs). The first result indicates that a decrease in buzz rate is 3.6 times more likely than no change given the data (Section 7.3.5 of the SWSS Summary Report). This Bayes factor is considered to be "substantial" or "positive" evidence for an effect (see Ellison 1996). The second analysis indicates that a decrease in pitching movement is 2.9 times more likely than no change. Additional CEEs are necessary to increase the sample size to numbers yielding the desired statistical power (see Tyack 2005 for a detailed discussion of the statistical power of this analysis). However, this analysis suggests that the odds favor the conclusion that there is a 20% decrease in foraging attempts at exposure levels ranging from 111 to 147 dB re 1 μPa (rms) (131 to 164 dBp-p re 1 μPa; see Table II in Madsen et al. 2006) at distances of roughly 1-13 km from the sound source than that there is no effect.

DeRuiter et al. (Section 6.2 of this report) used statistical methods to assess further the effects of airgun exposure on the foraging rates of each individual sperm whale in the experiment. They used both parametric testing and nonparametric rotation testing to test the null hypothesis that the buzz rate (the proxy for foraging rate) is constant for each whale with the alternative hypothesis being that the buzz rate is reduced during exposure to airgun sounds. They found the two test approaches were in relatively good agreement, and that the airgun exposures resulted in statistically significant reductions of up to 60% in foraging rates for some individuals, but that small reductions in foraging rates could not be detected given the statistical power of the test. They concluded that to test for smaller changes in foraging rates, the statistical power of the tests would have to be increased. Additional CEEs are needed to increase both the sample size and the duration of the control and exposure periods that are compared.

6.1.2 Opportunistic Studies of Seismic Survey Activity and Sperm Whales

Seismic Survey Activity and the Proximity of S-Tagged Whales

One possible indication of avoidance by sperm whales of seismic airgun sounds is whether whales occurred less frequently than expected in the vicinity of active seismic vessels. In Section 8.1 of the SWSS Summary Report (Jochens et al. 2006), Winsor and Mate assessed this by statistically comparing whale locations from the S-tags to positions of active seismic vessels in the Gulf of Mexico at corresponding times. High-quality locations, numbering 1167, from S-tags on 33 sperm whales were correlated with 6821 seismic lines from 6 June 2002 through 16 August 2004. A total of 30 high quality locations from 12 animals were determined to be within

25 km of an active vessel. The time differences between start of the seismic line and whale location varied from 0.65 h to 4.8 h, with a mean of 2.2 h and standard deviation of 1.24 h. Distances were tabulated into 5 km classes. No distances were less than 5 km and five of the 30 locations were 5 to 10 km from a vessel. When more than one observation was obtained from an individual, its contribution to the distance class was inversely weighted by the total number of observations for that animal. This addressed possible effects of pseudoreplication, maintaining a total sample size of 12 animals yet utilizing all the observations.

Chi-square testing and Monte Carlo simulations were applied to compare the observed with the expected number of observations for the various distance classes. There was no evidence for non-randomly distribution of distances between whales and active vessels, but due to a lack of sufficient sample size, these results cannot refute a possible avoidance or other behavioral response. A sample size of 25, double what was available, would be needed to have the statistical power to detect a non-random distribution from 5 km and further. A much larger sample size (75) is needed for analysis closer than 5 km. An additional source of uncertainty is the positional error from the Argos-derived locations.

Winsor and Mate (Section 6.3 of this report) extended their analysis to include all data obtained through 2006. The augmented data set of distances <25 km from active seismic sources showed no evidence of a non-random distribution, provided no distances less than 5 km are considered. However, it did not provide a sample size (n=17) large enough to sufficiently increase the statistical power to confidently assume a random distribution. Therefore results were consistent with those reported in the SWSS Summary Report, as summarized above.

Fine Scale Movements in Response to Seismic Line Starts

In the course of work surveying for sperm whales and keeping track of groups at the surface to support tagging, genetic sampling and photo-identification, the visual teams on the R/V *Gyre* logged the location, general behavior, and heading of every cluster of sperm whales seen at the surface. Gordon et al. (Section 8.2 of the SWSS Summary Report) analyzed the 2002-2004 data to investigate medium term responses of whales to seismic surveys which were occurring in the area. Matched pairs of data on whale and seismic line locations were determined for two hours before and two hours after line starts and line ends for survey lines within 100, 50, and 25 miles of the whales. Within the limits of the data sets available, no significant responses were detected in (1) heading relative to the bearing to the seismic survey locations, (2) time spent at the surface, or (3) surfacing rate in the comparisons of matched pairs.

6.1.3 Summary

The CEE results detected no horizontal avoidance to exposure levels to seismic airgun sounds of <150 dB re 1 μPa (rms); similarly, opportunistic studies detected no apparent horizontal avoidance or displacement of whales associated with operational seismic surveys. The CEE data do not support the assumption that whales swim away from an airgun array as it ramps up or approaches the whale at full power. However, there were no exposures above 164 dBp-p re 1 μPa (147 dB re 1 μPa (rms)). Further research would be required to test for avoidance at higher received levels. Further, the whales were tagged in a region with substantial human activity, and so they are not naïve to human-generated sounds. Gulf of Mexico sperm whales, at least in the area studied, may have some level of acclimation to seismic airgun sounds. Follow-on studies in regions not as affected by human activities are needed to address the issue of habituation.

In contrast to the lack of avoidance responses, the CEE results showed there may be statistically significant changes in the swimming and foraging behavior of sperm whales exposed to the sounds of airgun arrays in the exposure range of 111 to 147 dB re 1 µPa (rms) (131 to 164 dBp-p re 1 µPa; see Table II in Madsen et al. 2006) at distances of approximately 1.4-12.6 km from the sound source. The responses studied were selected for likelihood of biological significance, and are of particular interest given the small size of sperm whales in the northern Gulf. The acoustic measurements from D-tags demonstrate the necessity to measure exposure at the animal to detect critical responses – signals measured at the animal were very different from those predicted. The likelihood of an effect of seismic survey on foraging of sperm whales suggests the need for a larger sample of CEEs with longer exposure and control periods to increase the power of the test to detect effects. The discovery of a statistically significant 60% reduction in foraging for one whale coupled with evidence that other whales are less sensitive, emphasizes the need for statistical techniques to assess responses for each individual subject and for a broad coverage of age and sex classes of whales selected as subjects.

6.2 Modeling Sperm Whale Responses to Airgun Signals

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6.2.1 Introduction

We have developed several statistical methods to analyze data from the 2002 and 2003 SWSS experiments in which sperm whales were tagged with D-tags and exposed to airgun signals. This work has allowed us to assess the effects of airgun exposure on sperm whale foraging rates. Ultimately, we plan to use a similar statistical approach to quantify the relationship between noise exposure level and change in foraging rate. Once that relationship has been established, this approach could use literature data and established modeling methods to relate changes in whale foraging rate to changes in reproductive success, and finally to relate individual reproductive success rates to population growth rates. Such a modeling approach would facilitate a noise-management approach in which managers can regulate noise exposure levels based on the predicted effects of noise level on population growth rate.

6.2.2 Methods

Data Collection

The data analyzed in this study were collected during controlled exposure experiments conducted on the 2002 and 2003 SWSS cruises. During the experiments, eight sperm whales were tagged with D-tags, which recorded sound and movement data. The tags recorded data for approximately 4-17 hours per whale, including 1-2 hours of airgun exposure. The distance between the tagged whales and the airgun source vessels varied from about 1-13 km, and the received levels of airgun signals recorded on the D-tags ranged from <131-164 dB re 1 µPa peak-peak (many airgun arrivals were so quiet that it was impossible to quantify their received level above background noise). Data from seven of the eight whales were analyzed in this study, since one whale did not forage at all during airgun exposure. More detailed information on the experimental methods and the quantification of received sound levels is available in the SWSS 2002 and 2003 cruise reports (Jochens and Biggs 2003, 2004) and in Madsen et al. (2006).

For all statistical analyses, we used the rate of echolocation buzzes recorded on the D-tags (which indicate attempted or successful prey capture events) as a proxy for foraging rate (Miller et al. 2004a). We are confident that when a whale switches from regular clicks to a buzz, it has made a decision to attempt to capture a prey. Some capture attempts may not be successful, but use of buzz rate as a proxy for foraging in the context of a disturbance study would only be misleading if animals had higher success rates when disturbed, which seems unlikely.

Statistical Analyses – Parametric Test

In order to apply a traditional parametric test to determine whether sperm whale buzz rate changes during airgun exposure, we had to assume that the buzzes were Poisson distributed. That assumption is probably invalid, since buzz production rate will vary if a whale's food is patchy in either space or time and since inter-buzz intervals do not fit a negative exponential distribution (as would be expected for a Poisson process). However, we present the methods and results of the parametric test here for comparison with the nonparametric rotation test we have developed, which uses the empirical distribution of buzz rates and does not require any assumptions about how well the buzz rate dataset fits an analytical distribution.

Under the assumption that buzz production is a Poisson process, the number of buzzes during the control period (N_c) should have a negative exponential distribution. Our null hypothesis was that the foraging rate is constant for each whale; our alternate was that foraging rate is reduced during airgun exposure. Conditioning on n (the total number of buzzes produced during the experiment), N_c will have a Binomial distribution. The p-value of the test is the probability of getting the observed number of control buzzes, N_c, from the appropriate Binomial distribution. We used Fisher's method to account for multiple statistical tests and obtain a combined p-value indicating whether at least one of the seven whales showed a statistically significant reduction in foraging rate during airgun exposure (Fisher 1948). We also tested the hypothesis that all seven whales showed a concerted reduction in foraging rate in response to the airgun exposure. Assuming a normal approximation to the Binomial distribution, the sum of all seven whales' N_c values ($N_{c,all}$) will have a normal distribution. The p-value of the test is the probability of obtaining the observed value of $N_{c,all}$ from the appropriate Normal distribution. We calculated a method-of-moments estimate of the reduction in foraging rate during airgun exposure, and we estimated the power of the parametric tests using synthetic datasets.

Statistical Analyses – Nonparametric Rotation Test

We also developed a nonparametric method to test the null hypothesis that an individual whale maintains a constant buzz rate through control and airgun conditions. This test did not require us to make any assumptions about the distribution of the buzzes in the time series, and could therefore deliver accurate results even if the buzzes occurred in clumps or if the buzz time-series was autocorrelated.

The test statistic was again the observed number of buzzes during control conditions (N_c). To get a distribution for the test statistic, we used a "rotation test" method to resample the data. Our rotation test is similar to randomization or bootstrapping procedures in that it involves resampling the dataset to determine a distribution (or confidence bounds) for a parameter of interest. For each rotation of the dataset, we kept the time-series of buzzes intact, and held the duration of the airgun exposure constant, but randomly shifted the nominal start time of the exposure to any time within the experiment. We then calculated $N_{c,rotated}$ for the rearranged dataset. We repeated the process 10,000 times to construct a distribution of $N_{c,rotated}$ and to calculate the p-value of the test (the probability of $N_{c,rotated}$ being at least as large as the N_c value observed in the data). We again used Fisher's method to obtain a combined p-value for all seven whales. We also tested the hypothesis that all seven whales showed a concerted reduction in foraging rate during airgun exposure; for that test we used the sum of N_c (for all whales) as our test statistic, and again determined its distribution with a rotation test.

6.2.3 Results

Table 6.2.1 shows the p-values of all statistical tests; Figure 6.2.1 shows the results in graphical form, including 95% confidence intervals for the expected buzz rate during airgun exposure (based on the distribution of values obtained by applying the rotation test). Applying Fisher's method to either the parametric or rotation test results indicated that at least one of the seven whales reduced its foraging rate by about 60% during airgun exposure, and that reduction was statistically significant at the $p=0.05$ level. However, we found no evidence for a concerted reduction in foraging rate during airgun exposure by all seven whales ($p=0.19$, rotation test). Figure 6.2.2 shows the power of the parametric test to detect changes in foraging rate in response to airgun exposure. (We do not present a similar figure for the rotation test because it is impossible to calculate the power of the test without specifying the process (Poisson, Autoregressive, etc.) that generated the data, and the actual process which generated our sperm whale data is unknown.) The test has more power to detect a concerted change by seven whales that to detect a change by a single whale, and it does not have sufficient power to detect small changes in foraging rate (power > 0.8 only for >15% reduction by all seven whales or >40% reduction by a single whale).

6.2.4 Conclusions

Results of the parametric and rotation tests are in relatively good agreement, although the rotation test gives slightly larger p-values in some cases. We believe that the rotation test method of statistical analysis is superior to the parametric method, which depends on the assumption that buzz production is a Poisson process. That assumption is probably invalid, since buzz production rate will vary if a whale's food is patchy in either space or time. In fact, inter-buzz intervals do not fit a negative exponential distribution (as would be expected for a Poisson process).

Table 6.2.1

Results of Statistical Analyses

Whale	p-value (parametric test)	p-value (rotation test)
1	0.78	0.70
2	0.54	0.54
3	1.40e-4	0.069
4	5.20e-5	0.0021
5	0.93	0.92
6	0.88	0.72
7	0.13	0.13
Group of 7 whales		
Fisher's method	0.0001	0.036
Concerted change	0.083	0.19

Our data seem to indicate that airgun exposure – even at the low exposure levels observed in this experiment – can result in large reductions in foraging rate for some individual sperm whales. The ability of our method to statistically analyze the response of each individual whale is well suited to our long term goal of interpreting the effect of changes in foraging on population parameters. If the reduction in foraging tends to occur in reproductive females, this could have a larger impact on reproduction than if it occurs among males. It is also reasonable to expect that different age/sex classes, and individual whales with different histories of exposure would have different patterns of behavioral response. Unfortunately, the power of our statistical tests to detect small reductions in foraging rate was quite low. In future experiments, increasing the duration of the experiment (both control and airgun exposure periods) and increasing the number of animals involved would increase the power to detect changes.

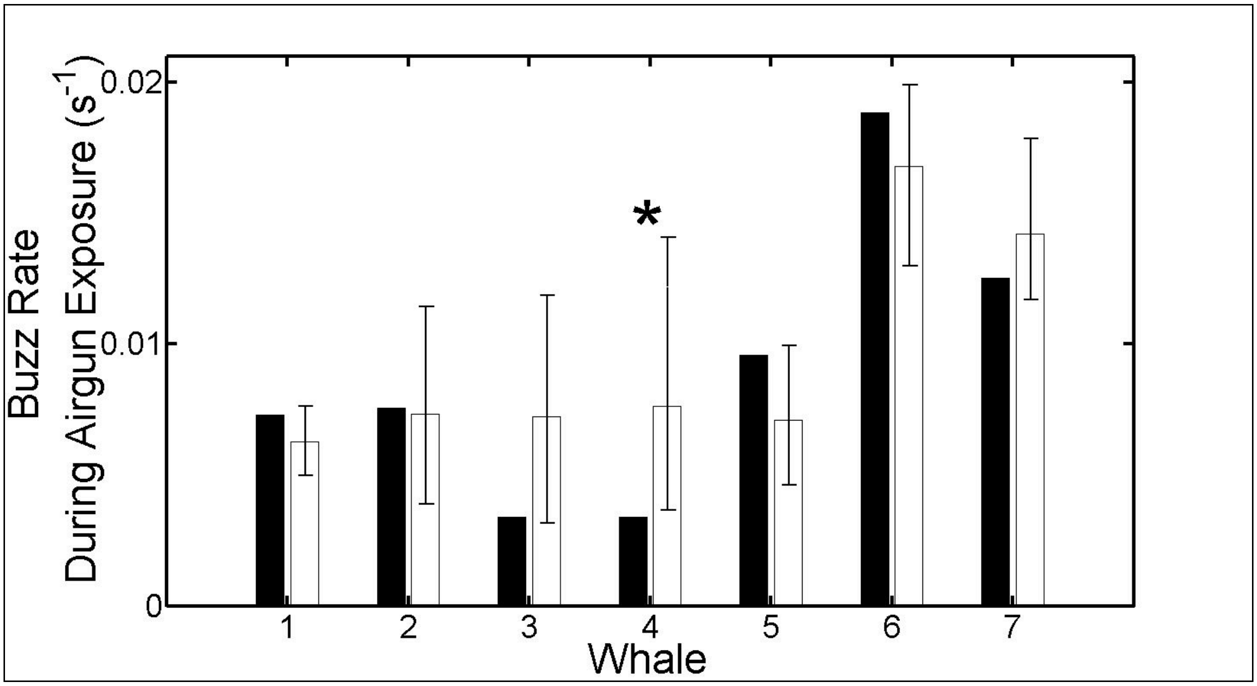

Figure 6.2.1. Rate of buzz production during airgun exposure. Black columns show observed buzz rate during airgun exposure for each whale. White columns show expected buzz rate during airgun exposure (under the null hypothesis that airgun exposure did not affect buzz production rate; column height is mean value from rotation tests, and error bars indicate 95% confidence intervals). An asterisk indicates results that are statistically significant at the $p<0.05$ level.

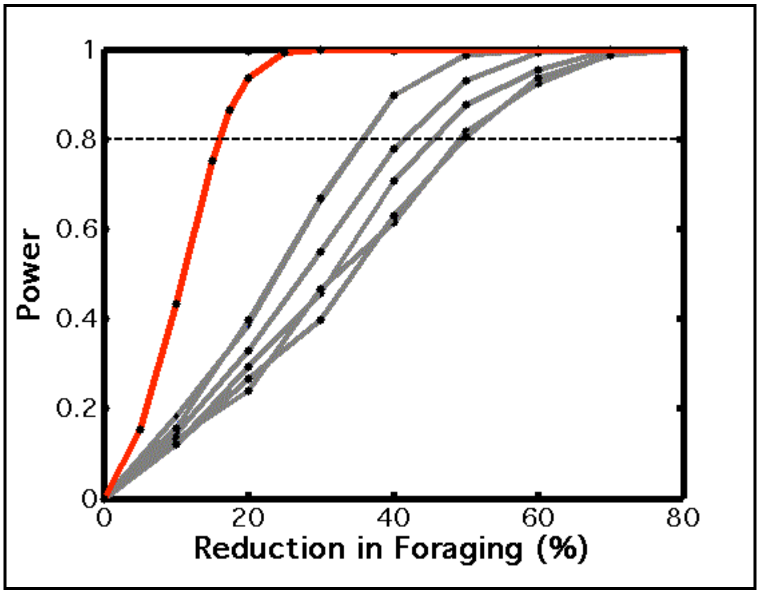

Figure 6.2.2. Power of the parametric test to detect reductions in foraging rate at the p = 0.05 level. Red line: power to detect concerted change by a group of 7 whales; gray lines: power to detect change by an individual whale.

