

UNITED STATES DEPARTMENT OF COMMERCE National Oceanic and Atmospheric Administration NATIONAL MARINE FISHERIES SERVICE

Alaska Fisheries Science Center 7600 Sand Point Way N.E. Bldg. 4, F/AKC Seattle, Washington 98115-0070

DATE:

March 12, 2008

MEMORANDUM FOR:

Douglas Mecum

Acting Alaska Regional Administrator

FROM:

↑ Douglas P. DeMaster

Science & Research Director, Alaska Region

SUBJECT:

Lynn Canal Herring ESA Petition: Transmittal of

Biological Review Team Report

I am pleased to submit the report of AFSC's Biological Review Team entitled, *Status Review of Pacific herring (Clupea pallasii) in Lynn Canal, Alaska*. The report incorporates the results of a peer review of its contents that was conducted by seven independent scientific experts (three non-federal, four federal) who were selected in compliance with the requirements of the Data Quality Act and the corresponding NOAA Information Quality Guidelines (NOAA IQ Guidelines).

The BRT concluded that Pacific herring in Lynn Canal are not a distinct population segment (DPS) as defined by the ESA. Examination of all available data by the BRT did not convince the majority of members that herring in Lynn Canal were markedly discrete from other populations of the same taxon in southeast Alaska. In addition, no members perceived Lynn Canal herring to be significant with respect to the taxon, although all recognized the importance of herring to the local ecosystem. A risk analysis was not conducted for Lynn Canal herring because the BRT did not find them to be a DPS.

Please let me know if there are items in the report needing to be clarified or otherwise addressed, or if the Center may be of further assistance in this matter.

Enclosure

cc:

Kaja Brix, AKR/PRD Usha Varanasi, NWC/SD



Status Review of Lynn Canal Herring (Clupea pallasii)

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March 2008

Acknowledgements

This document was prepared at the request of the Regional Office of the National Marine Fisheries Service. The purpose is to review the status of Lynn Canal herring and to determine if Lynn Canal herring are a distinct population segment of Pacific herring as defined by the Endangered Species Act. To accomplish this goal, the National Marine Fisheries Service assembled a knowledgeable biological review team: Mark G. Carls, Jeffrey T. Fujioka, Scott W. Johnson, Stanley D. Rice, Johanna Vollenweider, and Bruce L. Wing at the Alaska Fisheries Science Center; Richard G. Gustafson and Robin S. Waples at the Northwest Fisheries Science Center; Jamie N. Womble, National Park Service; and Erika Phillips at the Alaska Regional Office. We thank all team members for their contributions. The Alaska Department of Fish and Game (ADFG), the agency that manages Pacific herring in Alaska, provided considerable data and advice; important assistance was obtained from Marc Pritchett and Kevin Monagle and we thank them for this. Analysis of some of these data were contracted to Brian Bue, formerly at ADFG, and we thank him for his assistance.

Table of Contents

List of Tables	iii
List of Figures	iii
Chapter contents	v
List of Tables	
3.1. Mean growth rates in SEAK Pacific herring stocks	3.17
4.1. Seine hauls, fish catch, temperature, and salinity in SEAK.4.2. Summary of major <i>ShoreZone</i> habitat classifications	
List of Figures	
2.1. Pacific herring illustration	2.20
2.2 a,b. Global distribution of Pacific herring	
2.3. Herring stocks in the eastern north Pacific	
2.4 a,b. Herring spawning movement, small and large scale	
2.5. Comparison of spawning fidelity rates among areas in British Columbia	
2.6. Offshore herring in the Gulf of Alaska	
3.1. Pacific herring spawning locations and management areas in SEAK	3.18
3.2. Relationship between geographic area and fidelity in British Columbia	
3.3. Lynn Canal management area as defined by ADFG	
3.4. Seasonal Pacific herring biomass change in Lynn Canal	
3.5. Biomass estimates in tons for Lynn Canal herring	
3.6. Total nautical miles of herring spawn in Lynn Canal	
3.7. Relationship between biomass estimates obtained by dive survey and aerial survey	
3.8. Estimated historical biomass of Lynn Canal herring	
3.9 a,b. Pacific herring age structure in SEAK	
3.10. Larval herring distribution in SEAK	
3.11. Juvenile Pacific herring distribution in SEAK	
3.12. Adult non-spawning Pacific herring distribution in SEAK	
3.13. Total herring biomass and human harvest at major spawning locations in SEAK	
3.14. Genetic measures involving SEAK herring	
3.15. Spawn timing by location in SEAK	
3.16. Range of spawn timing in Pacific herring aggregations along North America	
3.17. Typical sea surface temperature gradient in SEAK in spring	
3.18 a,b. Differences in recruitment in SEAK herring	
3.19. Length-at-age data from 1929	3.38

3.20. Relationship between age and body size among SEAK herring stock	3.39
3.21 a,b. Differences among Pacific herring weight-at-age in SEAK	3.40
3.22. Trends in size (length) at age in SEAK Pacific herring stocks	
3.23. Cohort growth in northern SEAK	
3.24. Vertebrae number in SEAK herring	
3.25. Pacific herring migration in SEAK	
4.1. Ten study areas for herring in SEAK	4.17
4.2. Locations of beach seine sites sampled for herring in SEAK	4.18
4.3. Berners Bay: ShoreZone coastal habitat maps	
4.4. Shoreline kilometers of herring spawn in Lynn Canal	
4.5. Berners Bay: ADFG records of herring spawn	
4.6. Location and habitat type of beach seine sites in Berners Bay	4.22
4.7. Favorite Channel: <i>ShoreZone</i> coastal habitat maps	
4.8. Favorite Channel: ADFG records of herring spawn	
4.9. Location and habitat type of beach seine sites in Favorite Channel	
4.10. Auke Bay: <i>ShoreZone</i> coastal habitat maps	
4.11. Auke Bay: ADFG records of herring spawn	
4.12. Location and habitat type of beach seine sites in Auke Bay	
4.13. Tenakee Inlet: <i>ShoreZone</i> coastal habitat maps	
4.14. Tenakee Inlet: ADFG records of herring spawn	
4.15. Location and habitat type of beach seine sites in Tenakee Inlet	
4.16. Northern Sitka Sound: ShoreZone coastal habitat maps	
4.17. Northern Sitka Sound: ADFG records of herring spawn	
4.18. Location and habitat type of beach seine sites in Northern Sitka Sound	
4.19. Central Sitka Sound: ShoreZone coastal habitat maps	
4.20. Central Sitka Sound: ADFG records of herring spawn	
4.21. Location and habitat type of beach seine sites in Central Sitka Sound	
4.22. Southern Sitka Sound: ADFG records of herring spawn	
4.23. Location and habitat type of beach seine sites in Southern Sitka Sound	
4.24. Craig: <i>ShoreZone</i> coastal habitat map	
4.25. Craig: ADFG records of herring spawn	
4.26. Location and habitat type of beach seine sites in Craig	
4.27. Duke Island: <i>ShoreZone</i> coastal habitat maps	
4.28. Duke Island: ADFG records of herring spawn	
4.29. Location and habitat type of beach seine sites in Duke Island	
4.30. Kah Shakes: <i>ShoreZone</i> coastal habitat maps	
4.31. Kah Shakes: ADFG records of herring spawn	
4.32. Location and habitat type of beach seine sites in Kah Shakes	
4.33. General global sea surface temperature distribution	
4.34. Sea surface temperature in SEAK	
4.35. <i>ShoreZone</i> bioareas for SEAK	
4.36. Alaska marine ecoregions	4.52
5.1 Summary of biological information	5.1

Chapter 1. Executive summary	1.1
Introduction	1.1
Deliberation	1.2
Conclusion	1.2
Reference	1.3
Chapter 2. Pacific herring life history and ecology	2.1
Distribution	
Habitat requirements	2.1
Trophic interactions	2.2
Reproduction	
Mortality and survival	2.3
Diurnal movements	2.6
Migratory movements	2.7
Factors limiting productivity	2.8
Genetics	
Stocks, populations, metapopulation	2.9
References	
Figures	2.20
Chapter 3. Description of Pacific herring in Lynn Canal and southeastern Alaska	
Abstract	
Introduction	
Lynn Canal herring	
Pacific herring biomass in Lynn Canal	
Age structure, age structured models, and estimation of recruitment	
Estimate discrepencies	
SEAK herring Distribution	
Age structure	
Genetics	
Spawn timing	
Biomass	
Recruitment	
Size-at-age and growth rate	
Morphological or meristic variability	
Migration	
Metapopulation	
Summary	
References	
Table	
Figures	
o	
Chapter 4. Pacific herring habitat in southeastern Alaska	4.1
Abstract	
Introduction	4.1

Pacific herring habitat utilization in SEAK	4.1
Comparisons among study areas	4.2
Lynn Canal	4.2
Berners Bay	
Favorite Channel	4.3
Auke Bay	4.4
Tenakee Inlet	4.5
Sitka	
Northern Sitka Sound	
Central Sitka Sound	
Southern Sitka Sound	
Craig	
Duke Island	
Kah Shakes Cove	
Sea surface temperature and climate	
Marine zoogeographic provinces	
Summary	
References	
Tables	
Figures	4.17
Chapter 5. Are Lynn Canal herring a discrete population segment?	5 1
Abstract	
Introduction	
Endangered Species Act	
Evaluation of discreteness	
Evaluation of discreteness Evaluation of significance	
DPS decision by the BRT	
Are Lynn Canal herring discrete?	
Evidence against discreteness	
Evidence for discreteness	
Are SEAK herring discrete?	
Evidence for SEAK discreteness	
Are SEAK herring significant with respect to the taxon?	
References	
Figure	
1 15010	
Appendix A, Summary of Pacific herring genetic studies	A.1
-rr	
Appendix B. Analysis of ADFG age-length-weight data	B.1

Chapter 1 Executive Summary

Mark G. Carls

Introduction

On April 2, 2007 the National Marine Fisheries Service (NMFS) received a petition from the Sierra Club to list Pacific herring (*Clupea pallasii*) in Lynn Canal as endangered or threatened under the Endangered Species Act (ESA). The agency found that the petition presented substantial scientific and commercial information indicating the petitioned action may be warranted and initiated a status review (NMFS 2007).

The purpose of this document was to review the status of Lynn Canal herring and specifically to determine if Lynn Canal herring are a Distinct Population Segment (DPS) of Pacific herring as defined by the ESA. To accomplish this goal, NMFS assembled a knowledgeable biological review team (BRT): Mark G. Carls, Jeffrey T. Fujioka, Scott W. Johnson, Stanley D. Rice, Johanna Vollenweider, and Bruce L. Wing, at the Alaska Fisheries Science Center; Richard G. Gustafson and Robin S. Waples at the Northwest Fisheries Science Center; Jamie N. Womble, National Park Service; and Erika Phillips at the Alaska Regional Office. The Alaska Department of Fish and Game (ADFG), the agency that manages Pacific herring in Alaska, provided considerable data and advice; important assistance was obtained from Marc Pritchett and Kevin Monagle. Analysis of some of these data were contracted to Brian Bue, formerly at ADFG. Additional data were obtained from various sources, generally associated with scientific papers or reports.

After compiling and analyzing pertinent data, the BRT met on January 29, 2008 to discuss them and to determine if Lynn Canal herring are a DPS as defined by the ESA or if not, to determine the DPS to which Lynn Canal herring belong. In order to be classified as a DPS, a vertebrate population must fulfill two criteria – discreteness and significance. To be considered "distinct," a population, or group of populations, must first be "discrete" from other populations and then "significant" to the entire taxon (species or subspecies) to which it belongs. Evaluation was based on criteria in the ESA; a population segment of a vertebrate species may be considered discrete if it is markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors. Quantitative measures of genetic or morphological discontinuity may also provide evidence of this separation. A population may also be considered discrete if it is delimited by international governmental boundaries, between which exist differences in control of exploitation, management of habitat, conservation status, or regulatory mechanisms that are significant in light of Section 4(a)(1)(D) of the ESA.

Under the ESA, once a population segment is determined to be discrete under one or more of the above conditions, its biological and ecological significance to the taxon must then be considered. Criteria that can be used to assess whether the discrete population segment is significant include: 1) persistence of the discrete population segment in an ecological setting unusual or unique for the taxon; 2) evidence that loss of the discrete population segment would result in a significant gap in the range of a taxon; 3) evidence that the discrete population segment represents the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historic range; or, 4) evidence that the discrete population segment differs markedly from other populations of the species in its genetic

characteristics. A discrete population segment needs to satisfy only one of these criteria to be considered significant. However, the list of criteria is not exhaustive; other criteria may be used as deemed appropriate. The ESA and NMFS do not provide any guidance on what these additional criteria might be.

Deliberation

To examine the possibility that Lynn Canal herring are discrete, the BRT first briefly reviewed southeastern Alaska (SEAK) habitat, climate, and utilization by Pacific herring, thus allowing discussion of Lynn Canal herring in context.

Marine habitat in SEAK is variable, yet Pacific herring essentially occupy all of it. Organics and semi-protected, partially mobile substrate are the most common shore type and habitat class among all areas. Marine waters of SEAK are characterized by an inshore-offshore salinity gradient and a north-south temperature gradient. Inside waters are more estuarine, more protected from wave action, and have more extreme seasonal fluctuations in temperature and salinity than outside waters. Herring were captured in essentially all areas of SEAK; occasional capture failures were interpreted as insufficient sampling, not an absence of herring. Eelgrass meadows, kelp communities, sand-gravel beaches, and bedrock outcrops comprise a continuum of habitat types available to herring throughout southeastern Alaska. The percent shoreline extent of kelps (canopy and understory) and eelgrass are less in Lynn Canal than in all other areas but herring continue to spawn in Berners Bay and juveniles continue to utilize nearshore habitats in Auke Bay, Favorite Channel, and Berners Bay.

Beaches Pacific herring spawn on are not continuous in SEAK; some are repeatedly utilized, thus ADFG eventually began to manage herring in these areas as discrete stocks. However, available biological data, including genetics, spawn timing, biomass, recruitment, growth, meristics, and migration do not identify definitive divisions among SEAK stocks, rather apparent geographic groupings were variable and often rather arbitrary. Limited tagging studies within SEAK demonstrate fish migrate and mix over most of the region but were not designed to study spawning fidelity. Migration data from British Columbia, a region to the south of SEAK and reasonably similar in structure and climate, were used to roughly predict repeat spawning fidelity of herring stocks in SEAK; these approximations suggest considerable mixing among stocks (about 60 to 80%), possibly explaining the lack of definitive differences among stocks and suggesting that SEAK herring are part of an interrelated metapopulation. Clearly more work remains to understand the relationships among SEAK herring stocks, such as more detailed genetic analysis and more detailed, spawn-oriented and seasonal tagging studies.

Conclusion

The BRT concluded that Pacific herring in Lynn Canal are not a DPS as defined by the ESA. Examination of all available data by the BRT did not convince the majority of members that herring in Lynn Canal were markedly discrete from other populations of the same taxon in SEAK (the vote was 6 to 4). In addition, no members perceived Lynn Canal herring to be significant with respect to the taxon (although all recognized the importance of herring to the local ecosystem), thus even if the team had concluded that Lynn Canal herring were discrete the ESA significance criterion precludes its definition as a distinct population segment. A risk analysis was not completed for these fish because the BRT did not find that Lynn Canal herring are a DPS

The team concluded the smallest defensible DPS that includes Lynn Canal is SEAK. Although the team recognized the possibility that there may be subdivisions within SEAK, available biological data are either too incomplete or too similar to definitively separate herring populations within this region. The southern limit of the DPS, Dixon Entrance, is identified by genetic differences between herring in SEAK and those in British Columbia and by differences in parasitism between herring stocks north and south of the Queen Charlotte Islands. Genetics did not provide a definitive northern separator, rather the northern border is defined by a physical barrier: mobile, open ocean beaches are inadequate as spawning and rearing habitat. The northern boundary is near Icy Point. Glacier Bay and Lynn Canal are both included in the SEAK Pacific herring DPS.

The BRT based its decision on the best available science, yet recognizes that the science behind these decisions is imperfect. They also recognize that precautionary management of animals and ecosystems is a wise approach that goes beyond the language of the ESA. Precautionary management is the current stance of ADFG, the agency responsible for Pacific herring in Lynn Canal; the fishery has not been open since 1982. The information assembled in this report will further enable ADFG to appropriately manage this stock and it will enable Federal agencies responsible for the permitting of shoreline development to manage Lynn Canal herring in a precautionary manner.

Reference

NMFS 2007. Endangered and threatened species; notice of finding on a petition to list the Lynn Canal stock of Pacific herring as a threatened or endangered species. Fed Regist 72(174): 51619-51621.

Chapter 2 Pacific herring (*Clupea pallasii*) life history and ecology

Mark G. Carls

Pacific herring (*Clupea pallasii*): body elongate, depth about 4.5 into standard length, considerably and variably compressed. Head compressed about 4.0 to 4.5 into standard length. Mouth terminal, moderate in size, and directed moderately upward, upper jaw extending to around middle of eye. Teeth, none on jaws, a patch of fine teeth on volmer. Interorbital space slightly rounded, about 1.3 into eye. Eye diameter about equal to snout and about 3.5 to 4.0 into length of head. Opercles smooth (Hart 1973).

Pacific herring are one of about 330 species of fish classified within the family Clupeidae (Whitehead 1985). Pacific and Atlantic herring are the northernmost clupeids and the only ones in Arctic waters (Hay et al. 2001). They are dark bluish green to olive on the dorsal surface and fade to silver on the sides and belly (Fig. 2.1). Adult herring total length ranges from 13 to 46 cm and increases with latitude (Hart 1973; Garrison and Miller 1982; Emmett et al. 1991; Mecklenburg et al. 2002). For example, herring are rarely >25 cm in British Columbia; lengths >30 cm are common in Togiak (Hart 1973; Brazil 2007). Maximum age also increases with latitude. Until recently, Pacific, Atlantic, and Baltic herring were considered separate subspecies instead of species (*Clupea harengus harengus*, *C. h. pallasii*, and *C. h. membras*, respectively) (Hay et al. 2001; Mecklenburg et al. 2002).

Distribution

The species ranges from northern Baja California to the Arctic (Beaufort Sea) in the eastern Pacific (Mecklenburg et al. 2002) (Fig. 2.2). Pacific herring on the Asian coast range from Korea to the estuary of the Lena River in the Arctic Ocean (Laptev Sea) (Hart 1973). However, Pacific herring apparently mix with Atlantic herring as far west as the Barents sea, where two genetically different groups have been described (Jorstad 2004). Pacific herring populations in the Barents Sea, White Sea, and Kara Sea are apparently relics from an earlier dispersion of Pacific herring into the Atlantic associated with Pleistocene glaciation and are considered subspecies of *C. pallasii* (McQuinn 1997). Herring likely originated in the Atlantic Ocean and moved through the Bering Strait into the Pacific during the Pliocene (about 3 million years ago) (Novikov et al. 2001). In the postglacial period about 5000 y ago, Pacific herring dispersed and were distributed along the estuaries of the northern ocean, reaching the White Sea and some northern Norwegian fjords (Derjugin 1929; Jorstad et al. 1984; Novikov et al. 2001).

Habitat requirements

The habitat requirements of Pacific herring are diverse. For example, three different life history forms of Pacific herring are recognized in the northwestern Pacific: 1) a long-lived, migratory sea form; 2) a coastal form that undergoes little or no migration; and 3) a lagoon Pacific herring that is associated throughout its life with low salinity estuarine areas (Hay et al. 2001). Some Baltic herring also inhabit low salinity areas (<5 ppt) (Hay et al. 2001). Resident and migratory forms are thought to inhabit British Columbia and Washington (Taylor 1964; Trumble 1983; Hay 1985). Habitat requirements vary considerably with life stage and seasonally within life stage as should become clear in the ensuing text. Also clear is their adaptability; eggs for example, are not preferentially spawned on a single type of substrate,

rather whatever substrate is available at selected spawning sites is acceptable to these fish. How herring choose their repeatedly utilized spawning sites is a long-standing, unresolved puzzle.

Trophic interactions

Pacific herring are relatively small, schooling, abundant, mobile planktivores (forage fish) that provide a key link between lower trophic levels (typically crustaceans and small fish) and higher tropic levels [whales, sea lions, birds, and other fish; (Hart 1973; Hourston and Haegele 1980; Bakun 2006)]. Their position between first- or second-order consumers and larger predators essentially guarantees that the herring population is responsive to seasonal, oceanographic, and climate-driven changes in producer (phytoplankton) and predator populations and distributions. Intra- and interspecific competition are also important factors with an important nuance: herring may prey on early life stages of their predators, leading to trophic instability and possible abrupt regime shifts (Bakun 2006). Thus, the balancing act between trophic worlds explains in part why this relatively short-lived fish (about 20 y maximum) generally survives no more than 9 y (Ware 1985; Hay et al. 2001) and why population abundance is highly variable. However, survival during earlier life stages may be an even more important influence on population size; strongly recruiting year classes typically influence population size and age structure until senescence. Early life stages are particularly vulnerable to physical variability, resulting in high inter-annual variability and reproductive success (Bakun 2006).

Reproduction

From the human perspective, spawning is arguably the crucial event in the herring life cycle, for this is when the reproductive biomass concentrates in predictable, distinct regions at predictable times (Hay and Outram 1981) and is most easily enumerated. Spring spawning herring also represent a rich source of food for at least 25 vertebrate predators just emerging from winter (Willson and Womble 2006). Some species may consume only eggs, others both eggs and fish, and some consume adult fish only. Pacific herring are gonochoristic, oviparous, and iteroparous with external fertilization and spawn once a year (Emmett et al. 1991; Hay et al. 2001). Fecundity increases with female size, producing on average 19,000 eggs annually at 19 cm standard length and 29,500 at 22 cm (Hart 1973). Unfertilized Pacific herring eggs are about 1.0 mm in diameter; fertilized eggs are 1.2-1.5 mm in diameter (Outram 1955; Hart 1973; Hourston and Haegele 1980).

Adult herring typically congregate near spawning grounds weeks or months in advance of spawning and leave immediately thereafter, though some herring remain in inside waters near spawning grounds throughout the year (Haegele and Schweigert 1985). Ripe and spent herring can travel considerable distances in a short period of time [150 km in 6 d and 350 km in 16 d, respectively (Haegele and Schweigert 1985)].

Spawning areas (inlets, sounds, bays, and estuaries) are typically protected from ocean surf, probably an adaptation to minimize egg loss (Haegele and Schweigert 1985). No spawning has been reported in the relatively unsheltered Gulf of Alaska shoreline between northern southeastern Alaska and Yakutat or between Yakutat and Prince William Sound (Fig. 2.3). Herring typically spawn along the same shoreline each year although areas spawned can shift at various scales (e.g., small scale movement in Berners Bay or larger scale movement among Kah Shakes, Cat Island, and Annette Island in southeastern Alaska (SEAK) in the 1990s; Fig 2.4). Also variable are the volume of eggs deposited and shoreline spawn distances, easily visible

because the milt turns water milky white. For example, cumulative miles of spawn in Seymour Canal ranged from about 14 to 31 km between 1985 and 1989 (Bergmann et al. 1993).

Herring apparently do not favor specific vegetation types, rather the type of vegetation utilized is a function of spawn depth and the type of vegetation found in a given area (Haegele and Schweigert 1985). Adherent eggs are deposited on eelgrass, kelp, rockweed, other seaweed and sometimes rock, pilings, or trash (Hart 1973). Soft sediment is avoided (Stacey and Hourston 1982; Lassuy 1989). Herring in Lynn Canal spawn more heavily on large brown kelps (e.g., *Laminaria*, *Alaria*) than on eelgrass (*Zostera marina*) (Blankenbeckler and Larson 1987). Deposition depth ranges from high tide to subtidal; in Prince William Sound, 90% of the eggs are deposited between -2 and +5 m mean lower low water (Brown and Carls 1998). However, <25% of the spawn typically becomes exposed to air by tidal movement (in British Columbia) and this for only about 10% of the total incubation time (Haegele et al. 1981).

Spawn timing is related to winter and spring sea surface temperatures (Brown and Carls 1998) and varies according to latitude; it begins in November in the southern part of the range (California) and extends to August in the north (Kotzebue Sound, Alaska) (Lassuy 1989; Emmett et al. 1991). Spawning temperature ranges from 3.0°C to 12.3°C on the Pacific coast of North America (Scattergood et al. 1959). However, other factors may also influence spawn timing, such as tides (Hay 1990; Hay et al. 2001). Spawning typically occurs within a 3 to 6 week period within a given geographical area (Haegele and Schweigert 1985). Both males and females contact the substrate during spawning (Haegele and Schweigert 1985). Single spawning events are generally completed within 1 to 3 d (Hay 1985). Two or more spawning events are common at a given location; larger fish spawn before smaller, presumably younger fish, and these spawning events may be separated by 10 to 15 d (Hay 1985). Eggs hatch in 11 to 12 d at 10.7° C, 14 d at 8.5° C and 28 to 40 d at 4.4° C (Outram 1955). The optimal incubation temperature is roughly 5 to 9°C (Alderdice and Velsen 1971; Ojaveer 2006).

Herring eggs are euryhaline; the optimal salinity range for fertilization is about 12 to 24 ppt; sperm motility is reduced at low and high salinities [4 to 8 ppt and 28 to 32 ppt, respectively (Griffin et al. 1998)]. Maximum embryo survival was reported at 13 to 19 ppt and a spawning range of 8 to 28 ppt is typical (Alderdice and Velsen 1971). However at 32 ± 1 ppt, we routinely observed good fertility (80 to 96%), successful hatch (generally about 80%) and viable larvae (>95%) in herring from SEAK and Prince William Sound (Johnson et al. 1997).

Mortality and survival

Herring eggs must survive both 'top down' and 'bottom up' predation. Egg mortality is high (about 75%, range 67 to 100%) and tends to be greatest in upper intertidal areas and lowest at intermediate depths (Palsson 1984; Rooper et al. 1999). The amount of time eggs are exposed to air may be related to susceptibility to wave action and predation by birds and hypoxia, desiccation, and air-water temperature differentials: exposure to ultraviolet light may also increase risk factors for eggs in the upper intertidal (Alderdice and Velsen 1971; Hunter et al. 1979; Alderdice and Hourston 1985; Rooper et al. 1999). Crabs, sea anemones, sea cucumbers, and snails consume significant amounts of herring eggs (Haegele 1993). Perhaps lower survival at the lowest spawn depths (compared to the optimal intermediate depths) can be explained by greater access time by water-oriented predators because immersion time is longer and possibly because lower incubation temperatures prolong that access. In addition, low oxygen and microorganism invasions may kill large numbers of eggs; eggs in the middle of multiple layers

have reduced survival (Alderdice and Hourston 1985; Hay 1985). Surviving herring eggs hatch as larvae and are advected from natal areas by water movement.

Newly hatched larvae carry a yolk sac that is typically depleted in the first week and to survive they must begin feeding before depletion of endogenous energy stores and irreversible starvation. At 6 to 10°C, irreversible starvation occurs about 1 week after yolk resorption (McGurk 1984). The earliest larval stages begin feeding on invertebrate eggs and small zooplankton such as copepods, invertebrate eggs, and diatoms (Hart 1973). While the larval Pacific herring grow and congregate nearshore (generally in water <5 m deep) through their first summer, they continue to live mainly on copepods but may also eat other crustaceans, barnacle larvae, mollusk larvae or young fishes (Hart 1973; Brown and Carls 1998).

Larval mortality is caused by advection, predation, limited food availability, and other factors (McGurk 1993; McGurk et al. 1993; Norcross and Frandsen 1996). Loss of planktonic stages caused by diffusive and advective processes may explain large variations in population abundance; geographic patterns may be partially maintained in areas that limit egg and larval advection (Sanvicente-Anorve et al. 2006). A broad range of invertebrates and fish prey upon larvae by filtration, entrapment (e.g., ctenophores and jellyfish), or targeted feeding (Hart 1973; Alderdice and Hourston 1985). Suitable food must be located before irreversible starvation occurs if larvae are to survive. This observation forms the basis of the critical period hypothesis (Hjort 1914), that larval survival is the prime determinant of year-class strength, dependent on larval transition from endogenous to exogenous food. Low growth rates result in a longer exposure time for mortality through predation or transport out of favorable oceanographic regions (Cushing 1990; Leggett and DeBlois 1994). A longer larval period could result in poor condition for juvenile herring that must prepare for winter (Paul et al. 1998; Foy and Paul 1999; Norcross et al. 2001). Transport offshore can lead to increased mortality from lack of food, salinity intolerance, or increased predation pressure (Stevenson 1962; Alderdice and Hourston 1985; Schweigert et al. 1985; McGurk 1989; Wespestad and Moksness 1990). The larval stage may be the determinant of year class strength (Norcross et al. 2007).

When herring larvae become nektonic, they are able to swim to favorable habitats rather than follow currents (Gallego and Heath 1994). Metamorphosis to juveniles begins when larvae reach approximately 26 mm total length (about 10 weeks in Prince William Sound) and is complete by about 35 mm (Hourston and Haegele 1980; Hay 1985; Brown and Carls 1998; Stokesbury et al. 2002). Juveniles form and maintain schools as their primary defense against predation (Blaxter and Hunter 1982; Pitcher 1986) and spend the first two three years of their lives in nearshore waters (Tanasichuk et al. 1993; Hay et al. 2001). They occupy a variety of nearshore habitat types including steep bedrock outcrops, eelgrass, kelps, and sand-gravel beaches (Johnson and Thedinga 2005). Copepods remain an important food for juvenile herring. From August to October, age 0 juvenile herring survival depends on food availability, competition, predation, and disease (Stokesbury et al. 2002). Schooling is a mechanism that helps minimize the risks of the first three. During winter, as temperature and light decrease, food supply becomes limited and both young and adult year classes stop feeding functionally (Blaxter and Holiday 1963; Hay et al. 1988; Huse and Ona 1996; Paul et al. 1998).

To survive, juveniles must escape predation and accumulate sufficient energy for winter starvation. Predation is the greatest source of mortality for age 0 juvenile herring from the time of metamorphosis through fall (Stokesbury et al. 2000; Stokesbury et al. 2002). Sufficient energy storage to maintain age 0 and age 1 juveniles over winter is critical to juvenile herring survival in Prince William Sound and likely throughout northern waters. Food availability

declines in winter [the highest percentage of empty stomachs is in December (Norcross et al. 2001) and fish in cold regions often fast or reduce feeding (Blaxter and Holiday 1963; Hay et al. 1988; Paul et al. 1998)]. Consequently, whole body energy content drops over winter; YOY juveniles either consume relatively less energy than adults during this period or only those with the highest energy content in the fall survive (Paul et al. 1998). Juveniles begin recruiting to the adult population at about age 3 in the Gulf of Alaska (age 4 in the Bering Sea) (Williams and Quinn 2000; Hay et al. 2001). Age of first maturity increases with latitude, as early as 2 y in California, and as late as 8 y in the Bering Sea (Spratt 1981; Brazil 2007).

Apparent natural mortality is lower at the onset of adulthood than in juvenile and senescent adults, thus the overall mortality function is U-shaped (Vetter 1988; Hampton 2000; Tanasichuk 2000). The relationship between size and predation may in part explain declining natural mortality rates as herring approach adulthood. Increased body size may be a survival strategy to avoid predation (Houde 1997; Pedersen 1997) and larger-bodied juvenile herring are more likely to have sufficient energy reserves to survive winter starvation periods (Foy and Paul 1999; Stokesbury et al. 1999; Metcalfe and Monaghan 2003). Schooling is another survival strategy, common both to juveniles and adults. It is apparently an anti-predator tactic that increases survival odds for individual fish and schooling may have a sentry effect by increasing awareness of predators (Blaxter 1985). Schooling may increase feeding effectiveness and have hydrodynamic, migration, reproduction, and learning advantages (Freon et al. 2005). Survival of adult herring is dependent on both intrinsic and extrinsic factors; these are related because populations adapt to extrinsic pressures (Reznick et al. 2002; Reznick et al. 2006).

Intrinsic factors that may influence adult fish survival include growth rate, body size, genetics, reproductive effort, and senescence. Growth rate and longevity are influenced by water temperature (Terzibasi et al. 2007). Pacific herring are relatively small [about 70 g at maturation (≥3 y) and 200 g maximum in the oldest age classes]; growth becomes asymptotic at roughly 10 y (Tanasichuk 2000). The total herring lifespan is fairly short (6 or 7 y in extreme southern populations to 20 y or more in northern populations), consistent with the typical relationship between life span and body size among all species (Roff 1992; Hay et al. 2001; Metcalfe and Monaghan 2003). Genetic heritage determines how fast fish grow, how they utilize and store energy, their innate behavior, reproduction, and lifespan, and thus is arguably the central intrinsic factor. Reproductive stress and age-related reduction in metabolic efficiency might destabilize homeostasis and predispose adult herring to death (Woodhead 1979; Tanasichuk 2000). In particular, Tanasichuk (2000) demonstrates that increasing proportions of surplus energy in Pacific herring are allocated to gonads and argues that this demonstrates progressively greater reproductive strain in aging fish. However, because the rate of somatic growth becomes asymptotic, allocation of proportionally more energy to reproduction might simply mean that proportionately less energy is required for growth, leaving relatively more for reproduction without necessarily causing life-threatening physiological stress. Senescence, representing a combination of genetic heritage, accumulating physiological defects, and possibly growth history, ultimately limits individual lifespans. In fish species with gradual senescence (such as herring), age-dependent organ and cellular degeneration occur, including loss of muscle fiber and endocrine abnormalities (Patnaik et al. 1994; Terzibasi et al. 2007), probably a result of the progressive failure of physiological repair mechanisms to repair damage and maintain homeostatis (Valdesalicil and Cellerino 2003). These factors explain increased mortality rates as mature fish age.

Extrinsic (habitat) factors responsible for adult herring mortality include predation, starvation, disease, inter-specific competition, and contaminants. These in turn are influenced by ocean conditions, climate change, and intricate ecological relationships involving predators, prey, and intra- and inter-specific competition. This leads to a complex question: can the relative importance of each source of natural mortality be determined? The solution is not easy and may be impossible; natural mortality is one of the most difficult parameters to assess in fish populations (Vetter 1988; Tanasichuk 2000; Hewitt and Hoenig 2005). Most dead fish disappear without a trace. Instead of biologically based estimates of natural mortality, stock assessment models depend on modeled parameters or other estimates (Tanasichuk 2000; Cotter et al. 2004).

Diurnal movements

Diurnal movement in herring presumably evolved to maintain maximal access to prey, avoid predators, and conserve energy by digesting at colder temperatures. Adult herring schools remain near the seabed during daylight hours and move to the surface at dusk (Blaxter and Holiday 1963; Blaxter 1985; Hay et al. 2001). Feeding activity increases as the fish near the surface; as light levels decrease, visual attraction among school members relaxes and the fish disperse (Blaxter 1985). Small, less cohesive schools are best for optimum foraging (Blaxter and Hunter 1982). Herring can apparently switch to filter feeding during the night if particle sizes are suitable (Blaxter 1985). Many invertebrate prey follow a diel cycle and are most concentrated near the surface at night, suggesting this is an opportune place and time for herring to feed. Peak feeding is at dawn and dusk and herring actively feed on the way up and down in the water column, giving them access to a wide variety of foods and currents (Zusser 1958).

The swim bladder (or gas or air bladder) may play a role in herring buoyancy and be advantageous for diel movement. Herring, as are all clupeids, physostomous; the swim bladder has both stomach and anal ducts. Herring cannot excrete gas, rather they acquire it at the surface by swallowing air (Brawn 1962; Blaxter and Batty 1984; Thorne and Thomas 1990). This gas may persist for weeks or months, depending on the pressure regime (Blaxter and Batty 1984). Some researchers indicate swim bladders are rarely filled to volumes sufficient for neutral buoyancy, even at the surface (Blaxter and Batty 1984). Others conclude that herring can adjust their density through changes in swim bladder volume and that the swim bladder acts as a hydrostatic organ at least in fish near the surface (Brawn 1962). In theory, sufficient intake of surface air is unlikely to yield neutral buoyancy at depth, rather herring may adjust to an intermediate depth, thus minimizing energy expenditure by compensatory movement (Brawn 1962). Under this scenario, herring would expend energy to reach the intermediate depth [about 60 m (Thorne and Thomas 1990)] and they would expend energy at greater depths to offset gravity. Herring release some gas as they ascend but most gas is released after reaching the depth where they remain throughout the night suggesting adjustment to reach neutral buoyancy (Thorne and Thomas 1990). Intriguingly, a recent study suggests that Pacific herring produce rapid sound bursts associated with anal bubble expulsion (either from the gut or swim bladder) and that these sounds may have a social function (Wilson et al. 2004). In any case, the variable air volume in herring swim bladders means acoustic reflectivity varies, thus influencing population assessment by hydroacoustic measurement, thus careful compensation for varying target strength is required.

Migratory movements

Most adult herring tend to migrate between summer feeding areas on shelf waters to overwintering areas, often in protected nearshore water, and then to spawning locations (Hay et al. 2001). Juvenile herring remain isolated in bays through their first two winters in northern areas such as Prince William Sound and do not begin migratory behavior until they recruit to the adult population (Stokesbury et al. 2000). [First year juveniles (age 0+) school together and do not associate with larger juveniles (age 1+)]. Adult herring form small dynamic feeding schools in summer that move extensively to utilize relatively ephemeral aggregations of copepods (Kvamme et al. 2000; Sigler and Csepp 2007). In late fall, copepod densities are reduced and herring begin to aggregate into large schools and migrate to wintering areas (Huse and Ona 1996). The shift to wintering depths may be linked to breakup of the thermocline (Carlson 1980). Herring move little in wintering areas, apparently to conserve energy (Sigler and Csepp 2007), though as noted earlier, they can swim > 150 km/week immediately before or after spawning.

Herring schools have coherence. Individuals from different schools do not simply mix and migrate randomly, rather there is a positive association among tagged individuals released at the same site that can persist for several years (Hay and McKinnell 2002). An alternative explanation, that fish mix randomly and then home to specific spawning sites is not supported because the degree of homing (fidelity) to specific locations is low [Fig. 2.5; (Hay et al. 2001)]. Thus, there must be cohesion among conspecific herring, a phenomenon recognized in some other pelagic fish [e.g., yellowfin tuna] but the biological mechanisms for this cohesion are unclear (Hay and McKinnell 2002). An alternative, speculative, explanation is that because herring rarely segregate as individuals, small groups of fish may remain together as schools mix, thus the social behavior that binds individuals together may operate without requiring individual recognition of conspecifics (Hay and McKinnell 2002).

"If conspecifics associate together, it follows from the results that there may be a level of structure, perhaps dynamic and subtle, that occurs in large aggregations of herring that prevents thorough mixing. If so, large aggregations of herring typical of summer feeding concentrations could represent conglomerations of different populations, with different biological origins, destinations, and other characteristics. In B.C. [British Columbia] and most other areas inhabited by herring, dense aggregations also form during the overwintering period. In general, these aggregations appear to be larger but fewer in number and spatial scale than aggregations observed at other times of the year, particularly during spawning periods (Hay and McCarter 1997). This indicates that when these aggregations break up, herring move into smaller components and move away. perhaps to spawning or feeding areas. Therefore, we think that it is reasonable to assume that herring from different origins could merge or "appear" to merge into large loose aggregations. Subsequently they might dissociate into smaller units that retain some or much of the original membership. This would explain the patterns of matched tag recoveries observed after considerable periods (>200 days) and spatial ranges (>100 n.mi.). This interpretation supports the view that smaller aggregations may consist of fish with some common heritage, although not necessarily genetic. If so, when such small aggregations of relatively homogeneous fish (conspecifics) join with others to form larger conglomerations, they may not mix thoroughly. If so, conglomerations may confound attempts to take representative biological samples random[ly] from such mixtures. Instead such conglomerations of herring may contain components that exhibit a range of different biological attributes, such as different sizes and ages, nutritional states and

conditions, and maturation schedules, and perhaps even some form of spatial imprinting for approximate spawning sites (McQuinn 1997; Hay et al. 2001). It follows that fisheries directed on such mixed groups would have uncertain consequences, with the risk of relatively higher mortality among the smaller components." (Hay and McKinnell 2002)

Factors limiting productivity

Available energy (food) and sheltering from predation likely play critical roles in population productivity and these factors likely vary among life stages. Larval mortality may be the primary determinant of Pacific herring population recruitment and growth (Hjort 1914; Norcross et al. 2007). The hydrodynamic and meteorological events that influence water movement affect year class recruitment by affecting the vertical stability of the water column, thereby providing concentrations of suitable food (Lasker 1978), and by affecting transport of larvae to areas of good or bad food supply and predator fields (Fortier and Leggett 1982; Frank and Leggett 1982; Crecco et al. 1983; Crecco and Savoy 1984; Lambert and Ware 1984; Leggett et al. 1984; Sherman et al. 1984), estuarine nursery areas (Nelson et al. 1977; Shaw et al. 1985), and areas of recruitment to adult stocks (Bailey 1981; Parrish et al. 1981; Boltz and Lough 1984; Power 1986). Juvenile herring require adequate nearshore habitat to survive and the abundance of this habitat is likely to play a critical role in population success.

Adult herring may not be confined to spawning-related areas such as SEAK, rather they may range onto the continental shelf, thus greatly expanding feeding opportunities [inferred from Hay (Hay 2008)]. Although utilization of continental shelf waters by SEAK herring has not been documented, herring have been captured on shelf waters throughout the Gulf of Alaska, including areas near SEAK (Fig. 2.6). This suggests that like other eastern Pacific herring stocks, the habitat of SEAK herring may be considerably larger than is generally assumed.

Genetics

There is good evidence that some populations of Pacific herring in some geographic areas are locally distinctive genetically, albeit on a scale that is modest compared to the differences found between the two major lineages of Pacific herring. Atlantic and Pacific herring are characterized by genetic differences that are consistent with a separation of a few million years (Grant 1986). Within Pacific herring, by far the largest genetic distinction is between populations from Asia and the Bering Sea versus those inhabiting the remainder of North America (Fig. 2.2a) (Grant and Utter 1984). With the exception of some differentiated populations from the Alaskan Peninsula, genetic differences among localities within these two major lineages are smaller by an order of magnitude or more (Grant 1986). Among herring from the Alaska Peninsula to California, some very modest evidence of population structure exists [estimated with protein electophoresis (Grant and Utter 1984; Kobayashi 1993)]. Herring from some geographic areas can be distinguished in a statistical sense from herring from other areas (Burkey 1986; Schweigert and Withler 1990; Beacham et al. 2002; Bentzen 2004; Small et al. 2005). However, in some instances allele frequency differences between years were as large or larger than those between localities: temporal DNA variation among spawning aggregations may dominate the genetic variability at spatial scales of about 700 km (Seeb et al. 1999). In one case (Cherry Point herring in Washington), temporally replicated samples provided consistent evidence for population subdivision. Physical or behavioral isolation may explain consistent genetic differences. See Appendix A for a more complete review of Pacific herring genetics.

Large populations might be demographically independent but have only very modest levels of population genetic differentiation. At presumably neutral markers such as those discussed here, population genetic differentiation (as measured by indices such as F_{ST}) is a function of the product of the effective population size (N_e) and the migration rate (m = fraction)of the population that migrates each generation) (Gustafson et al. 2006). Based on Wright's (Wright 1978) commonly used (albeit very rough) approximation that at equilibrium, F_{ST} = $1/(1+4N_e m)$, the $F_{ST} = 0.0032$ reported by (Beacham et al. 2002) for NE Pacific herring implies $N_e m \sim 78$ migrant individuals per generation. In a small population, that could represent a high migration rate (m), but in a population with 10^6 individuals it equates to $m = 7.8 \times 10^{-5}$ – that is, less than one individual in ten thousand is a migrant each generation. Because of the inverse relationship between F_{ST} and $N_e m$ and the numerous assumptions underlying Wright's formula, robust estimation of migration parameters associated with low F_{ST} values is very difficult (Waples 1998; Whitlock and McCauley 1999), so any quantitative estimates should be treated with caution. Nevertheless, the point remains that in very large populations, very low levels of genetic differentiation could be associated with migration rates that have little influence in shaping the demographic parameters of the population. That is, large populations might be demographically independent but have only very modest levels of population genetic differentiation. Whether this scenario represents one in which it is reasonable to identify different 'populations' is not a question that has a single, scientifically correct answer; rather, the conclusions drawn for any practical application should be guided by desired conservation/management goals and the concept of 'population' that is most suitable to that application (Waples and Gaggiotti 2006).

Stocks, populations, metapopulation

The pan-Pacific herring population is a composite of many smaller stocks and is consistent with the metapopulation concept. Herring populations in the eastern Pacific consist of a relatively large number (>20) of relatively small populations (most <100,000 t) (Hay et al. 2001). Several herring stocks are evident along the Gulf of Alaska, including several population centers in British Columbia, SEAK, Yakutat, Prince William Sound, Kodiak, Cook Inlet, and along the Aleutian chain (Fig. 2.3). Herring in the Bering Sea are distinctly different from populations in the Gulf of Alaska and more southern regions of the eastern Pacific; they complete longer migrations, grow to 500 g (about twice the size of herring in the Gulf of Alaska), and are genetically distinct (Grant and Utter 1984; Williams and Quinn 2000; Hay et al. 2001) (Fig. 2.2a). Allozyme data also suggest differences among herring in south-central Alaska including those in SEAK and stocks in British Columbia (Grant and Utter 1984).

Two of the central characteristics of a metapopulation as originally defined were that local subpopulations are linked by migration and are subject to periodic extinction (extirpation) and recolonization (Levins 1969; Levins 1970). Consequently, not all suitable habitats would be simultaneously occupied. This ideal metapopulation included the assumptions that subpopulations have independent dynamics, that the exchange rate between subpopulations is so low that it has no affect on local subpopulation dynamics, and that all habitat patches have equal isolation and equal area (Levins 1970). In practice, most of these assumptions have been relaxed and no real metapopulation has been identified that satisfies all these criteria (Hanski and Simberloff 1997).

Local subpopulations within a metapopulation are spatially structured and migration among the subpopulations has some effect on local subpopulation dynamics (Hanski and

Simberloff 1997). The underlying concept in the many refinements to the original metapopulation model is that "persistence of species depends on their existence as sets of local populations, largely independent yet interconnected by migration" (Harrison and Taylor 1997). Others have advocated that linkage of local- and regional-scale population processes beyond extinction-recolonization analysis can be considered under the metapopulation concept for marine fishes and that "the critical feature of metapopulations is the coupling of spatial scales, whereby local populations experience partially independent dynamics but receive some identifiable demographic influence from other populations" (Kritzer and Sale 2004).

An 'adopted-migrant' variant of the metapopulation hypothesis applied to Atlantic herring suggests that juveniles that associate with and synchronize their maturation with adult schools will adopt the migration and homing patterns of the adults (McQuinn 1997). Thus local spawning populations are maintained by "repeat rather than natal homing to spawning areas, while local population persistence is ensured through the social transmission of migration patterns and spawning areas from adults to recruiting individuals" (McQuinn 1997). Under the adopted-migrant hypothesis, hydrographic forces on larvae and the effects of schooling of juveniles lead the majority of individuals to spawn in their native population. Thus differences in the mean values of meristic and morphometric measurements that reflect environmental differences during development are maintained, although strays from other populations are adopted by local populations and gene flow is significant(McQuinn 1997). The adopted-migrant hypothesis is consistent with genetic studies on Atlantic herring that have not observed temporally persistent differences, since no genetic differences would be expected between Atlantic herring populations with the hypothesized level of gene flow (McQuinn 1997). Although this metapopulation concept and adopted-migrant hypothesis were first formulated for Atlantic herring, they have equal application in the case of Pacific herring (Gustafson et al. 2006). Along these lines, several investigators have provided evidence indicating the major migratory stocks of Pacific herring in British Columbia are spatially structured and interact as a metapopulation (Ware et al. 2000; Ware and Schweigert 2001; Ware and Schweigert 2002; Ware and Tovey 2004). Dispersal rate and straying in both Atlantic and Pacific herring appear to be density dependent and increase with abundant recruitment, resulting in periodic waves of dispersal that radiate throughout the metapopulation (Huse et al. 2002; Ware and Schweigert 2002).

To be considered a metapopulation a system must meet the following two criteria: 1) local populations must be shown to exchange low levels of individuals, and 2) extinction and recolonization must be documented (Smedbol 2002). Both of these metapopulation criteria have been met, for example, by Georgia Basin Pacific herring to the south of SEAK. Evidence supporting the hypothesis that the five major migratory stocks of British Columbia Pacific herring form a spatially structured metapopulation include: 1) the spatially fragmented distribution of spawning habitat (Hay et al. 1989; Ware et al. 2000; Hay and McCarter 2004), 2) evidence of disappearance and recolonization events (Ware and Tovey 2004), 3) evidence of significant migration (straying) between the five main stock assessment regions as indicated by tagging data (Hay et al. 1999; Ware et al. 2000; Hay et al. 2001), and 4) high levels of gene flow as shown by DNA microsatellite analyses (Beacham et al. 2001; Beacham et al. 2002).

References

- Alderdice, D. F. and A. S. Hourston 1985. Factors influencing development and larval survival of Pacific herring (*Clupea harengus pallasi*) eggs and larvae to beginning of exogenous feeding. Can J Fish Aquat Sci 42(Supplement 1): 56-68.
- Alderdice, D. F. and F. P. J. Velsen 1971. Some effects of salinity and temperature on early development of Pacific herring (*Clupea pallasi*). J Fish Res Bd Can 28: 1545-1562.
- Bailey, K. M. 1981. Larval transport and recruitment of Pacific hake. Mar Ecol Prog Ser 6: 1-9.
- Bakun, A. 2006. Wasp-waist populations and marine ecosystem dynamics: navigating the "predator pit" topographies. Prog Oceanog 68(2-4): 271-288.
- Beacham, T. D., J. F. Schweigert, C. MacConnachie, K. D. Le, K. Labaree and K. M. Miller. 2001. Population structure of herring (*Clupea pallasi*) in British Columbia: an analysis using microsatellite loci. Fisheries and Oceans Canada, Canadian Science Advisory Secretariat. Research Document 2001/128 Retrieved December 2004, from http://www.dfo-mpo.gc.ca/csas/Csas/Csas/English/Research_Years/2001/2001_128e.htm.
- Beacham, T. D., J. F. Schweigert, C. MacConnachie, K. D. Le, K. Labaree and K. M. Miller 2002. Population structure of herring (*Clupea pallasi*) in British Columbia determined by microsatellites, with comparisons to southeast Alaska and California, Fisheries and Oceans Canada, Canadian Science Advisory Secretariat.
- Bentzen, P. 2004. Analysis of mtDNA polymorphism in Puget Sound herring: A preliminary summary provided for WDFW. March 13, 2004, memorandum. Portland, OR, National Marine Fisheries Service, Protected Resources Division.
- Bergmann, W. R., R. Timothy and R. Larson 1993. 1989 Seymour Canal sac roe herring fishery. Alaska Fish Game Regional Information Report(No. 1J93-07): 1-33.
- Blankenbeckler, D. and R. Larson 1987. Pacific herring (*Clupea harengus pallasi*) harvest statistics, hydroacoustical surveys, age, weight, and length analysis, and spawning ground surveys for southeastern Alaska, 1980-1983. Juneau, Alaska Department of Fish and Game, Division of Commercial Fish. Technical Data Report 202: 121.
- Blaxter, J. H. S. 1985. The herring: a successful species? Can J Fish Aquat Sci 42, Supplement No. 1: 21-30.
- Blaxter, J. H. S. and R. S. Batty 1984. The herring swimbladder: loss and gain of gas. J Mar Biol Assoc UK 64: 441-459.
- Blaxter, J. H. S. and F. G. Holiday 1963. The behavior and physiology of herring and other clupeids. Adv Mar Biol 1: 261-393.
- Blaxter, J. H. S. and J. R. Hunter 1982. The biology of clupeoid fishes. Adv Mar Biol 20: 1-223.
- Boltz, G. R. and R. G. Lough 1984. Growth of larval Atlantic cod, *Gadus morhua*, and haddock, *Melanogromus aegolfinis* on Georges Bank, spring 1981. Fish Bull 81:827-836
- Brawn, V. M. 1962. Physical properties and hydrostatic function of the swimbladder of herring (*Clupea harengus* L.). J Fish Res Bd Can 19: 635-656.
- Brazil, C. 2007. Abundance, age, sex, and size statistics for Pacific herring in the Togiak district of Bristol Bay, 2005. Alaska Fish Game Fishery Data Series No. 07-36: 1-55.
- Brown, E. D. and M. G. Carls 1998. Pacific herring (*Clupea pallasi*). Rest Notebook, EVOSTC: 1-8.

- Burkey, C. J. 1986. Population structure of Pacific herring (*Clupea harenqus pallasi*) in Eastern Prince William Sound, Alaska, University of Alaska, Juneau. masters.
- Carlson, H. R. 1980. Seasonal distribution and environment of Pacific herring near Auke Bay, Lynn Canal, southeastern Alaska. Trans Am Fish Soc 109(1): 71-78.
- Cotter, A. J. R., L. Burt, C. G. M. Paxton, C. Fernandez, S. T. Buckland and J. X. Pax 2004. Are stock assessment methods too complicated? Fish Fish 5(3): 235-254.
- Crecco, V. A. and T. F. Savoy 1984. Effects of fluctuations and hydrographic conditions on year class strength of American shad (*Alosa sapidissima*) in the Connecticut River. Can J Fish Aquat Sci 41: 1216-1223.
- Crecco, V. A., T. F. Savoy and L. Gunn 1983. Daily mortality rates of larval and juvenile American shad (*Alosa sapidissima*) in the Connecticut River with changes in year class strength. Can J Fish Aquat Sci 40: 1719-1728.
- Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv Mar Biol 26: 249-293.
- Derjugin, K. M. 1929. Fauna of the White Sea and the conditions of its origin. Priroda 9: 17-28.
- Emmett, R. L., S. L. Stone, S. A. Hinton and M. E. Monaco 1991. Distribution and abundance of fishes and invertebrates in West Coast estuaries, Volume II: species life history summaries. ELMR. Rockville, MD, NOAA/NOS SEA Division: 329.
- Farley, E. 2008. Personal communication.
- Fortier, L. and W. C. Leggett 1982. Fickian transport and the dispersal of fish larvae in estuaries. Can J Fish Aquat Sci 39: 1150-1163.
- Foy, R. J. and A. J. Paul 1999. Winter feeding and changes in somatic energy content of age-0 Pacific herring in Prince William Sound, Alaska. Trans Am Fish Soc 128(6): 1193-1200.
- Frank, K. T. and W. C. Leggett 1982. Coastal water replacement: its effect on zooplankton dynamics and the prey- predator complex associated with larval capelin (*Mallotus villosus*). Can J Fish Aquat Sci 39: 979-990.
- Freon, P., P. Cury, L. Shannon and C. Roy 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. Bull Mar Sci 76(2): 385-462.
- Gallego, A. and M. R. Heath 1994. The development of schooling behavior in Atlantic herring *Clupea harengus*. J Fish Biol 45: 569-588.
- Garrison, K. J. and B. S. Miller 1982. Review of the early life history of Puget Sound fishes. Fish Res Inst U Wash: 729.
- Grant, W. S. 1986. Biochemical genetic divergence between Atlantic, *Clupea harengus*, and Pacific, *C. pallasi*, herring. Copeia 1986: 714-719.
- Grant, W. S. and F. M. Utter 1984. Biochemical population genetics of Pacific herring (*Clupea pallasi*). Can J Fish Aquat Sci 41(6): 856-864.
- Griffin, F. J., M. C. Pillai, C. A. Vines, J. Kaaria, T. Hibbard-Robbins, R. Yanagimachi and G. N. Cherr 1998. Effects of salinity on sperm motility, fertilization, and development in the Pacific herring, *Clupea pallasi*. Biol Bull 194(1): 25-35.
- Gustafson, R. G., J. Drake, M. J. Ford, J. M. Myers, E. E. Holmes and R. S. Waples 2006. Status review of Cherry Point Pacific herring (*Clupea pallasii*) and updated status review of the Georgia Basin Pacific herring distinct population segment under the Endangered Species Act. Seattle, WA, Northwest Fisheries Science Center: 182.

- Haegele, C. W. 1993. Epibenthic invertebrate predation of Pacific herring, *Clupea pallasi*, spawn in British Columbia. Can Field-Nat 107(1): 83-91.
- Haegele, C. W., R. D. Humphreys and A. S. Hourston 1981. Distribution of eggs by depth and vegetation type in Pacific herring (*Clupea harengus pallasi*) spawnings in southern British Columbia. Can J Fish Aquat Sci 38(4): 381-386.
- Haegele, C. W. and J. F. Schweigert 1985. Distribution and characteristics of herring spawning grounds and description of spawning behavior. Can J Fish Aquat Sci 42: 39-55.
- Hampton, J. 2000. Natural mortality rates in tropical tunas: size really does matter. Can J Fish Aquat Sci 57(5): 1002-1010.
- Hanski, I. and D. Simberloff, Eds. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. Metapopulation biology: ecology, genetics, and evolution. London, Academic Press.
- Harrison, S. and A. D. Taylor, Eds. 1997. Emperical evidence for metapopulation dynamics. Metapopulation biology: ecology, genetics, and evolution. London, Academic Press.
- Hart, J. L. 1973. Pacific fishes of Canada. Bulletin 180. Ottawa, ON, Fisheries Research Board of Canada.
- Hay, D. 2008. Herring enhancement in Prince William Sound: feasibility, methodology,
 biological and ecological implications. Prince William Sound herring restoration plan. R.
 B. Spies. Anchorage, AK, Exxon Valdez Oil Spill Trustee Council: Appendix B.
- Hay, D. E. 1985. Reproductive biology of Pacific herring (*Clupea harengus pallasi*). Can J Fish Aquat Sci 42: 111-126.
- Hay, D. E. 1990. Tidal influence on spawning time of Pacific herring (*Clupea harengus pallasi*). Can J Fish Aquat Sci 47(12): 2390-2401.
- Hay, D. E., J. R. Brett, E. Bilinski, D. T. Smith, E. M. Donaldson, G. A. Hunter and A. V. Solmie 1988. Experimental impoundments of prespawning Pacific herring (*Clupea harengus pallasi*) effects of feeding and density on maturation, growth, and proximate analysis. Can J Fish Aquat Sci 45(3): 388-398.
- Hay, D. E. and P. B. McCarter 1997. Larval retetion and stock structure of British Columbia herring. J Fish Biol 51: 155-175.
- Hay, D. E. and P. B. McCarter. 2004. Herring spawn areas of British Columbia: a review, geographic analysis and classification. Revised edition 2004 (HTML format). Retrieved December 2004, from http://www.pac.dfo-mpo.gc.ca/sci/herring/herspawn/pages/project_e.htm.
- Hay, D. E., P. B. McCarter and K. Daniel 1999. Pacific herring tagging from 1936-1992: a reevaluation of homing based on additional data, Fisheries and Oceans Canada: 1-58.
- Hay, D. E., P. B. McCarter and K. S. Daniel 2001. Tagging of Pacific herring *Clupea pallasi* from 1936-1992: a review with comments on homing, geographic fidelity, and straying. Can J Fish Aquat Sci 58(7): 1356-1370.
- Hay, D. E., P. B. McCarter, R. Kronlund and C. Roy 1989. Spawning areas of British Columbia herring: a review, geographical analysis and classification. Canadian Manuscript Report of Fisheries and Aquatic Sciences I-VI (No. 2019).
- Hay, D. E. and S. M. McKinnell 2002. Tagging along: association among individual Pacific herring (*Clupea pallasi*) revealed by tagging. Can J Fish Aquat Sci 59(12): 1960-1968.
- Hay, D. E. and D. N. Outram 1981. Assessing and monitoring maturity and gonad development in Pacific herring. Canadian Technical Report Fisheries and Aquatic Sciences(988): 1-31.

- Hay, D. T., R. Toresen, R. Stephenson, M. Thompson, R. Claytor, F. Funk, E. Ivshina, J. Jakobsson, T. Kobayashi, I. McQuinn, G. Melvin, J. Molloy, N. Naumenko, K. T. Oda, R. Parmanne, M. Power, V. Radchenko, J. Schweigert, J. Simmonds, B. Sjostrand, D. K. Stevenson, R. Tanasichuk, Q. Tang, D. L. Watters and J. Wheeler 2001. Taking stock: an inventory and review of world herring stocks in 2000. Herring: expectations for a new millennium, Alaska Sea Grant College Program.
- Hewitt, D. A. and J. M. Hoenig 2005. Comparison of two approaches for estimating natural mortality based on longevity. Fish Bull 103(2): 433-437.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. Rapp P-V Reun Cons Int Explor Mer 20: 1-228.
- Houde, E. D. 1997. Patterns and trends in larval stage growth and mortality of teleost fish. J Fish Biol 51: 52-83.
- Hourston, A. S. and C. W. Haegele 1980. Herring on Canada's Pacific coast. Can Spec Publ Fish Aquat Sci 48: 23.
- Hunter, J. R., J. H. Taylor and H. G. Moser 1979. Effect of ultraviolet irradiation on eggs and larvae of the northern anchovy, *Engraulis mordax*, and the Pacific mackerel, *Scomber japonicus*, during the embryonic stage. Photochem Photobiol 29: 325-338.
- Huse, G., S. Railsback and A. Ferno 2002. Modelling changes in migration pattern of herring: collective behaviour and numerical domination. J Fish Biol 60(3): 571-582.
- Huse, I. and E. Ona 1996. Tilt angle distribution and swimming speed of overwintering Norwegian spring spawning herring. ICES J Mar Sci 57: 903-910.
- Johnson, S. W., M. G. Carls, R. P. Stone, C. C. Brodersen and S. D. Rice 1997. Reproductive success of Pacific herring, *Clupea pallasi*, in Prince William Sound, Alaska, six years after the *Exxon Valdez* oil spill. Fish Bull 95(4): 748-761.
- Johnson, S. W. and J. F. Thedinga 2005. Fish use and size of eelgrass meadows in southeastern Alaska: a baseline for long-term assessment of biotic change. Northwest Sci 79: 141-155.
- Jorstad, K. E. 2004. Evidence for two highly differentiated herring groups at Goose Bank in the Barents Sea and the genetic relationship to Pacific herring, *Clupea pallasi*. Enviorn Biol Fish 69: 211-221.
- Jorstad, K. E., G. Dahle and O. I. Paulsen 1984. Genetic comparison between Pacific herring (*Clupea pallasi*) and Norwegian fiord stock of Atlantic herring (*Clupea harengus*). Can J Fish Aquat Sci 51(Suppl. 1): 233-239.
- Kobayashi, T. 1993. Biochemical analyses of genetic variability and divergence of populations in Pacific herring. Bull Nat Res Inst Far Seas Fish 30: 1-77.
- Kritzer, J. P. and P. F. Sale 2004. Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. Fish Fish 5(2): 131-140.
- Kvamme, C., L. Nottestad, A. Ferno, O. A. Misund, A. Dommasnes and B. E. Axelsen 2000. A sonar study of the migration pattern of Norwegian spring-spawning herring (*Clupea harengus* L.) in July. ICES J Mar Sci CM2000: 1-24.
- Lambert, T. C. and D. M. Ware 1984. Reproductive strategies of demersal and pelagic spawning fish. Can J Fish Aquat Sci 41: 1565-1569.
- Lasker, R. H. 1978. The relation between oceanographic conditions and larval anchovy food in the California current: identification of factors contributing to recruitment failure. Rapports et Proces-Verbaux des Reunions Council Permanent International pour L'Exploration de la Mer 173: 212-230.

- Lassuy, D. M., D 1989. Species profiles. Life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest). Pacific herring US Fish Wildl. Serv. Biol. Rep. 82(11.126); US Army Corps of Engineers TR-EL-82-4: 1-18.
- Leggett, W. C. and E. DeBlois 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? Netherland Journal of Sea Research 32: 119-134.
- Leggett, W. C., K. T. Frank and J. E. Carscadden 1984. Meteorological and hydrographic regulation of year class strength in capelin (*Mallotur mallotus*). Can J Fish Aquat Sci 41: 1193-1201.
- Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. B Entomol Res 15: 237-240.
- Levins, R. 1970. Extinction. Some mathematical problems in biology, Providence, RI, American Mathematical Society.
- McGurk, M. D. 1984. Effects of delayed feeding and temperature on the age of irreversible starvation and on the rates of growth and mortality of Pacific herring larvae. Mar Biol 84(1): 13-26.
- McGurk, M. D. 1989. Advection, diffusion and mortality of Pacific herring larvae *Clupea harengus pallasi* in Bamfield Inlet, British Columbia. Mar Ecol Prog Ser 51(1-2): 1-18.
- McGurk, M. D. 1993. Allometry of herring mortality. Trans Am Fish Soc 122(6): 1035-1042.
- McGurk, M. D., A. J. Paul, K. O. Coyle, D. A. Ziemann and L. J. Haldorson 1993. Relationships between prey concentration and growth, condition, and mortality of Pacific herring, *Clupea pallasi*, larvae in an Alaskan sub-arctic embayment. Can J Fish Aquat Sci 50(1): 163-180.
- McQuinn, I. H. 1997. Metapopulations and the Atlantic herring. Rev Fish Biol Fisher 7(3): 297-329.
- Mecklenburg, C. W., T. A. Mecklenburg and L. K. Thorsteinson 2002. Fishes of Alaska. Am Fish Soc: 1-134.
- Metcalfe, N. B. and P. Monaghan 2003. Growth versus lifespan: perspectives from evolutionary ecology. Exp Gerontol 38: 935-940.
- Nelson, W. R., M. C. Ingraham and W. E. Schaff 1977. Larval transport and year-class strength of Atlantic menhaden, *Brevoortia tyrannus*. Fish Bull(75): 23-42.
- Norcross, B. L., E. D. Brown, R. J. Foy, M. Frandsen, S. M. Gay, T. C. Kline, D. M. Mason, E. V. Patrick, A. J. Paul and K. D. E. Stokesbury 2001. A synthesis of the life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska. Fish Oceanogr 10: 42-57.
- Norcross, B. L. and M. Frandsen 1996. Distribution and abundance of larval fishes in Prince William Sound, Alaska, during 1989 after the *Exxon Valdez* oil spill. Am Fish Soc Symp 18: 463-486.
- Norcross, B. L., S.-B. Kelly, P.-J. F. Hulson and T. J. Quinn II 2007. An early life history model for Pacific herring in Prince William Sound, Alaska. Prince William Sound herring: an updated synthesis of population declines and lack of recovery. S. D. Rice and M. G. Carls. Juneau, AK, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Auke Bay Laboratories: 7.1-7.18.
- Novikov, G. G., A. K. Karpov, A. P. Andreeva and A. V. Semenova 2001. Herring of the White Sea. 18th Lowell Wakefield Symposium, Anchorage, AK, University of Alaska Sea Grant College Program.

- Ojaveer, E. 2006. On the external and parental effects in early development of herring (*Clupea pallasi*) at the NE Kamchatka. Fish Res 81(1): 1-8.
- Orsi, J. A. 2008. Personal communication.
- Orsi, J. A., J. A. Harding, S. S. Pool, R. D. Brodeur, L. J. Haldorson, J. M. Murphy, J. H. Moss, E. V. J. Farley, R. M. Sweeting, J. F. T. Morris, M. Trudel, R. J. Beamish, R. L. Emmet and E. A. Fergusson 2007. Epipelagic fish assemblages associated with juvenile Pacific salmon in neritic waters of the California current and the Alaska current. Am Fish Soc Symp 57: 105-155.
- Outram, D. N. 1955. The development of the Pacific herring egg and its use in estimating age of spawn. Fish Res Bd Can Pacific Biological Station(Circular 40): 9.
- Palsson, W. A. 1984. Egg mortality upon natural and artificial substrata within Washington State spawning grounds of Pacific herring (*Clupea harengus*). Seattle, University of Washington. Masters: 191.
- Parrish, R. H., C. S. Nelson and A. Bakun 1981. Transport mechanisms and reproductive success of fishes in the California current. Biol Oceanog 1(175-203).
- Patnaik, B. K., N. Mahapatro and B. S. Jena 1994. Aging in Fishes. Gerontology 40(2-4): 113-132.
- Paul, A. J., J. M. Paul and E. D. Brown 1998. Fall and spring somatic energy content for Alaskan Pacific herring (*Clupea pallasi Valenciennes* 1847) relative to age, size and sex. J Exp Mar Biol Ecol 223(1): 133-142.
- Pedersen, B. H. 1997. The cost of growth in young fish larvae, a review of new hypotheses. Aquaculture 155(1-4): 259-269.
- Pitcher, T. J., Ed. 1986. Functions of shoaling behavior in teleosts. The Behavior of Teleost Fishes. Baltimore, Maryland, Johns Hopkins University Press.
- Power, J. H. 1986. A model of the drift of northern anchovy, *Engraulis mordax*, larvae in the California current. Fish Bull 84: 585-603.
- Pritchett, M. 2006. Historic spawn herring database. Alaska Department of Fish and Game, Juneau, AK.
- Reznick, D., M. Bryant and D. Holmes 2006. The evolution of senescence and post-reproductive lifespan in guppies (*Poecilia reticulata*). Plos Biol 4(1): 136-143.
- Reznick, D., C. Ghalambor and L. Nunney 2002. The evolution of senescence in fish. Mech Ageing Dev 123(7): 773-789.
- Roff, D. A. 1992. The evolution of life histories. New York, Chapman and Hall.
- Rooper, C. N., L. J. Haldorson and T. J. Quinn II 1999. Habitat factors controlling Pacific herring (*Clupea pallasi*) egg loss in Prince William Sound, Alaska. Can J Fish Aquat Sci 56: 1133-1142.
- Sanvicente-Anorve, L., L. A. Soto, M. L. Espinosa-Fuentes and C. Flores-Coto 2006. Relationship patterns between ichthyoplankton and zooplankton: A conceptual model. Hydrobiologia 559: 11-22.
- Scattergood, L. W., C. J. Sindermann and B. E. Skud 1959. Spawning of North American herring. Trans Am Fish Soc 88: 164-168.
- Schweigert, J. F., C. W. Haegele and M. Stocker 1985. Optimizing sampling design for herring spawn surveys in the Strait of Georgia, BC. Can J Fish Aquat Sci 42(11): 1806-1814.
- Schweigert, J. F. and R. E. Withler 1990. Genetic differentiation of Pacific herring based on enzyme electrophoresis and mitochondrial DNA analysis. Am Fish Soc Symp 7: 459-469.

- Seeb, J., S. E. Merkouris, L. W. Seeb, J. B. Olsen, P. Bentzen and J. M. Wright 1999. Genetic discrimination of Prince William Sound herring populations. Anchorage, AK, Alaska Department of Fish and Game, Genetics Laboratory: 1-111.
- Shaw, R. F., W. F. Wiseman, R. E. Turner, L. R. Rouse and R. E. Condrey 1985. Transport of larval gulf menhaden *Brevoortia patronus* in continental shelf waters of western Louisiana: a hypothesis. Trans Am Fish Soc 144: 452-460.
- Sherman, K., W. Smith, W. Morse, M. Berman, J. Green and L. Ejsymont 1984. Spawning strategies of fishes in relation to circulation, phytoplankton production, and pulses of zooplankton of the northeastern United States. Mar Ecol Prog Ser 18: 1-19.
- Sigler, M. F. and D. J. Csepp 2007. Seasonal abundance of two important forage species in the North Pacific Ocean, Pacific herring and walleye pollock. Fish Res 83(2-3): 319-331.
- Small, M. P., J. L. Loxterman, A. E. Frye, J. F. Von Bargen, C. Bowman and S. F. Young 2005. Temporal and spatial genetic structure among some Pacific herring populations in Puget Sound and the southern Strait of Georgia. Trans Am Fish Soc 134(5): 1329-1341.
- Smedbol, R. M., A; Hansen, MM; Kenchington, E 2002. Myths and moderation in marine 'metapopulations'? Fish and Fisheries [Fish Fish.] 3(1): 20-35.
- Spratt, J. D. 1981. Status of the Pacific herring, *Clupea harengus pallasi*, in California to 1980. Calif. Fish Game Fish Bull 171(1-104).
- Stacey, N. E. and A. S. Hourston 1982. Spawning and feeding behavior of captive Pacific herring, *Clupea harengus pallasi*. Can J Fish Aquat Sci 39: 489-498.
- Stevenson, J. C. 1962. Distribution and survival of herring larvae (*Clupea pallasi* Valenciennes) in British Columbia waters. J Fish Res Bd Can 19: 735-789.
- Stokesbury, K. D. E., R. J. Foy and B. L. Norcross 1999. Spatial and temporal variability in juvenile Pacific herring, *Clupea pallasi*, growth in Prince William Sound Alaska. Enviorn Biol Fish 56(4): 409-418.
- Stokesbury, K. D. E., J. Kirsch, E. D. Brown, G. L. Thomas and B. L. Norcross 2000. Spatial distributions of Pacific herring, *Clupea pallasi*, and walleye pollock, *Theragra chalcogramma*, in Prince William Sound, Alaska. Fish Bull 98(2): 400-409.
- Stokesbury, K. D. E., J. Kirsch, E. V. Patrick and B. L. Norcross 2002. Natural mortality estimates of juvenile Pacific herring (*Clupea pallasi*) in Prince William Sound, Alaska. Can J Fish Aquat Sci 59(3): 416-423.
- Stout, H. G., RG; Lenarz, WH; McCain, BB; VanDoornik, DM; Builder, TL; Methot, RD 2001. Status Review of Pacific Herring (*Clupea pallasi*) in Puget Sound, Washington. NOAA Technical Memorandum NMFS NWFSC. no. 45: 1-200.
- Tanasichuk, R. W. 2000. Age-specific natural mortality rates of adult Pacific herring (*Clupea pallasi*) from southern British Columbia. Can J Fish Aquat Sci 57(11): 2258-2266.
- Tanasichuk, R. W., A. H. Kristofferson and D. V. Gillman 1993. Comparison of some life history characteristics of Pacific herring (*Clupea pallasi*) from the Canadian Pacific Ocean and Beaufort Sea. Can J Fish Aquat Sci 50(5): 964-971.
- Taylor, F. H. C. 1964. Life history and present status of British Columbia herring stocks. Fish Res Bd Can Bulletin No. 143.
- Terzibasi, E., D. R. Valenzano and A. Cellerino 2007. The short-lived fish *Nothobranchius furzeri* as a new model system for aging studies. Exp Gerontol 42: 81-89.
- Thorne, R. E. and G. L. Thomas 1990. Acoustic observations of gas bubble release by Pacific herring (*Clupea harengus pallasi*). Can J Fish Aquat Sci 47(10): 1920-1928.