6.3 Seismic Survey Activity and the Proximity of Satellite Tagged Sperm Whales

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Sperm whales (*Physeter macrocephalus*) frequent the lower continental slope (>1000 m) off the Mississippi River Delta, which is an area of interest to offshore oil industries and is extensively surveyed by seismic vessels. Because sperm whales are highly acoustically-oriented animals there have been concerns about possible changes in behavior when subjected to airgun noise from seismic vessels.

During summer in 2002-2006, 53 sperm whales in the Gulf of Mexico were tagged with satellite-monitored radio tags (S-tags) as part of SWSS. One objective was to determine possible changes in the behavior of sperm whales when subjected to man-made noise produced by airguns during seismic surveys. Though the S-tag study was designed principally to describe long-term (months to seasonal) movements and distributions of sperm whales, the proximity of seismic vessel activity near S-tag locations provided an opportunity to explore possible behavioral response.

The Argos Data Location and Collection System was used to obtain position data from the S-tags (see Section 4.3). High quality (Argos location class 1-3) whale locations from the S-tags (N= 1559 locations) were compared to positions of active seismic vessels with vessel information provided by the International Association of Geophysical Contractors (IAGC). IAGC data consisted of the start and end times and locations of central shot points of the airgun array for 9958 seismic lines from January 2002 through October 2006 (Figure 6.3.1).

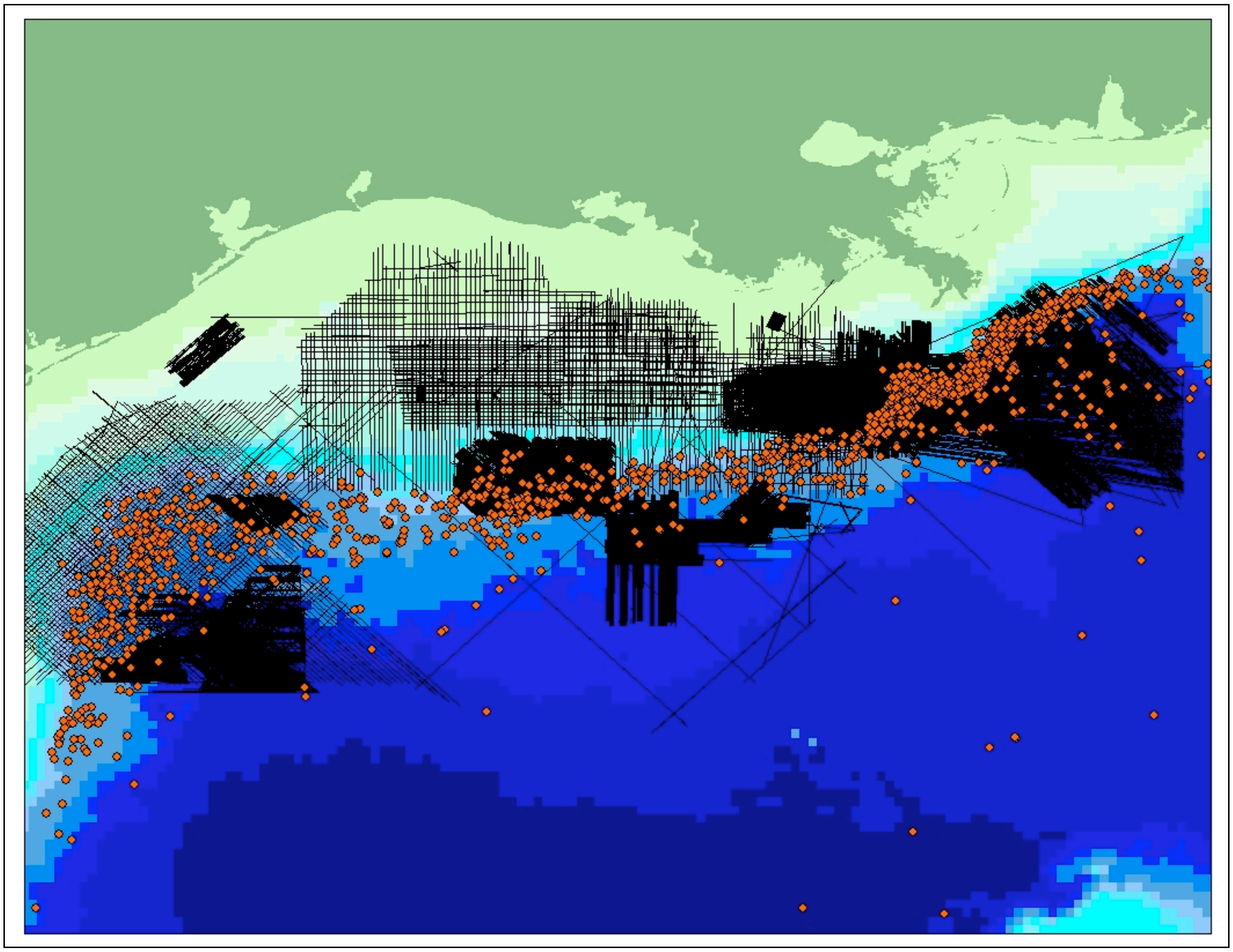

Figure 6.3.1. Map of all seismic lines provided by IAGC members from January 2002 through October 2006 (black lines) and high-quality (Argos LC1, LC2, and LC3) locations (red dots) from S-tagged sperm whales from July 2002 through October 2006.

When a whale location occurred between the start and end time of a seismic line, the position of the central shot point of the airgun array, at the time of the whale location, was interpolated from the line's start and end locations. The distance between the whale and central shot point location was then calculated. Vessels' track bearings and bearings from shot point to the whale were calculated using the interpolated shot point location. Only locations within 100 km of active airguns were considered in this analysis under the assumption that exposure to sound from closer distances would be of more interest in studying whale behavior. Additionally, vessel speeds and headings were assumed to be constant so that interpolated positions for central shot points were accurate.

Locations from 34 S-tagged whales were within 100 km of active airguns. The number of locations for each whale varied from 1 to 40. There was a total of 334 temporal matches of whale locations with seismic lines. Forty locations were within 100 km of two active vessels and three were within 100 km of three active vessels simultaneously. The minimum distance of any animal was 5.01 km and the total weighted (by individual sample size) mean was 66.3 km (standard deviation, S.D.=14.7). Fifteen individuals had more than seven locations fitting the criteria. These had an average minimum distance of 16.5 km (S.D.=7.3 km) with a range of 5.01 to 62.5 km.

Distances to shot points for each individual animal were compiled and compared to determine whether there were significant (*p*=.05) differences between individuals and/or sex. Whales with more than seven locations had sufficient sample sizes for comparisons. Data from the 15 cases that met this criterion showed significant differences between the mean distances of several individuals (ANOVA; *p*-value 0.01) but no significant difference between sexes (General Linear Models; *p*-value=0.23, 3 males, 8 females, 4 unknowns).

The relative bearing of the 15 whales to the vessel's track was also calculated and categorized into one of three bearing classes: Class A - in front of the sound source (60° to either side); Class B - to the side of the source (60°–120° and 240°–300°); and Class C - to the rear of the source (120°–240°) providing equal coverage in the three categories (Figure 6.3.2). Bearing classes were compared to determine whether whales were equally distributed in the three classes or whether there was an orientation to the sound source track occurring more frequently than others. There was no significant relationship between whale ande bearing class (Pearson's R; *p*=0.12).

A subset of the data, consisting of locations within 25 km of the central shot point (37 locations from 17 animals) was further analyzed to determine if locations were randomly distributed closer to the sound source. We hypothesize that if there is no evidence of avoidance to active airgun noise, the distances between whales and seismic vessels should be randomly distributed. Conversely, if the distribution is non-random, it may be an indication of a response of the whales to the presence of airgun noise.

Distances from these locations were tabulated into 5 km classes. No tagged whale distances were less than 5 km and five of the 30 locations were 5-10 km from the central shot point. When more than one location was obtained from an individual, its contribution to the distance class was inversely weighted by the total number of observations for that animal. This addressed possible effects of pseudoreplication (or data pooling) (Machlis et al. 1985) maintaining a total sample size of 17 animals yet utilizing all the observations.

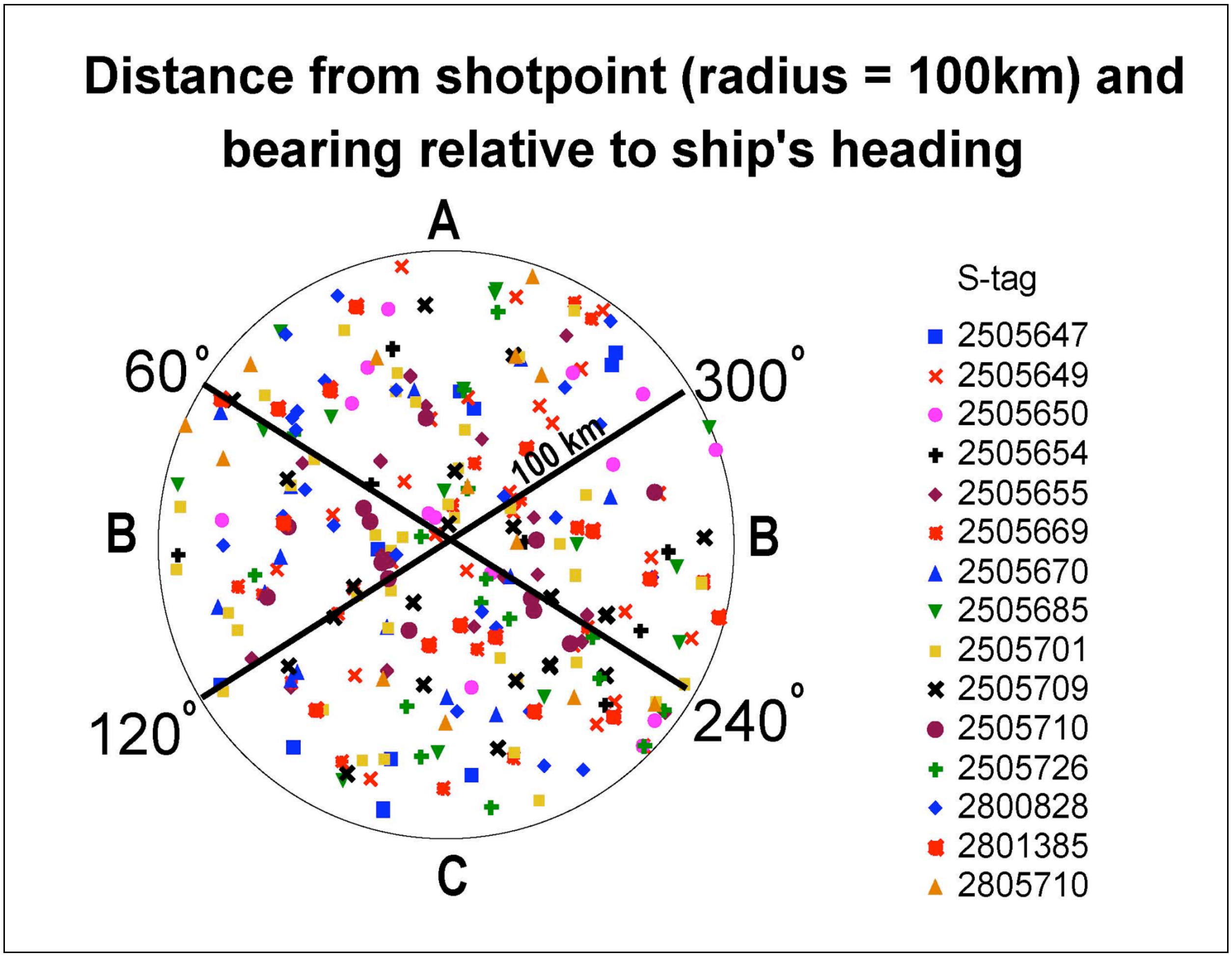

Figure 6.3.2. Relative bearings of whale locations to vessels' track using data from S-tags with more than 7 locations within 100 km of an active seismic vessel. S-tag locations were partitioned into 3 orientation categories: A = in front of; B = to either side of; and C = behind the sound source.

Assuming a random distribution, the expected number of locations in each 5-km class, was calculated by normalizing to the proportion of area the class represented in a 25-km radius circle. A chi-square test was performed comparing the observed frequencies with the normalized expected frequencies. There was no evidence (*p*-value=0.85) that the data were non-randomly distributed.

Because of the relatively small sample size available, it is important to consider the potential power of the statistical tests. To determine if 17 values are sufficient to detect a non-random distribution, additional Monte Carlo simulations of varying sample sizes were performed. Results indicate a sample size of at least 75 is needed to determine whether the lack of observations in the <5 km class indicates the data are non-randomly distributed.

Distances and bearings between whales and the central shot point of an active seismic vessel appear to be randomly distributed. From a distance greater than 5 km, there were no apparent patterns in the distances and bearings from the whale locations to the central shot that suggested a movement response to the presence of an active seismic vessel. These results, however, cannot totally refute a possible behavioral response at distances less than 25 km because of a lack of sufficient sample size. A much larger sample size (N=75) is needed for analysis closer than 5 km. An additional source of uncertainty is the lack of controlled positional errors from the Argos derived locations. Future studies would greatly benefit from the use of GPS derived locations and expanded sampling efforts.

7 CONCLUSIONS AND RECOMMENDATIONS

The three objectives of SWSS—establish baseline information on sperm whale biology and behavior, characterize habitat use, and determine possible behavioral changes from seismic airgun arrays—formed the basis for an ambitious study of the sperm whale in the northern Gulf of Mexico. After four years of field work and the analysis and interpretation of the data collected, SWSS has provided important new insights into the sperm whale population of the northern Gulf of Mexico. The resulting conclusions, together with an identification of continuing gaps in knowledge, lead to a number of recommendations and these are presented for each of the three SWSS objectives.

Sperm whales were the focus of this study because of their endangered listing under the U.S. Endangered Species Act. There are other marine mammal species and habitat components that may have been or could be affected in biologically significant ways by the various human activities in the Gulf of Mexico (c.f., NRC 2005). It is important to recognize that, while SWSS detected no apparently biologically significant effects of seismic activities on sperm whales, this cannot be viewed as conclusive evidence that neither sperm whales nor other ecosystem components have not and are not being affected in biologically significant ways by oil and gas exploration and production or other human activities in the Gulf of Mexico. Follow-up studies, as recommended, are necessary to elucidate and determine how to minimize or mitigate possible biologically significant effects.

Section 7.1 presents findings and recommendations on our understanding of the behavior of sperm whales of the Gulf of Mexico. Section 7.2 covers the relationship between habitat characteristics and the sperm whales. Section 7.3 gives the conclusions and recommendations on the effects of airgun sounds on the behavior of the Gulf's sperm whale population.

7.1 Understanding the Biology and Behavior of Gulf of Mexico Sperm Whales

The first objective of SWSS was to establish the "normal" behavior of sperm whales in the northern Gulf of Mexico. This behavior was studied using satellite-tracked tags for seasonal movements over large distances, digital-recording tags for fine scale movements over hours, and group follow photo-ID to elucidate group structure and movements over days. This research allowed a description of the sperm whale population and its structure in the northern Gulf (see Section 4 of this report and Sections 4, 5, 6.1, 7.3.1, and 7.3.2 of the SWSS Summary Report (Jochens et al. 2006) for detailed results). As the questions and recommendations that follow in this section 7.1 will detail, our combined results indicate the existence of a relatively small population of northern Gulf sperm whales with a rather limited home range that overlaps almost completely with areas of current and future oil related activity. It is clear that this population is living in close proximity to offshore oil and gas exploration and production and to all of the activities that come with this for many decades, so an ongoing monitoring project would be extremely useful to measure and track population parameters and ensure that any problems are identified and dealt with quickly. SWSS has shown that classical techniques used on the mesoscale population study (MPS), supplemented by the newer methods used for tagging and acoustic monitoring, are capable of providing the information required for management.

General Recommendation: Implement a monitoring program to continue and extend SWSS understanding of biology and behavior of Gulf whales, focused on providing information required for effective sperm whale population conservation. As the questions and recommendations that follow will illustrate, relatively low-cost methods like sailboat charter should be considered to augment use of more specialized but higher cost platforms like oceanographic research vessels.

What is the level of habituation to human activity of sperm whales in the Gulf?

Ideally, studies should be initiated years before industrial activity starts in a sperm whale habitat, so that sufficient baseline can be established in the population before initial impacts, and such studies should aim to study effects over the scale of potential impacts, typically several decades. However, this is not the case with the Sperm Whale Seismic Study. The SWSS study area was focused along and about the 1000-m isobath in the region between Mississippi Canyon and De Soto Canyon. This region is one that for many decades has been the location of human activity in the form of marine transportation, recreational activities, commercial and recreational fishing, and other anthropogenic disturbances. The expansion of oil and gas exploration and production into these deep waters is a fairly recent addition to the human activities there. Thus, individuals in the sperm whale population that was most studied during SWSS have certainly been pre-exposed to anthropogenic sounds, including those from seismic airgun arrays. SWSS data, therefore, cannot be considered as representative of the behavioral response that could be expected from animals with no exposure to anthropogenic sounds. The most sensitive individuals might have left this area, and the animals remaining may be habituated to exposure. SWSS was not designed to determine what level of effects these activities and their associated sounds may have already had on the Gulf's sperm whale population. The animals that were encountered during SWSS fieldwork forage, socialize, and move in the Gulf, so the information found in SWSS relates specifically to this population.

Recommendation: Gulf sperm whale populations in the Dry Torugas region may be a population that has not been exposed to intensive seismic surveys or oil and gas industrial activities; a study similar to SWSS in this region may provide information useful for comparison with the SWSS results. Socioeconomic studies that identify the historical development of human activities (e.g., marine transportation, fishing, seismic surveys, and oil and gas) in the SWSS study area should be assessed relative to the (sparse) historical data on sperm whale populations.

What is the effect of the temporal and spatial limitations of sampling on the study results?