- Trumble, R. 1983. Habitat protection. Proceedings of the fourth Pacific coast herring workshop, October 1981, Canadian Manuscript Report Fisheries and Aquatic Science.
- Valdesalicil, S. and A. Cellerino 2003. Extremely short lifespan in the annual fish *Nothobranchius furzeri*. Proc R Soc London, B 270: S189-S191.
- Vetter, E. F. 1988. Estimation of natural mortality in fish stocks: a review. Fish Bull 88(1): 25-42.
- Waples, R. S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. J Hered 89(5): 438-450.
- Waples, R. S. and O. Gaggiotti 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. Mol Ecol 15: 1419-1439.
- Ware, D. M. 1985. Life history characteristics, reproductive value, and resilience of Pacific herring (*Clupea harengus pallasi*). Can J Fish Aquat Sci 42, Supplement No. 1: 127-137.
- Ware, D. M. and J. F. Schweigert 2001. Metapopulation structure and dynamics of British Columbia herring, Fisheries and Oceans Canada, Canadian Science Advisory Secretariat: Online at http://www.dfo-mpo.gc.ca/csas/CSAS/DocREC/2001/RES2001 127e.pdf.
- Ware, D. M. and J. F. Schweigert 2002. Metapopulation dynamics of British Columbia herring during cool and warm climate regimes, Fisheries and Oceans Canada, Canadian Science Advisory Secretariat: Online at http://www.dfo-mpo.gc.ca/csas/CSAS/DocREC/2002/RES2002 107e.pdf.
- Ware, D. M. and C. Tovey 2004. Pacific herring spawn disappearance and recolonization events, Fisheries and Oceans Canada, Canadian Science Advisory Secretariat: Online at http://www.dfo-mpo.gc.ca/csas/CSAS/DocREC/2004/RES2004 008 E.pdf.
- Ware, D. M., C. Tovey, D. Hay and P. B. McCarter 2000. Straying rates and stock structure of British Columbia herring. Online at http://www.dfo-mpo.gc.ca/csas/CSAS/DocRec/2000/PDF/2000_006e.pdf, Canadian Science Advisory Secretariat.
- Wespestad, V. G. and E. Moksness 1990. Observations on growth and survival during the early life history of Pacific herring *Clupea pallasii* from Bristol Bay, Alaska, in a marine mesocosm. Fish Bull 88(1): 191-200.
- Whitehead, P. J. P. 1985. King herring: his place amongst the clupeoids. Can J Fish Aquat Sci 42(Suppl. 1): 3-20.
- Whitlock, M. C. and D. E. McCauley 1999. Indirect measures of gene flow and migration: FST doesn't equal 1/(4Nm+1). Heredity 82: 117-125.
- Williams, E. H. and T. J. Quinn 2000. Pacific herring, *Clupea pallasi*, recruitment in the Bering Sea and northeast Pacific Ocean, I: relationships among different populations. Fish Oceanogr 9(4): 285-299.
- Willson, M. F. and J. N. Womble 2006. Vertebrate exploitation of pulsed marine prey: a review and the example of spawning herring. Rev Fish Biol Fisher 16: 183-200.
- Wilson, B., R. S. Batty and L. M. Dill 2004. Pacific and Atlantic herring produce burst pulse sounds. Proc R Soc London, B 271: S95-S97.
- Woodhead, A. D. 1979. Senescence in fishes. Fish phenology; anabolic adaptiveness in teleosts, London, Symposium of the Zoological Society of London.
- Wright, S. 1978. Evolution and the genetics of populations. Chicago, University of Chicago Press.

Zusser, S. G. 1958. A study of the causes of diurnal vertical migration in fishes. Akademiia Nauk SSSR. Ikhtiologi-Cheskaia Kommissia 8: 115-120.

Fig. 2.1. Pacific herring (*Clupea pallasii*); actual photo (anterior) combined with a colorized scientific drawing (Hart 1973).

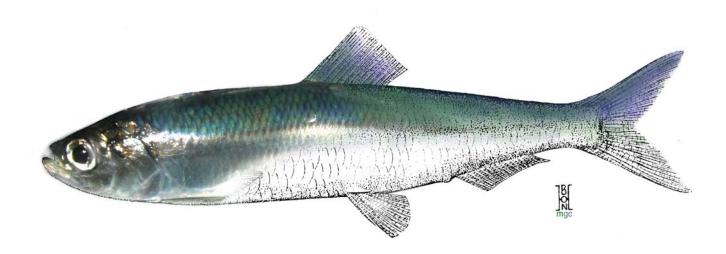


Fig. 2.2a. Global distribution of Pacific herring [adapted from Hay (1985)]. The genetic distance inset is from Grant and Utter (1984) (protein allozyme analysis); the red ellipses on the map identify these groupings.

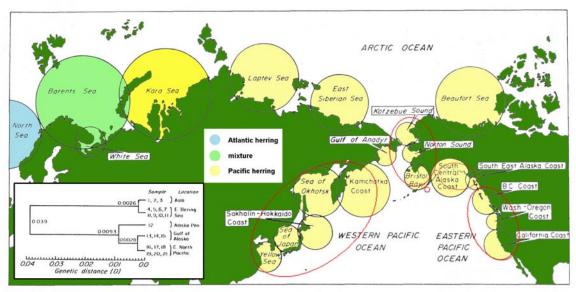


FIG. 13. Schematic view of the distribution of herring throughout the eastern North Atlantic, Arctic, and Pacific oceans. Spawning locations and distributions of Arctic herring are not well documented; therefore, sizes of the circles are not intended to represent either the range or abundance in these waters.

Fig. 2.2b. Global distribution of Pacific herring generated by FishBase (unreviewed; http://fishbase.sinica.edu.tw/tools/aquamaps/receive.php).

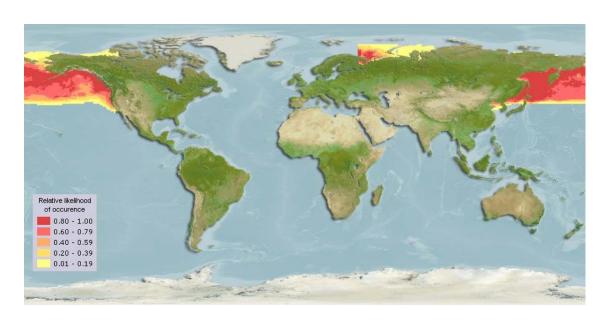


Fig. 2.3. Herring stocks in the eastern North Pacific, separated by solid, dashed, or dotted lines. The dark areas indicate the approximate centers of spawning and overwintering [from (Hay et al. 2001)]. The area circled in red has been defined as a discrete population segment using Endangered Species Act (ESA) criteria (Stout 2001; Gustafson et al. 2006).

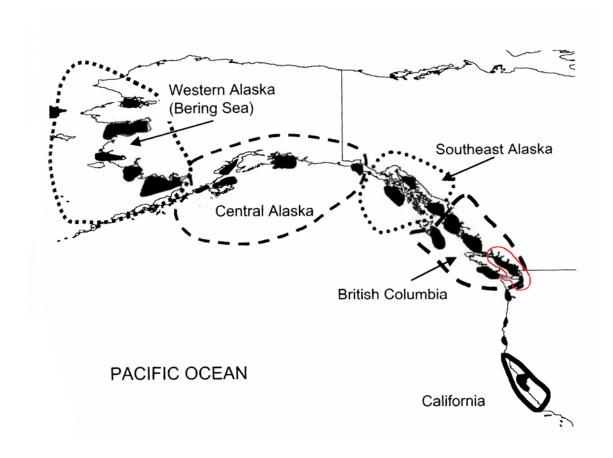


Fig. 2.4a. Small scale spawning movement in Berners Bay 1976 (blue) and 1977 (red).

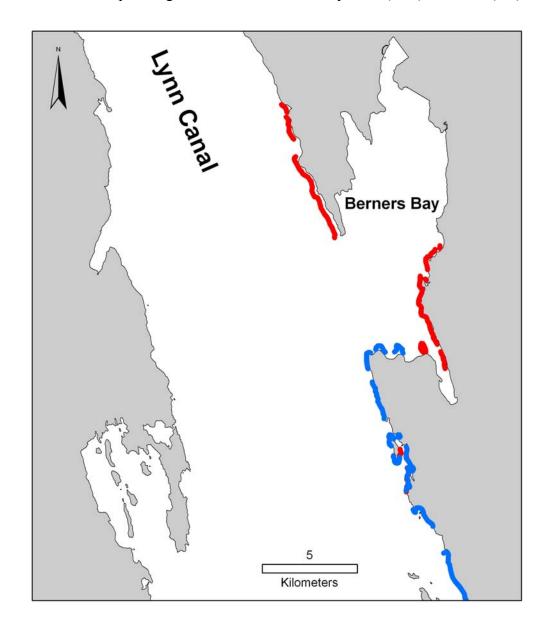


Fig. 2.4b. Large scale spawning movement in the Kah Shakes, Cat Is., and Annette Island area of SEAK. Red indicates spawning location (Pritchett 2006).

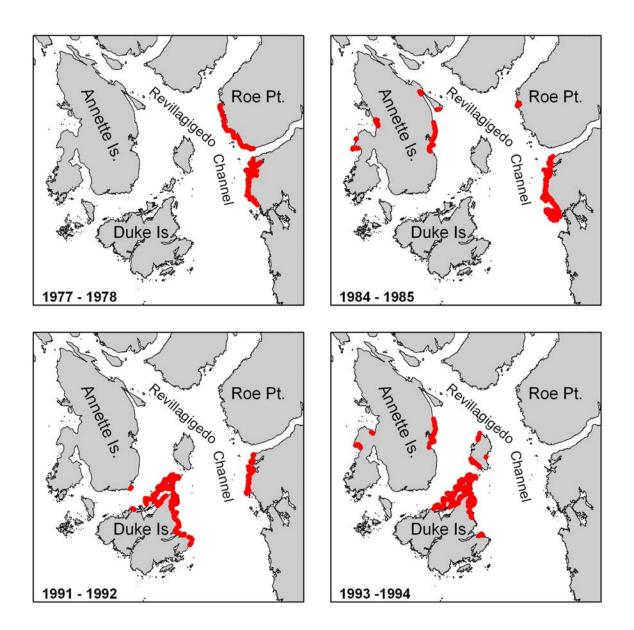
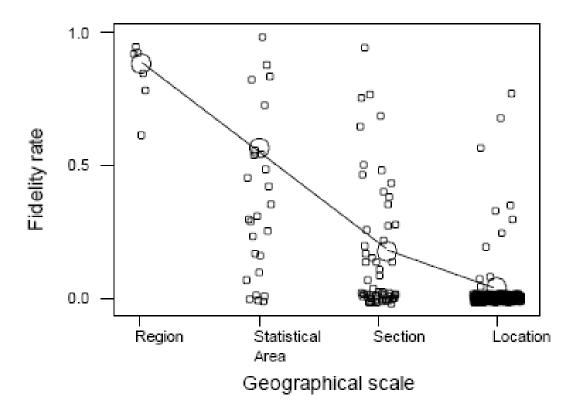
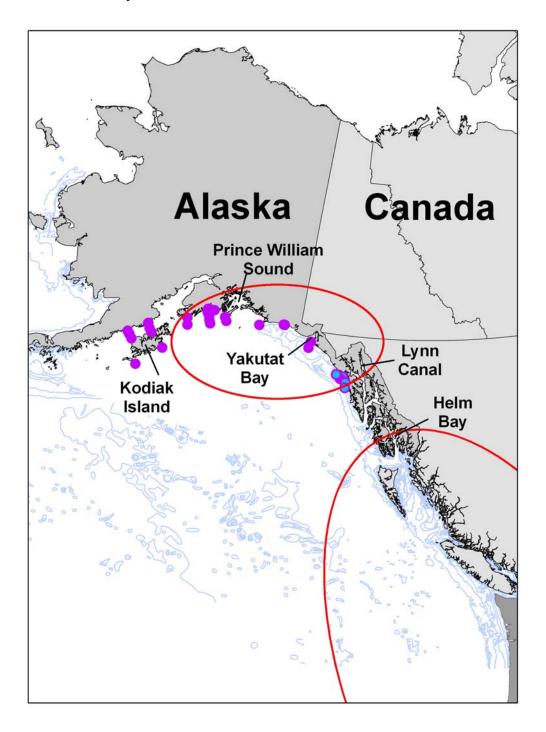


Fig. 2.5. Redrawn from Hay et al. (1999). "Comparison of fidelity rates by regions, statistical areas, sections, and locations. The array of small points (jittered horizontally to reduce overlap) each represent the mean fidelity of different geographic units within each geographic category (i.e., there are 6 regions and 6 points). Some of the highest points in the statistical area and section categories are based on very small sample sizes. The larger circles represent the overall mean fidelity for each geographic category" (Hay et al. 1999). Regions vary from 3000 to 10000 km², statistical areas from 500 to 2500 km², and most sections are <300 km² (Hay et al. 2001).



2.25

Fig. 2.6. Offshore herring in the Gulf of Alaska. Purple symbols are adult herring (Orsi et al. 2007; Farley 2008); blue symbols are juvenile herring (Orsi et al. 2007; Orsi 2008). Illustrated groupings (red ellipses) are based on allozyme analysis by Grant and Utter (1984); herring collected in Helm Bay, Lynn Canal, Yakutat Bay, Prince William Sound and west of Kodiak were included in that analysis.



Chapter 3

Description of Pacific herring in Lynn Canal and southeastern Alaska

Mark G. Carls

Abstract

All life stages of Pacific herring (*Clupea pallasii*) utilize much of southeastern Alaska (SEAK) waters as habitat. The beaches used for spawning are not continuous; some are repeatedly utilized, thus the Alaska Department of Fish and Game (ADFG) eventually began to manage herring in these areas as discrete stocks. However, available data do not identify definitive divisions among SEAK stocks, rather apparent geographic groupings were variable and often rather arbitrary. Limited tagging studies within SEAK demonstrate fish migrate and mix over most of the region but were not designed to demonstrate repeat spawning fidelity. Migration data from British Columbia, a region to the south of SEAK and reasonably similar in structure and climate, are used here to roughly predict repeat spawning fidelity at SEAK stock scales; these approximations suggest considerable mixing among stocks (59 to 84%), possibly explaining the lack of definitive differences among stocks and suggesting that SEAK herring are part of an interrelated metapopulation. Clearly more work remains to understand the relationships among SEAK herring stocks, such as more detailed genetic analysis and more detailed, spawn-oriented and seasonal tagging studies.

Introduction

Pacific herring in southeastern Alaska (SEAK) are managed as discrete stocks by the Alaska Department of Fish and Game (ADFG; Fig. 3.1). Management boundaries are based on major historic spawning areas. These boundaries are not contiguous, and how stocks outside them relate to identified stocks is unclear and unknown. Estimated stock areas range from about 100 to 1100 km² (water only). Of these, the Sitka management area is the largest, Lynn Canal is second and Craig is third.

In this chapter Lynn Canal herring are examined first, then herring throughout SEAK are examined to place Lynn Canal herring in context. Migration studies competed in British Columbia are used to roughly predict spawning fidelity within SEAK, a topic that has not been addressed by research in SEAK. For each of the variables considered (distribution, biomass, recruitment, size at age (a surrogate for growth rate), spawn timing, morphological variability, migration, and genetics) the question is asked, are there substantial differences among stocks, and if so do these differences form a cohesive pattern? The underlying goal is to determine if separately managed SEAK herring stocks are one population or metapopulation, or if they are sufficiently different to be considered separate populations.

Herring spawning fidelity studies in British Columbia provide estimates of conditions in SEAK

The spawning fidelity of Pacific herring has been extensively studied in British Columbia but not in SEAK. These fidelity estimates can reasonably be used to interpret conditions in SEAK. Located adjacently, both domains stretch along the north Pacific in the Gulf of Alaska, about 860 km (SEAK) to 900 km (British Columbia). Both are temperate rain forests bounded on the east by coastal mountains, ice fields and glaciers. Both have complex coastlines with many islands and fjords. Both domains may be partially or wholly in the same zoogeographic province (see Chapter 4 for a more complete discussion of this topic), although located further to the south, average water temperatures in British Columbia are likely warmer than those in SEAK

(e.g., Chapter 4, Figs 4.33 and 4.34). The distance between 'outside' and 'inside' waters (those along the Pacific Ocean and those along the mainland behind barrier islands) is roughly 100 to 150 km in SEAK. This distance is more variable in British Columbia, roughly 15 to 190 km, where the outside barrier islands are larger, fewer in number, and do not completely shield the mainland from the Gulf of Alaska as they do in SEAK.

On large scales, fidelity of Pacific herring approaches 100% and declines to near 0 as geographic scales decline to beach size [Chapter 2, Fig. 2.5; (Hay et al. 1999)]. This suggests that fish that mingle in summer areas mix and do not all return to the same spawning beaches. However, a nonrandom association of herring over considerable distances for up to several years is evident (Hay and McKinnell 2002), suggesting that herring schools have coherence; individuals from different schools do not simply mix and migrate randomly. (See Chapter 2 for a more complete discussion of school interaction.)

To roughly estimate spawning fidelity in SEAK, the relationship between fidelity and area in British Columbia was estimated by regression. Mean fidelity was estimated from the original x-y plot of Hay et al. (1999) using CAD. Areas for each category (water only) were reported by Hay and McKinnell (2002); the smallest area ("location") was estimated by dividing the mean region size by the number of locations (1800). Regression of ln(fidelity) against ln(area) was used to estimate the relationship between fidelity and area; $r^2 = 0.975$ (Fig. 3.2) and the resultant equation was used to roughly predict the spawning fidelity of SEAK stocks. The approximations are considered rough for two reasons 1) application of observations from one large geographic region to another and 2) scatter in the British Columbia data is high (Chapter 2, Fig. 2.5), though central tendencies at the smallest scales are rather clear.

Lynn Canal herring

The historic Lynn Canal spawning area, as defined by ADFG ranges from Berners Bay south to Taku Harbor and encompasses an area of about 950 km² (Fig 3.3). The Lynn Canal Pacific herring stock was one of the larger stocks in SEAK prior to 1983 [third in the 1930s; (Rounsefell and Dahlgren 1935)] but declined through the 1970s and has been depressed since 1982 (Pritchett et al. 2008). Studies by Carlson (1980), who summarized earlier work and is frequently referenced, focused his study primarily on a considerably smaller subset (16%) of this region (Fig. 3.3). Spawning in Lynn Canal was previously distributed from Juneau (Auke Bay) north to Berners Bay; since 1990, however, most spawning has been concentrated in Berners Bay north of Cascade Point and from Point Bridget south to Mab Island (Moulton 1999). Summer feeding areas are on the west side of Douglas Island with most fish found at depths of 5 and 37 m, whereas in winter, herring move into deeper waters and remain in dense concentrations near the bottom (73 to 110 m) (Carlson 1980). Herring biomass in Lynn Canal peaks in winter (December to February, variable among years) and decreases sharply thereafter (Sigler and Csepp 2007) (Fig. 3.4). The fish move around during this period; schools formed in the Benjamin Island area in November, then shifted south toward Amalga Trench (Sigler and Csepp 2007). Because marine mammal activity (in winter) was confined to these areas, the authors assumed few herring were elsewhere. They also assumed that observed herring were all from Lynn Canal because the nearest stocks occur "more than 100 km away." [Actual distance to the nearest spawning stock, in Port Frederick, is about 60 km, and distances to the nearest summer feeding areas are <5 km (near Point Retreat on the Mansfield Peninsula) to 24 km (Couverden Island), less than the net average yearly movement of herring, 89 km (Hay et al. 2001; Hay and McKinnell 2002). Herring have utilized Fritz Cove in winter for three decades but abundance in Auke Bay has declined, offset by an increase near Benjamin Island and in the Amalga Trench (Carlson 1980; Sigler and Csepp 2007). The submarine gully in this area is apparently critical winter habitat for the Lynn Canal herring stock and presumably offers benefits by reducing energy expenditure (sheltering from tidal currents) and predation (lower light levels may reduce predation by visual feeders) (Sigler and Csepp 2007).

Pacific herring biomass in Lynn Canal

Accurate biomass estimates for Pacific herring stock in Lynn Canal do not exist, though available data do indicate the present status. Biomass estimates of Lynn Canal herring have been made intermittently since the winter of 1971 to 1972 beginning with hydroacoustics (ADFG), although the estimates are most likely not comparable for all years (Fig. 3.5). Winter surveys had the apparent advantage of observing large aggregations of herring in deep water, a situation advantageous to echo integration techniques. Efforts during the first four years of surveys concentrated on equipment development and survey design while the remaining years used designed systematic surveys. Harvest quotas for the Lynn Canal herring sac roe fishery were based on these biomass estimates; fishery performance indicated that they were overestimates. In addition, recent work by Sigler and Csepp (2007) demonstrated a seasonal abundance pattern of herring in the Lynn Canal area with winter aggregations being much greater than the number of herring remaining in the spring to spawn (Fig. 3.4). Possibly herring from outside the Lynn Canal area also winter in the trench, and although the need to conserve energy during winter argues against this hypothesis, herring seem to disappear from wintering areas and reappear at often distant spawning areas (Thorne 2008).

Biomass estimates based on actual herring spawn by dive survey are better indicators of the true biomass and these surveys were conducted in the Juneau area during the mid to late 1980s (Fig. 3.5). Unfortunately, because the Lynn Canal herring biomass is at a level much lower than the threshold required for a commercial fishery and the limited stock assessment resources of ADFG are typically used in areas where fisheries are likely to occur, these surveys are incomplete and have recently been confined to Berners Bay.

Aerial surveys provide the longest time series of relative herring abundance data for the Lynn Canal area (Fig. 3.6). These data are collected by mapping observed spawning activity along the coastline. Survey frequency and the area to be flown are not standardized and as such, the total nautical miles of spawn observed for a given year can be a function of weather and survey effort. In addition, not all areas where spawning is observed are of equal value in regards to spawning requirements; the type of substrate is important as well as the width of usable substrate. No reliable observations of spawn intensity are available from aerial surveys. Because of these limitations biomass observations are typically not made using aerial surveys alone

Uncertainty is high in Lynn Canal biomass estimates. An estimate of the historic biomass of spawning herring in Lynn Canal was made using the eight estimates of spawning biomass from the dive surveys (Fig. 3.5) and the time series of nautical miles of spawn obtained from the aerial survey program (Fig. 3.6). The estimated tons of herring per nautical mile of spawn was considerably greater in the mid to late 1980s than what has been observed recently (256 tons of herring per nautical mile of spawn for the mid to late 1980s compared to 130 tons recently; Fig. 3.7). This disparity could be due to the differences in areas used for spawning between the time periods, where and how intensely the aerial surveys were conducted, as well as differences in herring biomass. However, given the small amount of data and high variance,

these estimates are not statistically different (P = 0.802). An average of the estimated tons of herring per nautical mile of spawn (176 tons) was used to estimate the historic spawning biomass time series (Fig. 3.8). Although this method may underestimate the early years and overestimate the more recent years, it is based on data collected during the spring spawning season. Earlier biomass estimates relied heavily on winter hydroacoustics, which most likely dramatically overestimated the spawning biomass, led to overfishing, and contributed to the stock collapse. Perhaps the most obvious result of the limited and variable data is that Lynn Canal biomass estimates are uncertain (Fig. 3.8).

Age structure, age structured models, and the estimation of recruitment

There are insufficient data available to construct an age structured model for the Lynn Canal herring population (Fig. 3.9) (Carlile et al. 1996; Quinn and Deriso 1999). Approximately 10 years of good biomass estimates and corresponding age composition estimates would be required to begin modeling this population. Typically, ADFG reliably ages herring in Southeast Alaska through age 8 with ages greater than age 8 grouped into a group called age 8+. Ten years of complete data would allow for observation of two complete cohorts.

Estimate discrepencies

An apparent discrepancy in estimated Lynn Canal herring biomass by ADFG (Carlile et al. 1996) (Fig. 3.5) and Sigler and Csepp (2007) (Fig. 3.4); alternatively it may be due to method differences, differences in observation timing coupled with possible outmigration, or inclusion of juvenile fish in the Sigler and Csepp (2007) data set. Peak estimates by Sigler and Csepp (2007) were roughly 400 times greater than those estimated from ADFG (Carlile et al. 1996; Pritchett 2007) data. Adjustment for juveniles in estimates of Sigler and Csepp (2007), roughly 5 to 20% of the total biomass, does not explain the difference between estimates. Apparently each time series can be considered an index of biomass and may form a time series consistent with itself but not necessarily with other data sets. At least some of the ADFG hydroacoustic data were collected in March (Moberly and Thorne 1974), likely missing the peak biomass observed more recently (Sigler and Csepp 2007) and differences between acoustic gear types, survey strategies, and other unknown factors may also contribute to the discrepancy.

SEAK herring

Distribution

Herring are ubiquitous throughout SEAK and utilize this habitat at all life stages (e.g., Fig. 3.1). Shoreline is utilized for spawning and egg incubation primarily in spring; there are many spawning aggregations throughout SEAK with the greatest biomass near Sitka (Fig. 3.1). (At least 9 of these aggregations are fished commercially.) Glacier Bay may be the only major area in SEAK without spawning, though northern Lynn Canal may also generally fall into this category. Bays and inlets along both the outer coast (e.g., Sitka) and inner coast (e.g., Lynn Canal) are utilized for spawning. In general, herring that spawn on the outer coastal areas are more productive than those in inside waters (Pritchett 2005).

Limited larval habitat utilization data have been collected in SEAK. Most larval studies have focused on Glacier Bay (Arimitsu et al. 2007; Piatt 2008) and Auke Bay (Haldorson et al. 1986; Haldorson et al. 1987; Haldorson et al. 1988); few other data exist (Fig. 3.10). Despite the limited surveys, we suspect many bays in SEAK are utilized by larval herring as rearing habitat

as they are elsewhere, such as Prince William Sound (Stokesbury et al. 1999; Stokesbury et al. 2000). Advection will control the destinations of these weak swimmers and bays proximal to spawning areas are logical places to expect larvae. Even bays without spawning events, such as Glacier Bay provide evidence of rearing habitat (with the caveat that the presence of larvae in the bay does not necessarily mean they will survive there). However, juveniles are also well represented in Glacier Bay, strongly suggesting it is adequate habitat. (Larvae, juveniles, and adults were categorized by size, <35 mm = larvae, 35-180 mm = juveniles, and >180 mm = adults). Larvae are also advected offshore from SEAK (Fig. 3.10) and based on observations in British Columbia and Prince William Sound, these are likely to die from lack of food, salinity intolerance, or increased predation pressure (Stevenson 1962; Alderdice and Hourston 1985; Stocker et al. 1985; McGurk 1989; Wespestad and Moksness 2002; Norcross et al. 2007). Peak larval abundances are in May or June in Auke Bay (Haldorson et al. 1986; Haldorson et al. 1987; Haldorson et al. 1988).

Juvenile herring evidently utilize many of the bays in SEAK as rearing habitat (Fig. 3.11). Sampling for juvenile herring in SEAK is more thorough than for larvae, though again coverage is not complete. Capture of juvenile herring by nearshore seine hauls is hit or miss; relative herring abundances tend to be high when a school is captured and low when schools are missed by the net. The incidence of capture in one study was about 132 times out of 600 hauls (Johnson 2007). In Glacier Bay, an area repeatedly resampled for 5 y (1999 to 2004), juveniles evidently utilize the entire area and were captured more often than not (Arimitsu et al. 2007; Piatt 2008).

Non-spawning adult Pacific herring are likely widespread throughout SEAK (Fig. 3.12). Although non-spawning sampling has been confined to limited areas [the summer reduction fishery in the 1930s (Rounsefell and Dahlgren 1933; Rounsefell and Dahlgren 1935; Skud 1963; Carlson 1977), winter hydroacoustic surveys generally in the vicinity of Juneau (Vollenweider 2008), and midwater trawls completed in Glacier Bay (Arimitsu et al. 2007)], anecdotal evidence suggests most of the waters in SEAK are utilized by Pacific herring throughout the year. More detail, and particularly comprehensive coverage of winter and summer schooling areas segregated by season, is desirable and would contribute to the general understanding of species utilization and population structure within SEAK.

The contemporary distribution of herring in SEAK is not identical to that in the past. At one time Kootznahoo Inlet (near Angoon) was of great importance (Rounsefell and Dahlgren 1935) but spawning activity is not even monitored there today. On the other hand, Sitka Sound and San Alberto Bay (near Craig) were considered the largest stocks in the 1930s (Rounsefell and Dahlgren 1935) and that is also true today (Fig. 3.13). Icy Strait was important herring habitat in the summer in the 1930s (Rounsefell and Dahlgren 1935) as it is today (Arimitsu et al. 2007). The distribution of herring plants in the 1900s may provide a rough index of historic herring distribution; however, where commercial fishing occurred was influenced by plant location and fishing intensity was less on large stocks impractically distant from the plants (Rounsefell and Dahlgren 1935).

Age structure

As in other herring populations (Williams and Quinn 2000; Funk 2007), strong age classes generally occur every few years in SEAK stocks (Fig. 3.9). For example, strong year classes (cohorts) were evident beginning in 1980, 1987, and 1996 at Kah Shakes. Synchrony among stocks is evident, consistent general patterns in the North Pacific Ocean and strongly

influenced by environmental conditions (Hollowed et al. 1987). For example, synchronous strong year classes were evident in 1996 in every SEAK stock except Sitka (Fig. 3.9). Interestingly, the largest, most actively growing stock (Sitka) is apparently the least reliant of all SEAK stocks on strong year classes.

Genetics

Current data do not support definitive genetic differences among SEAK stocks (Fig. 3.14). Available genetic data for SEAK stocks is largely peripheral to studies focused on other areas (Beacham et al. 2002) or on population separation on a coarse scale (Grant and Utter 1984); these do not suggest differences among SEAK populations. The first of these studies was a Pacific Ocean scale allozyme survey that provided modest evidence of population structure among herring from the Alaska Peninsula to California (Grant and Utter 1984). Within the northern Gulf of Alaska, herring near Kodiak, Yakutat, and Lynn Canal were grouped together; herring from Helm Bay (Cleveland Peninsula, north of Ketchikan) were grouped with populations to the south. Later, a microsatellite study identified genetic differences between herring in SEAK and British Columbia; SEAK samples included fish from Sitka, Kirk Point and Mary Island (in the Kah Shakes area), and Seymour Canal (Beacham et al. 2002). Genetic work on SEAK herring stocks is ongoing at the Auke Bay Laboratory but data collection and analysis are not complete.

Spawn timing

Differences in spawn timing suggest possible northern and southern groupings of SEAK herring (Fig. 3.15). The primary cause is likely temperature; marine waters of SEAK are characterized by an inshore-offshore salinity gradient and a north-south temperature gradient (Quast 1968; Murphy and Orsi 1999).

Pacific herring respond to their thermal environment; residence within a given area will drive spawning behavior. Most spawning in SEAK occurs between mid-March and mid-April; in Lynn Canal, herring spawn from late April to early May (Davidson et al. 2005; Pritchett 2006; Coonradt 2008). To understand how spawn timing in SEAK relates to spawning elsewhere in the eastern Pacific, the relationship between latitude and spawn timing was examined from California to Kotzebue Sound. Approximate latitudes were added to the data (Rounsefell 1930; Chapman et al. 1941; Miller and Schmidtke 1956; Scattergood et al. 1959; Skud 1960; Alderdice and Velsen 1971; Barton and Wespestad 1980; Hourston 1980; ADFG 1985; Hay 1985; Lemberg et al. 1997; Davidson et al. 2005) summarized by (Stout et al. 2001). All spawn dates were expressed as Julian days; negative values are those that extend into the previous year (e.g., December spawning in California). Data from SEAK data were updated from recent sources; data from Yakutat were unavailable (Davidson et al. 2005; Pritchett 2006; Coonradt 2008). Midpoint data were regressed against latitude. To compare timing specifically in SEAK with the overall pattern, data were divided into two groups, SEAK only and all other eastern Pacific herring and analyzed with analysis of covariance (latitude × midpoint × group).

The time Pacific herring spawn in the eastern Pacific Ocean is correlated with latitude (r = 0.950, P < 0.001). The relationship between latitude and spawn timing within SEAK was the same as all other eastern Pacific herring (slopes were not significantly different; P = 0.262, Fig. 3.16). Spawning throughout SEAK may be slightly earlier than predicted by the general relationship (P = 0.003); however, spawn timing in bordering areas (just north and south of SEAK) entirely overlapped timing in SEAK, suggesting the latter result may have little meaning.

Clearly, spawn timing in SEAK conforms to the overall cline evident along the coast and a spawn timing cline exists within SEAK (r = 0.918; Fig. 3.15 to 3.17). Temperature is likely the primary driver (Brown and Carls 1998). For example, annual sea surface temperatures are highest near the equator and decrease toward the poles (NOAA 2008), strong evidence that temperature gradients occur throughout the analysis region and within SEAK.

Spawn timing in SEAK is broader than captured by ADFG data, though the official data set likely by far captures most of the spawning activity. Only large scale spawning events are recorded in these data. Spawning outside the spring timing has been observed over many years. Spawning was observed in mid June (Gut Bay, Baranof Island) in the 1930s. In recent years, we have observed Pacific herring spawning in Auke Bay in June [1997, 2000, 2003; (Wing 2008)]. To the best of our knowledge, no one has attempted to record this additional spawning activity in SEAK. Rounsefell and Dahlgren (1935) imply that small groups of herring such as these may be nonmigratory residents, different in habit to the earlier migratory spawners.

Biomass

Temporal changes in biomass are not synchronous among SEAK herring stocks, suggesting at least some level of discreteness among them. Since the 1990s, herring spawning biomass in SEAK has increased in several stocks (Sitka Sound, Hoonah Sound, Seymour Canal, Craig, Ernest Sound); shown no trend (Hobart Bay / Port Houghton, Lynn Canal) or fluctuated (Tenakee, West Behm Canal; Figs. 3.8 and 3.13). The largest herring spawning biomass in SEAK is at Sitka, presently >4 times that of any other stock. Only one stock appears to be in decline (Kah Shakes) but this is likely not true. The Kah Shakes stock has moved from place to place over a many year period and is now spawning on Annette Island, outside the jurisdiction of ADFG, hence is unavailable for biomass estimates (see Chapter 2, Fig. 2.4b for an example). There are no apparent geographic groupings among increasing, fluctuating, or static stocks (not illustrated). In particular, temporal changes in Lynn Canal biomass are not synchronous with nearby stocks (Sitka, Hoonah Sound, and Seymour Canal). Unfortunately, biomass estimates for other nearby stocks are not available for comparison [Olivers Inlet (within the Lynn Canal Management Area), Port Frederick, and Lisianski Inlet]. Asynchronous biomass changes suggest that herring do not simply randomly disperse into areas with lower population density and there is no evidence that Lynn Canal herring are being repopulated by excesses from nearby, growing populations.

Recruitment

Recruitment synchrony, analyzed with multidimensional analysis (Williams and Quinn 2000), suggests divisions among SEAK herring, though coverage was not comprehensive (only Seymour Canal, Sitka Sound, Craig, and Kah Shakes were represented) and results differed among the several analyses provided (Figs. 3.18). Neither Lynn Canal nor Yakutat herring were included in the analysis. Geographic divisions suggested by recruitment synchrony do not follow the thermal gradient pattern, but how temperature may influence synchrony is unknown, and relative thermal conditions in SEAK through annual cycles remains to be described.

Differences in recruitment among SEAK stocks may divide the area into two or three regions (Fig 3.18). Comparison of recruitment similarities within SEAK was based on an analysis by Williams and Quinn (2000); data were obtained from several sources (Reid 1971; Funk et al. 1992; Schweigert et al. 1997; Williams and Quinn II 1998), and included samples from British Columbia north to Norton Sound (Alaska). Sites included in SEAK were Seymour

Canal, Sitka Sound, Craig, and Kah Shakes. [An additional 'site' was designated SEAK in their analysis (Williams and Quinn 2000); this is simply the sum of recruitment at Sitka and Craig and is not an independent measure.] Conspicuously absent from the analysis was Lynn Canal recruitment. Several multidimensional analyses and dendograms provided slightly differing results. Division may indicate differences between "inside" and "outside" populations, the latter directly exposed to the Gulf of Alaska and the former protected by barrier islands. However, the analysis provides no insight regarding the northern portion of SEAK and Lynn Canal in particular. A more complete data set for SEAK is available [ADFG; (Pritchett 2007)] and is currently under examination but insufficient time precluded a more detailed analysis and, as explained earlier, recruitment in Lynn Canal is not estimable, so the expanded data set does not improve the interpretation of this particular area.

Size-at-age and growth rate

Some size-at-age data suggest no consistent geographic differences among herring in SEAK, another suggests division but does not include northern SEAK. Four data sets were available to compare size-at-age within SEAK: 1) data from 1929 and 1930 (Rounsefell and Dahlgren 1935), 2) a relatively small experimental data set collected for research purposes (Johnson et al. 1997; Carls et al. 1998), 3) data ranging from Nome, Alaska, to British Columbia (Williams and Quinn 2000), and 4) raw data from ADFG (Pritchett 2007). The fourth set is the largest and most comprehensive. No geographic groupings were evident in the 1929 and 1930 length data (e.g., Fig. 3.19, illustrating the year of the most comprehensive coverage). No distinct geographic groupings emerged from the limited experimental set. Shelter Island (Lynn Canal) and Sitka fish were generally the largest at a given age; Seymour Canal fish tended to be the smallest but overlapped Cat Island (Kah Shakes) fish in some year classes (Fig 3.20). An analysis of weights by Williams and Quinn (2000) suggests southern and central divisions but did not include Lynn Canal fish [samples were collected from Seymour Canal, Sitka Sound, Craig, and Kah Shakes (Fig. 3.21)]. Based on applicable, completed analyses, the size at age of Lynn Canal herring did not differ from other nearby stocks.

The current trend in size-at-age in SEAK herring stocks is downward and there is no evidence that Lynn Canal stock is different from the others (Fig. 3.22). To determine trends, mean deviation from mean length [by stock and age; ADFG dataset (Pritchett 2007)] were calculated; age classes were restricted to 3 through 8 to avoid poor resolution (few fish) in younger and older year classes [(Williams and Quinn 2000); see Appendix B for complete analysis detail]. Size at age has been decreasing for several decades in some stocks, e.g., Kah Shakes. In others there was a general increase in the 1980s or 1990s; all are now in apparent decline (Fig 3.22).

Growth rates were not significantly different among SEAK Pacific herring stocks (P = 0.577, Fig. 3.23 and Table 3.1). Growth rates were estimated by cohort (year class) for each stock [ADFG data, (Pritchett 2007)]; analysis was restricted cohorts with ≥ 15 length measurements in ≥ 3 y to provide robust estimates (see Appendix B for complete analysis detail). The number of growth estimates for each stock ranged from 3 to 24 (Table 3.1); Lynn Canal had the fewest estimates. Mean growth rates ranged from 0.107 to 0.142 ln(mm)/ln(year) and varied significantly among cohorts, though most slopes were similar. The same conclusion, that growth rate does not vary significantly among stocks, was reached when only cohorts common to those in Lynn Canal (1983, 1995, and 1996) were analyzed (P = 0.223).

One interpretation of the growth data is that herring are too mobile to develop meaningful size differences among SEAK stocks. If there is a consistent thermal gradient in SEAK, as suggested by satellite sensing and spawn timing, and fish remain within given areas for extended periods, then a relationship between latitude (or longtitude) and fish size might develop. Correlation of length to either was not obvious in the Rounsefell and Dahlgren (1935) study r = 0.150 and r = 0.559, respectively. Clearly in this analysis longtitude appears to be more important; however, inspection suggests there is no relationship and that two outlying values drive the apparent relationship. When these forcing points are removed, r = 0.214 [data from table 9 of Rounsefell and Dahlgren (1935), age 4 fish in 1929, the most comprehensive set]. The failure of fish growth to respond to the typical thermal gradient in SEAK may suggest significant movement from location to location.

Morphological or meristic variability

The number of vertebrae a herring develops is negatively correlated with temperature (r = -0.85) (Rounsefell and Dahlgren 1932; Rounsefell and Dahlgren 1935), thus allowing possible discrimination among SEAK stocks presumptively sensitive to a temperature gradient through the region. From samples collected between 1928 and 1931 and partitioned by year class, Rounsefell and Dahlgren (1935) concluded that there is more than one herring population in SEAK; age and gender did not influence results. However, their "evidence tending to prove a lack of admixture in samples from the individual localities" is not detailed enough for further analysis and is not completely convincing. The entire analysis would have been more compelling if the effect of sample year had been included as a factor in their ANOVA. Vertebrae number in fish from Juneau were generally not different from those elsewhere in SEAK (unknown in Yakutat), except the 1926 year class differed significantly from that in Petersburg; differences among the 1925 and 1927 year classes were not significant (Rounsefell and Dahlgren 1935).

Differences in vertebrae number suggest perhaps three geographic groups in SEAK, southern, central, and northern (Fig. 3.24). These boundaries, however, are highly subjective. Lower counts in the southern grouping may be driven by warmer spring temperatures; the highest counts in the central region may in part be caused by an occasional relatively cool central water mass as the region warms (Fig. 3.17). Relatively low vertebrae counts were also observed in the north but there were also some low counts in central SEAK. Counts in central SEAK (in the general vicinity of Cape Ommaney) were variable and changed among year classes. Thus, any tendency for linkage between capture location and thermal history appears to be weak, though admittedly the relationship between temperature (observed 2005 to 2007 by satellite) and vertebrae count (1928 to 1931) is speculation and is not proven.

Herring stocks in SEAK probably cannot be definitively distinguished by vertebrate count because a) the fish are too mobile, resulting in a mixed population (see also section "migration") or b) because thermal conditions within localized regions are not stable enough to develop a coherent signal, or c) the link between temperature and vertebrae number is not sufficient for a definitive outcome ($r^2 = 0.72$), or d) a combination of these and other unknown factors (Fig 3.24). There was no numerical correlation between vertebrae number and latitude ($r^2 = 0.076$ for the 1926 year class and $r^2 = 0.002$ for the 1927 year class, the two sets where n > 5).

Migration

Migration studies suggest herring from most of SEAK mix during the summer (Fig. 3.25) (Rounsefell and Dahlgren 1933; Rounsefell and Dahlgren 1935; Dahlgren 1936; Skud 1963; Carlson 1977); however, these studies were not designed to measure fidelity among spawning stocks. Instead, fish were tagged and released from spawning locations and observed in a summer fishery concentrated within a single area (near the southern end of Baranof Island). Fish tagged with either small metal operculum strap tags or internal belly tags were released near Sitka and Craig between 1932 and 1935 (Rounsefell and Dahlgren 1933; Rounsefell and Dahlgren 1935; Dahlgren 1936). Relatively few fish were tagged in the first year of study, < 4000; recovery times ranged from 2 to 149 d. Increased numbers of fish were released in subsequent years, about 41 000 in 1935, and fish were recovered over a 5 y period (Skud 1963). Most fish were released in spring, coincident with spawning, and captured in the summer, thus linking spawning grounds and summer feeding areas. An additional study was completed between 1960 and 1962; some fish were released in the area of previous study, others from Auke Bay (n = 615) and Seymour Canal (n = 1142). Fish from the latter sites were also captured near southern Baranof Island (Carlson 1977). Tag recovery ranged from 0 to 0.8% in the latter study and from 0 to 8% in the former; belly tags were superior to operculum tags (Dahlgren 1936). An alternative tagging method, coded-wire tags, was more recently but incompletely explored (Krieger 1982). The migration patterns of Yakutat herring have never been studied.

The mixing of southern SEAK herring with other SEAK stocks is unknown; the weak evidence of segregation [lack of tag recapture (Carlson 1977)] is insufficient to conclude mixing does not occur because few fish were tagged. Furthermore, percent tag recovery was related to the approximate distance between release and capture in that study ($r^2 = 0.613$) and fish released in the southernmost area (Cleveland Peninsula) were furthest from capture locations. Herring released from some sites were not recaptured and although the authors of the studies involved suggest this is evidence against migration (Rounsefell and Dahlgren 1933; Rounsefell and Dahlgren 1935; Dahlgren 1936; Carlson 1977), it is more likely evidence of an insufficient study design (relatively few fish were released and recapture was constrained to a single, limited geographic area). Not recovered were fish from Auke Bay [n = 1572; (Dahlgren 1936)], Cape Bendel [n = 1820; (Rounsefell and Dahlgren 1933; Rounsefell and Dahlgren 1935)], and the Cleveland Peninsula [near Ketchikan; n = 527; (Carlson 1977)]. Given the small release numbers and an average recapture rate of about 3% [derived from (Dahlgren 1936) and consistent with the more extensive tagging experience in British Columbia (mean annual rate 2.7%, range 0.5 to 11%; (Hay et al. 1999)], recapture of between 6 and 55 fish could be expected from these sites under average conditions. Given that only a limited area was searched for tags, the failure to recapture any of these fish is not surprising and cannot be used as evidence that they were isolated from other SEAK stock. Indeed, migration was evident in a subsequent release of Auke Bay herring [1961; (Carlson 1977)], demonstrating the limitations of data from the earlier release. Similarly, fish released at Cornwallis Point (Carlson 1977), 21 km from Cape Bendel, were recaptured; given the apparent migratory pathways of other fish (such as from Seymour Canal), there is no reason to believe the intervening Keku Strait represents a geographic barrier.

One author (who is often cited in this context) concluded that Lynn Canal herring spend the entire year in the same general vicinity (Carlson 1980), unlike the more migratory populations in Sitka, Craig, and British Columbia. Although there is some evidence that non-migratory resident stocks may exist (Hay et al. 1999), we question the veracity of this conclusion, particularly because the same author reported movement of tagged fish from Auke

Bay to Frederick Sound, south of Admiralty Island (Carlson 1977) where they mixed with stocks from other locations. The recovery of two fish tagged in Auke Bay does not imply two herring made the migration because herring remain in schools; single herring are presumably highly vulnerable to predation. As previously noted, Carlson (Carlson 1980) confined his surveys to a relatively small area and did not provide compelling evidence that fish remained within this narrow boundary.

Mixed summertime stocks do not eliminate the possibility that individual schools remain coherent and go their separate ways after summer. Tagging studies completed in SEAK were designed to only detect movement from spawning grounds to one summer feeding area. Thus, although they demonstrate that herring mix in this feeding area, they do not demonstrate that fish become mixed on spawning grounds, i.e., they do not eliminate the possibility that individual schools remain coherent and separate after summer. However, more extensive tagging studies in British Columbia strongly suggest some degree of mixing, albeit nonrandom, and that individual fish do not always return to the same spawning area (Hay et al. 1999; Hay et al. 2001; Hay and McKinnell 2002).

Estimates of territorial size suggest Pacific herring in most of SEAK can potentially be described as a single population. Pacific herring can move considerable distances, evident both in SEAK (up to 200 km) and net yearly movement in BC (up to 300 km, mean 89 km) (Dahlgren 1936; Hay and McKinnell 2002). Assuming these measured distance are radii of circles, the average territorial range is about 180 km and the maximum is 600 km, implying potential territorial areas of 25,000 to 280,000 km² (assuming circumscribed areas are entirely water). The BC record confirms these estimates are within reason; fidelity of herring is high (~88%) from a regional perspective, where regions represent areas of about 3000 to 10,000 km² (Hay et al. 2001). An ellipse bounding the entire observed area of migration in SEAK and extending north to Berners Bay is 31,600 km² (water only; Fig. 3.25), well within estimated territorial bounds but greater than the maximum region size in BC.

Metapopulation

Herring in SEAK are likely part of the eastern Pacific metapopulation: a) local stocks within SEAK exchange at least low levels of individual fish, suggested by tagging studies (Skud 1963; Carlson 1977), b) stocks have been depressed to near zero and recovered, such as at Tenakee (Fig. 3.13), c) spawning habitat is spatially fragmented into numerous areas (Davidson et al. 2006) (Fig. 3.1), and d) gene flow is likely high because no differences in alleles are evident across SEAK or in British Columbia and genetic structure varies temporally at spatial scales of about 700 km (Grant and Utter 1984; Seeb et al. 1999). Herring size at age and recruitment data provide limited evidence of population differences at smaller scales (Williams and Quinn 2000) but also support the metapopulation concept because groupings were consistent with geography. In the latter study, some SEAK herring (Sikta) grouped most closely with those in Prince William Sound, others (Seymour Canal, Kah Shakes, and Craig) were grouped more closely with Prince Rupert stock in British Columbia.

Summary

A variety of data do not evidence of separation among SEAK herring stocks, rather apparent geographic grouping were variable and often rather arbitrary. Limited tagging studies within SEAK demonstrate fish migrate and mix over most of the region but were not designed to determine repeat spawning fidelity. Migration data from British Columbia, a region to the south

of SEAK and reasonably similar in structure and climate, are used here to roughly predict repeat spawning fidelity at SEAK stock scales; these approximations predict considerable mixing among stocks (59 to 84%), possibly explaining the lack of definitive differences among stocks and suggesting that SEAK herring are part of an interrelated metapopulation.

To definitively understand migration and spawning behavior in SEAK, fish must be tagged and recovered on spawning grounds in ensuing years. Future tagging efforts could rely on physical tags as has been done in the past or some alternative technique, such as mass otolith marking could be used. The point is, if we truly wish to understand the population structure of Pacific herring in SEAK, a large-scale, multi-year study is necessary and it will require the cooperation of commercial fishing operations to be feasible. An ongoing, detailed genetic analysis of SEAK herring stocks may provide sufficient data for greater understanding; it may also lead to additional questions.

References

- ADFG 1985. Pacific herring *Clupea pallasi*. Volume 1: life histories and habitat requirements of fish and wildlife. Juneau, AK, Alaska Department of Fish and Game.
- Alderdice, D. F. and A. S. Hourston 1985. Factors influencing development and larval survival of Pacific herring (*Clupea harengus pallasi*) eggs and larvae to beginning of exogenous feeding. Can J Fish Aquat Sci 42(Supplement 1): 56-68.
- Alderdice, D. F. and F. P. J. Velsen 1971. Some effects of salinity and temperature on early development of Pacific herring (*Clupea pallasi*). J Fish Res Bd Can 28: 1545-1562.
- Arimitsu, M. L., J. F. Piatt, M. D. Romano and D. C. Douglas 2007. Distribution of forage fishes in relation to the oceanography of Glacier Bay. Proceedings of the fourth Glacier Bay science symposium, October 26-28, 2004, U.S. Geological Survey Scientific Investigations Report 2007-5047.
- Barton, L. H. and V. G. Wespestad 1980. Distribution, biology and stock assessment of western Alaska's herring stocks. Proceedings of the Alaska herring symposium, February 9-21, 1980, Anchorage, AK, Alaska Sea Grant Report.
- Beacham, T. D., J. F. Schweigert, C. MacConnachie, K. D. Le, K. Labaree and K. M. Miller 2002. Population structure of herring (*Clupea pallasi*) in British Columbia determined by microsatellites, with comparisons to southeast Alaska and California, Fisheries and Oceans Canada, Canadian Science Advisory Secretariat.
- Brown, E. D. and M. G. Carls 1998. Pacific herring (*Clupea pallasi*). Rest Notebook, EVOSTC: 1-8.
- Carlile, D. 2003. Southeast Alaska herring. Ecosystem considerations for 2004. J. Boldt. Anchorage, AK, Alaska Fisheries Science Center: 112-115.
- Carlile, D. W., R. C. Larson and T. A. Minicucci 1996. Stock assessments of Southeast Alaska herring in 1994 and forecasts for 1995 abundance. Juneau, Alaska Department of Fish and Game, Commercial Fisheries Management and Development Division.
- Carls, M. G., G. D. Marty, T. R. Meyers, R. E. Thomas and S. D. Rice 1998. Expression of viral hemorrhagic septicemia virus in prespawning Pacific herring (*Clupea pallasi*) exposed to weathered crude oil. Can J Fish Aquat Sci 55(10): 2300-2309.
- Carlson, H. R. 1977. Results of a tagging study of Pacific herring in southeastern Alaska in 1960-62 using radioactive body cavity tags. Seattle, WA, U.S. Department of Commerce,

- National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Northwest Fisheries Center: 9.
- Carlson, H. R. 1980. Seasonal distribution and environment of Pacific herring near Auke Bay, Lynn Canal, southeastern Alaska. Trans Am Fish Soc 109(1): 71-78.
- Chapman, W. M., M. Katz and D. W. Erikson 1941. The races of herring in the state of Washington. Wash Biol Rep No. 38A: 1-36.
- Cieciel, K. 2008. personal communication.
- Coonradt, E. 2008. Spawn timing in Sitka, AK, Alaska Dept of Fish and Game.
- Dahlgren, E. H. 1936. Further developments in the tagging of the Pacific herring, *Clupea pallasii*. J Conseil 11: 229-247.
- Davidson, W., W. Bergmann, P. Doherty, K. Monagle and D. Gordon 2006. Southeast Alaska sac roe herring fishery, 2006, Alaska Department of Fish and Game: 18.
- Davidson, W., D. Gordon, K. Monagle and D. Harris 2005. Northern southeast Alaska herring spawn-on-kelp pound fishery, 2005. Fishery Management Report No. 05-11, Alaska Department of Fish and Game: 29.
- Farley, E. 2008. Personal communication.
- Funk, F. 2007. Is recent Pacific herring recruitment in Prince William Sound, Alaska, unusually low compared to recruitment elsewhere on the west coast of North America? Prince William Sound herring: an updated synthesis of population declines and lack of recovery. S. D. Rice and M. G. Carls. Juneau, AK, National Oceanic and Atmospheric Administration, National Marine Fisheries Service: 60-77 (3.1 3.18).
- Funk, F., L. K. Brannian and K. A. Rowell 1992. Age-structured assessment of the Togiak herring stock, 1978-1992, and preliminary forecast of abundance for 1993. Juneau, Alaska Department of Fish and Game, Division of Commercial Fish: 52.
- Grant, W. S. and F. M. Utter 1984. Biochemical population genetics of Pacific herring (*Clupea pallasi*). Can J Fish Aquat Sci 41(6): 856-864.
- Haldorson, L. and J. Collie 1991. Distribution of Pacific herring larvae in Sitka Sound, Alaska. Proceedings of the International Herring Symposium October 1990, Alaska Sea Grant College Program, University of Alaska Fairbanks.
- Haldorson, L. J., J. D. Watts and D. A. Sterritt 1986. Larval fish production in Auke Bay, Alaska 1986. APPRISE: association of primary production and recruitment in a subarctic ecosystem. O. A. Mathisen, J. J. Goering and P. K. Bienfang. Juneau, AK, School of Fisheries and Science (University of Alaska-Juneau), Institute of Marine Science (University of Alaska-Fairbanks), the Oceanic Institute (Waimanalo, Hawaii), and NOAA/National Marine Fisheries Service (Auke Bay Laboratory): 321-360.
- Haldorson, L. J., J. D. Watts and D. A. Sterritt 1987. Larval fish production in Auke Bay, Alaska 1987. APPRISE: association of primary production and recruitment in a subarctic ecosystem. O. A. Mathisen, J. J. Goering and P. K. Bienfang. Juneau, AK, School of Fisheries and Science (University of Alaska-Juneau), Institute of Marine Science (University of Alaska-Fairbanks), the Oceanic Institute (Waimanalo, Hawaii), and NOAA/National Marine Fisheries Service (Auke Bay Laboratory): 301-360.
- Haldorson, L. J., J. D. Watts and D. A. Sterritt 1988. Larval fish studies. APPRISE: association of primary production and recruitment in a subarctic ecosystem. O. A. Mathisen, J. J. Goering and P. K. Bienfang. Juneau, AK, School of Fisheries and Science (University of Alaska-Juneau), Institute of Marine Science (University of Alaska-Fairbanks), the

- Oceanic Institute (Waimanalo, Hawaii), and NOAA/National Marine Fisheries Service (Auke Bay Laboratory): 147-183.
- Hay, D. E. 1985. Reproductive biology of Pacific herring (*Clupea harengus pallasi*). Can J Fish Aquat Sci 42: 111-126.
- Hay, D. E., P. B. McCarter and K. Daniel 1999. Pacific herring tagging from 1936-1992: a reevaluation of homing based on additional data, Fisheries and Oceans Canada: 1-58.
- Hay, D. E., P. B. McCarter and K. S. Daniel 2001. Tagging of Pacific herring *Clupea pallasi* from 1936-1992: a review with comments on homing, geographic fidelity, and straying. Can J Fish Aquat Sci 58(7): 1356-1370.
- Hay, D. E. and S. M. McKinnell 2002. Tagging along: association among individual Pacific herring (*Clupea pallasi*) revealed by tagging. Can J Fish Aquat Sci 59(12): 1960-1968.
- Herbert, K. and D. Carlile 2002. Southeast Alaska/Yakutat annual herring research report, 2000/2001 season. Alaska Fish Game Regional Information Report No. IJ02-36: 1-146.
- Hollowed, A. B., K. M. Bailey and W. S. Wooster 1987. Patterns in recruitment of marine fishes in the Northeast Pacific Ocean. Biol Oceanog 5: 99-131.
- Hourston, A. S. 109-. Timing of herring spawnings in British Columbia. Canadian Ind. Report Fisheries and Aquatic Science 118: 1-101.
- Hourston, A. S. 1980. Timing of herring spawnings in British Columbia, 1942-1979. Can Ind Rep Fish Aquat Sci 118: 1-101.
- Johnson, S. M., ML; Csepp, DJ; Harris, PM; Thedinga, JF 2003. Survey of fish assemblages in eelgrass and kelp habitats of southeastern Alaska U.S. Department of Commerce, NOAA Technical Memorandum NMFS AFSC-139: 1-50.
- Johnson, S. W. 2007. Nearshore fish atlas of Alaska, http://www.fakr.noaa.gov/habitat/fishatlas/.
- Johnson, S. W., M. G. Carls, R. P. Stone, C. C. Brodersen and S. D. Rice 1997. Reproductive success of Pacific herring, *Clupea pallasi*, in Prince William Sound, Alaska, six years after the *Exxon Valdez* oil spill. Fish Bull 95(4): 748-761.
- Krieger, K. J. 1982. Tagging herring with coded-wire microtags. Mar Fish Rev 44: 18-21.
- Lemberg, N. A., M. F. O'Toole, D. E. Penttila and K. C. Stick 1997. 1996 Forage fish stock status report. Wash Fish Wildlife Fish Management Prog., Dec. 1997(Stock Status Report No. 98-1).
- Leon, H. 1993. Stock discreteness of Pacific herring (*Clupea harengus pallasi*) in southeast Alaska. Seattle, WA, University of Washington. Master of Science: 128.
- Mattson, C. R. and B. L. Wing 1978. Ichthyoplankton composition and plankton volumes from inland coastal waters of southeastern Alaska, April-November 1972, U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service: 1-16.
- McGurk, M. D. 1989. Advection, diffusion and mortality of Pacific herring larvae *Clupea harengus pallasi* in Bamfield Inlet, British Columbia. Mar Ecol Prog Ser 51(1-2): 1-18.
- Miller, D. J. and J. Schmidtke 1956. Report on the distribution and abundance of Pacific herring (*Clupea pallasi*) along the coast of central and southern California. Calif Fish Game 42: 163-187.
- Moberly, S. A. and R. E. Thorne 1974. Assessment of southeastern Alaska herring stocks using hydroacoustical techniques 1970-71. Juneau, Alaska Department of Fish and Game: 1-24.

- Moulton, L. L. 1999. Review of Lynn Canal herring, MJM Research, prepared for SAIC, Inc.: 1-47.
- Muret-Woody, H. 2008. personal communication.
- Murphy, J. M. and J. A. Orsi 1999. Physical oceanographic observations collected aboard the NOAA ship John C. Cobb in the northern region of southeastern Alaska, 1997 and 1998, U.S. Dept of Commerce. NMFS-AFSC Proc. Rep. 99-02: 239.
- NOAA. 2008. Climate prediction center; monthly climatology.
- Norcross, B. L., S.-B. Kelly, P.-J. F. Hulson and T. J. Quinn II 2007. An early life history model for Pacific herring in Prince William Sound, Alaska. Prince William Sound herring: an updated synthesis of population declines and lack of recovery. S. D. Rice and M. G. Carls. Juneau, AK, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Auke Bay Laboratories: 7.1-7.18.
- Orsi, J. A. 2008. Personal communication.
- Orsi, J. A., J. A. Harding, S. S. Pool, R. D. Brodeur, L. J. Haldorson, J. M. Murphy, J. H. Moss, E. V. J. Farley, R. M. Sweeting, J. F. T. Morris, M. Trudel, R. J. Beamish, R. L. Emmet and E. A. Fergusson 2007. Epipelagic fish assemblages associated with juvenile Pacific salmon in neritic waters of the California current and the Alaska current. Am Fish Soc Symp 57: 105-155.
- Piatt, J. F. 2008. U.S.G.S. Alaska Science Center.
- Pritchett, M. 2005. 2006 Report to the Alaska Board of Fisheries: southeast Alaska -- Yakutat herring fisheries. Fishery Management Report No. 05-67, Alaska Department of Fish and Game: 25.
- Pritchett, M. 2006. Historic spawn herring database. Alaska Department of Fish and Game, Juneau, AK.
- Pritchett, M. 2007. Personal communication.
- Pritchett, M., K. Monagle and D. Harris 2008. Berners Bay area herring research, 2007, Alaska Department of Fish and Game, Division of Commercial Fisheries: 1-10.
- Quast, J. C. 1968. New records of thirteen Cottoid and Blennoid fishes for southeast Alaska. Pac Sci 22: 482-487.
- Quinn, T. J. and R. B. Deriso 1999. Quantiative fish dynamics. New York, NY, Oxford University Press.
- Reid, G. 1971. Age composition, weight, length and sex of herring, *Clupea pallasii*, used for reduction in Alaska, 1929-66. Spec. Sci. Rep. Fish. Natl. Oceanic Armos.Adm., Seattle. no. 634: 1-25.
- Rounsefell, G. A. 1930. Contribution to the biology of the Pacific herring, *Clupea pallasii*, and the condition of the fishery in Alaska. Bull US Bureau Fish 45: 227-326.
- Rounsefell, G. A. and E. H. Dahlgren 1932. Fluctuations in the supply of herring, *Clupea pallasii*, in Prince William Sound, Alaska. Bull US Bureau Fish XLVII: 263-291.
- Rounsefell, G. A. and E. H. Dahlgren 1933. Tagging experiments on the Pacific herring, *Clupea pallasii*. J Conseil VIII: 371-384.
- Rounsefell, G. A. and E. H. Dahlgren 1935. Races of herring, *Clupea pallasii*, in southeastern Alaska. Bull Bureau Fish 17.
- Scattergood, L. W., C. J. Sindermann and B. E. Skud 1959. Spawning of North American herring. Trans Am Fish Soc 88: 164-168.

- Schweigert, J. F., C. Fort and L. Hamer 1997. Stock assessments for British Columbia herring in 1995 and forecasts of the potential catch in 1997. Can. Tech. Rep. Fish. Aquat. Sci 2173: 1-73.
- Seeb, J., S. E. Merkouris, L. W. Seeb, J. B. Olsen, P. Bentzen and J. M. Wright 1999. Genetic discrimination of Prince William Sound herring populations. Anchorage, AK, Alaska Department of Fish and Game, Genetics Laboratory: 1-111.
- Sigler, M. F. and D. J. Csepp 2007. Seasonal abundance of two important forage species in the North Pacific Ocean, Pacific herring and walleye pollock. Fish Res 83(2-3): 319-331.
- Skud, B. E. 1960. Herring spawning surveys in southeastern Alaska. U.S. Fish and Wildlife Service Special Science Report Fish. No. 321: 16.
- Skud, B. E. 1963. Herring tagging experiments in southeastern Alaska. Fish Bull 63: 19-32.
- Stevenson, J. C. 1962. Distribution and survival of herring larvae (*Clupea pallasi* Valenciennes) in British Columbia waters. J Fish Res Bd Can 19: 735-789.
- Stocker, M., V. Haist and D. Fournier 1985. Environmental variation and recruitment of Pacific herring (*Clupea harengus pallasi*) in the Strait of Georgia. Can J Fish Aquat Sci 42: 174-180.
- Stokesbury, K. D. E., R. J. Foy and B. L. Norcross 1999. Spatial and temporal variability in juvenile Pacific herring, *Clupea pallasi*, growth in Prince William Sound Alaska. Enviorn Biol Fish 56(4): 409-418.
- Stokesbury, K. D. E., J. Kirsch, E. D. Brown, G. L. Thomas and B. L. Norcross 2000. Spatial distributions of Pacific herring, *Clupea pallasi*, and walleye pollock, *Theragra chalcogramma*, in Prince William Sound, Alaska. Fish Bull 98(2): 400-409.
- Stout, H. A., R. G. Gustafson, W. H. Lenarz, B. B. McCain, D. M. VanDoornik, T. L. Builder and R. D. Methot 2001. Status Review of Pacific Herring (*Clupea pallasi*) in Puget Sound, Washington. NOAA Technical Memorandum NMFS NWFSC. no. 45: 1-200.
- Thorne, R. E. 2008. Personal communication.
- Velleman, P. F. and D. C. Hoaglin 1981. Applications, basics, and computing of exploratory data analysis. Boston, MA, Duxbury Press.
- Vollenweider, J. J. 2008. Personal communication.
- Wespestad, V. G. and E. Moksness 2002. Observations on growth and survival during the early life history of Pacific herring, *Clupea pallasi* from Bristol Bay, Alaska, in a marine mesocosm. Fish Bull 88: 191-200.
- Williams, E. H. and T. J. Quinn II 1998. Age-structured analysis of Pacific herring from Norton Sound, Alaska. Alaska Fish. Research Bulletin 4: 87-109.
- Williams, E. H. and T. J. Quinn 2000. Pacific herring, *Clupea pallasi*, recruitment in the Bering Sea and northeast Pacific Ocean, I: relationships among different populations. Fish Oceanogr 9(4): 285-299.
- Wing, B. L. 2008. Personal communication, NMFS.
- Wing, B. L., C. W. Derrah and V. M. O'Connell 1997. Ichthyoplankton in the eastern Gulf of Alaska, May 1990, U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center: 1-54.
- Wing, B. L. and G. Reid 1972. Surface zooplankton from Auke Bay and Vicinity, southeastern Alaska, August 1962 to January 1964. Seattle, WA, U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service: 764.

Table 3.1. Mean growth rates [ln(mm)/ln(year)] in SEAK Pacific herring stocks. The data represented here are a subset of ADFG data (Pritchett 2007), fish captured during active spawn between March and May, thus describing local spawning stocks as closely as possible. (These selection criteria identified 78,971 fish of 188,628 in the database, 42%. Examination of a second category, pre-spawning fish captured within the same time period, is recommended. Time constrains have precluded this analysis.)

			95% confidence	
		mean		
stock	n	rate	bounds	
Sitka	18	0.127	0.114	0.139
Lynn Canal	3	0.142	0.098	0.186
Craig	12	0.115	0.100	0.130
Ernest Sound	9	0.110	0.087	0.133
Hobart-Houghton	12	0.107	0.079	0.135
Hoonah	10	0.114	0.097	0.130
Kah Shakes	19	0.134	0.117	0.151
Seymour Canal	24	0.136	0.121	0.151
West Behm	14	0.107	0.090	0.124
Tenakee	12	0.123	0.103	0.143

Fig. 3.1. Pacific herring spawning locations and management areas in SEAK (Carlson 1980; Grant and Utter 1984; Leon 1993; Herbert and Carlile 2002; Davidson et al. 2005; Pritchett 2005; Pritchett 2007). The red symbols are spawning data for herring from an Alaska Department of Fish and Game database (Pritchett 2006), 1964 through present, although time series are not continuous, particularly prior to the 1970s. Orange symbols are other reported spawn sites not mapped by ADFG. Management boundaries approximate where the managers may be conducting fisheries, historically where spawn has occurred for particular spawning stocks, and are for information purposes only; i.e. they are places where managers look for spawn and where a fishery might occur.

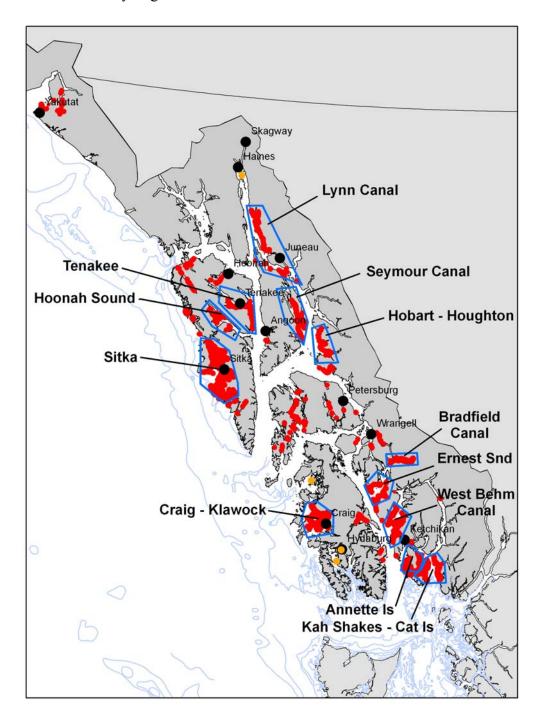


Fig. 3.2. Relationship between geographic area and herring fidelity in British Columbia ($r^2 = 0.975$, P = 0.013) (Hay et al. 1999).

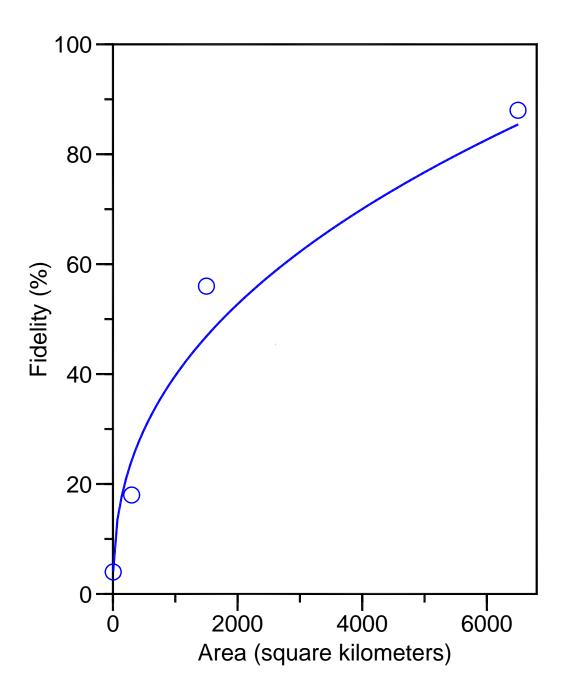


Fig. 3.3. Lynn Canal Management area as defined by ADFG (Pritchett et al. 2008) and the subset studied by Carlson (1980) (yellow). Non-spawning herring located by acoustic survey are indicated in green (summer) or blue (winter). Spawning is color coded by decade; however these lines often overlap and not all temporal detail is visible.

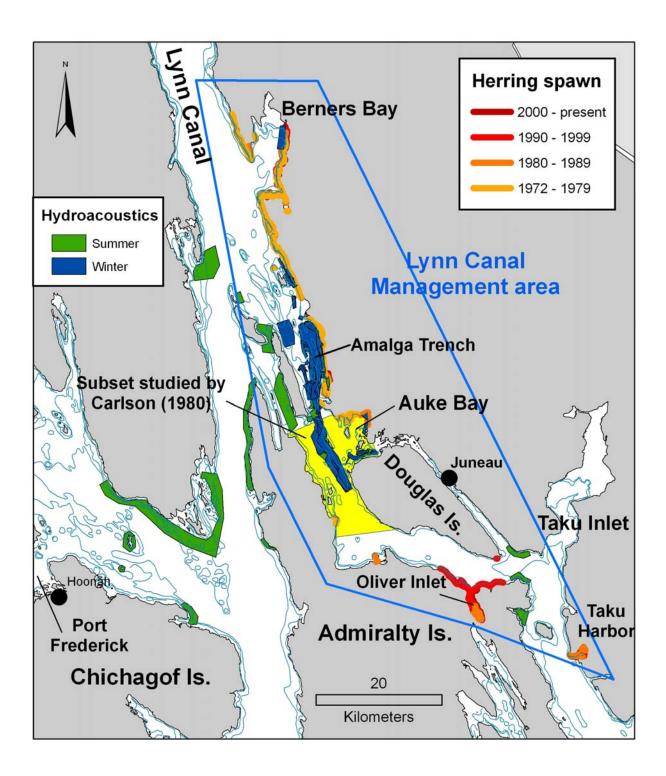


Fig. 3.4. Seasonal Pacific herring biomass change in Lynn Canal (Sigler and Csepp 2007); data were converted to short tons to be consistent with units used by ADFG. Noted in the text, there is a large discrepancy between these biomass estimates and those of ADFG (e.g., Figs. 3.4 and 3.7).

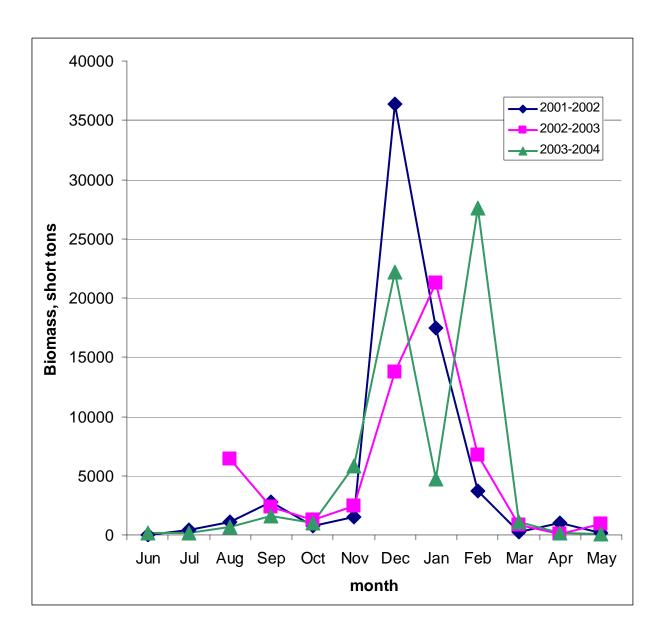


Fig. 3.5. Biomass estimates in tons for Lynn Canal herring, southeast Alaska (Moberly and Thorne 1974; Pritchett 2007).

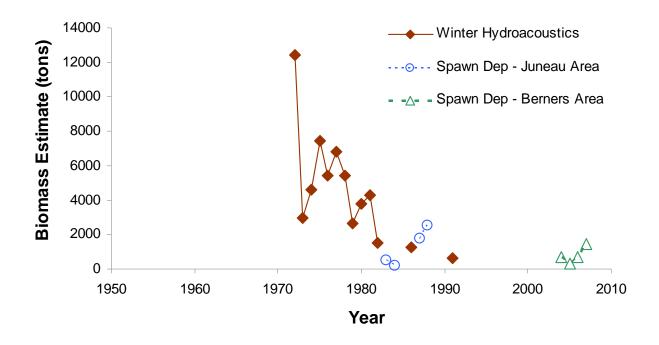


Fig. 3.6. Total nautical miles of herring spawn observed by year for aerial surveys of the Lynn Canal area, Southeast Alaska (Carlile et al. 1996; Pritchett 2007).