The SWSS field cruises were both seasonally and spatially restricted. They were conducted between June and early September and mainly along the 1000-m isobath between the Mississippi Canyon and De Soto Canyon. Thus they did not cover the full range of sperm whales in the Gulf in all seasons. Earlier, survey studies identified that sperm whales are present over the slope east of the Texas-Mexico border, north of the Florida Keys, and in deep waters throughout the northern Gulf (see e.g., Davis et al. 2002, Würsig et al. 2000, Waring et al. 2004, 2006). Some sperm whales, especially males tagged with S-tags in the main SWSS study area, also traveled to other portions of the Gulf and into deeper waters. However, there were strong indications that one or possibly two “core populations” were fairly restricted to the northern Gulf upper continental slope. It is these core “populations” – which will also be the ones most likely to be exposed to oil and gas related activities – that have been our focus of effort during SWSS. Other very fundamental information about sperm whale seasonality in this area, including the timing of mating and calving, remains unknown. While S-tagging did allow some individuals to be followed throughout the course of a year, it is unknown what effect the limitation of summertime-only S-tagging had on our study results. For example, we do not know whether individuals tagged in different seasons might have used the main SWSS study area differently than those that were tagged in summer. Broader geographic studies in all seasons will be needed to provide this information, particularly if and when oil and gas exploration expands into other geographic areas of the Gulf.

Recommendation: Conduct follow-on, SWSS-like detailed studies of sperm whale populations in parts of the Gulf outside the region along the 1000-m isobath between Mississippi Canyon and De Soto Canyon. Such studies should examine the animals off the Dry Tortugas, in the northwestern Gulf, in the deeper waters of the Gulf, and if possible in Mexican waters. Studies should be conducted in all seasons to determine seasonality of breeding and calving and whether important behaviors such as relative times spent in transit versus foraging may be different there.

What are the seasonal distributions and movements of the sperm whales in the northern Gulf?
Before our SWSS study, what was known about the movements and seasonal distributions of Gulf sperm whales came from surveys such as GulfCet (Davis et al. 1998, 2000). Their presence was known to be year-round as a population, but it was not known whether they left the Gulf or whether individual sperm whales had seasonal preferences for different geographical locations within the Gulf. A handful of photo-ID resightings suggested residency for individuals in particular areas, such as the Mississippi Canyon to De Soto Canyon region.

Rather than conducting surveys *per se*, SWSS collected substantial information on movements of individual whales from both S-tag and photo-ID studies. S-tag results (Section 4.3) suggest that movements of the females and most males in the Gulf of Mexico population studied are not migrations—routine seasonal movements that are repeated annually—but rather are more variable and possibly related to changes in food availability. Although there were no apparent repeated seasonal migrations, there are basin-wide movements along the slope of the northern Gulf. Additionally, there is apparent site-specific tenacity by many individuals, primarily females. Although the home ranges of some females tagged in the north central Gulf overlapped with some tagged in the northwestern Gulf, the core areas of females tagged in the two locations did not. This suggests the site-centric behavior observed in the north central and northwest Gulf females will likely be found in females from other areas of the Gulf.

Females showed great affinity for the areas in which they were found, and hence tagged, in summer. Tagging occurred generally about the 1000-m isobath. Females tagged here rarely went into waters deeper than 2000 m. Yet other studies have shown there are females with calves in those deeper waters (Mullin et al. 2004). This suggests there may be different distribution patterns for animals with possible depth preferences. Are there separate stocks based on water depth preferences? Data are insufficient to determine this.

SWSS collected no data on the distribution or movements of breeding mature males. Based on the S-tag results, movements of immature males had great variability. These results also indicate that males have larger individual home ranges and use deeper water habitats than females. For example, only two tagged whales known to be females actually moved out over deep water, while several males and individuals of unknown sex moved offshore and traveled to the Bay of Campeche in the southern Gulf and one male moved into the North Atlantic before returning to the Gulf of Mexico.

Recommendation: Conduct further S-tag and photo-ID studies in different parts of the Gulf, including deep waters, to determine the behavior and movements of whales in other areas and to assess whether distribution varies by age, sex, or reproductive status.

Recommendation: Conduct studies that re-tag individuals over several years to document sperm whale movement patterns over multiple years and provide information on interannual variability of movements and distributions. Individuals representative of different age and sex compositions of the population should be tagged in this program.

What is the genetic structure of the Gulf's sperm whales relative to those in the North Atlantic Ocean, Mediterranean Sea, and North Sea?

SWSS mtDNA results show population structuring between northern Gulf of Mexico, western North Atlantic Ocean, North Atlantic Ocean, Mediterranean Sea, and North Sea putative populations was highly significant (Section 4.2). The northern Gulf population structure supports the delineation of the northern Gulf into a female-dominated stock that is genetically distinct from those in other regions. Analyses of codas provide another "culturally based" insight into population structure (Section 4.8 of this report and Section 4.3 of the SWSS Summary Report). Coda and genetic data support the conclusion that the Gulf sperm whale is a unique population. These results warrant classification of this and the other putative populations as unique, biologically significant stocks. The Gulf of Mexico samples were mainly collected from the main SWSS study area in the north central Gulf. Areas in the southern, eastern and western Gulf were not well sampled. The limited data available hinders our efforts to further address the degree of structuring that may be present in these poorly sampled areas of the Gulf or to provide information on subpopulation structuring that might be occurring in the Gulf.

Recommendation: The four putative populations (Gulf, western North Atlantic, Mediterranean Sea, and North Sea) each should be treated as a unique stock for management and conservation purposes.

Recommendation: Conduct genetic sampling, coda recording, and photo-ID (mark-recapture) studies in the southern, eastern, and western Gulf of Mexico and the Caribbean Sea to allow determination of the interchange between the sperm whale populations of these areas with those of the north central Gulf, North Atlantic, and Mediterranean and North Seas and to allow identification of subpopulation structuring, if any, within the Gulf.

What is the size of the sperm whale population in the northern Gulf of Mexico?

Before SWSS, the population of the sperm whale in the northern Gulf of Mexico was studied through vessel and aerial surveys. These surveys provided population assessments for large areas. The current estimate, based mainly on transect surveys, is of approximately 1349 sperm whales Gulf-wide and a minimum abundance for the northern Gulf of 1114 (Mullin and Fulling

2004; Waring et al. 2004, 2005; see also NMFS (2007) for information on the stock assessment revision that estimates 1665 whales for the northern Gulf population). SWSS did not conduct grid surveys, but used an alternative technique of analyzing the resighting rates for individually identified whales, especially in the upper continental slope area between Mississippi and De Soto canyons where industrial activities are increasing (Section 4.7). Using maximum likelihood mark recapture analysis methods with all the available photo-ID data for the Gulf (mainly collected during SWAMP and SWSS) provided an estimated population of 285 with 95% confidence intervals of 202-434 for all of the animals in the study area and an estimated "core population" of mixed group members off the Mississippi Delta and Canyon region of 140 with 95% confidence interval of 103-200 (Section 4.7). Based on these numbers and the presumed composition of mixed groups we expect there to be approximately 88 females in the core population, with an expected annual calf production of 15-20.

What is the reproductive rate for Gulf sperm whales? Where are the breeding and calving grounds in the Gulf of Mexico for its sperm whale population? Where are the breeding males? Calf production and survival are very important measures of the well being of a population. However, several factors including the unknown and extended breeding season, unknown rate of individual growth of calves, and long period of dependency make this parameter difficult to measure. Prior to SWSS, little was known about the reproduction rate of the sperm whale in the Gulf of Mexico. In this study, animals were classified as calves based on size and behavior, due to lack of knowledge of breeding seasons and the possibly smaller size of sperm whales in general. Results from the SWSS mesoscale studies (Section 4.7) suggest that calves account for about 11% of the mixed groups encountered in the north central Gulf. This is similar to results found for the Indian Ocean with its relatively unexploited, healthy sperm whale populations (Whitehead et al. 1997). The studies also suggest that the calf production varies between years. However, due to our definition of calves based on size and behavior, results may be biased upward and should be viewed accordingly.

Due to the limited geographic and temporal scope of the study, SWSS did not identify the breeding or calving grounds or seasons for Gulf sperm whales. Nevertheless, new born calves were observed on two occasions in the summer months in the northern Gulf. SWSS researchers did not encounter large males of the size traditionally considered to be physically mature and breeding. Nevertheless, the S-tag data show that mature females normally remain within the northern Gulf and that implies that mating must occur in some portion of the year here.

Recommendation: Further research is needed to reliably measure calf production and mortality in the Gulf of Mexico sperm whale population. One way forward is to make all relevant data available to population modelers to evaluate uncertainties about the rates of reproduction and mortality, timing of sexual maturity, and population size in sperm whales of the Gulf. After evaluating these results, design a study which would reduce critical uncertainties the most. As a strawman, we suggest that any monitoring survey of sperm whales throughout the Gulf have among its goals to identify the breeding males and the breeding season. This should include genetic sampling of sexually mature males to identify the level of male-mediated gene flow between oceanic areas.

Is the body size of the Gulf's sperm whales smaller than that of other populations?

Before the SWSS study, assessments by eye by experienced naturalists suggested that the northern Gulf sperm whales were smaller (perhaps young) animals than in other sperm whale populations. During SWSS individuals were measured both photographically and by using an acoustic technique and these data confirm the small size of Gulf sperm whales. MPS results (Section 4, SWSS Summary Report) indicate the north central Gulf of Mexico sperm whales are smaller than those measured in similar populations in the Gulf of California (Jaquet 2006). It is not known why this size difference exists – whether it is an adaptive response to the environment or a cause for concern – as the size could be mediated by population-level genetic differences, prey differences, environmental stressors, or a combination of these. It is also not known if this size difference exists in sperm whales in other regions of the Gulf that were not studied as part of SWSS. If there is a preference of whales by depth regime, as suggested by comparison of S-tag data with other data sources (see Section 4.3), it is possible that the population studied is smaller because smaller animals may prefer the shallower waters relative to their diving ability and/or availability of suitable prey.

Recommendation: Determine the prey field, its abundance, and its nutritional value, as well as the feeding success of the sperm whale over multiple years, to capture natural variations in the nutrition available to the whales. As explained in Section 7.2, this is a very ambitious project, but one way forward at least with respect to body size is to analyze historical data from Yankee whaling logs to see whether whales were smaller in this area in the past. Another is to review body size data from sperm whales in less impacted areas that are otherwise ecologically similar (such as the Dry Tortugas) to investigate variation and thus better judge if feeding rates in the Gulf are particularly low.

What is the social organization?

The SWSS S-tag, photo-ID, and genetic relatedness data allow the beginnings of a detailed and coherent picture of the social organization of the northern Gulf sperm whale population to emerge. Repeated photo-identifications of some whales since 1994 are indicative of long-term residence. There are indications of preferred locations for individuals within the core range.

Social structure in sperm whales of the Gulf seems to parallel that from other areas, with small units staying together for an extended period of time, and larger groups consisting of several units joining for short periods. In contrast, typical group size in the Gulf (10 or so individuals) is approximately 1/3 the size of groups in other areas (Coakes and Whitehead 2004). However, the photo-ID dataset is still small compared to those typically used for such analyses of social structure. It is therefore not possible yet to determine the size of long-term units or how representative our results are of long-term social structures. For example, it is unclear how typical (or atypical) the changes in distribution and groups compositions are that were observed in 2005.

Genetic data on relatedness in the groups of sperm whales encountered in SWSS are incomplete because for most groups, not all members had both biopsy samples and photo-IDs taken. The genetic data on groups of sperm whales observed in SWSS showed that most were mixed-sex groups consisting of both related and unrelated females and young of both sexes (Section 4.2), and S-tag data show that some of these individuals traveled together for several months (Section

4.5). In contrast, no long-term associations occurred between males. Long-term association data are needed to accurately describe the social affiliations of group members; multi-year studies would allow a better evaluation of how groups disperse and under what conditions they might reassemble.

The contrast between group structures in the MPS study area in 2004 and 2005 was especially striking, and shows the need for multi-year studies to understand the group composition under varying environmental conditions. In all years except 2005, a strong segregation was found in the distribution between groups of female/immature sperm whales and bachelor or lone males. The former were mainly found in the region south of the Mississippi River Delta and Mississippi Canyon and in the western Gulf, while the latter were mainly found in the De Soto Canyon and along the Florida slope. Groups of females and immature sperm whales showed a high site fidelity for the region south of the Mississippi River Delta and Mississippi Canyon. In 2005, this region lacked the mixed groups of 2004 and instead the bachelor/lone males were seen; however, we do not know to where the mixed groups may have been displaced. One possible cause of this change was that the oceanographic conditions between the two years were significantly different, with the discharge from the Mississippi River being just 59% of average summer monthly outflow in 2005. Sea surface chlorophyll fields from summer 2005 indicate a corresponding reduction in amount of off-margin transport of base-of-the-food-chain biological production. Whether the female/immature sperm whales returned to the area after 2005 is unknown. Breeding Gulf males seem to have either a different behavior or a different seasonality to those in other regions, since no breeding males were observed in the northern Gulf.

Recommendation: A continuous, multi-year study of the Gulf's sperm whale population, both in the northern Gulf and in other Gulf areas such as farther offshore, should be conducted to improve understanding of the social structure of the Gulf's sperm whale population. Photography, photogrammetry, genetic analyses, acoustic recordings, and other classical observational techniques for observing groups of animals should be conducted to assess group and individual behavior under varying environmental conditions. These classical methods should be combined with S-tag data in order to gain detailed and long-term information on the social organization and movement patterns in the Gulf. A subset of S-tagged whales also should be tagged repeatedly to provide movement data over multiple years.

What do codas reveal about culturally-based population structure?

The analysis of acoustic recordings indicates a single acoustic clan within the core range of the northern Gulf of Mexico. This clan is distinct from that of the Caribbean Sea and North Atlantic (see Section 4.8 and Section 4.3 of the SWSS Summary Report). The recorded coda vocalizations indicate that the mixed groups in the Gulf of Mexico belong to an acoustic clan that is rarely encountered in other areas and, from this, it is inferred that groups from other clans rarely enter the northern Gulf of Mexico. Results from the one SWSS cruise in the northwestern Gulf suggest there may be a different acoustic clan in the western Gulf.

Recommendation: Continue to collect coda recordings in the core area in conjunction with photo-ID data to provide an improved picture of social units and their coda repertoires. Conduct similar research in other areas of the Gulf to expand the database that can be used to understand the populations in parts of the Gulf such as the deepest waters, the Dry Tortugas, the western Gulf, and, if possible, the off-shelf waters of Mexico.

What are typical short term movement patterns?

Many of the individual follows in D-tag cruises lasted 4-12 hours, and during the 2004 and 2005 MPS cruises, groups of sperm whales were followed closely for 4 to 50 hours. For 2004, the animals showed an average horizontal daily displacement of 35 km (Section 4.1 of the SWSS Summary Report); 2005 data averaged ~50 km a day, but results indicated little doubling back of movements (Section 4.4 of this report). These relatively small horizontal daily displacements, combined with frequent creak-buzz vocalization by individual whales during D-tag follows, appear to suggest a high feeding success. As compared to displacement patterns of sperm whales in other oceans, the pattern of movements of the observed Gulf whales consists of zigzags over a smaller area and longer periods during which the animal stays within a particular area. These results lead to the speculation that sperm whales may be feeding on small but dense patches of prey.

The D-tag data have greatly expanded our understanding of foraging behavior (see the question that immediately follows), and the fluke ups and other surface behaviors of individual whales have been examined using the MPS data (Section 4.4). A modal dive cycle of ~55 min was determined from the fluke ups of individual whales. This is in good agreement with the D-tag results of Watwood et al. (2006); see below. MPS data also indicated a mean speed of 3.3 km/hr while animals were engaged in diving behavior, with the speed of presumed maturing male whales being significantly lower than for adults, including nursing females. During 24-50 hour MPS follows, groups of sperm whales appeared to travel roughly parallel to bathymetric contours and to stay within a narrow water depth range.

What are typical diving and underwater behaviors?

The SWSS study has provided an extensive body of continuously sampled data on behavior of sperm whales throughout their dive cycles in the Gulf. Indeed, the detail provided in the D-tag data has revolutionized our understanding of underwater behavior. Watwood et al. (2006) and Miller et al. (2004b) used the D-tag data to assess aspects of diving and underwater behavior. Miller et al. (2004b) used data from 23 animals tagged in the north central Gulf of Mexico and the Ligurian Sea to study swimming behavior of the sperm whales. They conducted a detailed model study of drag and buoyancy on the relative periods of active thrusting versus gliding on swimming behavior. They thus examined "cost-of-transportation" for the animals. They found that the animals stroked steadily during descent and used stroke and glide behavior during ascents. The mean descent speeds (1.45 ± 0.19 m s^{-1}) were slower than mean ascent speeds (1.63 ± 0.22 m s^{-1}). Miller et al. (2004b) found that swimming behavior incorporated more glide time when the buoyancy aided movement.

Watwood et al. (2006) used data from 37 animals tagged in the north central Gulf, the Ligurian Sea, and the North Atlantic Ocean to study the deep diving foraging behavior of sperm whales (see also Section 7.3.1 of the SWSS Summary Report). They found that animals in all three regions had similar basic dive parameters. The dives fell into two distinct categories: dives of less than 150 m and "deep" dives to greater than 300 m. A typical deep dive of a tagged whale lasted 45 minutes with a range of 14-64 minutes followed by a surface interval of 9 min. Whales descended at an average vertical velocity of 1.2 m s^{-1}, and began producing regular clicks during the descent (on average at 215 m in the Gulf). The animals spent on average 64% of the descent producing regular clicks, which are thought to be used to search for prey. The animals continued descending and producing regular clicks until they reached the apparent depth of prey. When whales stopped descending and began the bottom phase of the dive, they began using buzzes, which Miller et al. (2004a; see below) concluded indicate attempts to capture prey. There were on average 18 buzzes per dive over an average of 28 minutes. Gulf whales started and ended the bottom phase at depths that were shallower than the animals in the Atlantic Ocean or Ligurian Sea; this may be related to the shallower water depths where Gulf whales were D-tagged, as compared to those in the other two regions. Gulf and Atlantic whales spent 72% of their time in foraging dive cycles, whereas those in the Ligurian Sea spent 97% of their time. Whales dove on average to 985 m in the Atlantic, 644 m in the Gulf, and 827 m in the Ligurian Sea. The deepest dive recorded was to 1202 m by a whale in the Atlantic.

What are typical feeding and foraging behaviors?

Miller et al. (2004a) related the diving and movement behavior of the sperm whale to its rapid-click buzzes (creaks) as recorded on the D-tag. Results supported the hypothesis that the buzz rates of the sperm whale could be used as a proxy for foraging activity and prey capture attempts. These data are corroborated by similar data from bats and beaked whales (see Griffin 1958 and Griffin et al. 1960 for bats and Johnson et al. 2004 for beaked whales; see also Section 7.2 of the SWSS Summary Report). The whales observed, which included both animals from the north central Gulf of Mexico and Ligurian Sea, spent most of the dive time within one or two depth bands at or near the bottom of the dive. Consistent with the expectation that feeding occurs during the bottom phase of the dive, Miller et al. (2004a) concluded these were layers of vertically stratified prey. They found that the animals produced most of their buzzes during the bottom phase of the dives and that the animals significantly changed their orientation in water in association with the buzzes. They further found that the onset of the buzzes was associated with increased movement of the animal and that the strongest activity occurred at the end of the buzz. They interpreted these movements as maneuvering to capture prey. Finally, they found that foraging animals spent more time at depths in which creak rates were higher. Miller et al. (2004a) concluded that buzzes indicate a shift in biosonar strategy as the whales attempt to capture a prey item. While this may be used to indicate intensity of foraging activity, they note that the study examines only the predator behavior aspects of the foraging activity and that studies of prey capture success rates and of caloric value of prey are needed for a quantitative energetic model of costs and benefits of foraging.

The D-tag dive and foraging data were compared to relative acoustic backscatter intensity (RABI) from the 38-kHz ADCP that gives a measure of biological scattering layers and to surface oceanographic features such as sea surface height, sea surface chlorophyll, and distance of whales from nutrient rich off-shelf flows (Section 5.2). Sperm whale dive depths (and by extension buzz rates) did not appear to be predicted by typical surface oceanographic variables, confirming a complex relation between deeper dense prey patches and surface oceanographic conditions that influence biological productivity over wider spatial and longer temporal scales. Sperm whale foraging dive depths were found to correspond to three depth layers: in the deep-scattering layer (DSL), and in a scattering layer below the DSL that both were indicated by elevated RABI, and at the sea floor. Whales foraging in the DSL at sunset exhibited movement that appeared to be associated with the diel vertical migration of the biological assemblages. Whales foraging below the DSL did not show this behavior. The results suggest that the dive and foraging depths of sperm whales relate quite strongly to the vertical distribution of biological assemblages, and acoustic technologies appear to have the potential to locate dense sperm whale prey patches.

The MPS cruise observations included data on the defecation rates of the individual animals that were followed (Section 4.4). For animals with at least 5 observed fluke ups, the mean defection rate was 0.209 per fluke up. This is high compared to other areas such as the South Pacific and the Galapagos, suggesting a high feeding success for Gulf of Mexico sperm whales. The difference in defection rate between the two years studied was significant, with a rate of 0.235 per fluke up in 2004 and a rate of 0.148 per fluke up in 2005. The relationship between these differences and oceanographic conditions (low river flow and apparent displacement of the typical mixed groups of whales from the Mississippi Canyon–DeSoto Canyon areas in 2005) is discussed further in Section 7.2. In contrast to the defecation rate finding of relatively high feeding success for Gulf whales, Watwood et al. (2006), using D-tag data sets from the Gulf of Mexico, North Atlantic and Ligurian Sea, found that the mean buzz rates, which may be an alternative to defecation rates as a proxy for foraging success, were similar in those three oceans.

<u>Recommendation</u>: Develop techniques to identify the actual benefits from feeding and to measure the energetic cost of foraging behavior. Then conduct studies of the cost/benefit ratios for feeding individuals as related to environmental factors, including oceanographic conditions and anthropogenic sources of possible behavioral disturbance.

<u>Recommendation</u>: Test whether deeper prey patches which can be detected acoustically are actually those being exploited by sperm whales when they forage at depths greater than the deep-scattering layer by using acoustic methodologies to track variations in the vertical distribution of prey simultaneously with techniques, such as the D-tag, to observe foraging by diving whales.

<u>Recommendation</u>: Any research studies to monitor populations over extended time periods and geographical areas of the Gulf should include collection of improved metrics for the feeding success of the animals.

7.2 Characterizing the Habitat Used by the Gulf of Mexico Sperm Whales

A second objective of SWSS was to characterize habitat use. The early studies that looked at habitat characterization found that the Gulf's sperm whales seemed to be located in regions influenced by cyclones, the confluence of cyclones with anticyclones, and in waters influenced by the outfall of the Mississippi River (e.g., Biggs et al. 2000; Davis et al. 1994, 1996, 2002). SWSS extended this work.

What are the characteristics of the habitats in which the Gulf sperm whales are found?
SWSS results support the findings of GulfCet and SWAMP (e.g., Biggs et al. 2000, Davis et al. 2002, Biggs et al. 2005) that led to the hypothesis that locally high chlorophyll features, particularly cyclonic eddies or eddy-induced off-margin flows, that persist for 3-4 months, provide sustained primary production that then can support the higher biological production that

is important for the development of feeding grounds for sperm whales along the continental slope. Preliminary findings from comparisons of the locations of sperm whales observed during the 2005 S-tag cruise with the acoustic backscatter from a fishery echosounder that operated at frequencies chosen to achieve acoustic returns from nekton and micronekton (Section 5.3), show that whales seem to go where the food is, as significantly higher backscatter was measured when whales were locally abundant. In summers 2002, 2003, and 2005, most sperm whales were encountered in regions of negative sea surface height anomaly and/or higher-than-average surface chlorophyll, as were the GulfCet and SWAMP animals. But this was not apparent every summer, for only a few of the whale encounters in summer 2004 were in regions of negative sea surface height anomaly and/or higher-than-average surface chlorophyll.

In addition to summer-to-summer variability, local oceanographic conditions also can change during the course of a single summer, with resultant changes in encounter rates with whales. This was the case in summer 2003 when the usual pattern of the presence of sperm whales in the Mississippi Canyon region was not present in early summer 2003, but was present approximately one month later. A large Loop Current eddy was located seaward of but in close proximity to Mississippi Canyon in early 2003, with resultant on-margin flow that effectively "flushed" the canyon with low chlorophyll, low nutrient Caribbean water originating from the Loop Current eddy. Approximately one month later, after this eddy had rebounded away from the continental margin re-establishing along-margin and off-margin flows, sperm whales were encountered in the Mississippi Canyon region (see Section 3.1 of the SWSS Summary Report).

Further, the interannual variability of the Mississippi River discharge itself may have significant impact on sperm whale distributions in the Mississippi Canyon to De Soto Canyon region. In 2005 animals anomalously were not found in the abundance or usual groupings in this main SWSS study area. The change in distribution may have been related to the lower discharge from the Mississippi River in 2005. Climate teleconnection indices may allow 5-12 month forecasts of such low river discharge conditions (see Section 5.5) and may provide an additional oceanographic condition to the eddy field that could be used to estimate the areas in which sperm whales may be abundant. Continuation of the federal satellite program for monitoring SSH and ocean color, in coordination with the ongoing monitoring of northern Gulf sperm whale biology and behavior that we proposed as a General Recommendation in Section 7.1, should permit additional habitat data to be conducted concurrently with data on sperm whale distribution/abundance during future years of lower than average river discharge.

<u>Recommendation</u>: Future sperm whale studies in the northern Gulf of Mexico should include a component that uses satellite data and river disharge data to examine the habitat characteristics concurrently with the locations of sperm whales.

What is the spatial distribution of sperm whales relative to habitat characteristics?

To study the use of physical habitat by S-tagged sperm whales in the northern Gulf of Mexico, three environmental variables (ocean bottom depth, bottom slope, and sea surface height) were analyzed at the spatial and temporal locations of whales tagged with satellite transmitters (see Section 6.2 of the SWSS Summary Report). Comparisons were made between sex classes (female and male) and movement types (meandering and transit). Statistically significant differences were observed in the median values of bottom depth for females and males, with the median depth of the females being almost 300 m shallower (884 m) than of the males (1171 m). Female sperm whales were located more frequently on the upper continental slope of the northern Gulf of Mexico. Males were also located in this region, but some moved into the central Gulf or over the lower continental slope and abyssal plain. Median values of bottom slope also were different between areas utilized by S-tagged females and S-tagged males. Females tended to be located where the bottom slope was steeper (3.06 degrees) than the slope at the locations of males (2.39 degrees). No significant differences between females and males were found in sea surface height values at animal locations. However, the median value of sea surface height was different between meandering (-3.9 cm) and transit (-7.1 cm) locations. Note that the median value for both types is negative, which is consistent with the hypothesis of a preference for regions of cyclonic circulation. Interestingly, the difference in mean sea surface height between meandering and transit movement types may indicate that sperm whales have differential use for various areas of the Gulf. This difference is statistically significant. Moreover, movements of tracked whales showed that, although most individuals frequented the Mississippi Canyon and the Mississippi River Delta regions, there are differences between males and females, as well as among individuals, in the specific areas frequented during the year. A trend was observed for satellite-tracked whales to aggregate near the Mississippi Canyon and Mississippi River Delta regions in the summer. While some individuals may spend several months in those areas, others disperse in different directions the rest of the year. Because most of the satellite tracked whales were tagged in the Mississippi Canyon and Mississippi River Delta regions, we do not know whether other groups of sperm whale have similar site-fidelity patterns in other regions of the Gulf. Studies in other regions (i.e., western, eastern, or deep water Gulf) are necessary to resolve this question.

<u>Recommendation</u>: Conduct S-tag studies of sperm whales and characterize their habitats in regions of the Gulf of Mexico outside the north central area along the 1000-m isobath studied in SWSS.

What are the prey of Gulf sperm whales and what are their temporal and spatial distributions? GulfCet, SWAMP, and SWSS noted the relationship of sperm whales to regions with circulation features that entrained or stimulated biologically productive surface waters. But, neither the eddy field at the surface nor the interannual variability of the nutrient-rich Mississippi River discharge reveal the complex food web associations that result in an apparent mid- to bottom-water prey field for the sperm whale in the otherwise oligotrophic Gulf. How deep below surface does the habitat influence of the cyclonic and anticyclonic oceanic eddies actually extend? The SWSS study had one 2003 cruise that included midwater trawling to compare and contrast zooplankton and midwater fish in the 0-400 m, 0-600 m and 0-800 m depth horizons, but results were marginal for assessing sperm whale prey fields (see Section 3.2 of the SWSS Summary Report for details). While squid are assumed to be the primary prey of Gulf whales, this assumption is based on stomach samples from whales hunted and killed mostly outside the Gulf. Backscatter returns from 38-kHz ADCP and fishery echosounders that have a range that extends below the main Deep Scattering Layer (DSL) are suggestive that these returns are presence or absence indicators of squid or the fish or crustacean prey of squid that are living below the daytime depth of the main DSL. However, the prey field itself requires study: What species are present and used by the sperm whale? Where are they found? What are their distribution patterns? What factors affect their populations? What is the relationship of the prey species to river discharge and the eddy field?

Recommendations: Conduct a workshop (1) to assess the knowledge of the sperm whale prey field that might be present in the Gulf and the methods that might be used to study this prey field and (2) to develop recommendations for a quantitative study of that prey field and the possible effects of oil and gas exploration and other human activities on sperm whale prey availability.

Recommendation: Using recommendations from the workshop, conduct a pilot study to examine the prey field of the Gulf of Mexico sperm whale, including species, isotopic analyses, factors determining the nutritional value of the prey, and the characteristics of the prey habitat. We expect that the most challenging part of such a prey field study will be making the direct linkage to what prey the sperm whales actually go for. For example, recent work on beaked whales has shown that these predators pass by thousands of targets before they select one to eat (Tyack et al. 2006). So, just measuring the presence or target strength of the presumed sperm prey layer may be of limited value in assessing kinds of prey that are selected.

7.3 Understanding the Effects of Anthropogenic Noise on Gulf of Mexico Sperm Whales

The third objective for SWSS was to determine possible changes in behavior of sperm whales when subjected to man-made noise, particularly from seismic airgun arrays. This objective encompassed the main motivation for SWSS as the efforts to explore for and produce the oil and gas, so necessary to our country's economic health, have extended farther into water depths where the endangered sperm whale is found.

What were typical responses to seismic airgun sounds?
The SWSS study used carefully planned controlled exposure experiments to assess whether there were behavioral changes at known received levels from airgun sounds (Section 6.2 of this report and Section 7 of the SWSS Summary Report). The results detected no horizontal avoidance to acoustic exposure that ranged from 111 to 147 dB re 1 µPa (rms) (131 to 164 dBp-p re 1 µPa). The typical diving behavior was curtailed during full-array firing for the one whale that was approached most closely, but seven other whales continued to make deep foraging dives during controlled acoustic exposure. Results of an ANOVA statistical test for changes in foraging behavior in the 7 whales that did foraging dives during exposure indicated a statistically significant decrease in pitching movements generated by swimming motion during full-array exposure as compared to post-exposure periods. Likewise an ANOVA of data on the buzzes produced when whales presumably attempt to capture prey indicated the buzz rate was lower during the exposure condition, but this effect was not statistically significant. The small sample size (7 animals) was too small to provide definitive results. To examine the odds-ratio of whether these data supported the conclusion of a change in behavior, Bayesian analyses were conducted. These analyses indicated that the odds favor that, during exposure, there was a decrease in foraging activity of approximately 20% rather than that there was no change in foraging activity. Statistical methods were developed to assess the effects of airgun exposure on the foraging rates of each individual sperm whale in the experiment. The airgun exposures were found to result in statistically significant reductions of up to 60% in foraging rates for some individuals, but it was found that small reductions in foraging rates could not be detected given the statistical power of

the test. Additional CEEs are needed to increase both the sample size and the duration of the control and exposure periods that are compared, particularly since only two instead of the planned for three summers of D-tag CEE fieldwork went forward during SWSS.

Recommendations: Controlled exposure experiments should be continued and expanded. They should include:

- a CEE continuation study with individual D-tagged animals to increase the sample size to numbers that improve the statistical power to resolve the effect of exposure at 120-150 dBrms re 1 μPa and then if the results justify such a step, to safely increase the sound testing levels to better assess behaviors as airgun sounds approach the 180 db re 1 μPa limit. Testing at these higher levels will require better specification and modeling of the sound field around airgun arrays in order to predict received levels at the whale, or would require real time telemetry of received level at the subject whale(s).

- a new CEE study of tagged animals outside the north central Gulf to assess populations that have not been heavily exposed to industrial noises in general and airgun sounds in particular.

- an extended CEE study that instruments groups of animals (giving simultaneous information on exposure to animals at a variety of ranges and received levels from an actual seismic track line) and that follows these instrumented individuals for several days to establish their normal behavior prior to exposure and several days after exposure to establish whether they return to normal behavior. Such a study should include monitoring the prey field (for example by using fishery echosounders) before, during, and after exposure to test whether behavioral variations among acoustically exposed sperm whales could be explained by changes in the prey field.

Recommendation: Continue development of sensor and instrument capabilities, including increasing attachment duration for the D-tag and addition of new sensor capability for the S-tag.

Recommendation: Passive acoustic monitoring (PAM) as well as visual observers should be used to monitor for cetaceans in future seismic surveys. Critical requirements for using PAM in mitigation include real time detection and classification, and the capability of estimating range to the whale(s).

Recommendation: Given the expense and limited opportunities to conduct CEEs using full seismic arrays, databases should be assembled and analyzed to determine what semi-opportunistic PAM observations might be feasible in conjunction with ongoing seismic surveys.

Recommendation: Using what is known about the distributions and movement patterns of Gulf sperm whales and seismic survey activity in the Gulf (present and projected for the future), a modeling effort should be designed to assess issues such as how often an individual would be affected by the survey activity and, given a worst case scenario, whether this effect would be deleterious; the model might then address population level effects, if the impact on individuals is biologically significant.

What did SWSS reveal about acoustic propagation and airgun sounds?

The SWSS CEEs included prediction of received levels to avoid potentially harmful exposure of any animal to airgun sounds of the experiment. When compared to the actual received levels as recorded by the D-tags, results showed there were important differences between the measured and predicted sounds from the airgun arrays in the spectrum, directionality, and propagation (DeRuiter et al. 2005; Section 7.3.4 of the SWSS Summary Report). A better understanding is required of the full bandwidth three dimensional beam pattern of airgun arrays during ramp up and full power. Data on sound propagation should be linked to models of sound exposure for different species in order to predict the amount of time sperm whales and other species are exposed to different levels of airgun sounds as they move in three dimensions. This information in combination with data on effects of exposure will be useful for development of models to assess whether effects observed are biologically significant to the population.

Recommendation: Measure airgun array source signatures at a full range of angles and at frequencies up to several kilohertz during ramp up and normal operation for all classes of array geometry that may vary in acoustic properties.

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APPENDIX: YEAR-BY-YEAR DESCRIPTIONS OF SLOPE EDDY FEATURES IN RELATION TO THE LOCATIONS WHERE SPERM WHALES WERE D-TAGGED

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A.1. Summer 2001

During summer 2001 (July 18-28) there was a persistent warm slope eddy (WSE), with a positive sea surface height (SSH) of about 15 cm, located at and off-shore of the 1000-m isobath in the northeastern Gulf of Mexico south of 28.5ºN between 88ºW to 90ºW (Figure A1.1). Associated with this WSE were two cyclonic circulating features, observed in the SSH field as regions of negative SSH. The cyclonic circulation to the north (C_N) of the WSE was observed along the upper slope from the Mississippi River Delta to about 87ºW. This circulation was present through out the cruise. The cyclone to the east (C_E) of the WSE was oriented approximately NW-SE off-shore of the 1000-m isobath between 86ºW and 87°W. The western boundary of this cyclone would induce southward currents. At the beginning of the cruise, this peanut-shaped cyclonic feature was initially between the eastern boundary of the Loop Current and the west Florida shelf and was disconnected from the cyclonic feature to the north. During the cruise, it split into two parts and the northern part contracted northward and interacted with the slope in the vicinity of the northern cyclonic feature (sequence not shown).