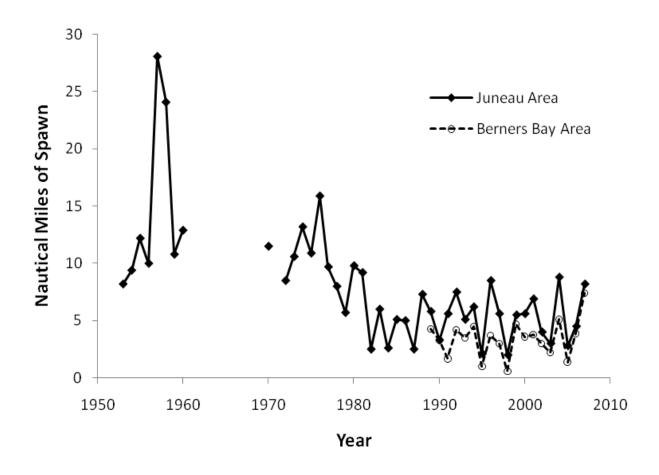


Fig 3.7. Relationships between the biomass estimates for Lynn Canal herring obtained from dive surveys (y) and the nautical miles of spawn obtained from aerial surveys (x).

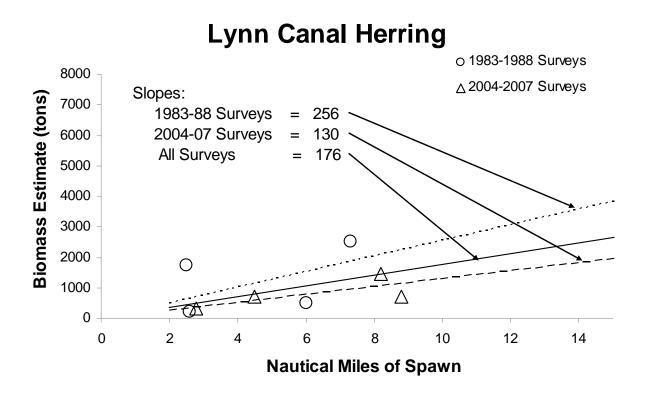


Fig. 3.8. Estimated historical biomass of Lynn Canal herring using miles of spawn observed during aerial surveys and the estimated biomass obtained from dive surveys. The aerial survey estimate is based on the slope describing all surveys, 176 tons/mile (Fig. 3.6). The vertical bars identify 95% confidence bounds.

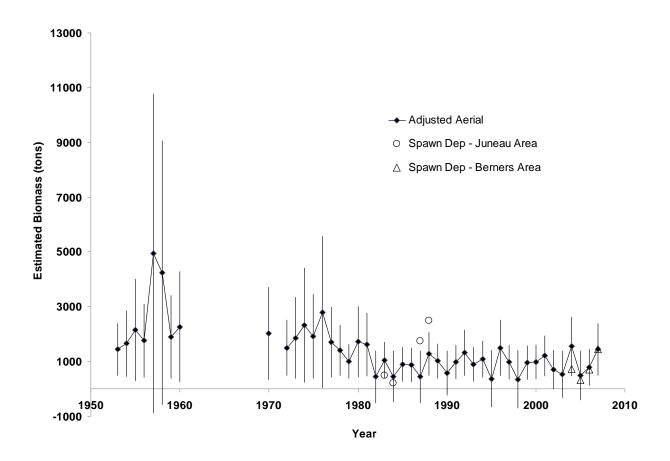


Fig. 3.9a. Pacific herring age structure in northern SEAK. The data represented here are a subset of ADFG data (Pritchett 2007), fish captured during active spawn between March and May, thus describing local spawning stocks as closely as possible. (These selection criteria identified 78,971 fish of 188,628 in the database, 42%. Examination of a second category, prespawning fish captured within the same time period is recommended. Time constrains have precluded this analysis.)

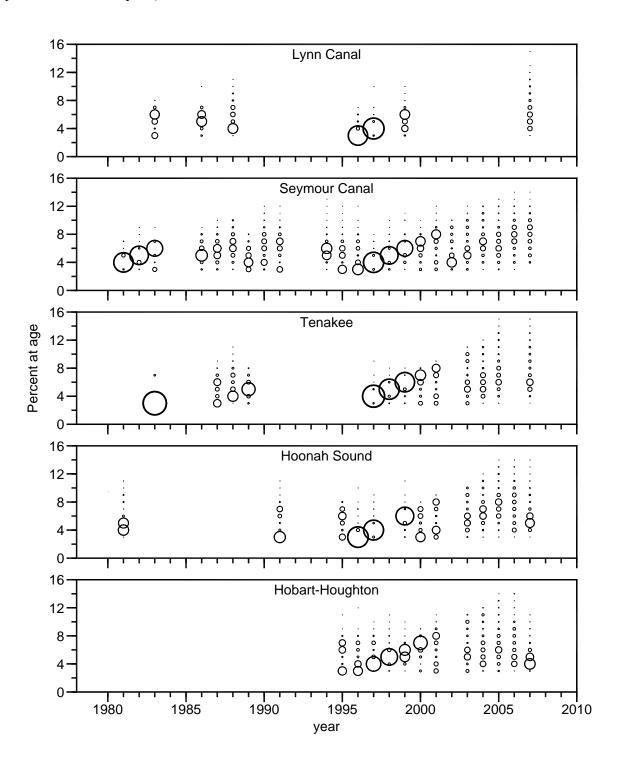


Fig. 3.9b. Pacific herring age structure in central and southern SEAK.

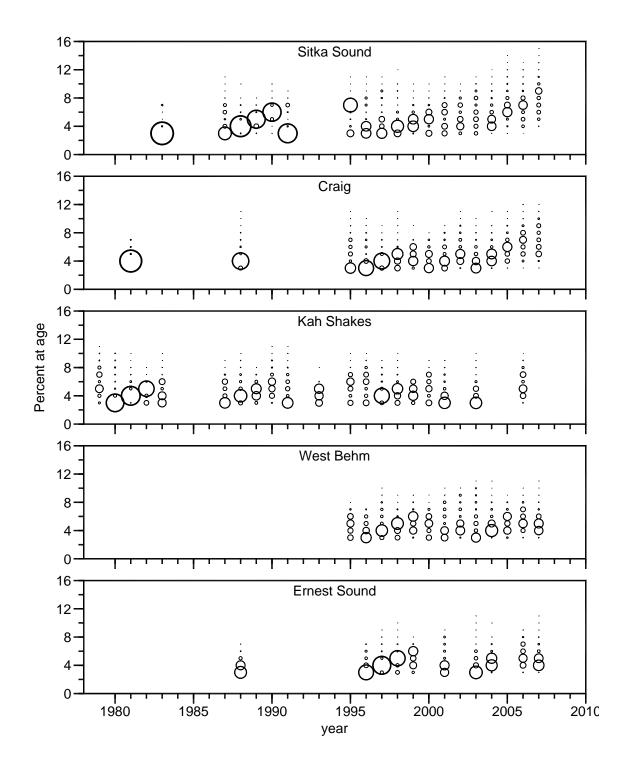


Fig. 3.10. Larval herring distribution in SEAK. Data are not synoptic and do not represent total habitat utilization; years are combined (Mattson and Wing 1978; Haldorson et al. 1986; Haldorson et al. 1987; Haldorson et al. 1988; Haldorson and Collie 1991; Wing et al. 1997; Johnson 2003; Arimitsu et al. 2007; Johnson 2007). Most observation efforts have been focused in Glacier Bay [1999 to 2004; (Arimitsu et al. 2007)], Sitka [1989 to 1990 (Haldorson and Collie 1991)], and Auke Bay [1986 to 1988; (Wing and Reid 1972; Haldorson et al. 1986; Haldorson et al. 1987; Haldorson et al. 1988)]. Those in Haines and Saginaw Bay were collected in 1972 (Mattson and Wing 1978). Offshore larvae were collected in 1990 (Wing et al. 1997). Some larvae are captured in ongoing habitat assessment research although these nets are too coarse for efficient larval capture (Johnson 2003; Johnson 2007).

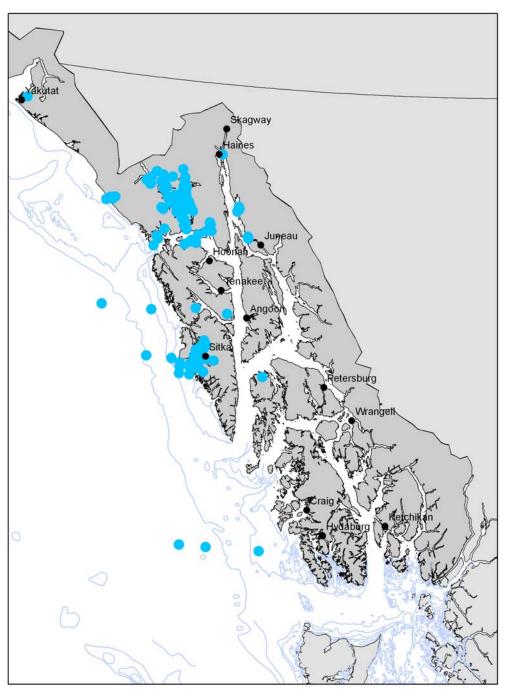


Fig. 3.11. Juvenile Pacific herring distribution in SEAK. Observation in Glacier Bay was extensive [1999 to 2004 (Arimitsu et al. 2007; Piatt 2008)]. Sampling in other SEAK habitat was less comprehensive (Johnson 2003; Johnson 2007; Orsi et al. 2007; Cieciel 2008; Muret-Woody 2008; Orsi 2008).

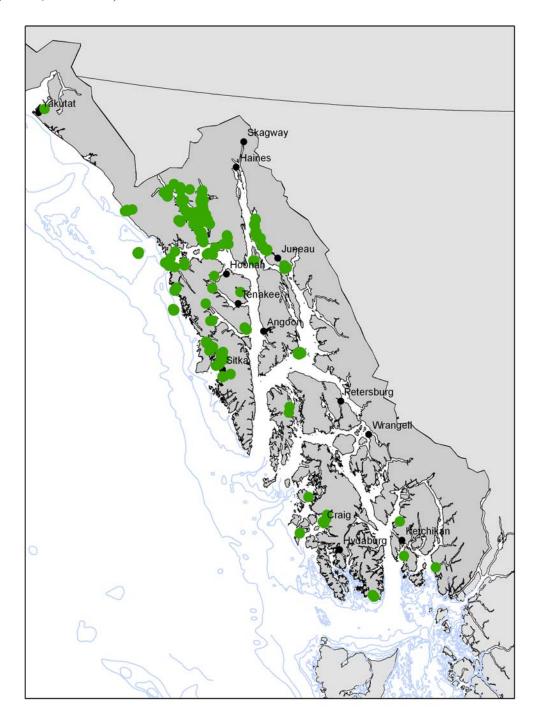


Fig. 3.12. Adult non-spawning Pacific herring distribution in SEAK (Rounsefell and Dahlgren 1933; Rounsefell and Dahlgren 1935; Skud 1963; Carlson 1977; Arimitsu et al. 2007; Orsi et al. 2007; Farley 2008; Orsi 2008; Vollenweider 2008). Not all areas have been sampled.

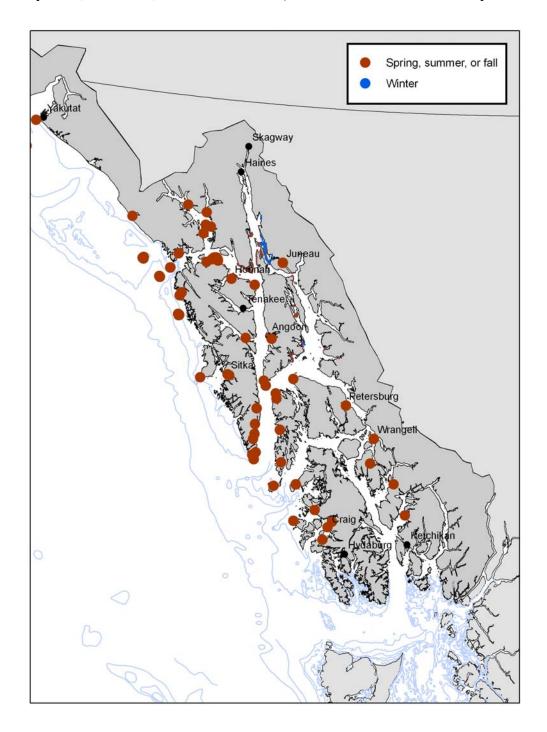
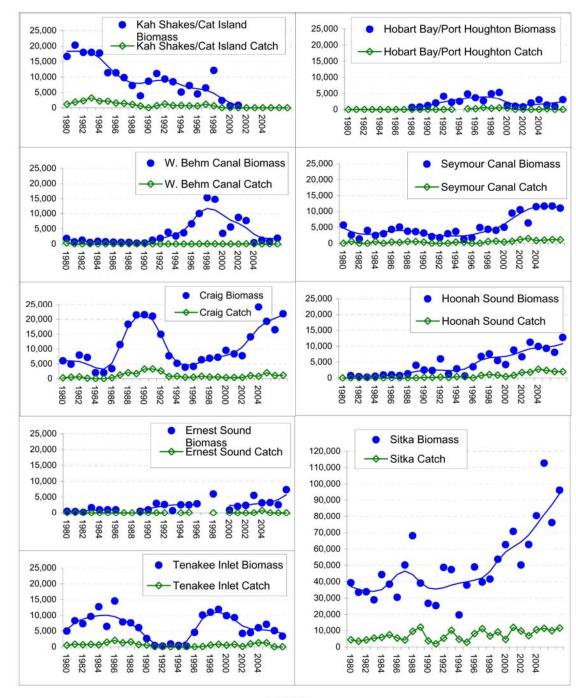


Fig. 3.13. Total mature herring biomass (tons) and human harvest (tons) at major spawning locations in SEAK (Carlile 2003; Pritchett 2007). See Fig. 3.7 for Lynn Canal biomass. Biomass is characterized with smoothed data [4235H method; (Velleman and Hoaglin 1981)].



TONS (note different scale for Sitka)

YEAR

Fig. 3.14. Genetic measures involving SEAK herring. Blue ellipses are the result of a Pacific Ocean scale allozyme analysis (Grant and Utter 1984) and the red ellipse is the SEAK grouping estimated by microsatellite analysis (Beacham et al. 2002).

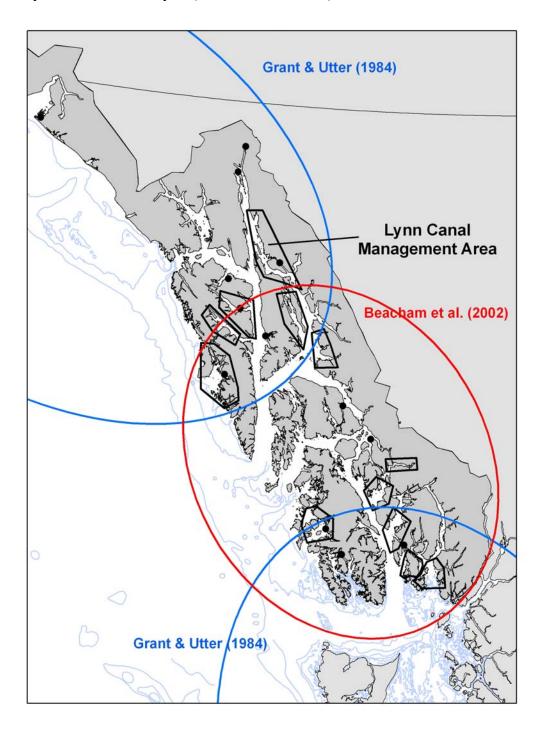


Fig. 3.15. Spawn timing (median Julian days) by location in SEAK (Davidson et al. 2005; Pritchett 2006; Coonradt 2008). The question mark indicates missing information. Circled areas divide the data into earlier and later spawning groups. Areas range from 11,500 to 37,800 km² (water only); predicted herring spawning fidelity is 100% in areas this size [derived from Hay et al. (Hay et al. 1999)].

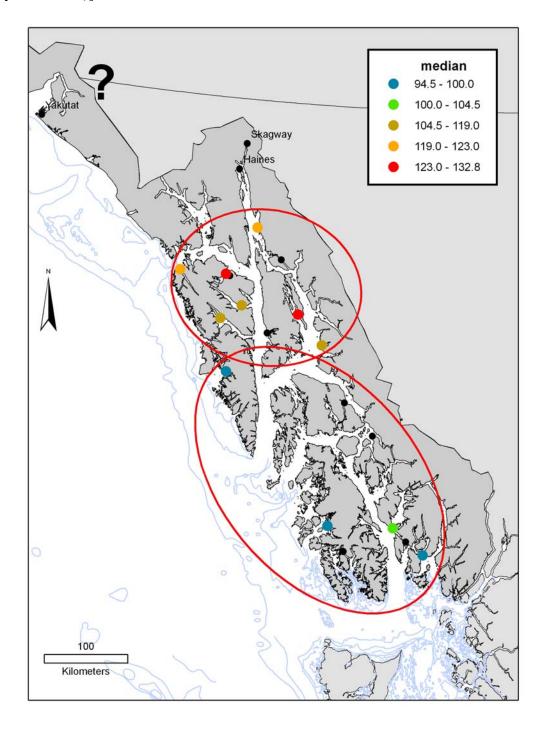


Fig. 3.16. Range of spawn timing of Pacific herring aggregations along the west coast of North America. Data from Stout et al. (Stout et al. 2001), a compilation of other authors (Hourston 109-; Rounsefell 1930; Chapman et al. 1941; Miller and Schmidtke 1956; Scattergood et al. 1959; Skud 1960; Alderdice and Velsen 1971; Barton and Wespestad 1980; ADFG 1985; Hay 1985; Lemberg et al. 1997; Davidson et al. 2005). SEAK data were updated (Davidson et al. 2005; Pritchett 2006; Coonradt 2008) and approximate latitude was added with reference to original work. Vertical bars indicate the range of spawn timing with symbols at the midpoints.

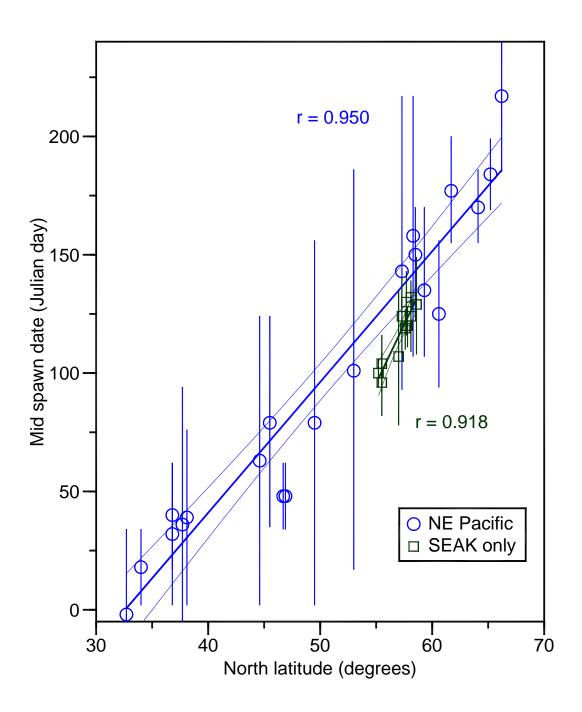


Fig. 3.17. Typical sea surface temperature gradient in SEAK in spring.

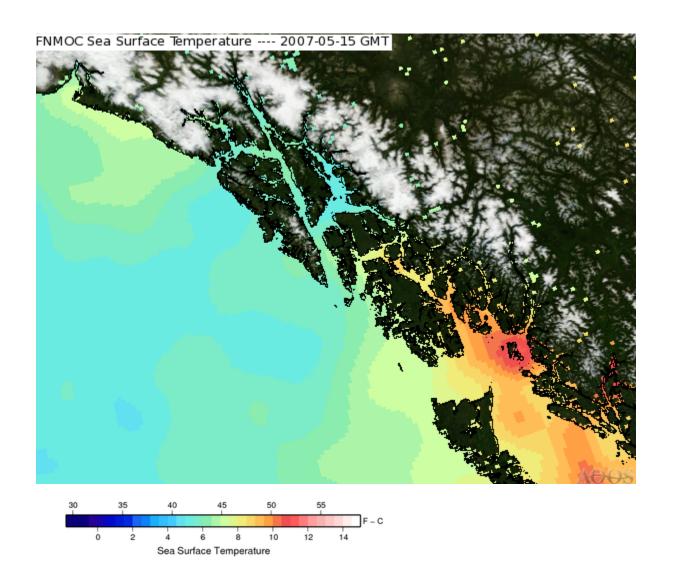


Fig. 3.18a. Differences in recruitment suggest herring in SEAK can be subdivided into more than one region. Illustrated areas are based on Figures 4 (red), 7 (black), 8 and 9 (blue) in Williams and Quinn (2000); see Fig. 3.17b. Question marks indicate missing information. Delineated areas entirely within SEAK range from 1100 to 49,500 km² (water only); predicted herring spawning fidelity ranges from 41 to 100% in areas this size [derived from Hay et al. (1999)].

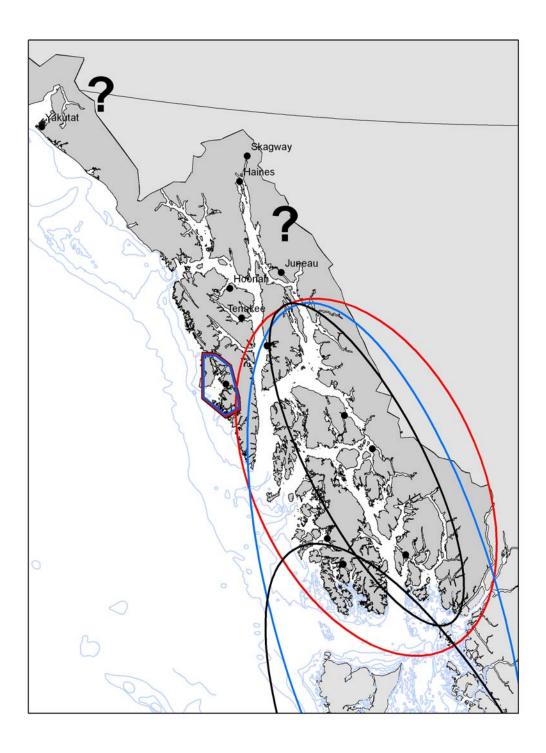


Fig. 3.18b. Recruitment analysis figures from Williams and Quinn (2000). SEAK = SIT + CRG in this analysis.

Figure 4. Scatterplot of the first two dimensions from a metric multidimensional scaling analysis of Bering Sea and NE Pacific herring recruitment estimates.

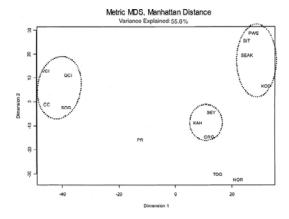


Figure 7. Dendrogram from divisive hierarchical analysis of NE Pacific herring recruitment estimates.

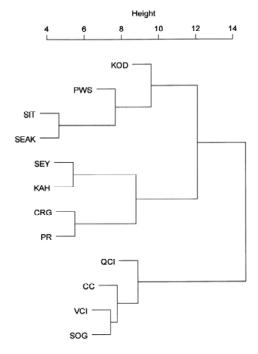


Figure 8, Scatterplot of first two dimensions from a metric multidimensional scaling analysis of NE Pacific herring recruitment estimates corresponding to the 1978-1993 year classes.

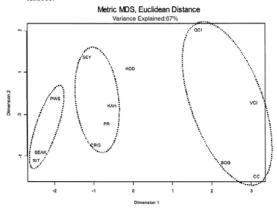


Figure 9. Dendrogram from divisive hierarchical analysis of NE Pacific herring recruitment estimates corresponding to the 1978–1993 year classes.

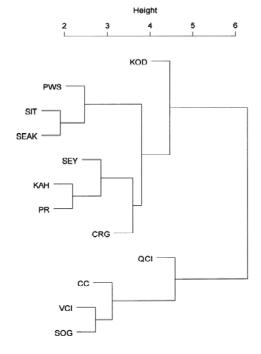


Fig. 3.19. Length-at-age data from 1929, year class 4 (Rounsefell and Dahlgren 1935), do not suggest definitive separation among herring in SEAK.

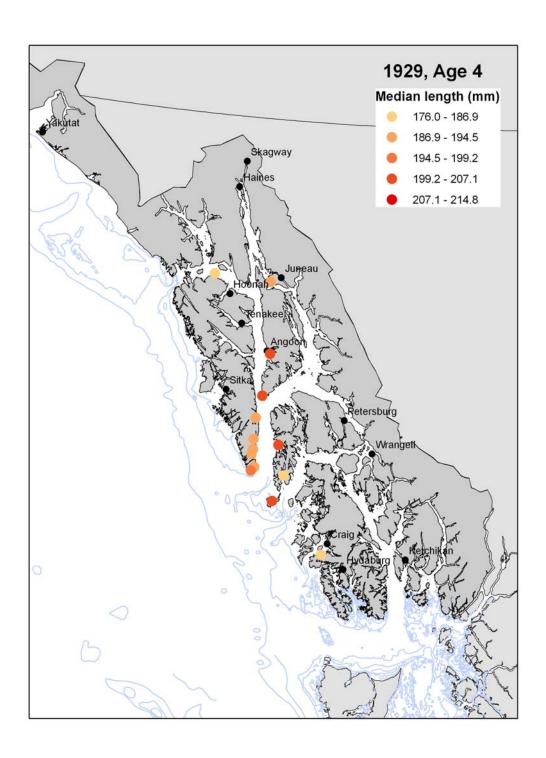


Fig. 3.20. Relationship between age and body size among SEAK herring stock (Johnson et al. 1997; Carls et al. 1998). Shelter Island is within the Lynn Canal management area; Cat Island is near Kah Shakes. Symbol size is related to number of fish; the smallest symbols represent single fish; interpretation of such data obviously requires caution.

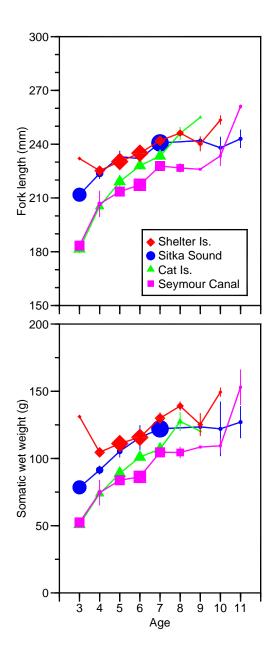


Fig. 3.21a. Differences among Pacific herring weight-at-age in SEAK. Illustrated areas are based on Williams and Quinn (2000) weight at age analysis. Question marks indicate missing information. The circled area in SEAK is 34,000 km² (water only); predicted herring spawning fidelity is 100% in an area this size [derived from Hay et al. (1999)].

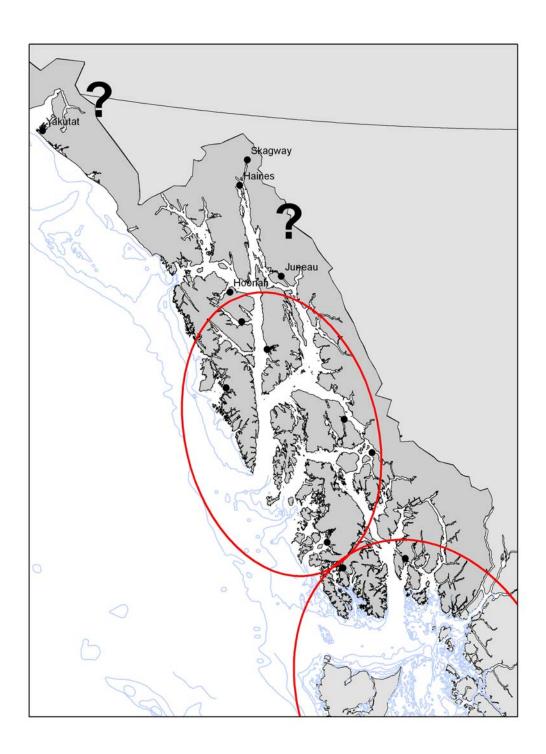


Fig. 3.21b. Figure 10 of Williams and Quinn (2000). Metric multidimensional scaling analysis of Pacific herring weight-at-age data for ages 3 to 8 from the Bering Sea and NE Pacific. SEAK = SIT + CRG in this analysis.

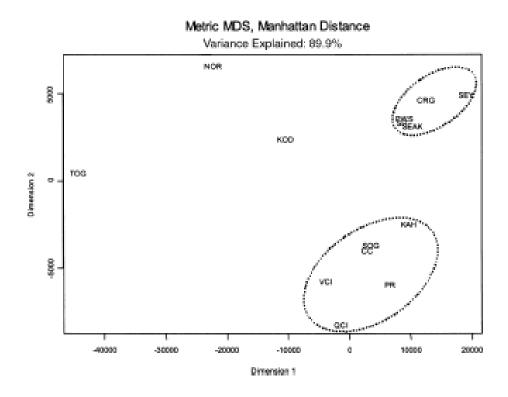


Fig. 3.22. Trends in size (length) at age in SEAK Pacific herring stocks; Lynn Canal (LYN), Seymour Canal (SEY), Tenakee (TEN), Hobart-Houghton (HOB), Ernest Sound (ERN), Craig (CRG), Hoonah Sound (HOO), Sitka Sound (SIT), Kah Shakes (KAH), and West Behm Canal (BEH). The data represented here are a subset of ADFG data (Pritchett 2007), fish captured during active spawn between March and May, thus describing local spawning stocks as closely as possible. (These selection criteria identified 78,971 fish of 188,628 in the database, 42%. Examination of a second category, pre-spawning fish captured within the same time period is recommended. Time constrains have precluded this analysis.)

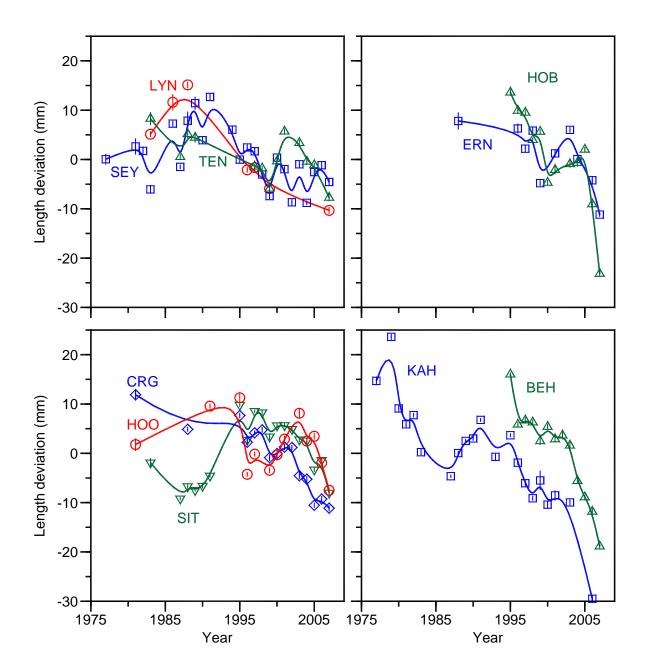


Fig. 3.23. Cohort growth in northern SEAK (power model); growth in remaining SEAK stocks is not illustrated. Individual cohorts are distinguished by color, symbol shape, and symbol fill. Symbol sizes correspond to the number of measurements (the largest indicate >100, the smallest ≤10). The data represented here are a subset of ADFG data (Pritchett 2007), fish captured during active spawn between March and May, thus describing local spawning stocks as closely as possible. (These selection criteria identified 78,971 fish of 188,628 in the database, 42%. Examination of a second category, pre-spawning fish captured within the same time period is recommended. Time constrains have precluded this analysis.)

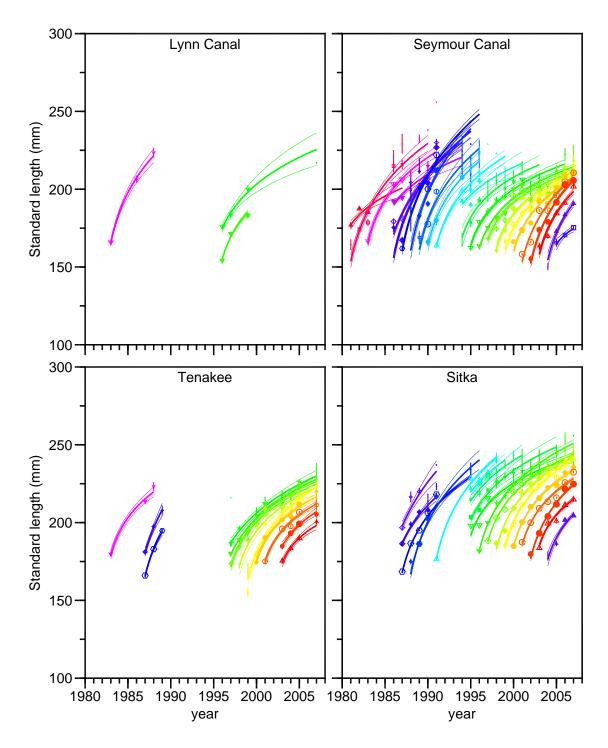


Fig. 3.24. Vertebrae number in SEAK herring (Rounsefell and Dahlgren 1935). Symbol sizes are largest for the earliest year classes so that variability in vertebrate number is evident for each location. The question mark indicates missing information. Circled areas divide SEAK into three possible regions, northern, southern, and central, the latter with a somewhat higher vertebrae count. Admittedly these divisions are highly subjective. Circled areas range from 3800 to 15,200 km² (water only); predicted herring spawning fidelity ranges from 69 to 100% in areas this size [derived from Hay et al. (1999)].

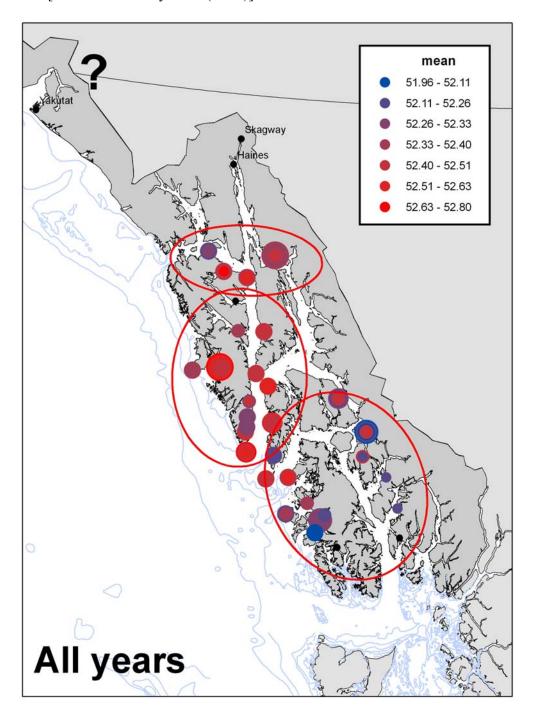
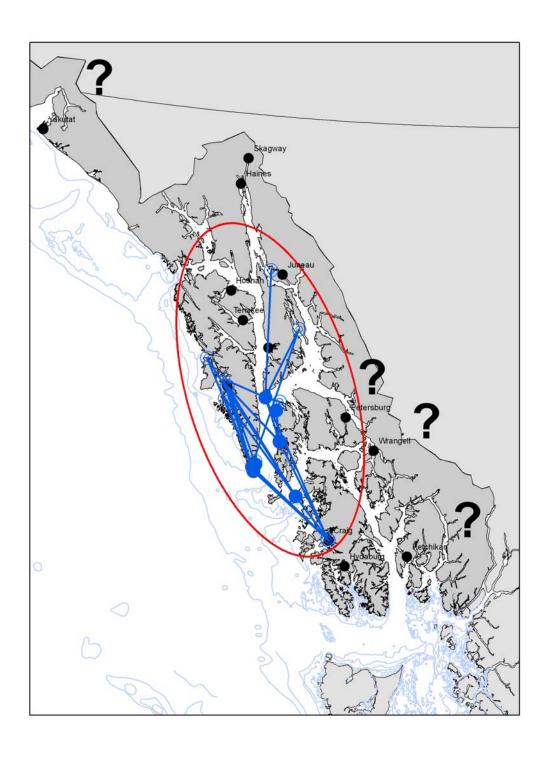


Fig. 3.25. Pacific herring migration in SEAK, observed by tagging studies (Rounsefell and Dahlgren 1933; Rounsefell and Dahlgren 1935; Dahlgren 1936; Skud 1963; Carlson 1977). Question marks indicate missing or incomplete information. The circled area identifies the approximate area of known mixing and is 31,600 km² (water only); predicted herring spawning fidelity within an area this large is 100% [derived from Hay et al. (1999)].



Chapter 4 Pacific herring habitat in southeastern Alaska

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Abstract

Marine habitat in southeastern Alaska (SEAK) is variable, yet Pacific herring essentially occupy all of it. Organic sediment and semi-protected, partially mobile substrate are the most common shore type and habitat class among all areas. Marine waters of SEAK are characterized by an inshore-offshore salinity gradient and a north-south temperature gradient. Inside waters are more estuarine, more protected from wave action, and have more extreme seasonal fluctuations in temperature and salinity than outside waters. Herring were captured in essentially all areas of SEAK; occasional capture failures were interpreted as insufficient sampling, not an absence of herring. Eelgrass meadows, kelp communities, sand-gravel beaches, and bedrock outcrops comprise a continuum of habitat types available to herring throughout SEAK. The percent shoreline extent of kelps (canopy and understory) and eelgrass are reduced in Lynn Canal compared to all other areas but herring continue to spawn in Berners Bay and juveniles continue to utilize nearshore habitats in Auke Bay, Favorite Channel, and Berners Bay.