Currents collected by a 300-kHz shipboard ADCP at a 12-m depth along approximately the 1000-m isobath of the slope illustrate the patterns of circulation associated with the circulating features observed in SSH field (Figure A1.2). The velocity vectors that are shown represent the average current velocity for 20 minutes of time of raw data collection along the 1000-m isobath. The anticyclonic flow around the WSE was evident from the current velocities shown. Currents along the northwestern boundary of the WSE were directed mostly to the north, or on-shelf, between 90ºW and 89.5ºW. The currents then changed direction toward the northeast and east, inducing along-shelf flow between 89.5ºW and 88ºW near the Mississippi River Delta; this marked the northern boundary of the WSE. Near about 88ºW currents changed direction to southward, or off-shelf, tracing the eastern limb of the WSE. The currents east of 88ºW and north of about the 29ºN were rotating counterclockwise in association with the cyclonic circulation of C_N. In the area where the confluence between WSE and C_N was located, currents were southward and southeastward, which would induce an off-margin flow across the slope into deep water. Although no currents are shown, the configuration of SSH indicates that the off-margin flow would be continued southeastward by the circulation formed from the Loop Current and the eastern cyclone, C_E.

The surface chlorophyll imagery derived from SeaWiFS ocean color data for the first part of the cruise (July 16-22) shows that currents on the northwest side of the WSE moved waters with very low chlorophyll concentrations (<0.2 mg m^{-3}) over the entire slope up to the shelf edge (200-m isobath) in the region west of about 89ºW (Figure A1.3). Currents in the confluence of the WSE and the cyclone to its north (89ºW to 88ºW) pulled high chlorophyll (> 2 mg m^{-3}) waters along the upper slope at and inshore of the 1000-m isobath. The SeaWiFS ocean color imagery for the first part of the cruise also shows a filament of water with high chlorophyll concentrations that has been transported offshore of the 1000-m isobath over the slope to water depth greater than 2000 m near about 87.4ºW (Figure A1.3; Feature 1 indicated by a red cross). This high chlorophyll filament is associated with the interaction of the southeastward currents, which are pulling productive waters off the shelf, with the eastern cyclone found at this location. South of this location, the anticyclonic circulation around the northeastern limb of the Loop Current, which would induce southeastward currents, transported the off-margin flow of biologically high productive water south of 27.5ºN.

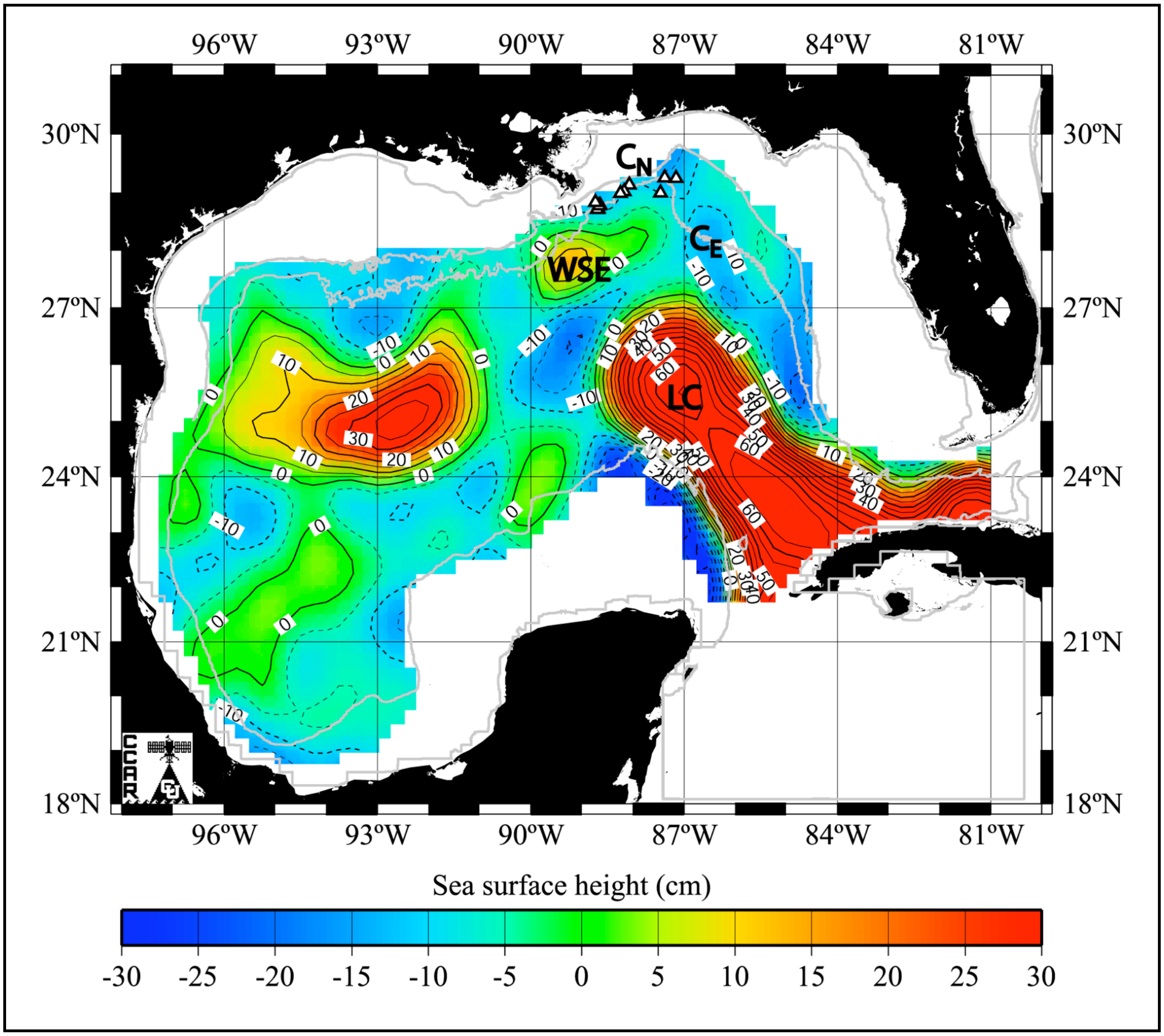

Figure A1.1. Sea surface height field for 23 July 2001, the mid point in time of the 2001 D-tag cruise (July 18-28). Triangles show locations of sperm whales tagged with the D-tag during the cruise. LC refers to Loop Current. WSE refers to Warm Slope Eddy. C_N refers to the cyclone north of the WSE. C_E refers to the cyclone east of the WSE. The 10-, 200- and 1000-m isobaths are shown.

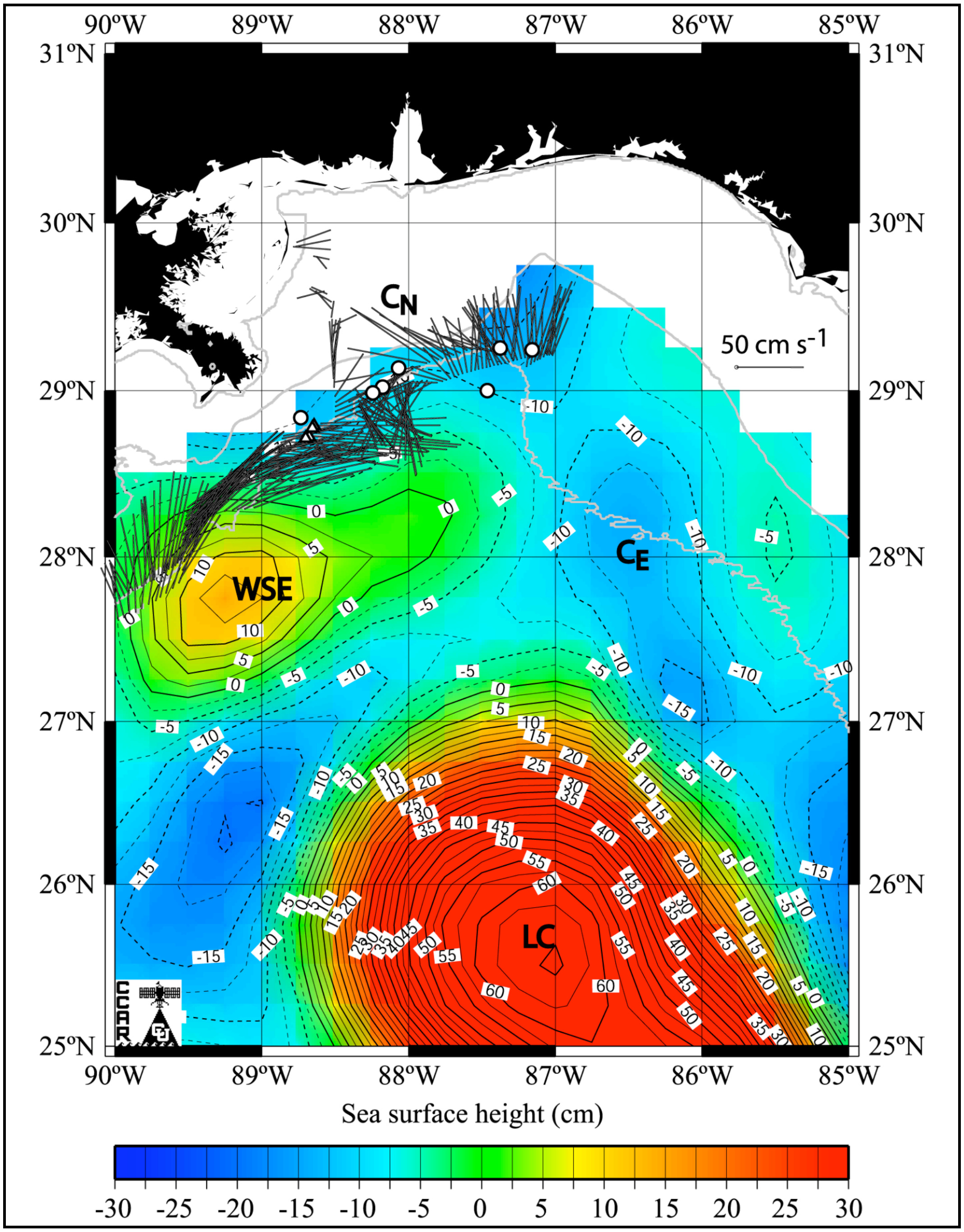

Figure A1.2. Current velocities, averaged over 20 minutes from 300-kHz ADCP data collected during the 2001 D-tag cruise, are overlain on the SSH field for 23 July 2001. Currents shown are from the 12-m depth. The triangles show the locations of sperm whales tagged on the 2001 D-tag cruise during the time period of 16-22 July 2001. The circles show the locations of the sperm whales tagged during the time period 23-29 July 2001. LC refers to Loop Current. WSE refers to Warm Slope Eddy. CN refers to the cyclone north of the WSE. CE refers to the cyclone east of the WSE. The 10-, 200-, and 1000-m isobaths are shown.

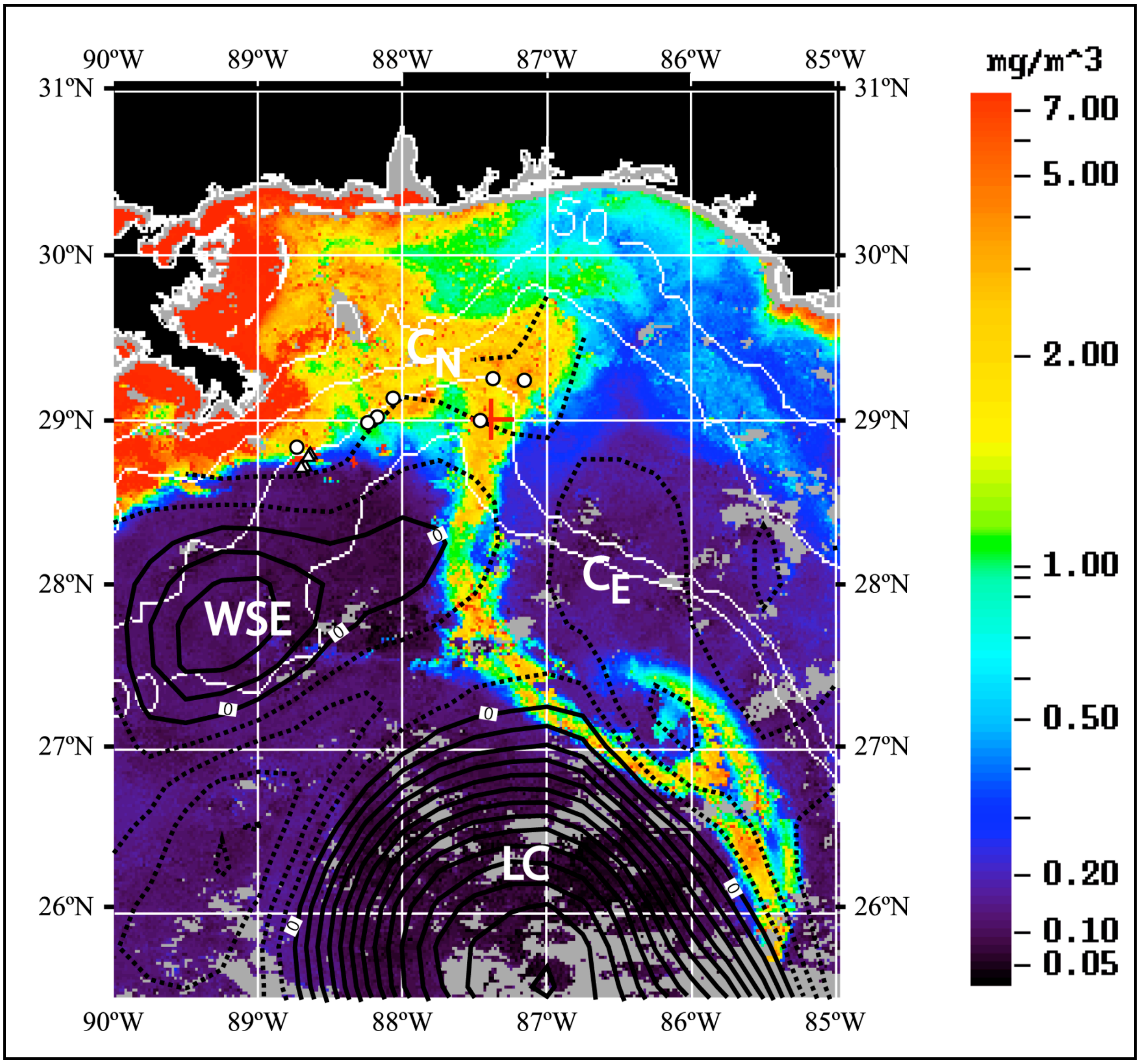

Figure A1.3. SeaWiFS 7-day composite of ocean color imagery centered on 19 July 2001. The contours of sea surface height for 23 July 2001 are shown in dark black lines. The contour intervals are every 5 cm; solid lines are positive SSH and dashed lines are negative SSH. The triangles show the locations of sperm whales tagged on the 2001 D-tag cruise during the time period of 16-22 July 2001. The circles show the locations of sperm whales tagged during the time period 23-29 July 2001. LC refers to Loop Current. WSE refers to Warm Slope Eddy. C_N refers to the cyclone north of the WSE. C_E refers to the cyclone east of the WSE. The red cross indicates Feature 1 referred to in the text. The 50-, 200-, 1000-, and 2000-m isobaths are shown.

SeaWiFS imagery of the last part of the cruise (July 23-29) differs from the earlier image, reflecting changes in the circulation pattern. By the time of the second half of the cruise, the intense off-margin transport of biologically productive waters into the deep Gulf was no longer present. This most likely was due to the change in the eastern cyclonic eddy as it interacted with the Loop Current. However, the transport of low-chlorophyll waters from the WSE onto the slope to the shelf edge west of 89°W remained. East of this, the region of intense productivity was still associated with the along-margin transport eastward adjacent to the Mississippi River Delta and with the confluence of the WSE and the northern cyclonic circulation. The off-margin flow of biologically productive waters had shifted westward from its location at Feature 1 in Figure A1.3 to about 87.8°W (Figure A1.4; Feature 2 indicated by a black cross). The waters over and adjacent to the 1000-m isobath in De Soto Canyon remained relatively productive throughout the period of the cruise.

Note that the anticyclone-cyclone geometry was changing rapidly in summer 2001. A month after the D-tag cruise, as the NOAA Ship *Gordon Gunter* continued with SWAMP Leg 3 fieldwork, there was again strong off-margin transport of green water in the region of Feature 1 in Figure A1.3. A SeaWiFS 7-day composite centered on 23 Aug 2001 shows two plumes of high color water, and Leg 3 whales were seen in and around each of them (see Plate 1, Panel D in Biggs et al. 2005).

The sperm whales tagged on the D-tag cruise were seen in water depths greater than 624 m (Table A1.1). All were tagged in regions of low sea surface height; most in regions where the SSH was < -10 cm. There were three animals tagged in the apex of the DeSoto Canyon. The other eight animals were located southeast of the Mississippi River Delta in the region of highest chlorophyll concentrations at or inshore of the 1000-m isobath. Although none were tagged directly coincident with Feature 1 in Figure A1.3 during the time period of the ocean color image showing the feature, these eight animals were found 29.8 to 93.3 km from the center of the offshelf productive water of Feature 2 (Figure A1.4).

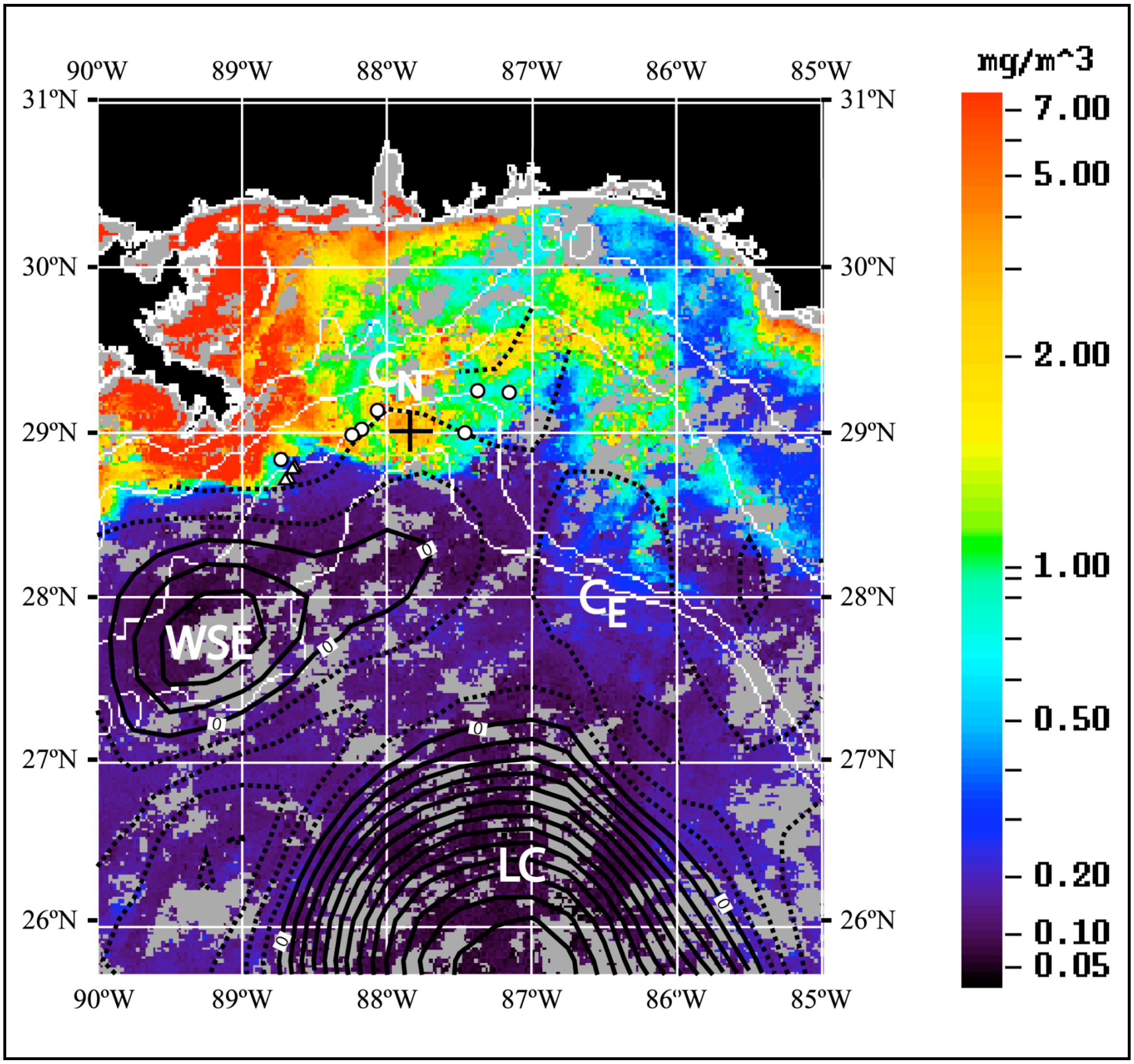

Figure A1.4. SeaWiFS 7-day composite of ocean color imagery centered on 26 July 2001. The contours of sea surface height for 23 July 2001 are shown in dark black lines. The contour intervals are every 5 cm; solid lines are positive SSH and dashed lines are negative SSH. The triangles show the locations of sperm whales tagged on the 2001 D-tag cruise during the time period of 16-22 July 2001. The circles show the locations of sperm whales tagged during the time period 23-29 July 2001. LC refers to Loop Current. WSE refers to Warm Slope Eddy. C_N refers to the cyclone north of the WSE. C_E refers to the cyclone east of the WSE. The black cross indicates Feature 2 referred to in the text. The 50-, 200-, 1000-, and 2000-m isobaths are shown.

Table A1.1

Locations of the Sperm Whales Tagged with D-tags during the Summer of 2001 Together with Data on the Water Depth, Slope, Distance to the Two Features Identified in Figures A1.3 and A1.4, and the Satellite-Derived Sea Surface Height and Chlorophyll Values for Each Location

Tag ID	**Date (m/d/y)**	**Longitude (ºW)**	**Latitude (ºN)**	**Depth (m)**	**Slope**	**SSH (cm)**	**Ocean Color (mg m^{-3})**	**Distance Feature 1 (km)**	**Distance Feature 2 (km)**
sw199	7/17/2001	-88.6758	28.7232	1038.3	0.025	-13.1	0.73	128	90.7
	7/18/2001	-88.6758	28.7232	1038.3			0.74		
	7/19/2001	-88.6758	28.7232	1038.3			21.65		
sw200	7/18/2001	-88.6438	28.7891	973.6	0.029	-13.3	2.24	123.4	85.5
	7/19/2001	-88.6438	28.7891	973.6			43.24		
sw203a	7/22/2001	-88.7	28.7133	1154.8	0.022	-13.2	CloudCover-NoData	130.6	93.3
sw203b	7/22/2001	-88.655	28.7766	996.1	0.03	-13.4	CloudCover-NoData	124.7	86.9
sw204	7/23/2001	-88.7345	28.8371	665.6	0.029	-14	CloudCover-NoData	131.2	92.8
sw207	7/26/2001	-87.46	29.2883	833.2	0.036	-12	CloudCover-NoData	32.6	46
	7/27/2001	-87.46	29.2883	833.2			0.82		
sw208a	7/27/2001	-87.155	29.2448	759.9	0.012	-14.4	1.15	36.2	68.3
sw208b	7/27/2001	-87.3733	29.255	901.4	0.029	-13.4	0.92	28.5	50.2
sw209a	7/27/2001	-88.0646	29.1355	624.2	0.043	-8.2	2.32	66.4	29.8
	7/28/2001	-88.0646	29.1355	624.2			CloudCover-NoData		
	7/29/2001	-88.0646	29.1355	624.2			0.92		
sw209b	7/27/2001	-88.1737	29.0203	1115.2	0.033	-7.2	0.76	75.3	36.4
	7/28/2001	-88.1737	29.0203	1115.2			CloudCover-NoData		
	7/29/2001	-88.1737	29.0203	1115.2			1.30		
sw209c	7/27/2001	-88.2416	28.9879	1015.5	0.031	-6.1	0.91	81.9	43
	7/28/2001	-88.2416	28.9879	1015.5			CloudCover-NoData		
	7/29/2001	-88.2416	28.9879	1015.5			1.72		

A.2. Summer 2002

During the D-tag cruise in summer 2002 (August 23–September 11) there was a persistent triad of eddy features, consisting of two regions of positive sea surface height and one of negative SSH, over the upper slope of the northern Gulf of Mexico between 91ºW and 85ºW (Figure A2.1). One region of positive SSH consisted of a weak, anticyclonically circulating warm filament eddy, derived from the Loop Current, which was centered south of the Mississippi Canyon and which extended northwest to the 1000-m isobath southwest of the Canyon. The second positive SSH region was an anticyclonic warm slope eddy centered at the western side of the DeSoto Canyon. The region of negative SSH was associated with cyclonic circulation south of the Mississippi River Delta and centered at about 88.5°W and 27.5°N.

Currents collected at 104-m depth by a shipboard ADCP illustrate the patterns of circulation associated with the features observed in the SSH fields (Figure A2.2). The currents were directed to the southeast or south along most of the upper slope between 90°W and 89°W, where the western anticyclone was present and the confluence of that anticyclone and the cyclone to its east was located. These circulation features created conditions for the off margin flow of biologically productive waters associated with the Mississippi river discharge. Currents associated with the eastern anticyclone were eastward along the northern edge of the eddy. This circulation also created conditions where riverine-influenced productive waters were moved along the edge of the upper slope.

The surface chlorophyll imagery, derived from SeaWiFS ocean color data, shows that the pair of anticyclones and the cyclone pulled biologically productive water off the continental shelf onto and/or along the upper slope (Figures A2.3 and A2.4). The SeaWiFS ocean color imagery for the first part of the cruise shows the region of highest chlorophyll concentration along the 1000-m isobath is directly off the Mississippi River Delta at about 89°W. It also shows a region of relatively high chlorophyll concentration, when compared with the surrounding water, that is centered near 89.2ºW and 27.8ºN (Figure A2.3; Feature 1 indicated by the red cross). This region is associated with the interaction of the southeastward currents, which are pulling productive waters off the shelf, with cyclonic circulation found at this location. Part of this production is likely to be new production induced by the upwelling of nutrient rich waters to near surface by the cyclone.

SeaWiFS imagery for the last part of the cruise shows that, by mid-September, the off-shelf productive waters had been transported over the slope to about 2000-m water depth at about 89°W (Figure A2.4). The currents around the northeastern limb of the elongated warm filament eddy and the northwestern limb of the cyclone resulted in this transport and entrainment of productive water off the shelf. This region likely includes cyclone-induced new production seen in the earlier SeaWiFS imagery, which indicates a temporal persistence of the cyclonic feature of at least weeks. The image also shows that the off margin production along the 1000-m isobath was best developed south of approximately 89ºW off the Mississippi River Delta (Figure A2.4; Feature 2 indicated by the black cross).

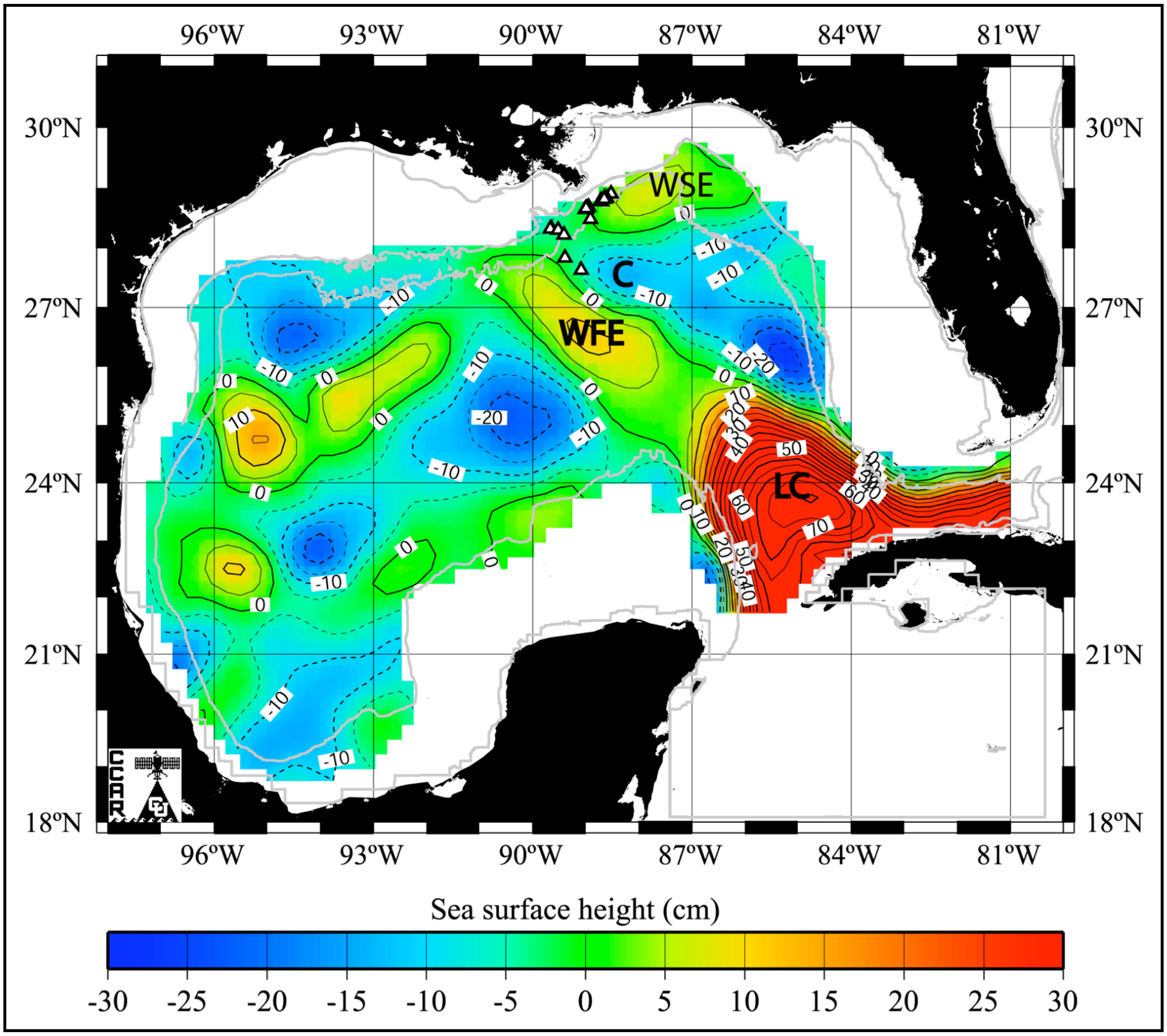

Figure A2.1. Sea surface height field for 2 September 2002, the mid point in time of the 2002 D-tag cruise (23 August-11 September). Triangles show locations of sperm whales tagged with the D-tag during the cruise. WSE refers to Warm Slope Eddy. LC refers to Loop Current. C refers to Cyclone. WFE refers to Warm Filament Eddy. The 10-, 200- and 1000- isobaths are shown.

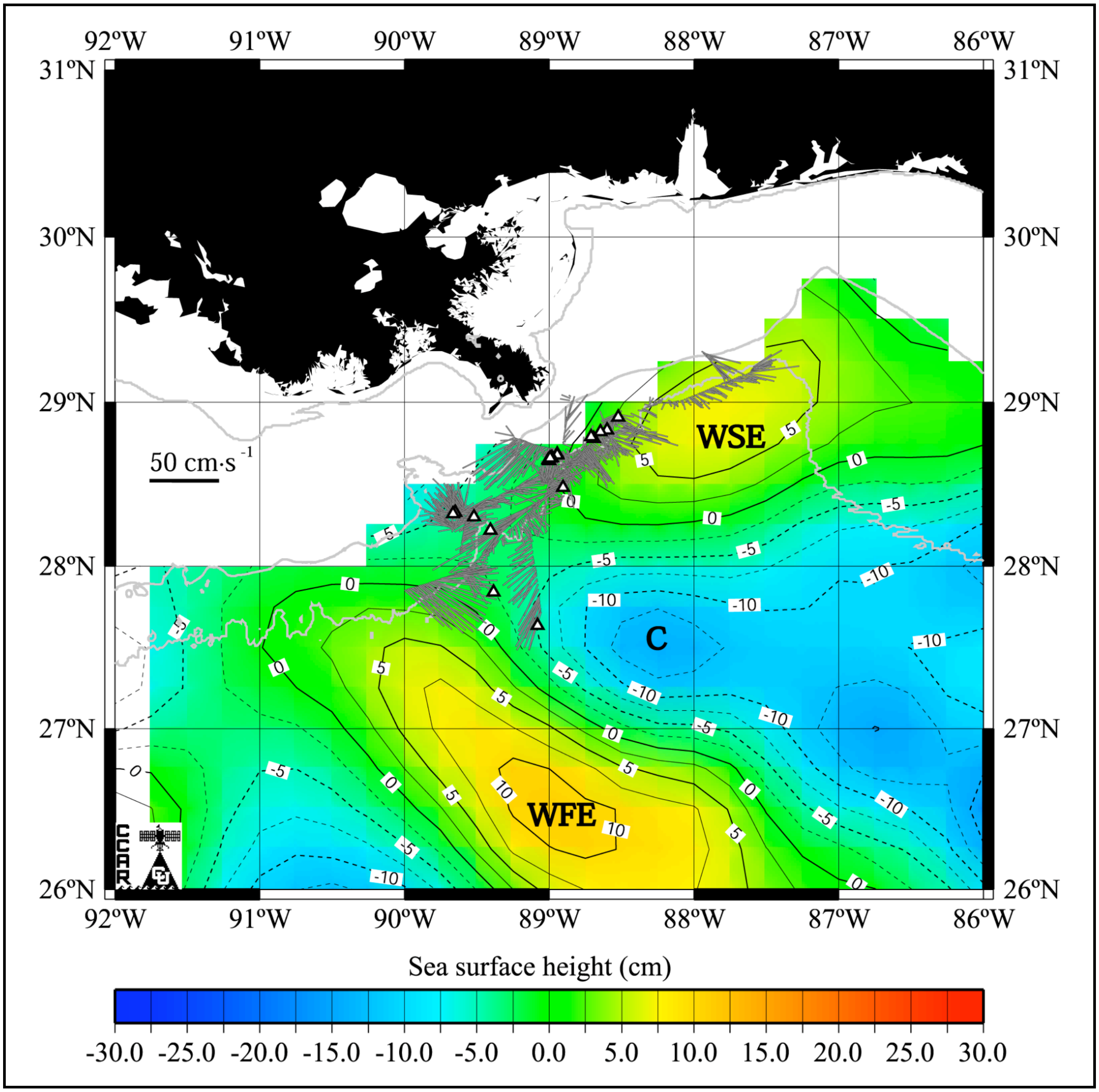

Figure A2.2. Current velocities determined from 150 KHz ADCP data collected during D-tag cruise 2002 are overlain on SSH field map for 2 September 2002. Currents shown are from the 104-m depth. Triangles show locations of sperm whales tagged with the D-tag during the cruise. WSE refers to Warm Slope Eddy. C refers to Cyclone. WFE refers to Warm Filament Eddy. The 10-, 200- and 1000- isobaths are shown.