Introduction

Because all life stages of Pacific herring (*Clupea pallasii*) are responsive to climatic and oceanographic conditions, areas that this species inhabits are linked to population survival and success. Spawn timing, for example, is related to winter and spring sea surface temperatures (Lassuy 1989; Emmett et al. 1991; Brown and Carls 1998). Hatching must coincide with sufficient zooplankton abundance or larvae will starve and survival may be the principal determinant of year class strength (Hjort 1914; McGurk 1984; Norcross et al. 2001). These fish, particularly first year juveniles, must accumulate enough energy before winter to survive winter starvation (Paul et al. 1998).

In this chapter, we focus on herring habitat and how it varies by region in southeastern Alaska (SEAK). The specific goal is to determine if habitat in Lynn Canal is unique or discrete compared to other areas. Ten areas with a history of known herring populations were used in habitat comparisons (Fig. 4.1). Lynn Canal was divided into three study areas (Berners Bay, Favorite Channel, and Auke Bay) and Sitka Sound was divided into three areas (northern, central, and southern). The other study areas were Tenakee Inlet, Craig, Duke Island, and Kah Shakes Cove (Fig. 4.1). Within each area we examined shore type, habitat class, extent of vegetation types (e.g., kelp, eelgrass), environmental data (temperature, salinity), general fish distributions, and historical herring spawning areas. The selection of the 10 areas was also based on the availability of data from three major datasets [*ShoreZone* aerial imagery (Harney et al. 2007), Nearshore Fish Atlas of Alaska (Nearshore Fish Atlas of Alaska. 2007) and ADFG spawning surveys (Leon 1993; Herbert and Carlile 2002; Davidson et al. 2005; Pritchett 2006)].

The habitat and shore type classifications referenced in this report are based on the classifications used by the Alaska *ShoreZone* program. There are 35 shore type classes; such as rock cliff, organic sediment, and man-made [Table 4.1; (Howes et al. 1994)]. Habitat classification relates dominant structuring processes (e.g., fluvial, glacial, and wave energy) to biologically based estimates of exposure (Table 4.2). A complete description of *ShoreZone* methods and habitat classifications is presented in Harney et al. (2007).

Pacific herring habitat utilization in SEAK

Juvenile herring occupy a variety of habitat types including steep bedrock outcrops, eelgrass, kelps, and sand-gravel beaches in SEAK. In surveys from 1998 to 2007, mean catch per seine haul for herring was greatest in bedrock outcrops, followed by kelp, eelgrass, and sand and gravel beaches (Fig. 4.2) (Johnson et al. 2005; Nearshore Fish Atlas of Alaska. 2007). In brief, bedrock outcrops are usually steep and located in exposed locations on the outside of bays—*Laminaria* and *Alaria* are usually attached to bedrock faces; eelgrass meadows are typically located inside protected bays and inlets in soft substrates of sand, silt, or mud; understory kelps (Laminariales) occupy more exposed locations, often near the entrance of bays; and sand or gravel beaches with no rooted vegetation are generally "pocket beaches" found inside protected bays—algae (e.g., filamentous) is occasionally present. Characteristic of schooling fishes, herring were captured infrequently with a beach seine (<20% of all hauls) but often in large numbers (Johnson et al. 2005; Johnson and Thedinga 2005). After hatching in spring, larvae scatter widely, both nearshore and offshore. At metamorphosis juvenile herring move into nearshore water [in late July and early August in Auke Bay (Jones 1978)] and spend the first three years of their lives in nearshore waters (Tanasichuk et al. 1993)

Herring tolerate a wide range of temperatures and salinities. Juvenile herring were captured in nearshore habitats throughout SEAK in seawater temperatures that ranged from 4.0°C to 16.9°C [Table 4.3; (Johnson and Lorenz)]. Temperature profiles from several locations in northern SEAK, including Lynn Canal, exhibited a similar pattern; mean monthly temperatures were usually lowest in March (about 4°C) and highest in August or September [about 13°C; (NMFS. 1974; Johnson and Thedinga 2005)]. Herring were captured in nearshore habitats throughout SEAK in salinities that ranged from about 7 PSS to 33 PSS (practical salinity scale) [Table 4.3; (Johnson and Lorenz)].

In Lynn Canal, herring commence spawning when sea-surface temperatures (SST) increase to 5 to 6°C (Carlson 1980). Sea surface temperatures in Auke Bay increased about 0.024°C per year between 1976 and 2004 (Wing et al. 2006). The greatest freshwater input is from April to November; surface salinity is highest (31 PSS) in March and usually lowest (10-15 PSS) in late July or August. Herring spawn from late April to early May in Lynn Canal, a time of relatively high salinity (USDA 2004).

Comparisons among study areas

For each study area, there are three maps: a four-panel map with shore type, habitat class, kelp distribution, and eelgrass distribution based on *ShoreZone* aerial imagery (see Appendix I for definitions); a four-panel map showing historical herring spawn locations from the early 1970s to 2007 [ADFG surveys (Pritchett 2006)]; and a map showing beach seine capture locations of juvenile herring by habitat type, overall fish species composition, and temperature data (not available for all areas) from NOAA Fisheries (Nearshore Fish Atlas of Alaska. 2007). On the *ShoreZone* imagery maps, boundaries included in habitat descriptions are depicted by large Xs. Study areas are described from north to south in SEAK (Fig. 4.1).

Lynn Canal

Berners Bay

The Berners Bay study area includes 89.3 km of shoreline (excludes Berners River delta) from Point Sherman to Sunshine Cove (Fig. 4.3a). Shoreline outside of Berners Bay is dominated by wide platforms with gravel beaches which are semi-protected and partially mobile.

Inside Berners Bay, beaches are dominated by organic sediment and wide sand and gravel flats. Dominant organic sediment (27%) are primarily associated with estuary habitats (29%) and other areas of the bay are mainly semi-protected, protected, or partially mobile (Figs. 4.3a,b). Less common shore types within the classification "other" (40%) represent 22 separate classes which are not dominated by one class or a uniquely different class (Fig. 4.3a). Semi-exposed or exposed habitats are not found in this area. The shoreline extent of kelps is dominated by *Fucus* (57%) followed by *Alaria* (34%), understory kelps (14%), and canopy kelps (5%) (Fig. 4.3c). Eelgrass is present on only about 5% of the shoreline (Echo Cove and Bridget Cove) (Fig. 4.3d), and total area of all eelgrass beds is about 10 ha (Harris et al. In prep). Limited development has occurred in Berners Bay (man-made or modified shoreline is <1% or 174 m) but future activities may include the enlargement of a marine terminal at Slate Creek Cove (Fig. 4.3a) to service the Kensington Gold Mine (Harris et al. 2005) and construction of an access road from Juneau to Skagway.

The Lynn Canal herring population has declined since the 1950s; mean shoreline extent of spawn averaged roughly 15 km in the 1950s compared to about 5 km in the 2000s (Fig. 4.4) (Williams et al. 2004). In 2007, about 12 km of spawn was observed in Lynn Canal (Alaska Department of Fish and Game. 2007). Presently, most Lynn Canal herring spawn in the vicinity of Berners Bay. In the 1970s and 1980s, herring spawned from south of Point Sherman to Sunshine Cove (Figs. 4.5a,b), whereas in the 1990s and 2000s, spawning was concentrated along the eastern shore of Berners Bay and from Point Bridget to Bridget Cove (Figs. 4.5c,d). No significant spawning in any year has been observed in Echo Cove on kelp or eelgrass

Juvenile herring utilize eelgrass and kelp in Berners Bay. Nearly 9,000 herring were captured in 16 of 54 beach seine hauls from 1998 to 2006; mean fish size was 44 mm FL (Fig. 4.6) (Nearshore Fish Atlas of Alaska. 2007). No herring were captured in northern Berners Bay on sand-gravel substrates void of vegetation. In addition to herring, 41 other species were captured; dominant species included young-of-the year (YOY) chum salmon (*Oncorhynchus keta*), coho salmon (*O. kisutch*) smolts, tubesnout (*Aulorhynchus flavidus*), and crescent gunnel (*Pholis laeta*) (Fig. 4.6). Temperature profiles in Berners Bay followed seasonal patterns similar to other areas in SEAK; mean monthly temperatures were usually lowest in February or March and highest in July or August (Fig. 4.6).

Favorite Channel

The Favorite Channel study area includes 60.7 km of shoreline from Sunshine Cove to Lena Point (Fig. 4.7a). The shoreline within Favorite Channel is dominated by rock ramps with gravel (21%), sand and gravel flats (10%), and by wide platforms with gravel (9%) that range from mostly semi-protected (53%) to protected (13%) from wave action, with partially mobile sediments. Estuaries (19%) and semi-protected shorelines with immobile substrates (8%) are also common in this area (Figs. 4.7a,b). Shore types within the classification "other" (60%) represent 20 separate classes mostly comprised of gently sloping wide sand and gravel flats that are concentrated near the Eagle River Delta and where most of the estuarine habitat is present (Fig. 4.7a). Semi-exposed or exposed habitats are not found in this area. The shoreline extent of kelps is dominated by *Fucus* (57%) followed by *Alaria* (27%), and understory kelps (26%); canopy kelps are absent (Fig. 4.7c). Eelgrass is present on less than 2% of the shoreline (Sunshine Cove and Tee Harbor) (Fig. 4.7d); total area of all eelgrass beds is about 1.4 ha (Harris et al. In prep). Development along Favorite Channel (man-made or modified shoreline is 1% or 552 m) is mostly limited to residential homes concentrated in Lena Cove and Tee Harbor. A

major Steller sea lion (*Eumetopias jubatus*) haulout is located on Benjamin Island (Fig. 4.7a); up to 800 sea lions may use this haulout from October to June (Thedinga et al. 2006).

Historically, spawning has been concentrated on the eastern side of Favorite Channel with no significant spawning on any of the nearby islands (Shelter Island, Lincoln Island) (Fig. 4.8a). In the 1970s, herring spawned along most of the shoreline from Sunshine Cove to Tee Harbor (Fig. 4.8a), whereas in the 1980s spawning was sparse and concentrated near Sunshine Cove and Tee Harbor (Fig. 4.8b). Spawning was almost nonexistent in the 1990s and sparse and concentrated near Sunshine Cove in the 2000s (Figs. 4.8c,d).

Juvenile herring use bedrock, kelp, and sand-gravel habitats in Favorite Channel. Nearly 5,000 herring were captured in 16 of 95 beach seine hauls from 2001 to 2006; mean fish size was 55 mm FL (Fig. 4.9) (Nearshore Fish Atlas of Alaska. 2007). In addition to herring, 37 other species were captured in Favorite Channel; dominant species included Pacific sand lance (*Ammodytes hexapterus*), walleye pollock (*Theragra chalcogramma*), tubesnout, and YOY pink salmon (*O. gorbuscha*) (Fig. 4.9). Temperature profiles in Favorite Channel followed seasonal patterns similar to other areas in SEAK; mean monthly temperatures were usually lowest in February or March and highest in July or August (Fig. 4.9).

Auke Bay

The Auke Bay study area includes 52.1 km of shoreline between Lena Point and Outer Point on Douglas Island (Fig. 4.10a). The shoreline within Auke Bay is dominated by gently sloping sand and gravel flats (23%), organic sediment (14%), estuaries (16%), and rock ramps with gravel and sand beaches (10%). These beaches are mostly semi-protected-partially mobile (43%), or semi-protected (8%) from wave action with mobile sediments and protected-partially mobile (8%) substrates (Figs. 4.10a,b). Less common shore types within the classification "other" (45%) represent 22 separate classes which are not dominated by one class or a uniquely different class (Fig. 4.10a). Steep rock cliffs and semi-exposed shoreline are mostly absent in this area. The shoreline extent of kelps is dominated by *Fucus* (60%) followed by *Alaria* (12%), and understory kelps (10%); canopy kelps are absent (Fig. 4.10c). Eelgrass is present on about 6% of the shoreline (Fig. 4.10d), and total area of all eelgrass beds in Auke Bay is about 8 ha (Harris et al. In prep). Auke Bay has a history of public, private, and commercial development including a ferry terminal, marina, docks, and housing complexes—about 16% of the shoreline has been subject to man-made alterations (Figs. 4.10a,b).

In the 1970s, most herring spawned in the vicinity of Indian Point, whereas in the 1980s spawning was concentrated near the present day marina (Figs. 4.11a,b). No significant spawning has occurred in Auke Bay since the 1980s (Figs. 4.11c,d). Historical spawning beaches overlap with public, private, and commercial development (Figs. 4.11a,b). In addition, historical spawning locations were near or in eelgrass beds (Figs. 4.10d, 4.11a,b). Loss of eelgrass from development in Auke Bay is unknown. Anecdotal evidence suggests that the size of the eelgrass bed in Auke Nu Cove (Fig. 4.10d) was about 5.7 ha in the early 1980s (USCOE. 1984) compared to 1.9 ha in 2007 (Harris et al. In prep).

Presently, juvenile herring still utilize eelgrass in Auke Bay. Over 800 herring were captured in 11 of 39 beach seine hauls from 1999 to 2007; mean fish size was 42 mm FL (Fig. 4.12) (Nearshore Fish Atlas of Alaska. 2007). Herring may use other habits in Auke Bay but they have not been sampled. In addition to herring, 36 other species were captured in Auke Bay; dominant species included YOY chum and pink salmon, tubesnout, crescent gunnel, and threespine stickleback (*Gasterosteus aculeatus*) (Fig. 4.12). Temperature profiles in Auke Bay

followed seasonal patterns similar to other areas in SEAK; mean monthly temperatures were usually lowest in February or March and highest in July or August (Fig. 4.12).

Tenakee Inlet

The Tenakee Inlet study area includes 116.0 km of shoreline between East Point and Tenakee Springs on the north side of the inlet and between South Passage Point and Saltery Bay on the south side of the inlet (Fig. 4.13a). The shoreline within Tenakee Inlet is dominated by organic sediment (42%) and estuarine habitats (45%). Gently sloping sand and gravel flats (20%) and wide platforms with gravel and sand (11%) are also common shore types. Habitat classifications in addition to dominating estuaries include protected with partially mobile (27%), semi-protected with partially mobile (4%), and semi-protected with mobile substrates (Figs. 4.13a,b). Less common shore types within the classification "other" (27%) represent 20 separate classes which are not dominated by one class or a uniquely different class (Fig. 4.13a). Habitat information is not currently available for the southern shoreline outside Tenakee Inlet, a known spawning area for herring. The shoreline extent of kelps is dominated by Fucus (54%) followed by understory kelps (44%), Alaria (6%), and canopy kelps (1%) (Fig. 4.13c). Eelgrass and surfgrass are present on about 57% and 1% of the shoreline (Fig. 4.13d). Development is minimal in Tenakee Inlet (man-made or modified shoreline is <1% or 526 m) and concentrated near the small community of Tenakee Springs with a population of about 100 people (Fig. 4.13a).

Records of herring spawn in Tenakee Inlet are limited to 1998 and later; most spawning has been on the south side of the inlet. In 1998, 1999, and 2000 most spawning was between Trap Bay and Basket Bay (Figs. 4.14a,b). In 2001, spawning was concentrated from Corner Bay to Saltery Bay (Fig. 4.14b). From 2002 to 2007, spawning occurred along much of the shoreline from Basket Bay to Saltery Bay (Figs. 4.14c,d). Based on the shoreline extent of eelgrass and kelp in Tenakee Inlet, herring likely spawn on both vegetation types.

Herring were not captured in Tenakee Inlet in 20 beach seine hauls from 1998 to 2006 (Fig. 4.15) (Nearshore Fish Atlas of Alaska. 2007). A total of 28 species were captured; dominant species included YOY chum and pink salmon, threespine stickleback, crescent gunnel, and Pacific cod (*Gadus macrocephalus*) (Fig. 4.15). Temperature profiles in Tenakee Inlet (Crab Bay) followed seasonal patterns similar to other areas in SEAK; mean monthly temperatures were usually lowest in February or March and highest in July or August (Fig. 4.15).

Sitka

Northern Sitka Sound

The northern Sitka Sound study area includes 314.2 km of shoreline encompassed by Sinitsin Cove, Kane Island, Lisianski Point, and Mountain Point (Fig. 4.16a). The shoreline within the northern Sitka Sound study area contains organic sediment (22%) and estuarine habitats (22%), narrow sand and gravel beaches (17%), and rock ramps with gravel (9%). Less common shore types within the classification "other" (52%) represent 27 separate classes of which sand and gravel flats or fans and rock cliffs with gravel beaches are prevalent (Fig. 4.16a). Dominate habitats include protected partially mobile (33%), estuaries, semi-protected partially mobile (17%), and protected immobile (7%) substrates (Figs. 4.16a,b). Less common habitat classifications within "other" (21%) are mostly current dominated habitats. The shoreline extent of kelps is dominated by *Fucus* (86%) followed by understory kelps (70%), canopy kelps (17%), and *Alaria* (12%) (Fig. 4.16c). Eelgrass and surfgrass are present on 39% and 1% of the

shoreline (Fig. 4.16d). Shoreline development is sparse in northern Sitka Sound (man-made or modified shoreline is <1% or 780 m) and limited mostly to cabins; ferry and recreational boat traffic can be high, especially in summer with the community of Sitka nearby.

From the 1960s to the 1990s, most spawning occurred on the north end of Partofshikof Island, southern Krestof Island, northern Halleck Island, and in the vicinity of Lisianski Peninsula (Figs. 4.17a,b,c). Since 2000, spawning has been much more extensive, especially in 2005, when almost all of northern Sitka Sound was covered with spawn (Fig. 4.17d). Based on the shoreline extent of eelgrass and kelp in northern Sitka Sound, herring likely spawn on both vegetation types.

Juvenile herring utilize bedrock, eelgrass, and sand-gravel habitats in northern Sitka Sound; herring likely also use kelp but only one kelp site was sampled. Over 5,000 herring were captured in 19 of 53 beach seine hauls from 1998 to 2006; mean fish size was 94.2 mm FL (Fig. 4.18) (Nearshore Fish Atlas of Alaska. 2007). In addition to herring, 45 other species were captured in northern Sitka Sound; dominant species included YOY chum and pink salmon, shiner perch (*Cymatogaster aggregata*), and Pacific sand lance (Fig. 4.18). No thermograph data are available from northern Sitka Sound.

Central Sitka Sound

The central Sitka Sound study area includes 369.3 km of shoreline from Lisianski Point to the vicinity of Redoubt Bay (excludes Silver Bay, Deep Bay, Redoubt Bay) (Fig. 4.19a). The shoreline within central Sitka Sound area has rock ramps with gravel (14%), rock cliffs (13%) and narrow rock ramp (13%) beaches. Less common shore types within the classification "other" (54%) represent 26 separate classes of which steep cliffs with gravel, sand and gravel flats or fans and estuaries are prevalent (Fig. 4.19a). Dominate habitats include semi-protected-partially mobile (29%), protected-partially mobile (15%), semi-protected-immobile (15%), and estuaries (5%) (Figs. 4.19a,b). Less common habitat classifications within "other" (29%) are not dominated by one class or a uniquely different class but semi-exposed habitats are present. The shoreline extent of kelps is dominated by *Fucus* (83%) followed by understory kelps (69%), *Alaria* (38%), and canopy kelps (38%) (Fig. 4.19c). Eelgrass and surfgrass are present on 32% and 11% of the shoreline (Fig. 4.19d). Shoreline development is concentrated around the community of Sitka (man-made or modified shoreline is 7% or 24,082 m). Sitka has a population of about 9,000 people; recreational and commercial boat traffic is high, especially during the summer months and numerous cabins are located on many islands in Sitka Sound.

In the 1960s and 1970s, most spawning occurred from Lisianski Peninsula (including Katlian Bay) and Middle Island south to the community of Sitka and in the vicinity of Eastern Channel (Fig. 4.20a). From the 1980s to the 2000s, spawning occurred throughout central Sitka Sound including Silver Bay and Deep Inlet in 2005 (Figs. 4.20b,c,d). Based on the shoreline extent of eelgrass and kelp in northern Sitka Sound, herring likely spawn on both vegetation types.

Juvenile herring utilize bedrock, eelgrass, kelp, and sand-gravel habitats in central Sitka Sound. Nearly 1,500 herring were captured in 10 of 58 beach seine hauls from 1998 to 2006; mean fish size was 84.6 mm FL (Fig. 4.21) (Nearshore Fish Atlas of Alaska. 2007). In addition to herring, 47 other species were captured in northern Sitka Sound; dominant species included shiner perch, YOY chum and pink salmon, and Pacific sand lance (Fig. 4.21). Temperature profiles from central Sitka Sound (Sandy Cove) followed seasonal patterns similar to other areas

in SEAK; mean monthly temperatures were usually lowest in February or March and highest in August or September (Fig. 4.21).

Southern Sitka Sound

Shore type and habitat class information is not available for southern Sitka Sound. Shoreline extent of kelps and eelgrass is likely very similar to northern and central Sitka Sound. Shoreline development is sparse in southern Sitka Sound; there are a few cabins and recreational boat traffic from the nearby community of Sitka is limited.

In the 1970s and 1990s most spawning was in the vicinity of Redoubt Bay and the Necker Islands (Figs. 4.22a,c). In the 1980s, spawning occurred from Redoubt Bay into West Crawfish Inlet (Fig. 4.22b). Since 2000, spawn has been extensive and in some years continuous throughout all of southern Sitka Sound (Fig. 4.22d).

About 3,000 herring were captured in only 1 of 23 beach seine hauls in southern Sitka Sound from 1998 to 2006; mean fish size was 31.3 mm FL (Fig. 4.23) (Nearshore Fish Atlas of Alaska. 2007). In addition to herring, 35 other species were captured in southern Sitka Sound; dominant species included Pacific cod, bay pipefish (*Syngnathus leptorhynchus*), shiner perch, and juvenile greenling (Hexagrammidae) (Fig. 4.23). No thermograph data is available from southern Sitka Sound.

Craig

The Craig study area includes 426.1 km of shoreline from Blanquizal Island to Craig (Fig. 4.24). Only shore type information is currently available for this area. The shoreline within the Craig area has organic sediment (19%) associated with estuaries, sand and gravel flats (17%), and rock ramps with gravel and sand (16%) beaches (Fig. 4.24). Less common shore types within the classification "other" (47%) represent 19 separate classes of which narrow sand and gravel beaches are prevalent including rock platforms with sand and gravel and rock ramps with gravel. Although not assessed, kelps and eelgrass are common habitat types in the Craig area (Murphy et al. 2000). Shoreline development is concentrated near the community (manmade or modified shoreline is 1% or 3,701 m); Craig has a population of about 1,400 people.

In the 1970s, spawning was concentrated on the western side of Wadleigh and Fish Egg Islands only (Fig. 4.25a) and in the 1980s expanded to include San Christoval Channel and San Fernando Island (Fig. 4.25b). Spawning has been relatively consistent since the 1990s in the vicinity of Wadleigh Island, Fish Egg Island, San Fernando Island, and San Juan Bautista Island (Figs. 4.25c,d).

Juvenile herring utilize eelgrass, kelp, and sand-gravel habitats near Craig. Nearly 9,000 herring were captured in 15 of 76 beach seine hauls from 1998 to 1999; mean fish size was 43.8 mm FL (Fig. 4.26) (Nearshore Fish Atlas of Alaska. 2007). In addition to herring, 45 other species were captured; dominant species included YOY pink salmon, Pacific sand lance, bay pipefish, threespine stickleback, and crescent gunnel (Fig. 4.26). No thermograph data is available from Craig.

Duke Island

The Duke Island study area includes 163.4 km of shoreline from Ryus Bay to Duke Point (includes Mary Island) (Fig. 4.27a). The shoreline within the Duke Island area contains organic sediment (27%) and estuarine habitats (21%), sand and gravel flats (14%), and wide platforms with gravel and sand beaches (12%). Less common shore types within the classification "other"

(47%) represent 16 separate classes of which wide platforms and ramps with gravel beaches are prevalent in the more exposed areas (Fig. 4.27a). Dominant habitats include semi-protected, partially mobile (56%), estuaries (21%), protected, partially mobile (16%) and semi-exposed, partially mobile (3%) beaches (Figs. 4.27a,b). The shoreline extent of kelps is dominated by *Fucus* (92%) followed by understory kelps (81%), canopy kelps (28%), and *Alaria* (23%) (Fig. 4.27c). Eelgrass and surfgrass are present on 32% and 3% of the shoreline (Fig. 4.27d). Shoreline development is absent in the vicinity of Duke Island (man-made or modified shoreline is 0%).

In the 1970s and 1980s, spawning was very sparse and limited to the eastern shore of Annette Island near Crab Bay (Figs. 4.28a,b). In the 1990s, spawning was extensive and included the eastern shore of Annette Island, Mary Island, Cat Island, and northern Duke Island (Fig. 4.28c). Since 2000, spawning has been sparse and limited mainly to Annette Island and Mary Island (Fig. 4.28d). Based on the shoreline extent of eelgrass and kelp near Duke Island, herring likely spawn on both vegetation types.

Herring were not captured in the Duke Island area; sampling was limited, however, to only three beach seine hauls in 2007 (Fig. 4.29) (Nearshore Fish Atlas of Alaska. 2007). A total of 28 species were captured; dominant species included YOY chum and pink salmon, crescent gunnel, English sole (*Parophrys vetulus*), and juvenile flatfish (Fig. 4.29). No thermograph data is available from Duke Island.

Kah Shakes Cove

The Kah Shakes Cove study area includes 68.3 km of shoreline from near Black Island to Foggy Point (excludes Boca de Quadra) (Fig. 4.30). Only shore type information is currently available for this area. The shoreline within the Kah Shakes Cove area has wide platforms with gravel and sand (22%) beaches, sand and gravel flats (21%), and beaches with organic sediment (11%) associated with estuarine habitats (Fig. 4.30). Less common shore types within the classification "other" (46%) represent 18 separate classes of which wide platforms and ramps with gravel beaches are prevalent in the more exposed areas. Shoreline development is absent in the vicinity of Kah Shakes Cove (man-made or modified shoreline is 0%).

From the late 1970s through the 1990s, spawning was concentrated on either side of the entrance of Boca de Quadra north to Black Island and south to Foggy Bay (Figs. 4.31a,b,c). Since 2000, spawning has been sparse and limited from Boca de Quadra south to Foggy Bay (Fig. 4.31d). No spawning information is available after 2003.

Only six herring were captured in the Kah Shakes Cove area; sampling was limited, however, to only four beach seine hauls in 2007 (Fig. 4.32) (Nearshore Fish Atlas of Alaska. 2007). In addition to herring, 20 other species were captured; dominant species included shiner perch, YOY pink salmon, kelp perch (*Brachyistius frenatus*), bay pipefish, and copper rockfish (*Sebastes caurinus*) (Fig. 4.32). No thermograph data is available from Kah Shakes Cove.

Sea surface temperature and climate

Solar energy input drives global temperatures and because the greatest net radiative gain is at the equator, a general temperature gradient is established from equatorial to polar regions. Sea surface temperatures are correlated with air temperatures [e.g., (Rounsefell and Dahlgren 1932)], explaining general sea surface temperature patterns Fig. 4.33. Southeast Alaska stretches about 860 km along the eastern Pacific in a primarily north-south orientation, thus a general sea surface temperature gradient is expected through the region, consistent with observation. Marine

waters of SEAK are characterized by an inshore-offshore salinity gradient and a north-south temperature gradient (Quast 1968; Murphy and Orsi 1999). Inside waters are more estuarine, more protected from wave action, and have more extreme seasonal fluctuations in temperature and salinity than outside waters (Pickard 1967; Pickard and Emery 1982; Rosenthal et al. 1982). Sea surface temperatures measured by infrared or microwave radiometry by satellites (Wentz et al. 2000) support these observations and suggest that a north-south thermal gradient is typical in SEAK and that inside waters may be cooler than outside waters at corresponding latitudes (Fig. 4.34).

Marine Zoogeographic Provinces

Distribution patterns of fauna in the northeastern Pacific and Bering Sea can be described in terms of zoogeographic provinces (Briggs 1974). Each province represents a distinct set of environmental conditions and species that have lived together during recent evolutionary history (Allen and Smith 1988). The coastal region from Puget Sound to Sitka, Alaska is considered a transition zone and is classified as either one of two provinces; Aleutian or Oregonian by some (Briggs 1974). The southern boundary of the Oregonian Province is generally recognized as Point Conception, California, and the northern boundary of the Aleutian Province is similarly recognized as either Nunivak or the Aleutian Islands (Allen and Smith 1988). Briggs (1974) placed the boundary between the Oregonian and Aleutian Provinces at Dixon Entrance in southern Southeast Alaska, based on the well-studied distribution of mollusks, but indicated that distributions of fishes, echinoderms, and algae gave evidence for placement of this boundary in the vicinity of Sitka, Alaska. Peden and Wilson (1976) investigated the distributions of inshore fishes in British Columbia and found Dixon Entrance to be of minor importance as a barrier to fish distribution. A more likely boundary between these faunas may occur near either Sitka, Alaska, or Cape Flattery, Washington (Peden and Wilson 1976; Allen and Smith 1988).

ShoreZone mapping has identified geographic bioareas with unique indicator and associated species in Alaska. For example, SEAK can be divided into four bioareas based on differences in bioband occurrence, species composition within biobands, and geographic boundaries (Fig. 4.35). Additional bioareas will develop as further ShoreZone mapping of SEAK is completed. Briefly, the Yakutat Bioarea (SEYA) is characterized by sparse biota, high wave exposure, and few canopy kelps. The Icy Strait Bioarea (SEIC) is the only area with significant amounts of the dragon kelp bioband (Alaria fistulosa). The Lynn Canal Bioarea (SEFJ) has milky, glacial-fed inlets, many with coralline reds in the red algae bioband, especially in areas with semi-protected exposures. The Sitka Bioarea (SESI) has fully marine waters with a wide range of wave exposures and a lush mixture of canopy kelps, particularly the giant kelp bioband (Macrocystis integrifolia).

An alternative marine ecoregion proposal (Piatt and Springer 2007) divides SEAK into northern and southern zones (Fig. 4.36); these correspond almost exactly with the two divisions suggested by the spawn timing of Pacific herring (Fig. 3.15). Divisions among marine ecoregions were based on biological indicators, topographic, bathymetric, and oceanographic features such as persistent fronts. The relationship between marine ecoregions and the preliminary and incomplete *Shorezone* bioareas is unclear; at present the *Shorezone* approach will result in a greater number of divisions. Both schemes are subject to modification and perhaps ultimately both schemes will be used to inform the other or be merged.

Distinct distribution patterns are evident for some fauna and flora in SEAK. For example, black rockfish (*S. melanops*) and shiner perch are absent in northern inside waters near

Juneau, but are relatively common in inside and outside waters south of Sitka, Alaska (Johnson 2003). Similarly, the Juneau area is more strongly dominated if not richer in both arcticamphiboreal and western North Pacific taxa of marine algae than near Sitka—cooler waters near Juneau than on the outer coast of the Alaska Panhandle may partially explain differences in distribution patterns of some marine algae (Lindstrom et al. 1986).

Summary

From a habitat perspective, *ShoreZone* mapping, historical spawning records, and nearshore fish sampling reveal no obvious pattern in habitat use by herring—adult and juvenile herring use a wide range of geographical areas (inside and outside waters), habitat types, beach exposures, temperatures, salinities, and vegetation types.

ShoreZone mapping revealed similarities and differences in habitat between Lynn Canal and other areas. For example, organic sediment and semi-protected, partially mobile substrate are the most common shore type and habitat class among all areas, whereas the percent shoreline extent of kelps (canopy and understory) and eelgrass is less in Lynn Canal than in all other areas (Table 4.4). These results are not surprising given differences in topography, oceanography, wave exposure, and glacial influence among areas. For example, turbid effluent from glacial rivers may partially explain the absence or near absence of eelgrass in some bays and inlets on or near the mainland (McRoy 1968). Nearshore, vegetated habitats are available to herring in Lynn Canal, however, and lack of vegetation does not seem to be a factor in limiting fish from spawning, especially in historical spawning areas such as Favorite Channel and north of Berners Bay.

Physical habitat parameters such as temperature and salinity can also play an important role for all life stages of herring. Spawn distribution and juvenile catch data in SEAK show that herring utilize a wide range of sea surface temperatures (SST) and salinities. Marine waters of SEAK are characterized by an inshore-offshore salinity gradient and a north-south temperature gradient (Quast 1968; Murphy and Orsi 1999). Inside waters are more estuarine, more protected from wave action, and have more extreme seasonal fluctuations in temperature and salinity than outside waters (Pickard 1967; Pickard and Emery 1982; Rosenthal et al. 1982). Observed patterns in SST in Lynn Canal (Berners Bay) (Fig. 4.6) were similar to observations in earlier years (NMFS. 1974) and similar to observations at other areas—maximum and minimum temperatures usually reach about 12°C to 14°C in August or September and 3°C to 5°C in February or March. Thus, changes in SST are probably not a reason why herring declined in Lynn Canal.

The possibility that human shoreline development has caused the Lynn Canal herring population to decline has been suggested but the evidence does not support this hypothesis. The decline in the Lynn Canal herring population occurred slowly from 1950 to 1980 prior to most major development projects, somewhat more rapidly from 1980 to 1990, and has remained relatively low and stable the last 25 years (Fig. 4.4). Development has long been considered a factor in the decline of Lynn Canal herring, particularly from loss of habitat in Auke Bay. Auke Bay has the highest percentage (16%) of human altered shoreline of any area (Table 4.4). Loss of habitat from development, however, does not explain fluctuations of the herring population in Tenakee Inlet; shoreline development in this area is minimal to nonexistent (Table 4.4). In addition, central Sitka Sound supports a robust herring population even with the second highest percentage (7%) of man-made alteration of shoreline. Decline of herring spawning in Auke Bay also does not account for the near absence of spawning in nearby Favorite Channel; herring used

to spawn extensively along the eastern shore of Favorite Channel until 1990 and the shoreline has remained relatively undisturbed.

Nearshore fish sampling showed that two to three fish species comprised the majority of the total catch at all areas. Herring were captured in all areas except Tenakee Inlet and Duke Island; juvenile herring were probably present in these two areas but not captured due to limited sampling. In areas where herring were captured, herring comprised from 1% (Kah Shakes Cove) to 70% (southern Sitka Sound) of the total catch. In Lynn Canal, herring comprised from 5% (Auke Bay) to 36% (Berners Bay) of the total catch. The spatially large and consistent capture of mostly age-0 herring in shallow water habitats of SEAK provides evidence of the importance of the nearshore as juvenile habitat. Some of the other abundant fish species captured with herring were YOY chum and pink salmon, tubesnouts, and crescent gunnels. Herring larvae and juveniles are eaten by many fish species, but no unusual or large fish predator populations were observed in any nearshore area.

Eelgrass meadows, kelp communities, sand-gravel beaches, and bedrock outcrops comprise a continuum of habitat types available to herring throughout SEAK (Johnson et al. 2005; Nearshore Fish Atlas of Alaska. 2007). The shoreline extent of some of these habitat types may be less in Lynn Canal than in other areas, but herring continue to spawn in Berners Bay and juveniles continue to utilize nearshore habitats in Auke Bay, Favorite Channel, and Berners Bay. With some habitat types such as eelgrass comprising only about 3% of 235 km of shoreline surveyed from Auke Bay to Berners Bay (Harris et al. In prep) and spawning limited mostly to Berners Bay (e.g., Cascade Point), habitat protection should be a management priority for the preservation of Lynn Canal herring.