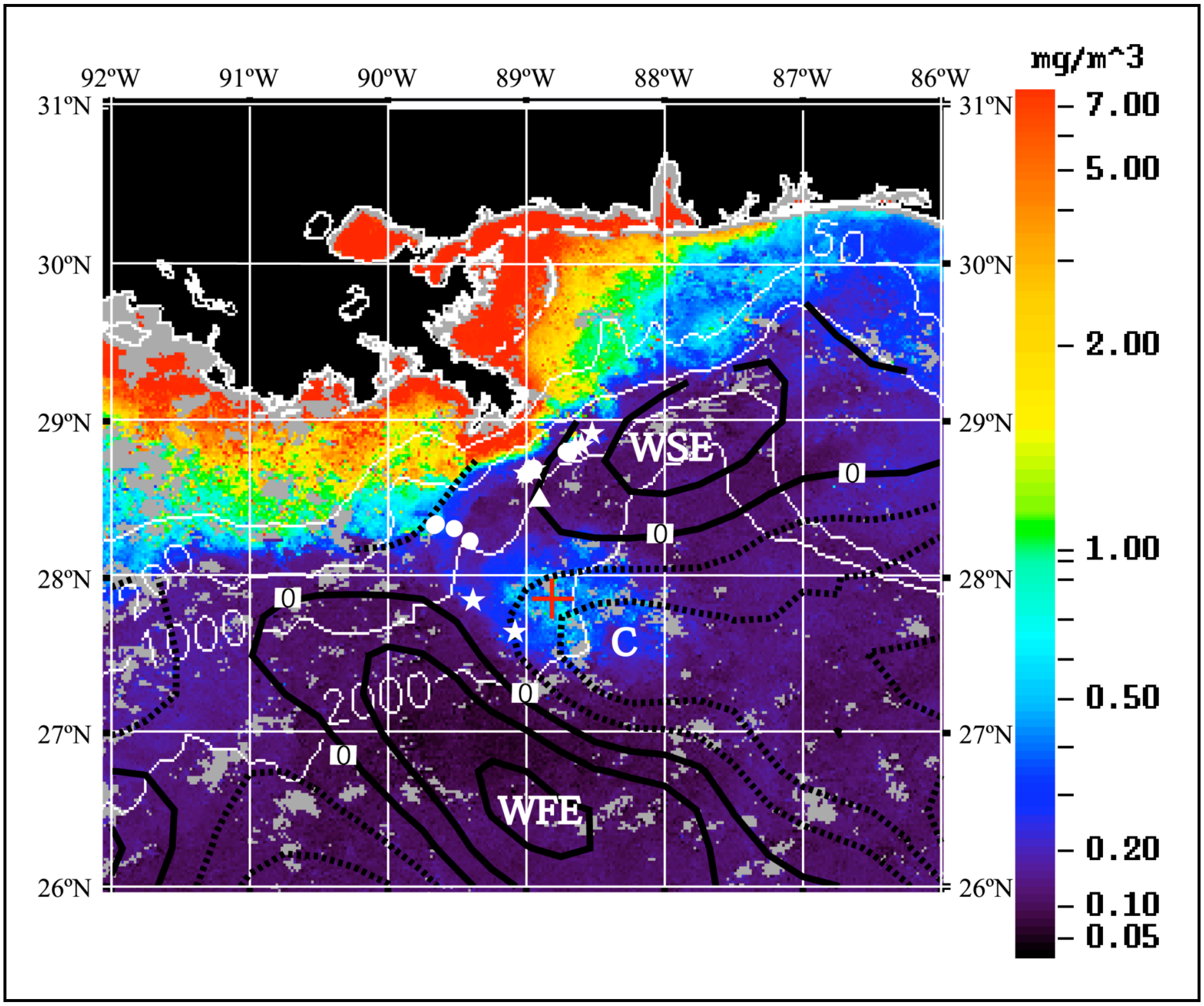

Figure A2.3. SeaWiFS 7-day composite of ocean color imagery centered on 23 August 2002. The contours of sea surface height for 2 September 2002 are shown in dark black lines. The contour intervals are every 5 cm; solid lines are positive SSH and dashed lines are negative SSH. White circles show the locations of sperm whales tagged on the 2002 D-tag cruise during the time period of 23-26 August 2002. White stars show the locations of sperm whales tagged during the time period 27 August-9 September 2002. White triangles show the locations of sperm whales tagged during the time period 10-16 September 2002. WSE denote Warm Slope Eddy. WFE denotes Warm Filament Eddy. C denotes Cyclone. The red cross indicates Feature 1 referred to in the text.

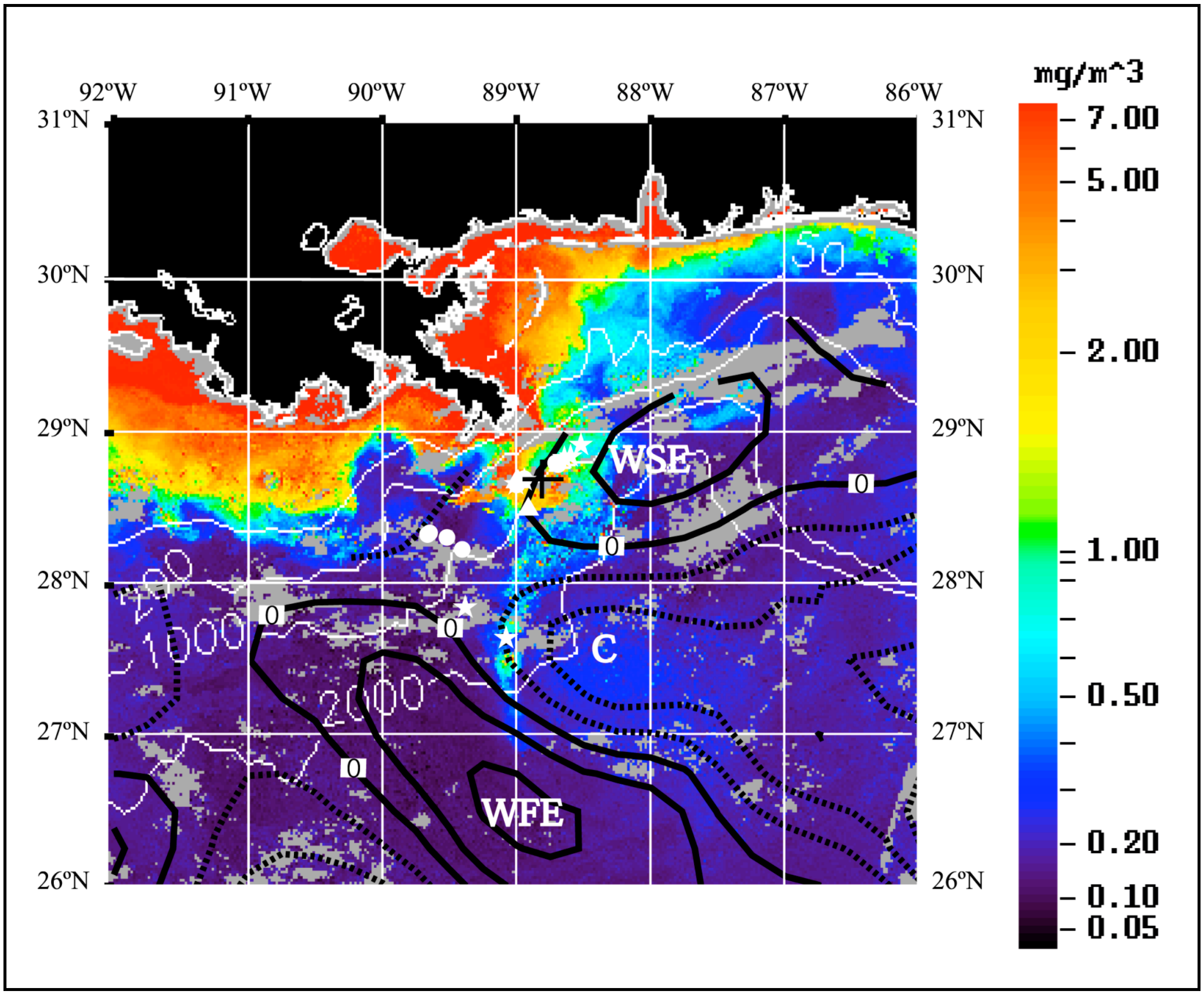

Figure A2.4. SeaWiFS 7-day composite of ocean color imagery centered on 13 September 2002 (earlier images had extensive cloud cover). The contours of sea surface height for 2 September 2002 are shown in dark black lines. The contour intervals are every 5 cm; solid lines are positive SSH and dashed lines are negative SSH. White circles show the locations of sperm whales tagged on the 2002 D-tag cruise during the time period of 23-26 August 2002. White stars show the locations of sperm whales tagged during the time period 27 August-9 September 2002. White triangles show the locations of sperm whales tagged during the time period 10-16 September 2002. WSE denote Warm Slope Eddy. WFE denotes Warm Filament Eddy. C denotes Cyclone. The black cross indicates Feature 2 referred to in the text.The off margin flow was also evidenced by near surface salinity data, collected during the cruise, near 89ºW where the off margin flow was seen. A CTD done at this location shows near surface salinities between 30 and 33 (not shown), confirming the entrainment of river-derived low salinity water off the shelf by the local circulation imposed by the triad of the anticyclones and the cyclone.

Table A2.1 shows the locations of the sperm whales tagged and gives data on the water depth, slope, distance to the two features identified in Figures A2.3 and A2.4, and the satellite-derived sea surface height and chlorophyll values for each location. The sperm whales tagged on the D-tag cruise were seen in water depths greater than 720 m, and all were on the negative side of the gradients between positive and negative SSH. The animals were in essentially three regional groupings. Two animals were located in water depths greater than 1200 m; both were located within approximately 20 km of the center of Feature 1. Four animals were located in the region of the Mississippi Canyon. The other 13 animals were located south of the Mississippi River Delta in the region of highest chlorophyll concentrations at or off-shelf of the 1000-m isobath.

The distance from the two features identified in Figures A2.3 and A2.4 and the tagged sperm whales were determined (Table A2.1). Sperm whales were found 21 to 123 km from the center of Feature 1 (Figure A2.3) with two of the tagged animals were in closest association with this feature. Sperm whales were found 22 to 108 km from the center the offshelf productive water of Feature 2 (Figure A2.4), with thirteen of the tagged animals were in close association with this feature.

Table A2.1

Locations of the Sperm Whales Tagged with D-tags during the Summer of 2002 Together with Data on the Water Depth, Slope, Distance to the Two Features Identified in Figures A2.3 and A2.4, and the Satellite-Derived Sea Surface Height and Chlorophyll Values for Each Location

Tag ID	Date (m/d/y)	Longitude (°W)	Latitude (°N)	Depth (m)	Slope	SSH (cm)	Ocean Color (mg m^{-3})	Distance Feature 1 (km)	Distance Feature 2 (km)
	8/22/2002	-89.6507	28.33	800.1			0.44		
235a	8/23/2002	-89.6507	28.33	800.1	0.017	-1.6	0.35	73.7	53.3
	8/22/2002	-89.6641	28.3203	756.1			0.46		
235b	8/23/2002	-89.6641	28.3203	756.1	0.019	-1.7	0.36	73.7	55
	8/22/2002	-89.5189	28.3014	935.6			0.21		
235c	8/23/2002	-89.5189	28.3014	935.6	0.013	-1.8	0.25	64	45.6
	8/23/2002	-89.4053	28.2208	1051.2			0.17		
236a	8/24/2002	-89.4053	28.2208	1051.2	0.011	-1	CloudCover-NoData	51	46.7
237a	8/25/2002	-88.693	28.78	1024.5	0.028	-0.2	0.14	119.8	53.4
237b	8/25/2002	-88.7102	28.7907	987	0.028	-0.2	0.15	120.2	52.3
	8/25/2002	-88.9441	28.6863	859.8			0.11		
238a	8/26/2002	-88.9441	28.6863	859.8	0.024	-3	CloudCover-NoData	101.7	26.8
	8/27/2002	-88.9441	28.6863	859.8			0.60		
	8/25/2002	-88.9992	28.6449	723.1			0.11		
238b	8/26/2002	-88.9992	28.6449	723.1	0.024	-2.5	CloudCover-NoData	96	20.2
	8/27/2002	-88.9992	28.6449	723.1			0.54		
239a	8/27/2002	-89.0052	28.6511	743.4	0.024	-7.6	0.46	96.6	19.9
239b	8/27/2002	-88.9459	28.6789	880.8	0.024	-7.3	0.62	100.9	26.3
240a	8/29/2002	-88.5236	28.9093	744.4	0.029	-6.2	CloudCover-NoData	140	74.4
	8/30/2002	-88.5236	28.9093	744.4			0.21		
240b	8/29/2002	-88.5995	28.8319	834.6	0.027	-5.8	0.36	129	64
240c	8/29/2002	-88.6455	28.8221	880.8	0.029	-6.2	0.31	126	59.5
248a	9/5/2002	-89.3839	27.8398	1285.7	0.013	-10.1	CloudCover-NoData	18.6	86.5
249a	9/6/2002	-89.08	27.6367	1631.1	0.012	-12	CloudCover-NoData	21.7	107.8
253a	9/10/2002	-88.9032	28.4815	1014.7	0.024	-3.3	CloudCover-NoData	81.2	31.9
	9/11/2002	-88.9032	28.4815	1014.7			1.04		
254a	9/11/2002	-88.9829	28.6644	821.4	0.024	-4.1	CloudCover-NoData	98.5	22.4
254b	9/11/2002	-88.9924	28.6617	794.3	0.024	-4.1	2.02	98	21.4
254c	9/11/2002	-88.9953	28.6612	782.5	0.024	-4	2.02	97.9	21.1

A.3. Summer 2003

During the D-tag cruise in summer 2003 (June 5-22), a strong Loop Current Eddy (LCE) named Sargassum with a sea surface height of more than 55 cm dominated the circulation over the slope in the northeastern Gulf of Mexico east of 91ºW (Figure A3.1). The northern periphery of the LCE extended almost to the shelf edge near 90ºW. The northern boundary was oriented along the 28°N latitude, which would induce eastward currents. The boundary of the LCE turned to a southeastward orientation at approximately 88°W. This would induce off-margin flow of waters influenced by the Mississippi River discharge. To the north of the LCE and east of about 90ºW, cyclonic circulation prevailed along the upper slope. The cyclone and anticyclone (LCE) observed in the SSH field persisted throughout the cruise period.

CTDs done north of 27ºN between 91ºW and 88ºW along with XBTs dropped in the same area confirmed the presence of the LCE and cyclone. Data from stations made in the northern limb of the LCE were marked by the presence of the Subtropical Underwater in the upper 200 m of the water column. Salinity values in this upper water mass were greater than 36.5 in the LCE region that was sampled. The depth of the 15ºC isotherm in the LCE was greater than 250 m. An XBT dropped north of the LCE showed the 15ºC depth was less than 150 m, confirming the presence of the cyclonic feature.

Currents collected by the 38-kHz shipboard ADCP at 73-m depth along approximately the 1000-m isobath of the slope illustrate the patterns of circulation associated with the anticyclonic and cyclonic features observed in the SSH field (Figure A3.2). Large currents with speeds of more than 75 cm/s were directed to the northeast between 90ºW and 88ºW, where the confluence of the anticyclone and cyclone was located approximately along the 1000-m isobath. West of 89ºW, these northeastward currents created conditions for the on-margin flow into in the Mississippi Canyon region of biologically poor, non-productive Loop Current water. Between 89°W and 88°W, the northeastward currents would tend to move waters influenced by the Mississippi River discharge along the slope adjacent to the shelf edge. At the northeast edge of the LCE, currents were southeastward. This occurred east of 88°W, where the LCE also was located farther off-shore. As a consequence, the currents along the 1000-m isobath east of 88ºW were more quiescent. This circulation created conditions for the off margin flow of biologically productive shelf waters associated with the Mississippi River discharge.

The surface chlorophyll imagery, derived from SeaWiFS ocean color data, shows that the pair of anticyclone and cyclone influenced the location of regions of both biologically rich and biologically poor waters along the 1000-m isobath (Figures A3.3 and A3.4). Currents on the northwest side of the LCE moved waters with very low chlorophyll concentrations (<0.20 mg m^{-3}) over the entire slope up to the shelf edge in the region of the Mississippi Canyon (Figure A3.3). Currents in the confluence of the LCE and cyclone (~89.25°W to 88.5°W) transported high chlorophyll ($\geq$ 2 mg m^{-3}) waters along the upper slope at and inshore of the 1000-m isobath. The SeaWiFS ocean color imagery for the first part of the cruise (June 4–10) shows the region of high chlorophyll concentrations along the 1000-m isobath has been transported over the slope to water depth greater than 2000 m at about 88ºW (Figure A3.3, Feature 1 indicated by a red cross). This region is associated with the southeastward currents of the LCE, which pulled productive waters over the continental slope.

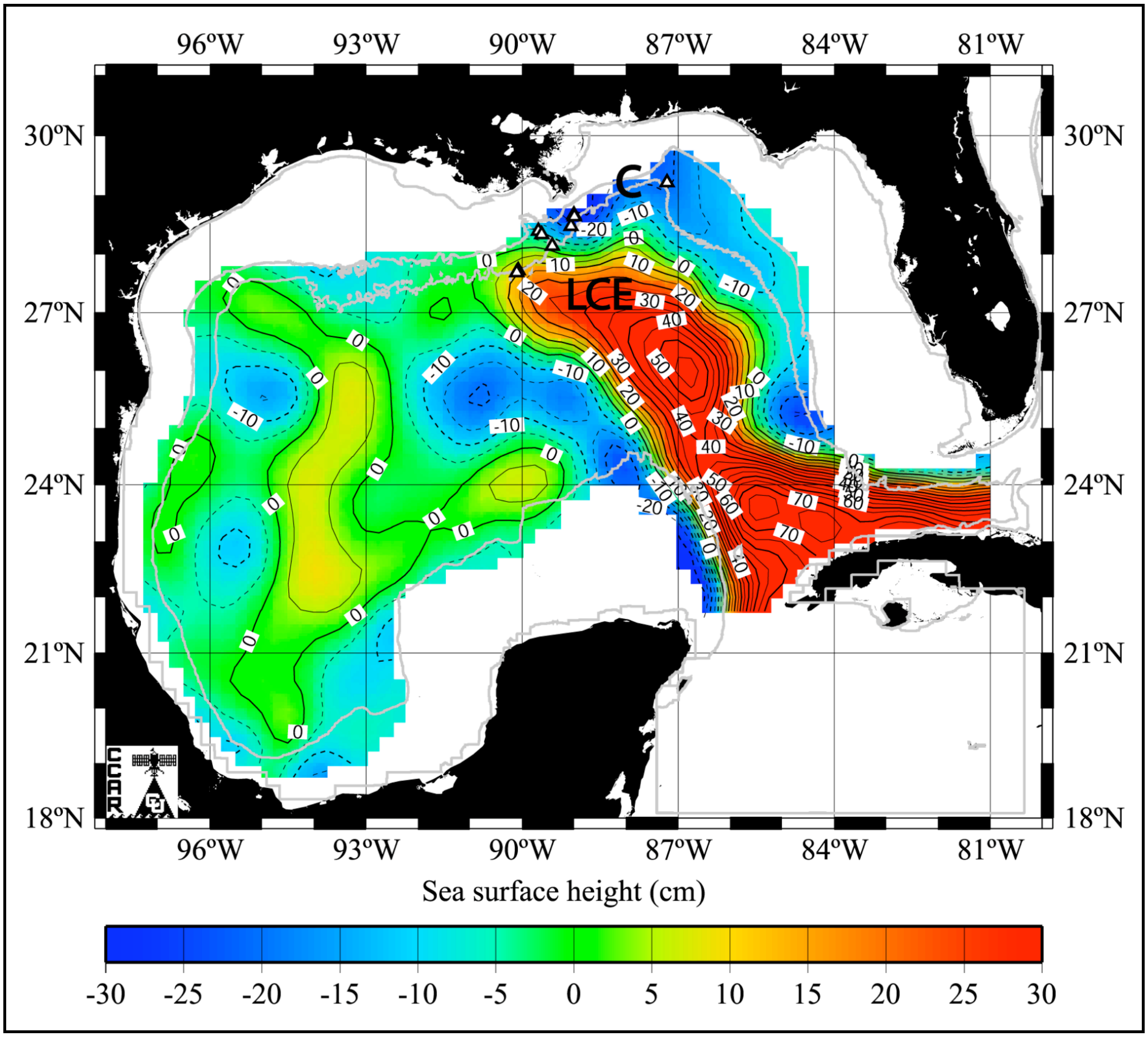

Figure A3.1. Sea surface height field for 14 June 2003, the mid point in time of the 2003 D-tag cruise (June 05-22). Triangles show locations of sperm whales tagged with the D-tag during the cruise. LCE refers to Loop Current Eddy. C refers to Cyclone. The 10-, 200- and 1000- isobaths are shown.

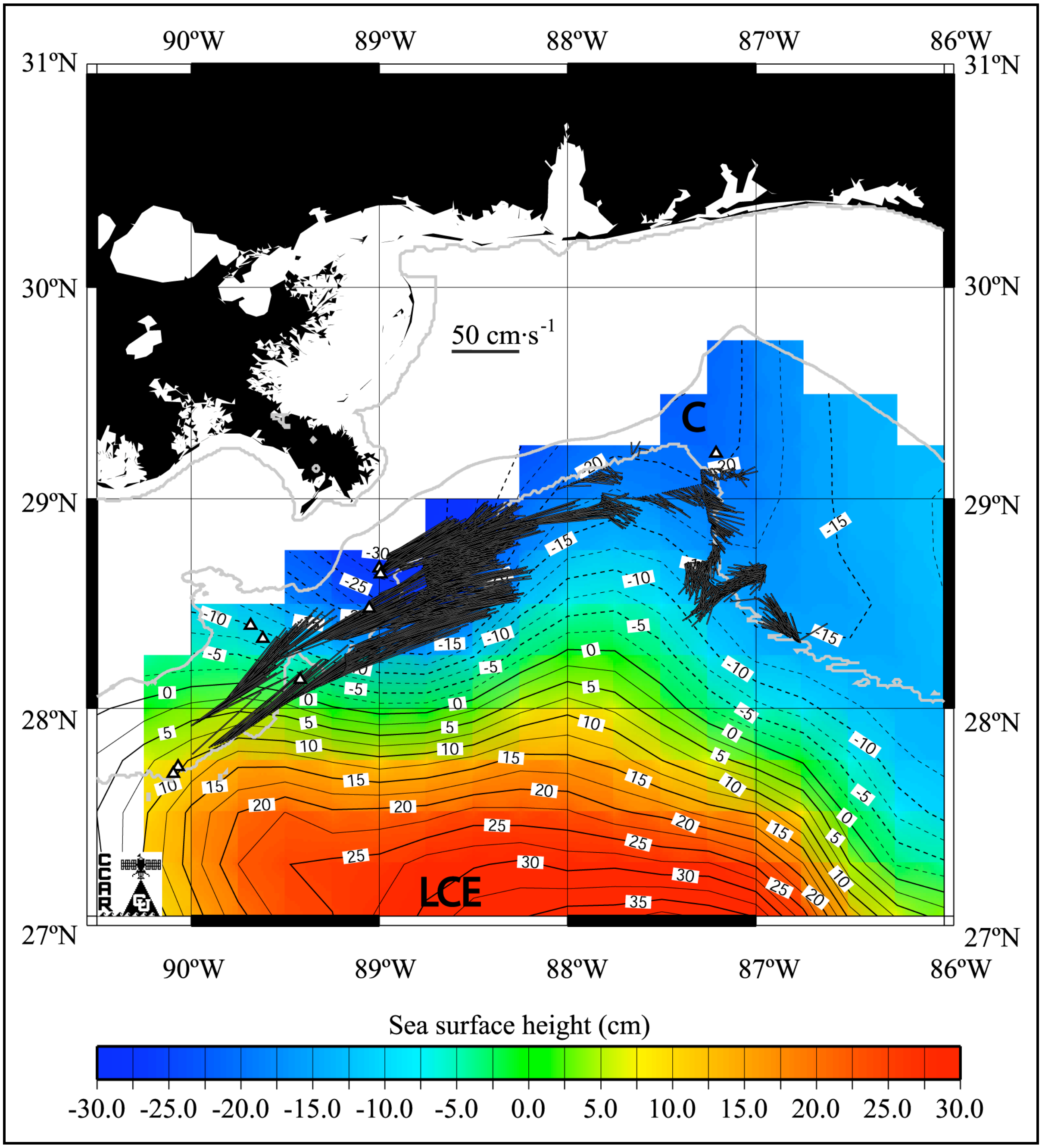

Figure A3.2. Current velocities, determined from 38-KHz ADCP data collected during the 2003 D-tag cruise, are overlain on the SSH field for 14 June 2003. Currents shown are from the 73-m depth. Triangles show locations of sperm whales tagged with the D-tag during the cruise. LCE refers to Loop Current Eddy. C refers to Cyclone. The 10-, 200- and 1000- isobaths are shown.

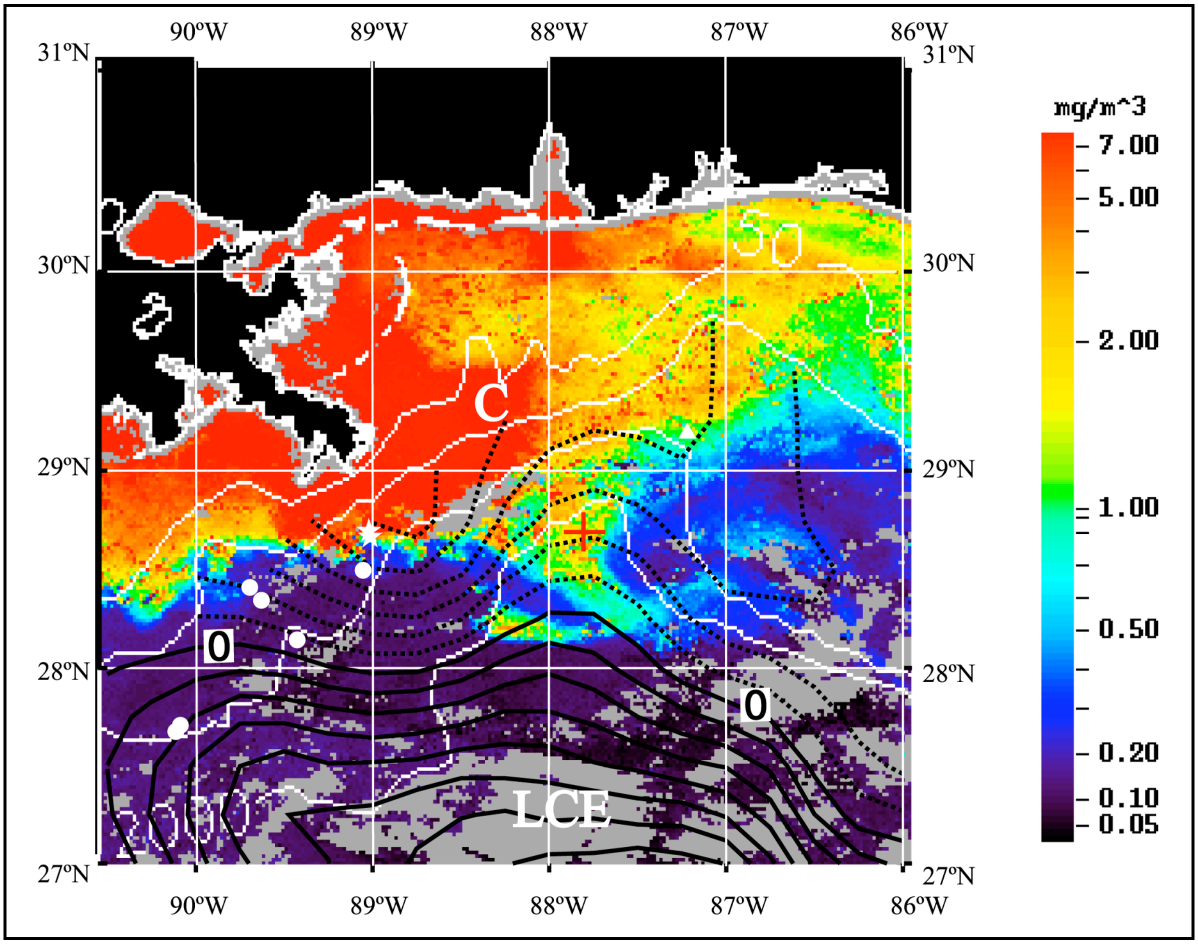

Figure A3.3. SeaWiFS 7-day composite of ocean color imagery centered on 7 June 2003. The contours of sea surface height for 14 June 2003 are shown in dark black lines. The contour intervals are every 5 cm; solid lines are positive SSH and dashed lines are negative SSH. The white triangle shows the location of a sperm whale tagged on the 2003 D-tag cruise during the time period of 4-10 June 2003. The white circles show the locations of sperm whales tagged during the time period 11-17 June 2003. The white stars show the locations of sperm whales tagged during the time period 18-24 June 2003. LCE denotes Loop Current Eddy. C denotes Cyclone. The red cross indicates Feature 1 referred to in the text.

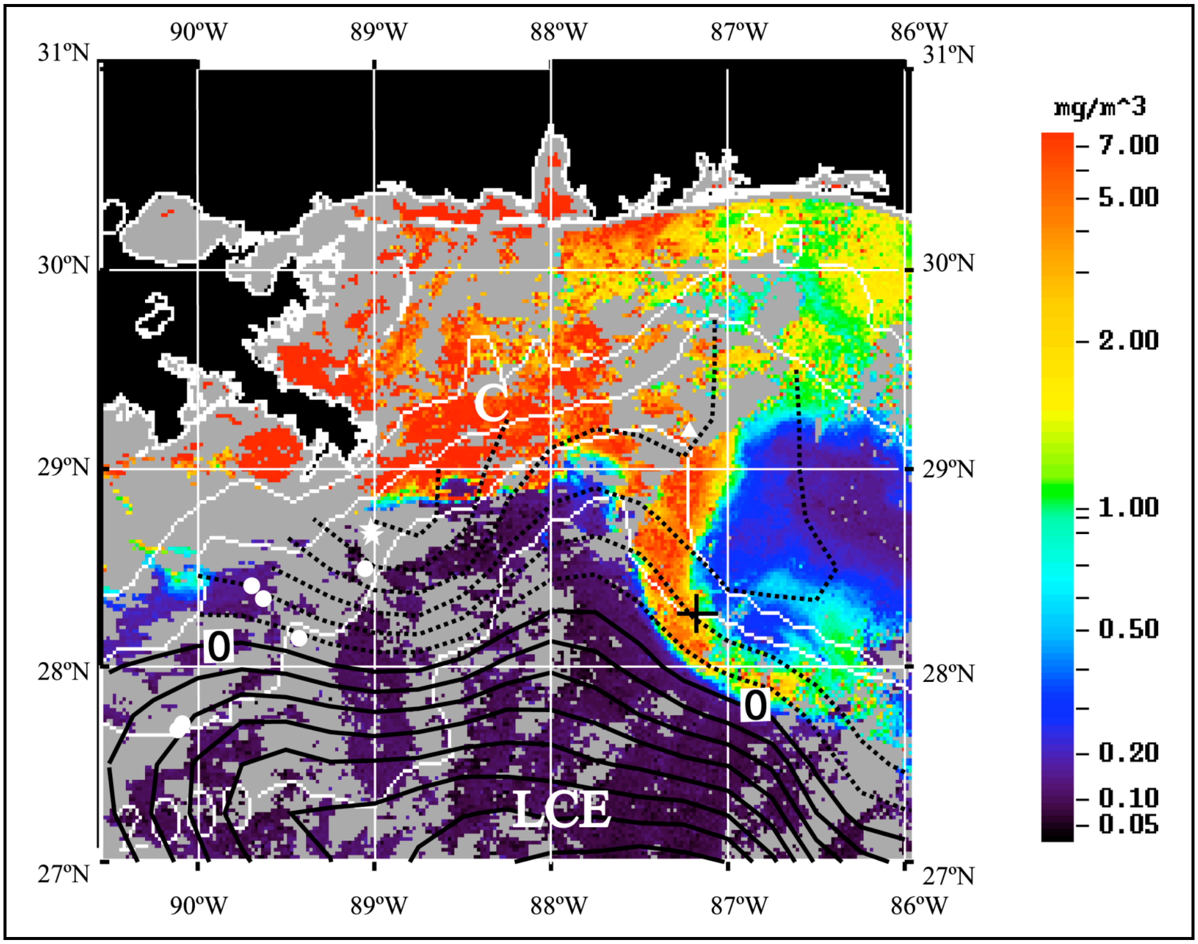

Figure A3.4. SeaWiFS 7-day composite of ocean color imagery centered on 14 June 2003. The contours of sea surface height for 14 June 2003 are shown in dark black lines. The contour intervals are every 5 cm; solid lines are positive SSH and dashed lines are negative SSH. The white triangle shows the location of a sperm whale tagged on the 2003 D-tag cruise during the time period of 4-10 June 2003. The white circles show the locations of sperm whales tagged during the time period 11-17 June 2003. The white stars show the locations of sperm whales tagged during the time period 18-24 June 2003. LCE denotes Loop Current Eddy. C denotes Cyclone. The black cross indicates Feature 1 at an advanced stage referred to in the text.

SeaWiFS imagery of the middle part of the cruise (June 11–17) is very similar to the earlier image with one distinct difference. Feature 1 in Figure A3.3 was more developed during the middle part of the cruise (Figure A3.4, Feature 1 indicated by a black cross). The off-margin flow of biologically productive waters has shifted from starting near 88ºW to about 87.3ºW and has developed into a more distinct, jet-like feature. This is shown as a tongue of very high cholorphyll (≥ 5 mg m^{-3}) water extending south of 28ºN and east of 87ºW in Figure A3.4.

SeaWiFS imagery of the last period of the cruise (June 18–24; not shown) also shows the off-margin flow at about 88ºW. So, this feature which is associated with the southeastward current of the LCE, persisted at least for several weeks. But in June this region was outside the main search area for the D-tag cruise.

The sperm whales tagged on the D-tag cruise were seen in water depths greater than 708 m (Table A3.1), and, as in previous summers, all were tagged on the negative side of the SSH gradient between the anticyclonic eddy and companion cyclone. The animals were observed in four different regions. One animal was found in the apex of the De Soto Canyon; it was located approximately 87 km from the center of Feature 1 in Figure A3.3. There were three animals tagged in the Mississippi Canyon and two animals along the northern limb of the LCE at about 90ºW and 27.8ºN. The five other animals tagged were observed directly south of the Mississippi River Delta in water depths greater than 722 m.

Sperm whales were found 87 to 278 km from the center of Feature 1, where the center of the latter is indicated by a red cross in Figure A3.3. By the time of the SeaWiFS ocean color imagery shown in Figure A3.4, the center of Feature 1 was displaced to the southeast, farther from the D-tag search area, and so the distances between the sperm whales and the center of the feature were greater and ranged from 107 to 327 km.

Table A3.1

Locations of the Sperm Whales Tagged with D-tags during the Summer of 2003 Together with Data on the Water Depth, Slope, Distance to the Center of Feature 1 Identified in Figures A3.3 and A3.4, and the Satellite-Derived Sea Surface Height and Chlorophyll Values for Each Location. Distance 1 is the Distance of the Tagged Whale to the Feature in Figure A3.3 (red cross); Distance 2 is the Distance of the Tagged Whale to the Feature in Figure A3.4 (black cross).

Tag ID	**Date (m/d/y)**	**Longitude (ºW)**	**Latitude (ºN)**	**Depth (m)**	**Slope**	**SSH (cm)**	**Ocean Color (mg m^{-3})**	**Distance 1 (km)**	**Distance 2 (km)**
	6/4/2003	-87.211	29.217	813.2			0.56		
sw156a	6/5/2003	-87.211	29.217	813.2	0.015	-7.9	CloudCover-NoData	81.2	107.6
sw162a	6/11/2003	-89.419	28.139	1111.7	0.009	-15.3	CloudCover-NoData	170.2	217.9
sw163a	6/12/2003	-89.684	28.397	708.9	0.018	-18.5	CloudCover-NoData	187.2	243.8
sw164a	6/13/2003	-89.618	28.334	844.5	0.012	-18.3	CloudCover-NoData	182.3	237
sw165a	6/14/2003	-89.054	28.48	816.4	0.025	-16.6	CloudCover-NoData	124.9	183.3
sw165b	6/14/2003	-89.054	28.48	816.4	0.025	-16.6	CloudCover-NoData	124.9	183.3
sw167a	6/16/2003	-90.069	27.72	1033.4	0.015	-10.8	CloudCover-NoData	247.7	287.9
sw167b	6/16/2003	-90.094	27.688	992.8	0.014	-12	CloudCover-NoData	251.5	291.1
sw170a	6/19/2003	-89.001	28.671	767.4	0.024	-9.1	CloudCover-NoData	117.2	182.3
sw173a	6/22/2003	-88.992	28.643	722.4	0.024	-9.1	CloudCover-NoData	116.5	180.6
	6/23/2003	-88.992	28.643	722.4			0.17		
sw173b	6/22/2003	-88.992	28.643	722.4	0.024	-9.1	CloudCover-NoData	116.5	180.6
	6/23/2003	-88.992	28.643	722.4			0.17		

The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

The Minerals Management Service Mission

As a bureau of the Department of the Interior, the Minerals Management Service's (MMS) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS), collect revenue from the Federal OCS and onshore Federal and Indian lands, and distribute those revenues.

Moreover, in working to meet its responsibilities, the **Offshore Minerals Management Program** administers the OCS competitive leasing program and oversees the safe and environmentally sound exploration and production of our Nation's offshore natural gas, oil and other mineral resources. The MMS **Minerals Revenue Management** meets its responsibilities by ensuring the efficient, timely and accurate collection and disbursement of revenue from mineral leasing and production due to Indian tribes and allottees, States and the U.S. Treasury.

The MMS strives to fulfill its responsibilities through the general guiding principles of: (1) being responsive to the public's concerns and interests by maintaining a dialogue with all potentially affected parties and (2) carrying out its programs with an emphasis on working to enhance the quality of life for all Americans by lending MMS assistance and expertise to economic development and environmental protection.