References

- Alaska Department of Fish and Game. 2007. Juneau herring season summary for 2007. http://documents.cf1.adfg.state.ak.us/AdfgDocument.po?DOCUMENT=11379.
- Allen, J. M. and G. B. Smith 1988. Atlas and zoogeography of common fishes in the Bering Sea and northeastern Pacific. NOAA Technical Report, National Oceanic and Atmospheric Administration, National Marine Fisheries Service: 1-151.
- Briggs, J. C. 1974. Marine zoogeography. New York, NY, McGraw-Hill Book Company.
- Brown, E. D. and M. G. Carls 1998. Pacific herring (*Clupea pallasi*). Rest Notebook, EVOSTC: 1-8.
- Carlson, H. R. 1980. Seasonal distribution and environment of Pacific herring near Auke Bay, Lynn Canal, southeastern Alaska. Trans Am Fish Soc 109(1): 71-78.
- Davidson, W., D. Gordon, K. Monagle and D. Harris 2005. Northern southeast Alaska herring spawn-on-kelp pound fishery, 2005. Fishery Management Report No. 05-11, Alaska Department of Fish and Game: 29.
- Emmett, R. L., S. L. Stone, S. A. Hinton and M. E. Monaco 1991. Distribution and abundance of fishes and invertebrates in West Coast estuaries, Volume II: species life history summaries. ELMR. Rockville, MD, NOAA/NOS SEA Division: 329.
- Harney, J. N., M. Morris and J. R. Harper 2007. ShoreZone coastal habitat mapping protocol for the Gulf of Alaska. Sidney, BC., Coastal & Ocean Resources, Inc.
- Harris, P. M., S. W. Johnson, L. G. Holland, A. D. Neff, J. F. Thedinga and S. D. Rice 2005. Hydrocarbons and fisheries habitat in Berners Bay, Alaska: baseline monitoring

- associated with the Kensington Gold Mine, U.S. Department of Commerce. AFSC Processed Report 2005-06: 1-44.
- Harris, P. M., A. D. Neff, S. W. Johnson and J. F. Thedinga In prep. Eelgrass habitat and faunal assemblages in the City and Borough of Juneau, Alaska, U.S. Department of Commerce, AFSC Report.
- Herbert, K. and D. Carlile 2002. Southeast Alaska/Yakutat annual herring research report, 2000/2001 season. Alaska Fish Game Regional Information Report No. IJ02-36: 1-146.
- Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe. Rapp P-V Reun Cons Int Explor Mer 20: 1-228.
- Howes, D. E., J. R. Harper and E. H. Owens 1994. Physical shore-zone mapping system for British Columbia. Victoria, BC, BC Ministry of Environment, Lands and Parks: 71.
- Johnson, S. M., ML; Csepp, DJ; Harris, PM; Thedinga, JF 2003. Survey of fish assemblages in eelgrass and kelp habitats of southeastern Alaska U.S. Department of Commerce, NOAA Technical Memorandum NMFS AFSC-139: 1-50.
- Johnson, S. W. and J. M. Lorenz Unpublished data, NOAA Fisheries, Auke Bay Laboratory.
- Johnson, S. W., A. D. Neff and J. F. Thedinga 2005. An atlas on the distribution and habitat of common fishes in shallow nearshore waters of southeastern Alaska, U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-157: 1-89.
- Johnson, S. W. and J. F. Thedinga 2005. Fish use and size of eelgrass meadows in southeastern Alaska: a baseline for long-term assessment of biotic change. Northwest Sci 79: 141-155.
- Jones, J. D. 1978. Growth of larval Pacific herring in Auke Bay, Alaska in 1975 and 1976. Juneau, AK, University of Alaska, Juneau. Masters: 23.
- Lassuy, D. M., D 1989. Species profiles. Life histories and environmental requirements of coastal fishes and invertebrates (Pacific Northwest). Pacific herring US Fish Wildl. Serv. Biol. Rep. 82(11.126); US Army Corps of Engineers TR-EL-82-4: 1-18.
- Leon, H. 1993. Stock discreteness of Pacific herring (*Clupea harengus pallasi*) in southeast Alaska. Seattle, WA, University of Washington. Master of Science: 128.
- Lindstrom, S. C., N. I. Calvin and J. R. Ellis 1986. Benthic marine algae of the Juneau, Alaska area. Contrib Nat Sci 6: 1-10.
- McGurk, M. D. 1984. Effects of delayed feeding and temperature on the age of irreversible starvation and on the rates of growth and mortality of Pacific herring larvae. Mar Biol 84(1): 13-26.
- McRoy, C. P. 1968. The distribution and biogeography of *Zostera marina* (eelgrass) in Alaska. Pac Sci 22: 507-513.
- Murphy, J. M. and J. A. Orsi 1999. Physical oceanographic observations collected aboard the NOAA ship John C. Cobb in the northern region of southeastern Alaska, 1997 and 1998, U.S. Dept of Commerce. NMFS-AFSC Proc. Rep. 99-02: 239.
- Murphy, M. L., S. W. Johnson and D. J. Csepp 2000. A comparison of fish assemblages in eelgrass and adjacent subtidal habitats near Craig, Alaska. AK Fish Res Bull 7: 11-21.
- Nearshore Fish Atlas of Alaska. 2007. http://www.fakr.noaa.gov/habitat/fishatlas/ National Oceanics and Atmospheric Administration, National Marine Fisheries Service.
- NMFS. 1974. Lynn Canal: a resource assessment. Juneau, AK, U.S. Department of Commerce, NMFS. Prepared for the Alaska Power Administration: 172.
- Norcross, B. L., E. D. Brown, R. J. Foy, M. Frandsen, S. M. Gay, T. C. Kline, D. M. Mason, E. V. Patrick, A. J. Paul and K. D. E. Stokesbury 2001. A synthesis of the life history and

- ecology of juvenile Pacific herring in Prince William Sound, Alaska. Fish Oceanogr 10: 42-57.
- Paul, A. J., J. M. Paul and E. D. Brown 1998. Fall and spring somatic energy content for Alaskan Pacific herring (*Clupea pallasi Valenciennes* 1847) relative to age, size and sex. J Exp Mar Biol Ecol 223(1): 133-142.
- Peden, A. E. and D. E. Wilson 1976. Distribution of intertidal and subtidal fishes of northern British Columbia and southeastern Alaska. Syesis 9: 221-248.
- Piatt, J. F. and A. M. Springer 2007. Marine ecoregions of Alaska. Long-term ecological change in the northern Gulf of Alaska. R. B. Spies. Amsterdam, Elsevier: 522-526.
- Pickard, G. L. 1967. Some oceanographic characteristics of the larger inlets of southeast Alaska. J Fish Res Bd Can 24: 1475-1506.
- Pickard, G. L. and W. J. Emery 1982. Descriptive physical oceanography: an introduction. New York, NY, Pergamon Press.
- Pritchett, M. 2006. Historic spawn herring database. Alaska Department of Fish and Game, Juneau, AK.
- Quast, J. C. 1968. New records of thirteen Cottoid and Blennoid fishes for southeast Alaska. Pac Sci 22: 482-487.
- Rosenthal, R. J., L. Haldorson, L. J. Field, V. M. O'Connell, M. G. LaRiviere, J. Underwood and M. C. Murphy 1982. Inshore and shallow offshore bottomfish resources in the southeastern Gulf of Alaska 1981-82. Alaska Coastal Research. Sitka, AK: 1-166.
- Rounsefell, G. A. and E. H. Dahlgren 1932. Fluctuations in the supply of herring, *Clupea pallasii*, in Prince William Sound, Alaska. Bull US Bureau Fish XLVII: 263-291.
- Tanasichuk, R. W., A. H. Kristofferson and D. V. Gillman 1993. Comparison of some life history characteristics of Pacific herring (*Clupea pallasi*) from the Canadian Pacific Ocean and Beaufort Sea. Can J Fish Aquat Sci 50(5): 964-971.
- Thedinga, J. F., S. W. Johnson and D. J. Csepp 2006. Nearshore fish assemblages in the vicinity of two Steller sea lion haulouts in southeastern Alaska. Sea lions of the world. A. W. Trites, S. K. Atkinson, D. P. DeMaster, L. W. Fritz, T. S. Gelatt, L. D. Rea and K. M. Wynne. Fairbanks, AK, University of Alaska, Fairbanks: 269-284.
- USCOE. 1984. Juneau, Alaska boat harbor improvements, final detailed project report and environmental impact statement. U.S. Army Engineer District, Alaska, ATTN: Records Manager, PO Box 6898, Elmendorf Airforce Bace, US Army Corps of Engineers (Alaska District). 1-85.
- USDA 2004. Kensington gold project, draft supplemental environmental impact statement, Vol. 1 of 2, U.S. Department of Agriculture, Forest Service.
- Wentz, F. J., C. Gentemann, D. Smith and D. Chelton 2000. Satellite measurements of sea surface temperature through clouds. Science 288(5467): 847-850.
- Williams, G. D., L. K. O'Rourke and W. H. Pearson 2004. Reconnaissance evaluation of ecological effects to forage fish populations associated with Juneau access improvements project. Sequim, WA, Battelle Marine Sciences Laboratory, PNWD-3419: 50.
- Wing, B. L., M. M. Masuda and S. G. Taylor 2006. Time series analyses of physical environmental data records from Auke Bay, Alaska, U.S. Department of Commerce, NOAA Technical Memorandum NMFS-AFSC-166: 75.

 Table 4.1. Classification of shore types (based on ShoreZone protocol).

SUBSTRATE	SEDIMENT	WIDTH	SLOPE	COASTAL CLASS	NO.
			STEEP (>20°)		
		WIDE (>30 m)	INCLINED (5-20°)		
ROCK	N/A		FLAT (<5°)	Rock Platform, wide	2
			STEEP (>20°)	Rock Cliff	3
		NARROW (<30 m)	INCLINED (5-20°)	Rock Ramp, narrow	4
			FLAT(<5°)	Rock Platform, narrow	5
	İ	İ	STEEP (>20°)	n/a	
		WIDE (>30 m)	INCLINED (5-20°)	Ramp with gravel beach, wide	6
	GRAVEL	,	FLAT (<5°)	Platform with gravel beach, wide	7
		NARROW (<30 m)	STEEP (>20°)	Cliff with gravel beach	8
			INCLINED (5-20°)	Ramp with gravel beach	9
			FLAT (<5°)	Platform with gravel beach	10
			STEEP (>20°)	n/a	
		WIDE (>30 m)	INCLINED (5-20°)	Ramp w gravel & sand beach, wide	11
ROCK &	SAND &	()	FLAT (<5°)	Platform with G&S beach, wide	12
SEDIMENT	GRAVEL		STEEP (>20°)	Cliff with gravel/sand beach	13
	3.0.022	NARROW (<30 m)	INCLINED (5-20°)	Ramp with gravel/sand beach	14
			FLAT (<5°)	Platform with gravel/sand beach	15
			STEEP (>20°)	n/a	+ **
		WIDE (>30 m)	INCLINED (5-20°)	Ramp with sand beach, wide	16
	SAND	WIDE (COM)	FLAT (<5°)	Platform with sand beach, wide	17
	SAND		STEEP (>20°)	Cliff with sand beach	18
		NARROW (<30 m)	INCLINED (5-20°)	Ramp with sand beach, narrow	19
			FLAT (<5°)	Platform with sand beach, narrow	20
	1	WIDE (>30 m)	FLAT (<5°)	Gravel flat, wide	21
	GRAVEL	WIDE (20 III)	STEEP (>20°)	n/a	- 21
	GRAVEL	NARROW (<30 m)	INCLINED (5-20°)	Gravel beach, narrow	22
		IVARRICOVI (SOUII)	FLAT (<5°)	Gravel flat or fan	23
		WIDE (>30 m)	STEEP (>20°)	n/a	- 25
	SAND		INCLINED (5-20°)	n/a	+-
SEDIMENT	&		FLAT (<5°)	Sand & gravel flat or fan	24
	GRAVEL		STEEP >20°)	n/a	- 24
	GRAVEL	NADDOM/<20 m)	INCLINED (5-20°)	10.0	25
		NARROW (<30 m)		Sand & gravel beach, narrow	26
		 	FLAT (<5°)	Sand & gravel flat or fan	20
	SAND / MUD	WIDE (>30m)	STEEP (>20°)	n/a Sand beach	+
			INCLINED (5-20°)	100 to 10	27
			FLAT (<5°)	Sand flat	28
			FLAT (<5°)	Mudflat	29
		NARROW (<30m)	STEEP (>20°)	n/a	
			INCLINED (5-20°)	Sand beach	30
	00000000	Total II	FLAT (<5°)	n/a	n/a
	ORGANICS	n/a	n/a	Estuaries	31
ANTHRO-	Man-made	n/a	n/a	Man-made, permeable	32
POGENIC			n/a	Man-made, impermeable	33
CHANNEL	Current	n/a	n/a	Channel	34
GLACIER	lce	n/a	n/a	Glacier	35

 Table 4.2. Habitat classification, based on ShoreZone protocol.

					Bic	logical Ex	Biological Exposure Category	gorv	
Structuring	Substrate	Coastal Type	Description	Very	Exposed	Semi- exnosed	Semi- nrotected	Protected	Very
Process				VE	E	SE	SP	Р	VP
	I.m. o. k.T.	Rock or	The epibiota in the immobile mobility categories is influenced by the wave exposure at the site. In high wave exposures, only considered the constitution of the const	10	20	30	40	50	09
	ттторие	or Sediment	solid oberack, stolerines with the classified as Imminotite. At the solid oberack, stolerines with the classified as Imminotite. At the lust exposures, even pebble/cobble beaches may show lust epibola, indicating an immobile Habitat Class.	$^{ m VE}_{-1}$	E_I	SE_I	SP_I	P_I	$^{\mathrm{VP}_{-\mathrm{I}}}$
			These units describe the combination of sediment mobility observed. That is, a sediment beach that is bare in the upper half of the intertidal with biobands occurring on the lower beach						
Wave Energy	Partially-	Rock & Sediment	would be classed as 'partially mobile'. This pattern is seen at moderate wave exposures.	11 1	21	31	41	51	61
3	mobile	or Sediment	Units with immobile bedrock outcrops interningled with bare mobile sediment beaches, as can be seen at higher wave exposures, could also be classified as 'partially mobile'.	VE_P	ਸ਼ ਮ	N A A	42 -	4	۲ م م
			These categories are intended to show the 'bare sediment beaches', where no epibenthic macrobiota are observed. Very	12	22	33	42	52	69
	Mobile	Sediment	fine sediment may be mobile even at the lowest wave exposures, while at the highest wave exposures, large-sized boulders will be mobile and bare of epibiota.	VE_M	E_{M}	SE_M	SP_M	$_{\rm M}^{\rm 2}$	VP_M
Fluvial/Estuarine		E	Units classified as the 'estuary' types always include wetland biobands in the upper intertidal, are always associated with a	13	23	33	43	53	63
Processes		Емату мешана	freshwater stream or river and often show a delta form. Estuary units are usually in lower wave exposure categories.	VE_E	E_E	SE_E	SP_E	$P_{-}E$	VP_E
Superior of Superior C		Current-	Species assemblages observed in salt-water channels are structured by current energy rather than by wave energy.	14	24	34	44	54	64
Current energy		channel	Current-dominated sites are limited in distribution and are rare habitats.	VE_C	E_C	SE_C	SP_C	P_C	VP_C
(7 Jania) managagas		Clanion	In a few places in coastal Alaska, saltwater glaciers form the intertial bakiter. These Habiter Classes are rore and include a	15	25	35	45	55	65
caecaooid renorm		Cuerce	small percentage of the shorline length.	VE_G	E_G	SE_G	SP_G	P_G	VP_G
		Anthropogenic –	Impermeable man-made Habitats are intended to specifically	16	26	36	46	56	99
Man-modified		Impermeable	note units classified as Coastal Class 33.	VE_X	E_X	SE_X	SP_X	P_X	VP_X
		Anthropogenic – Permeable	Permeable man-made Habitats are intended to specifically note shore units classified as Coastal Class 32.	17 VE Y	27 E Y	37 SE Y	47 SP Y	57 P Y	67 VP Y
-			Units classified as Lagoons in the Secondary Habitat Class contain activity or salty water that is contained within a basin	18	28	38	48	58	89
Lagoon		Lagoon	ura nas innited or amage. They are often associated with wellands and may include wetland biobands in the upper intertical.	VE_L	E_L	SE_L	SP_L	P_L	$^{-}$ NP $^{-}$ L

Table 4.3. Total number of beach seine hauls, total fish catch (all spp.), total herring catch, and mean temperature and salinity (practical salinity scale) ranges at several areas throughout SEAK from 1998 to 2007 (Johnson and Lorenz). Asterisk denotes herring study areas discussed in detail in this report.

		Total	catch		
	•		_	Mean	
Area				Temperature	Mean salinity
	No. hauls	All spp.	Herring	°C	(PSS)
Berners Bay*	54	24,339	8,804	8.3 - 12.8	16.9 - 18.3
Favorite Channel*	95	16,891	4,638	4.0 - 12.4	17.6 - 32.6
Auke Bay*	39	16,625	873	6.9 - 12.7	11.3 - 30.8
Sweetheart Creek	2	4,074	3,910	9.9 - 10.8	6.8 - 7.7
Farragut Bay	1	374	246	9.2	11.7
Flat Cove	2	5,412	5,358	13.8	33.6
Sitka Sound north*	53	31,098	5,145	6.5 - 13.3	22.4 - 31.0
Sitka Sound central*	58	23,722	1,472	6.3 - 13.7	19.7 - 33.0
Sitka Sound south*	23	4,370	3,050	14.2	23.7
Hamilton Bay	4	24,128	23,804	14.4 - 16.9	29.9 - 30.6
Dakaneek Bay	2	6,493	4,400	12.7 - 14.8	31.2 - 31.3
Craig*	76	28,952	651	9.7 - 12.5	25.4 - 27.5
Kah Shakes Cove*	1	509	6	13.6	19.3
Total	410	186,987	62,356		

Table 4.4. Summary of major *ShoreZone* habitat classifications found within the BRT study areas. Percentages relate to Figs. 4.3 to 4.30.

т.50.	Berners	Favorite	Auke		Northern	Central	Southern			Kah
	Bay	Channel	Bay	Tenakee	Sitka	Sitka	Sitka	Craig	Duke Is.	Shakes
Total Shoreline (km)	89.3	60.7	52.1	116.0	314.2	369.3	NA	426.1	163.4	68.3
Shore Type										
manmade	0%	0%	8%	0%	0%	6%	NA	1%	0%	0%
other	40%	60%	45%	27%	52%	54%	NA	47%	47%	46%
organic sediment	27%		14%	42%	68%		NA	19%	27%	11%
wide platform with gravel	19%	9%					NA			
sand and gravel flat	14%	10%	23%	20%			NA	17%	14%	21%
ramp with gravel beach		21%			9%	14%	NA			
ramp with gravel and sand wide platform with gravel and			10%				NA	16%		
sand				11%			NA		12%	22%
narrow sand and gravel					17%		NA			
rock cliff						13%	NA			
narrow rock ramp						13%	NA			
Habitat Class										
manmade	0%	1%	16%	0%	0%	7%	NA	NA	0%	NA
other	8%	6%	9%	7%	21%	29%	NA	NA	4%	NA
Semi-exposed partially mobile									3%	NA
Semi-protected partially mobile	37%	53%	43%	17%	17%	29%	NA	NA	56%	NA
semi-protected mobile			8%	4%			NA	NA		NA
semi-protected immobile	10%	8%				15%	NA	NA		NA
protected partially mobile	16%	13%	8%	7%	33%	15%	NA	NA	16%	NA
protected immobile					7%		NA	NA		NA
estuary	29%	19%	16%	45%	22%	5%	NA	NA	21%	NA
Kelps										
Canopy kelps	5%	0%	0%	10%	17%	38%	NA	NA	28%	NA
Understory kelps	14%	26%	11%	44%	70%	69%	NA	NA	81%	NA
Alaria (intertidal)	34%	27%	13%	6%	12%	38%	NA	NA	23%	NA
Fucus	57%	57%	64%	54%	86%	83%	NA	NA	92%	NA
Seagrasses										
Eelgrass	6%	2%	6%	57%	39%	32%	NA	NA	32%	NA
surfgrass	0%	0%	0%	1%	1%	11%	NA	NA	3%	NA

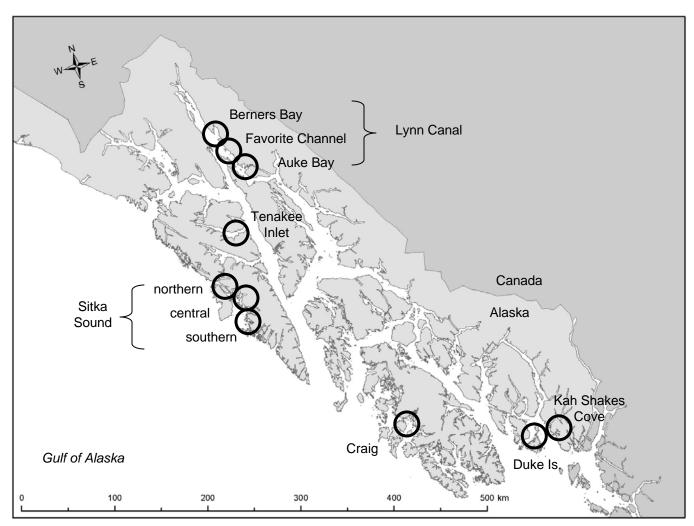


Figure 4.1. Ten study areas for herring in SEAK identified by the Lynn Canal herring Biological Review Team (BRT).

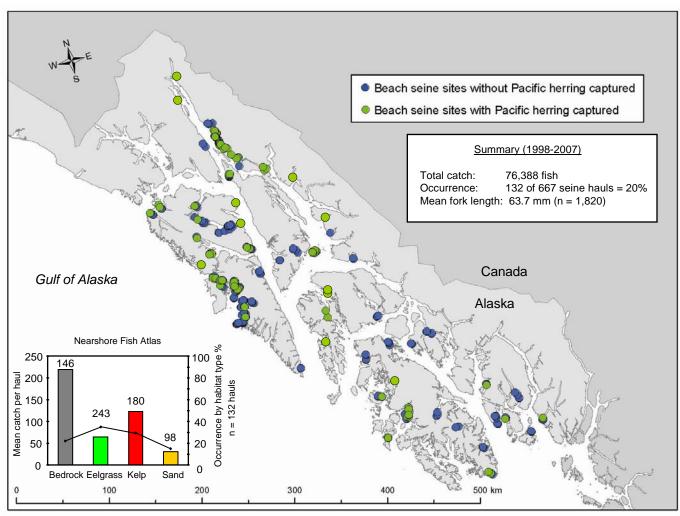


Figure 4.2. Locations of beach seine sites sampled for herring in SEAK from 1982 to 2007; summary data (1998-2007) and bar graph from Nearshore Fish Atlas of Alaska (2007). Numbers above bars are number of seine hauls. Other data sources are Orsi and Landingham (1985), and J. M. Lorenz, NOAA Fisheries, ABL, Juneau, AK unpublished data.

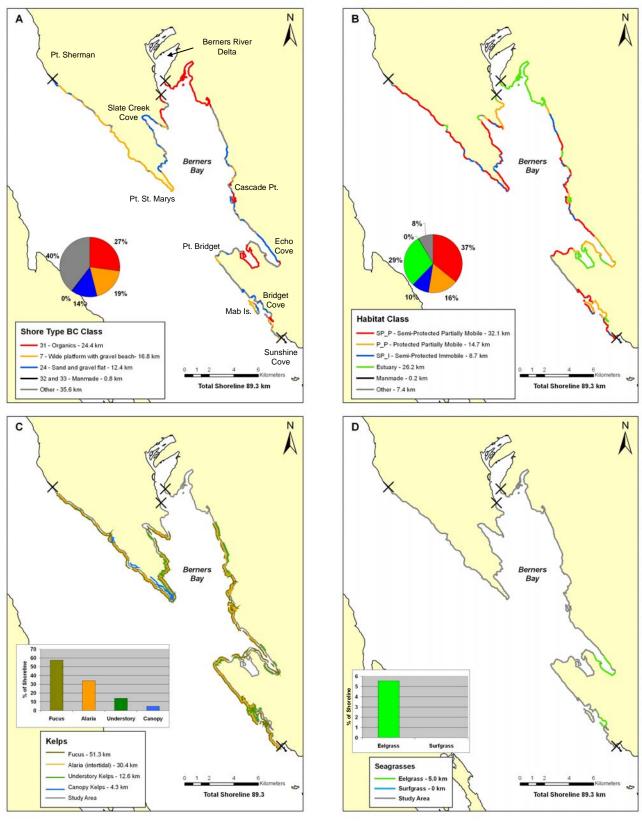


Figure 4.3. Berners Bay: *ShoreZone* coastal habitat maps. Proportions of dominant habitat classes are delineated in four panels - panel A (Shore Type), panel B (Habitat Class), panel C (kelps), and panel D (seagrasses). For definitions of *ShoreZone* habitat classifications see Appendix A.

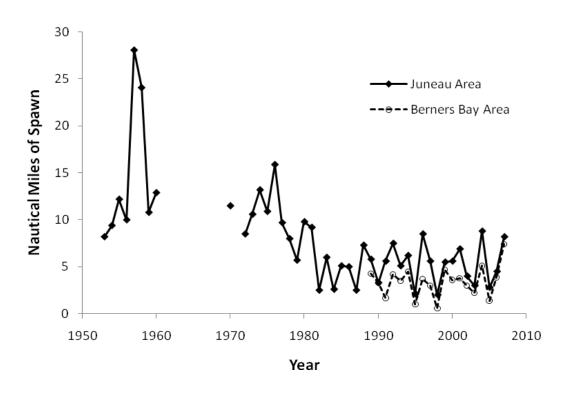


Figure 4.4. Shoreline kilometers of herring spawn in Lynn Canal from 1951 to 2007 (Pritchett 2007).

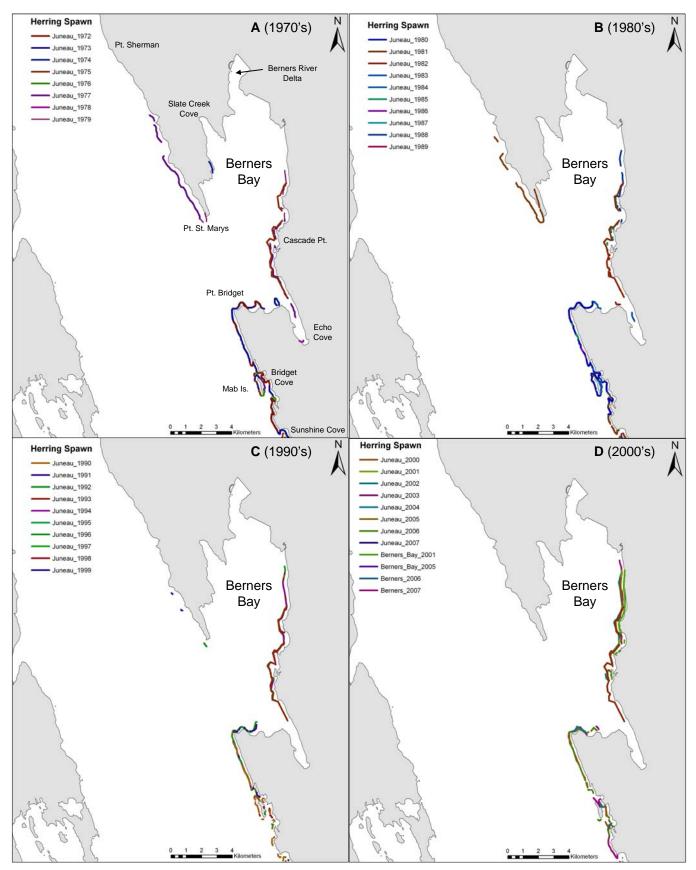


Figure 4.5. Berners Bay: ADFG records of herring spawn (Pritchett 2007). Panel A shows spawn records for 1970's, panel B for 1980's, panel C for 1990's, and panel D for 2000–2007. Some panels may not have spawn records for each year in a given decade. Refer to each panel's legend for color coded, annual spawn records.

4.22

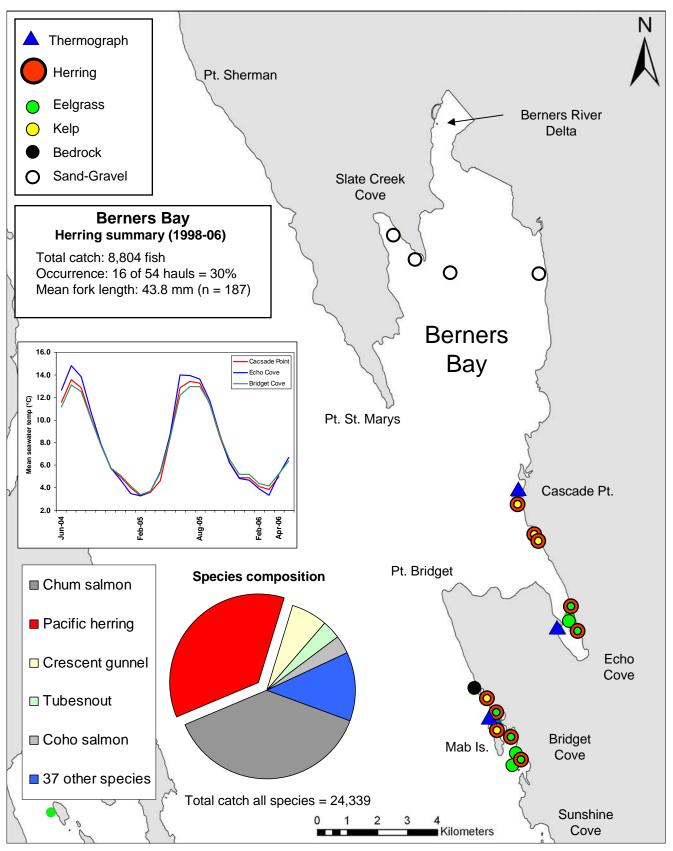


Figure 4.6. Location and habitat type of beach seine sites in Berners Bay (see legend). Herring are summarized by total catch, percent occurrence, and mean fork length. Seine catch data (pie graph) represents the percent species composition of 54 seine hauls from 1998 to 2006. Seawater temperature is from three locations within Berners Bay.

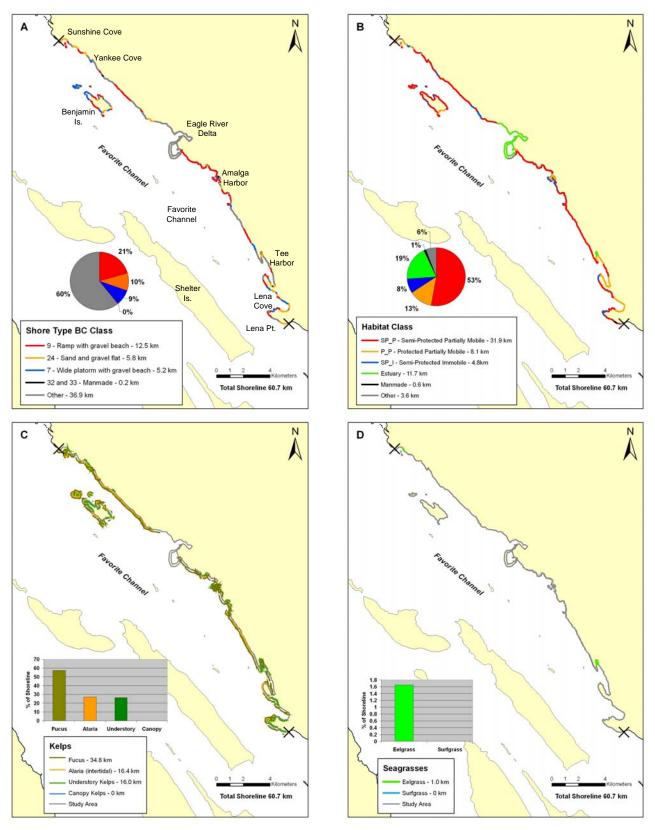


Figure 4.7. Favorite Channel: *ShoreZone* coastal habitat maps. Proportions of dominant habitat classes are delineated in four panels - panel A (Shore Type), panel B (Habitat Class), panel C (kelps), and panel D (seagrasses). For definitions of *ShoreZone* habitat classifications see Appendix A.

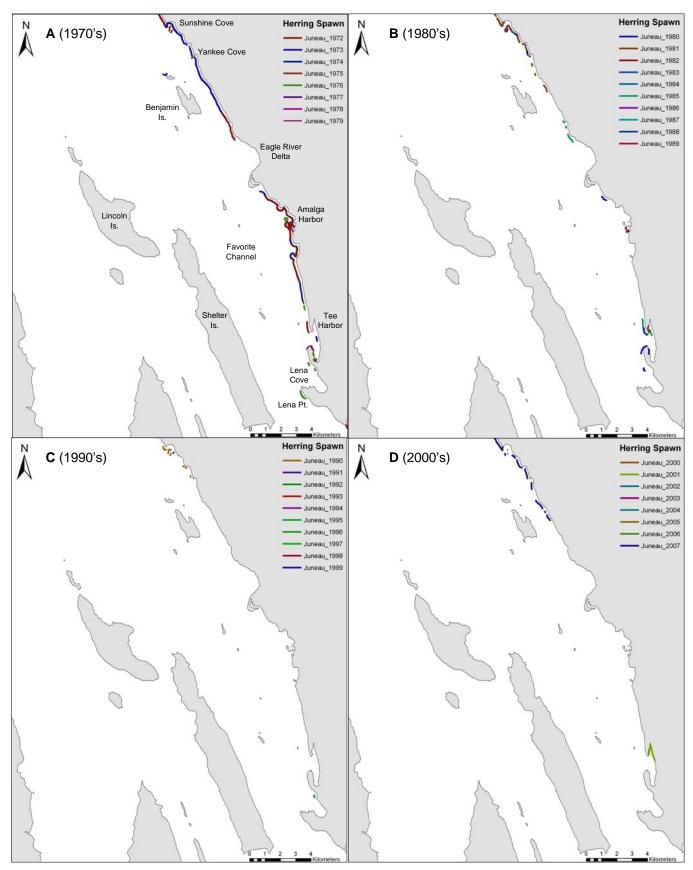


Figure 4.8. Favorite Channel: ADFG records of herring spawn (Pritchett 2007). Panel A shows spawn records for 1970's, panel B for 1980's, panel C for 1990's, and panel D for 2000–2007. Some panels may not have spawn records for each year in a given decade. Refer to each panel's legend for color coded, annual spawn records.

4.25

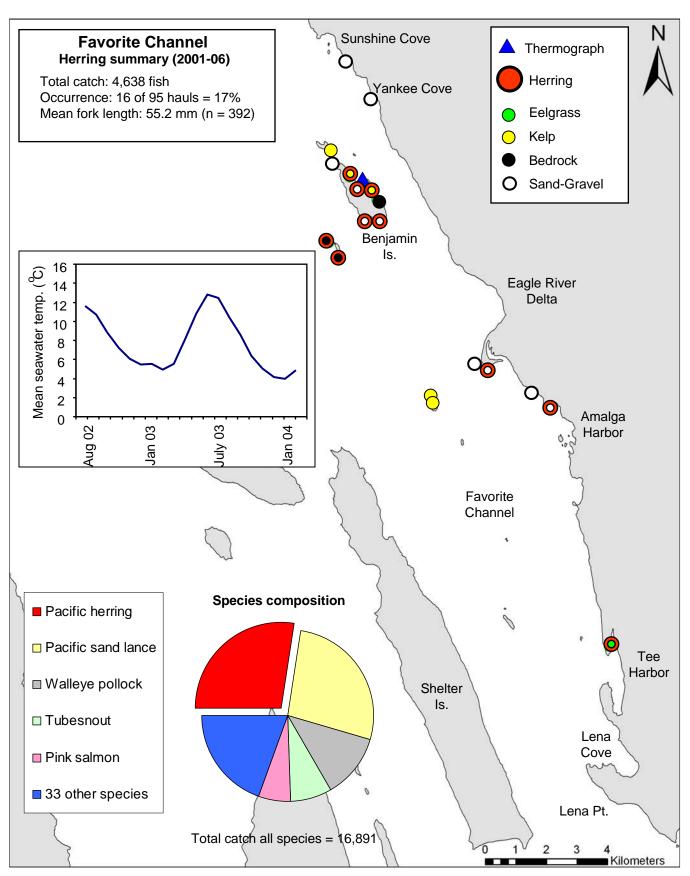


Figure 4.9. Location and habitat type of beach seine sites in Favorite Channel (see legend). Herring are summarized by total catch, percent occurrence, and mean fork length. Seine catch data (pie graph) represents the percent species composition of 95 seine hauls from 2001 to 2006. Seawater temperature is from Benjamin Island.

4.26

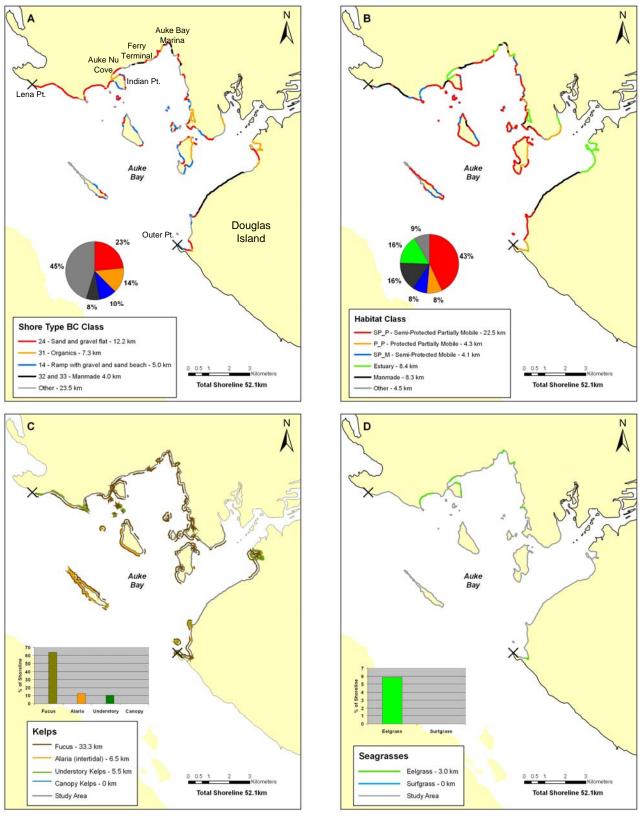


Figure 4.10. Auke Bay: *ShoreZone* coastal habitat maps. Proportions of dominant habitat classes are delineated in four panels - panel A (Shore Type), panel B (Habitat Class), panel C (kelps), and panel D (seagrasses). For definitions of *ShoreZone* habitat classifications see Appendix A.

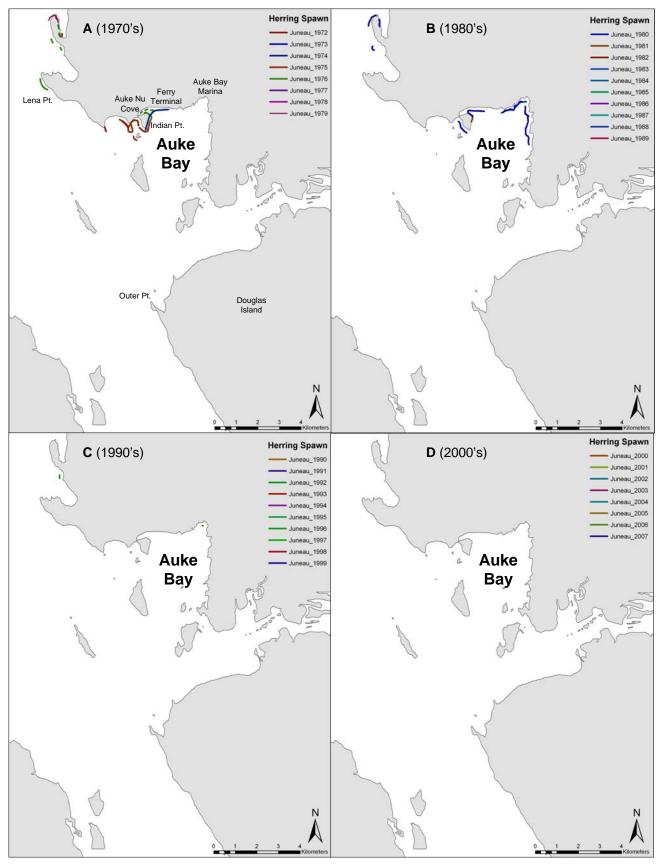


Figure 4.11. Auke Bay: ADFG records of herring spawn (Pritchett 2007). Panel A shows spawn records for 1970's, panel B for 1980's, panel C for 1990's, and panel D for 2000–2007. Some panels may not have spawn records for each year in a given decade. Refer to each panel's legend for color coded, annual spawn records.

4.28

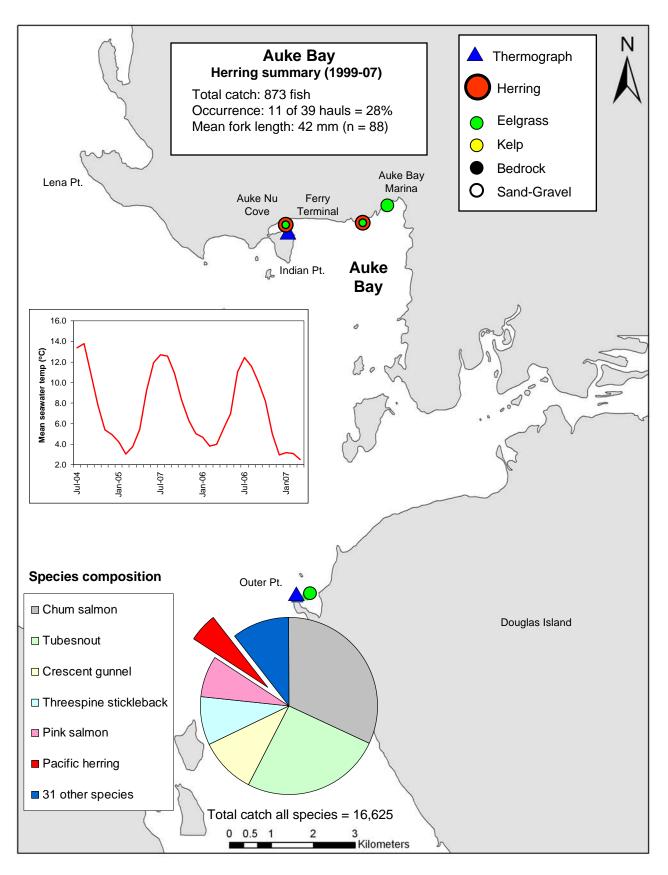


Figure 4.12. Location and habitat type of beach seine sites in Auke Bay (see legend). Herring are summarized by total catch, percent occurrence, and mean fork length. Seine catch data (pie graph) represents the percent species composition of 39 seine hauls from 1999 to 2007. Seawater temperature is from Indian Pt.

4.29

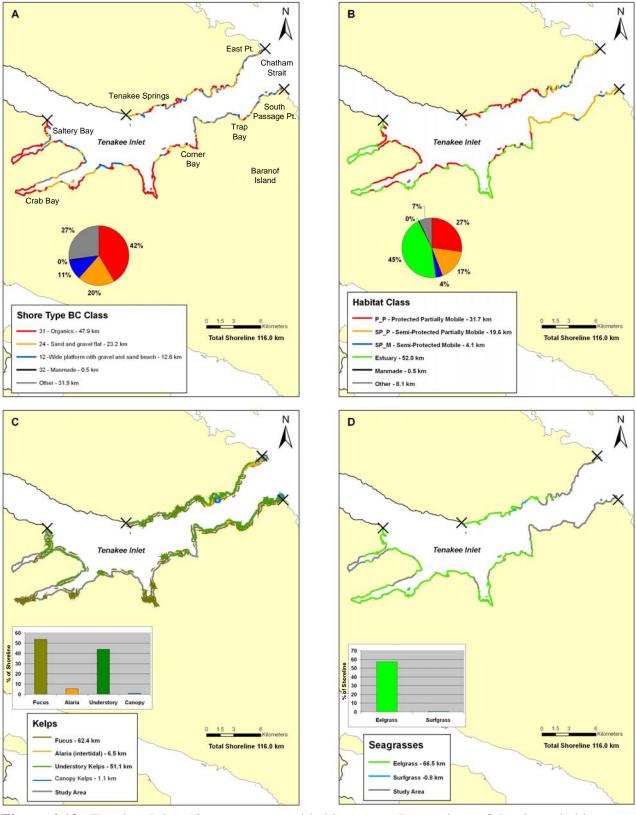


Figure 4.13. Tenakee Inlet: *ShoreZone* coastal habitat maps. Proportions of dominant habitat classes are delineated in four panels - panel A (Shore Type), panel B (Habitat Class), panel C (kelps), and panel D (seagrasses). For definitions of *ShoreZone* habitat classifications see Appendix A.

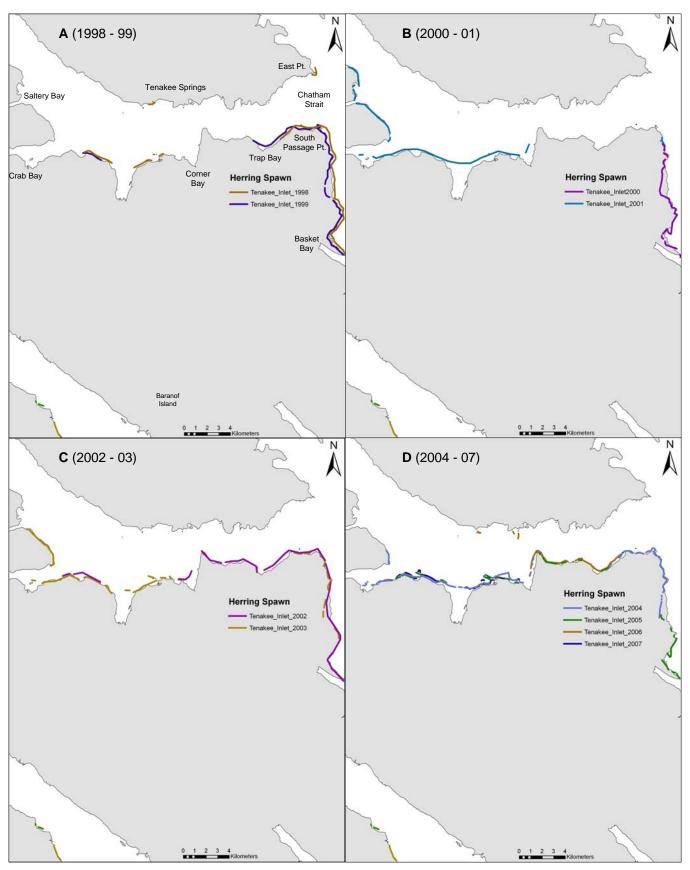


Figure 4.14. Tenakee Inlet: ADFG records of herring spawn (Pritchett 2007). Panel A shows spawn records for 1970's, panel B for 1980's, panel C for 1990's, and panel D for 2000–2007. Some panels may not have spawn records for each year in a given decade. Refer to each panel's legend for color coded, annual spawn records.

4.31

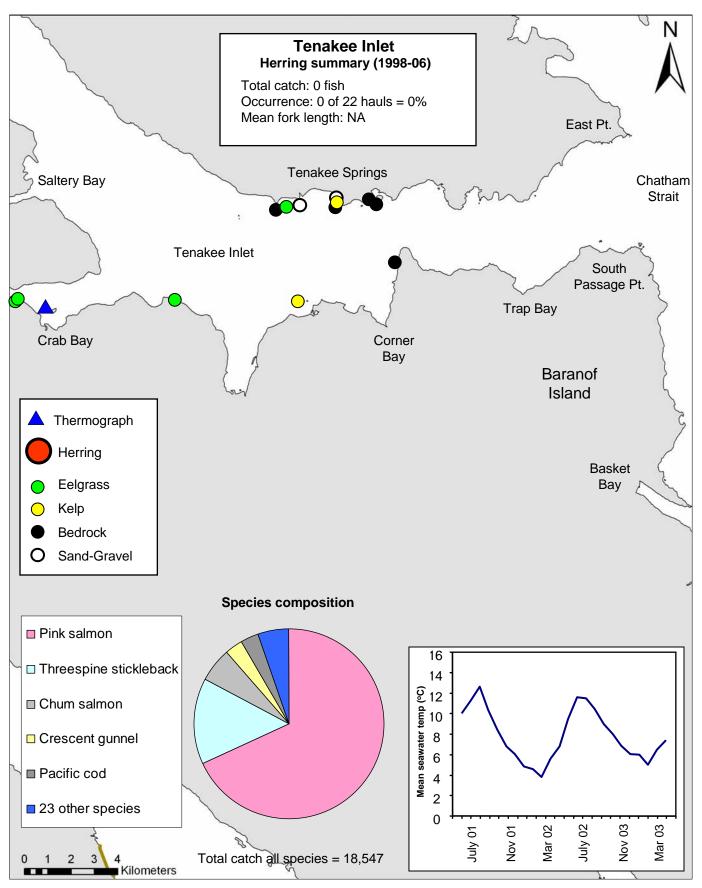


Figure 4.15. Location and habitat type of beach seine sites in Tenakee Inlet (see legend). Herring are summarized by total catch, percent occurrence, and mean fork length. Seine catch data (pie graph) represents the percent species composition of 22 seine hauls from 1998 to 2006. Seawater temperature is from Crab Bay.

4.32

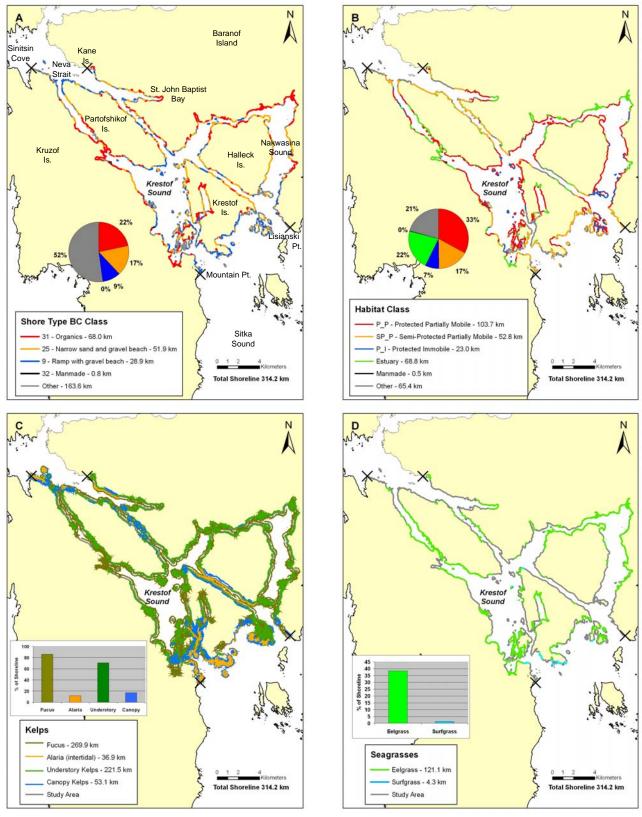


Figure 4.16. Northern Sitka Sound: *ShoreZone* coastal habitat maps. Proportions of dominant habitat classes are delineated in four panels - panel A (Shore Type), panel B (Habitat Class), panel C (kelps), and panel D (seagrasses). For definitions of *ShoreZone* habitat classifications see Appendix A.

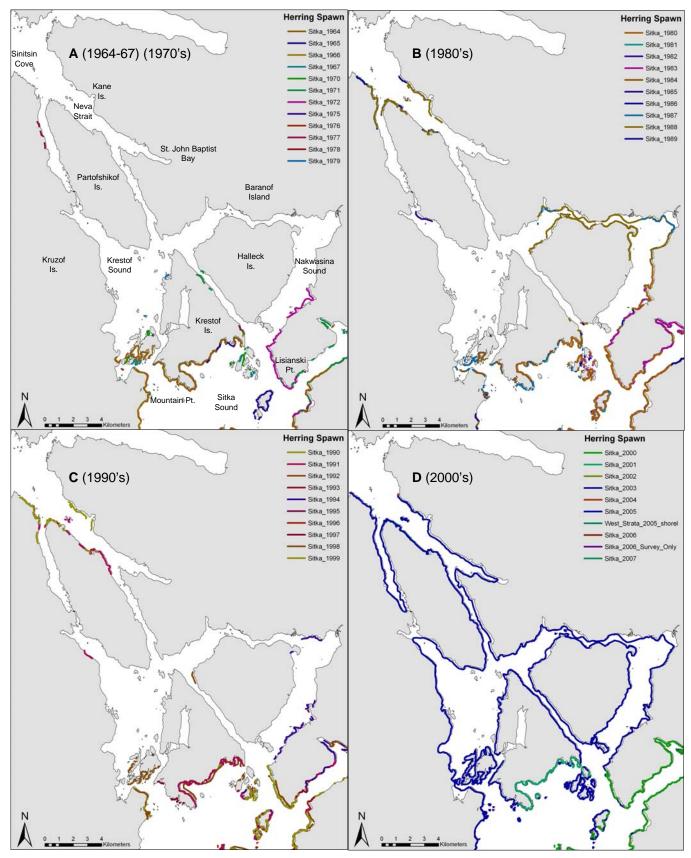


Figure 4.17. Northern Sitka Sound: ADFG records of herring spawn (Pritchett 2007). Panel A shows spawn records for 1970's, panel B for 1980's, panel C for 1990's, and panel D for 2000–2007. Some panels may not have spawn records for each year in a given decade. Refer to each panel's legend for color coded, annual spawn records.

4.34

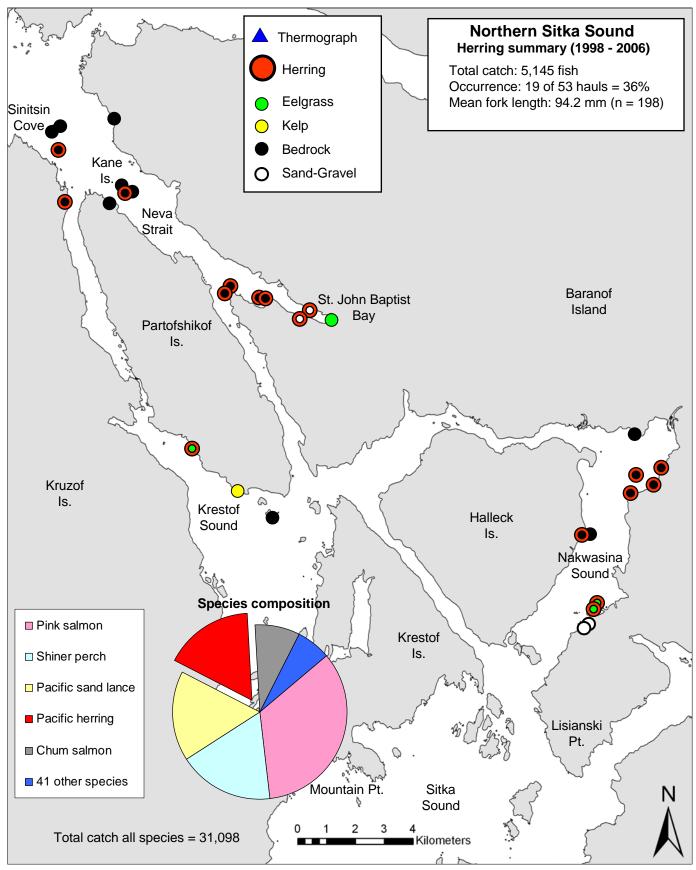


Figure 4.18. Location and habitat type of beach seine sites in Northern Sitka Sound (see legend). Herring are summarized by total catch, percent occurrence, and mean fork length. Seine catch data (pie graph) represents the percent species composition of 53 seine hauls from 1998 to 2006.

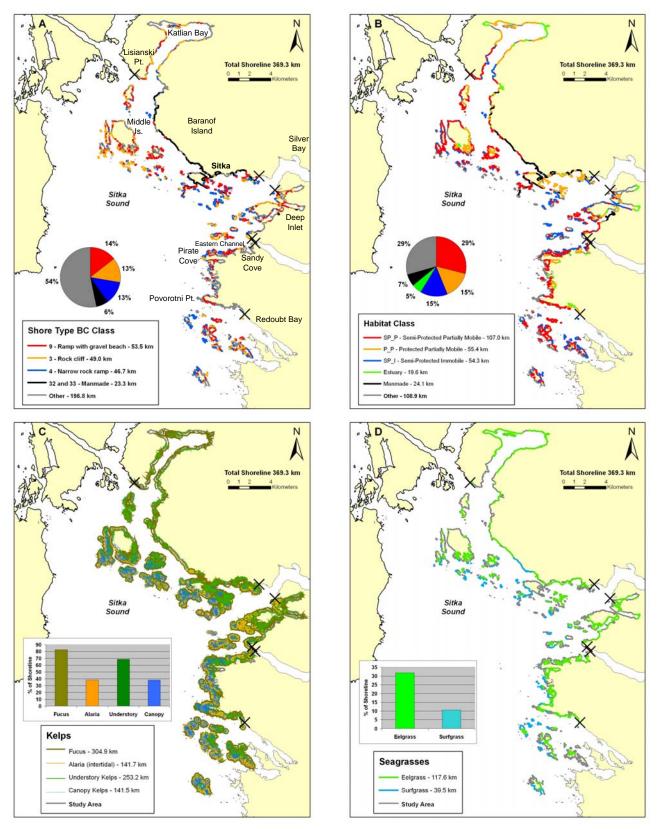


Figure 4.19. Central Sitka Sound: *ShoreZone* coastal habitat maps. Proportions of dominant habitat classes are delineated in four panels - panel A (Shore Type), panel B (Habitat Class), panel C (kelps), and panel D (seagrasses). For definitions of *ShoreZone* habitat classifications see Appendix A.

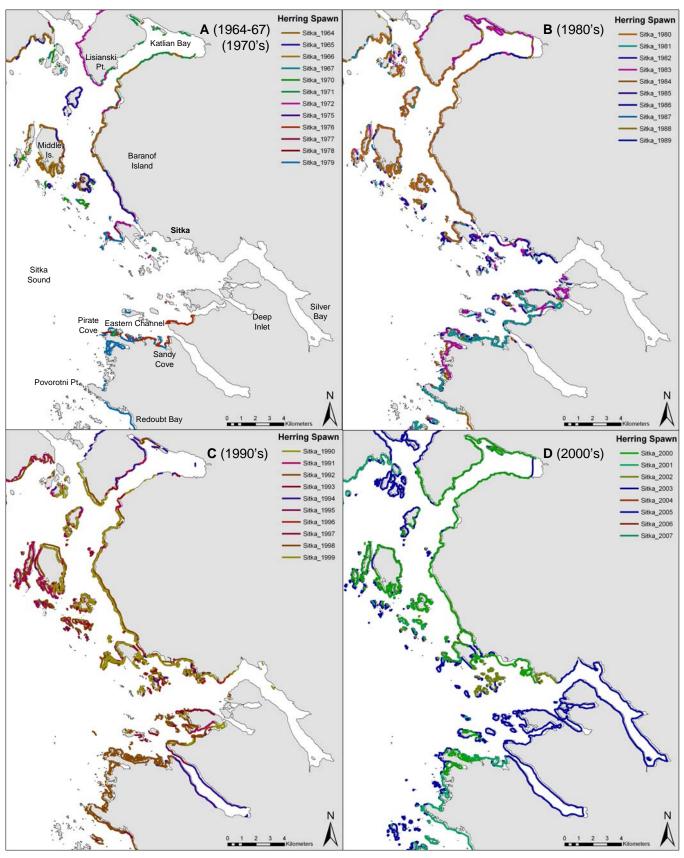


Figure 4.20. Central Sitka Sound: ADFG records of herring spawn (Pritchett 2007). Panel A shows spawn records for 1970's, panel B for 1980's, panel C for 1990's, and panel D for 2000–2007. Some panels may not have spawn records for each year in a given decade. Refer to each panel's legend for color coded, annual spawn records.

4.37

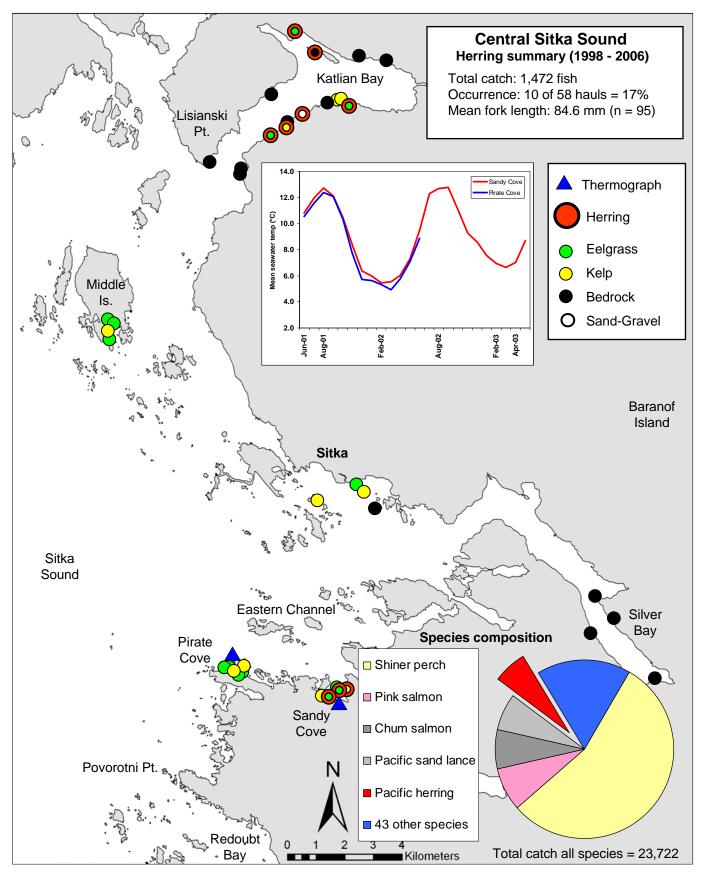


Figure 4.21. Location and habitat type of beach seine sites in Central Sitka Sound (see legend). Herring are summarized by total catch, percent occurrence, and mean fork length. Seine catch data (pie graph) represents the percent species composition of 58 seine hauls from 1998 to 2006. Seawater temperature is from two locations within Central Sitka Sound.

4.38

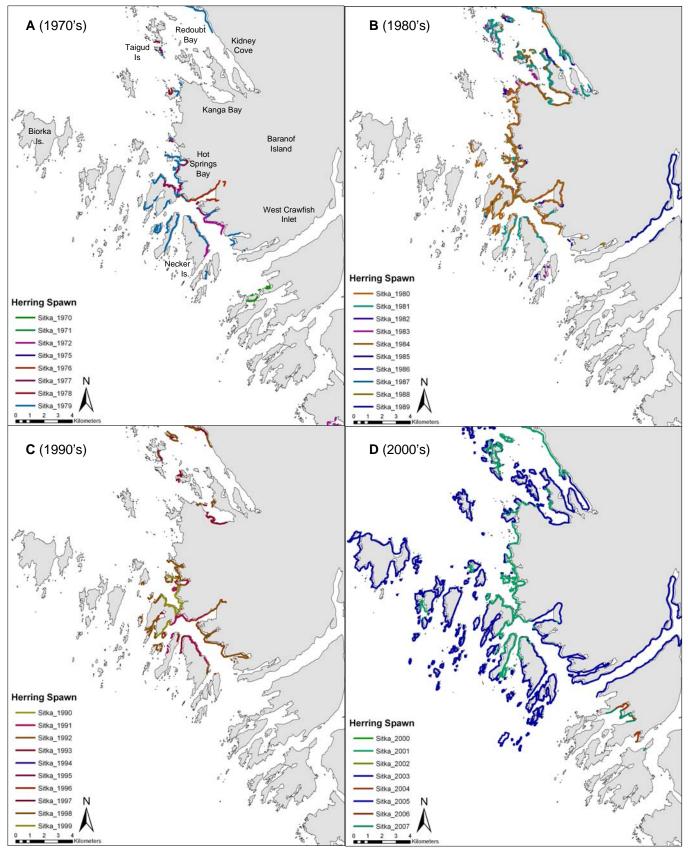


Figure 4.22. Southern Sitka Sound: ADFG records of herring spawn (Pritchett 2007). Panel A shows spawn records for 1970's, panel B for 1980's, panel C for 1990's, and panel D for 2000–2007. Some panels may not have spawn records for each year in a given decade. Refer to each panel's legend for color coded, annual spawn records.

4.39

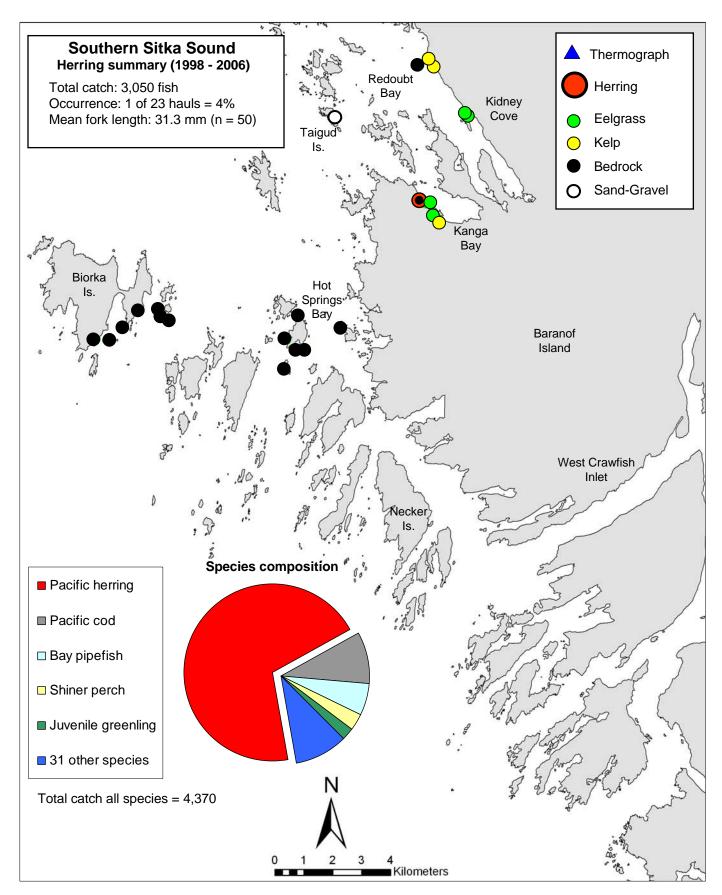


Figure 4.23. Location and habitat type of beach seine sites in Southern Sitka Sound (see legend). Herring are summarized by total catch, percent occurrence, and mean fork length. Seine catch data (pie graph) represents the percent species composition of 23 seine hauls from 1998 to 2006.

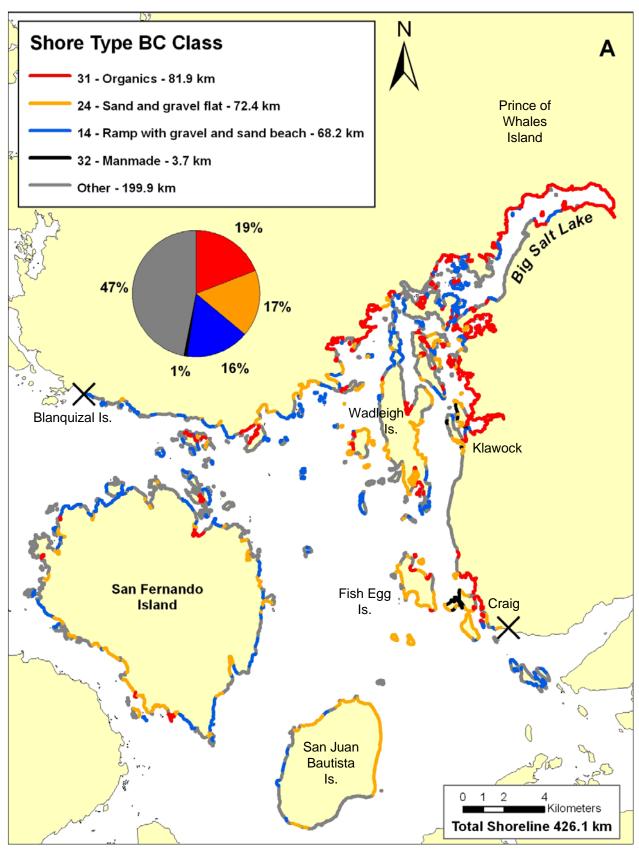


Figure 4.24. Craig: *ShoreZone* coastal habitat map. Proportion of dominant shore types are delineated in panel A. *ShoreZone* information for Habitat Class, kelps, and seagrasses are currently unavailable. For definitions of *ShoreZone* habitat classifications see Appendix A.

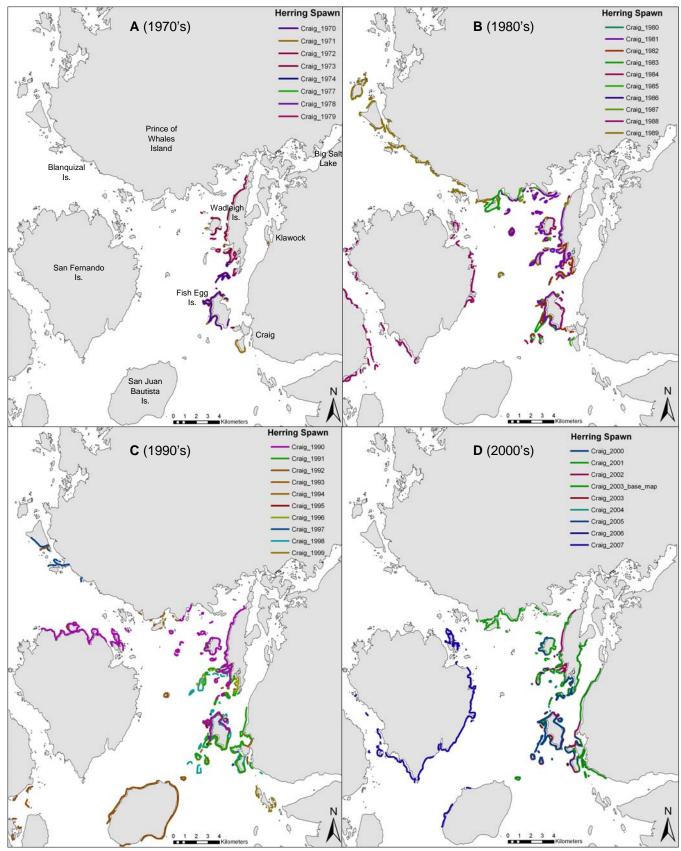


Figure 4.25. Craig: ADFG records of herring spawn (Pritchett 2007). Panel A shows spawn records for 1970's, panel B for 1980's, panel C for 1990's, and panel D for 2000–2007. Some panels may not have spawn records for each year in a given decade. Refer to each panel's legend for color coded, annual spawn records.

4.42

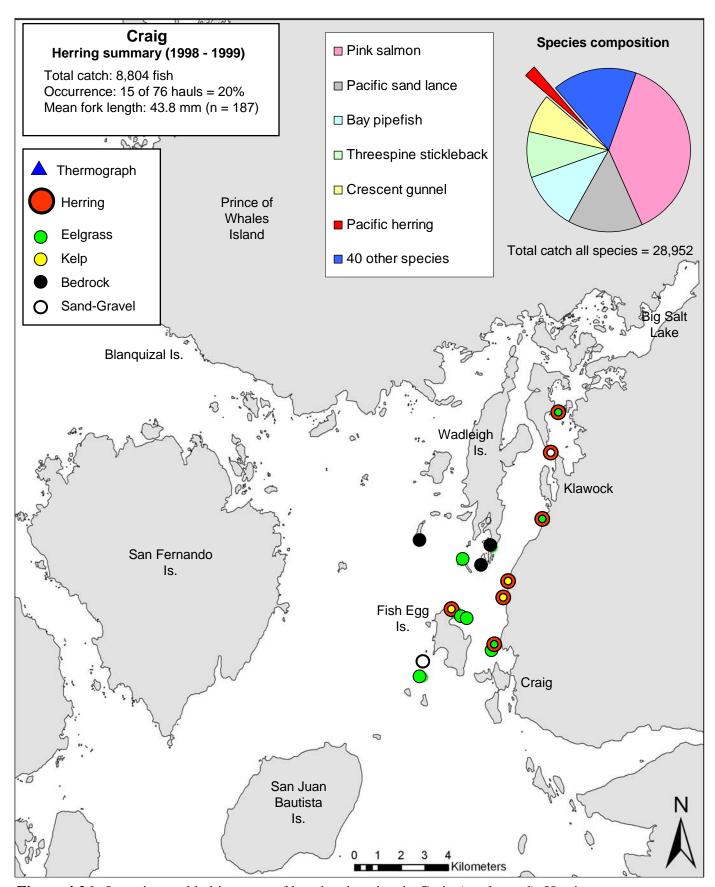


Figure 4.26. Location and habitat type of beach seine sites in Craig (see legend). Herring are summarized by total catch, percent occurrence, and mean fork length. Seine catch data (pie graph) represents the percent species composition of 76 seine hauls from 1998 to 1999.

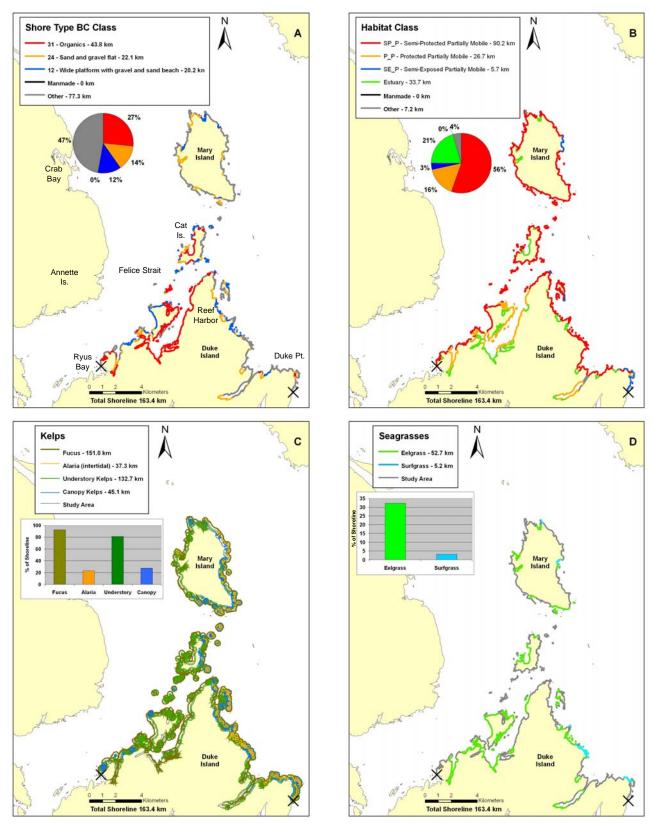


Figure 4.27. Duke Island: *ShoreZone* coastal habitat maps. Proportions of dominant habitat classes are delineated in four panels - panel A (Shore Type), panel B (Habitat Class), panel C (kelps), and panel D (seagrasses). For definitions of *ShoreZone* habitat classifications see Appendix A.

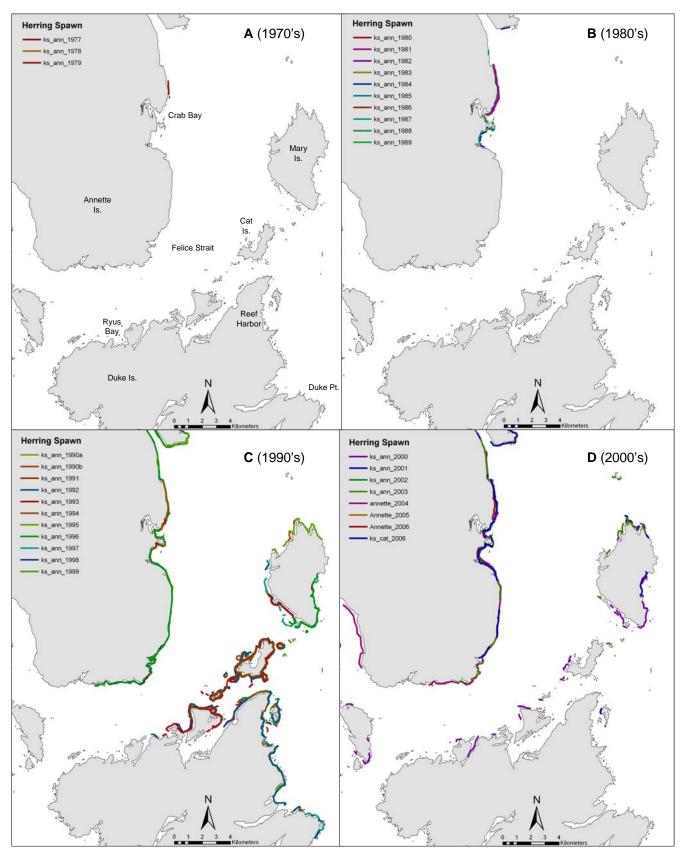


Figure 4.28. Duke Island: ADFG records of herring spawn (Pritchett 2007). Panel A shows spawn records for 1970's, panel B for 1980's, panel C for 1990's, and panel D for 2000–2007. Some panels may not have spawn records for each year in a given decade. Refer to each panel's legend for color coded, annual spawn records.

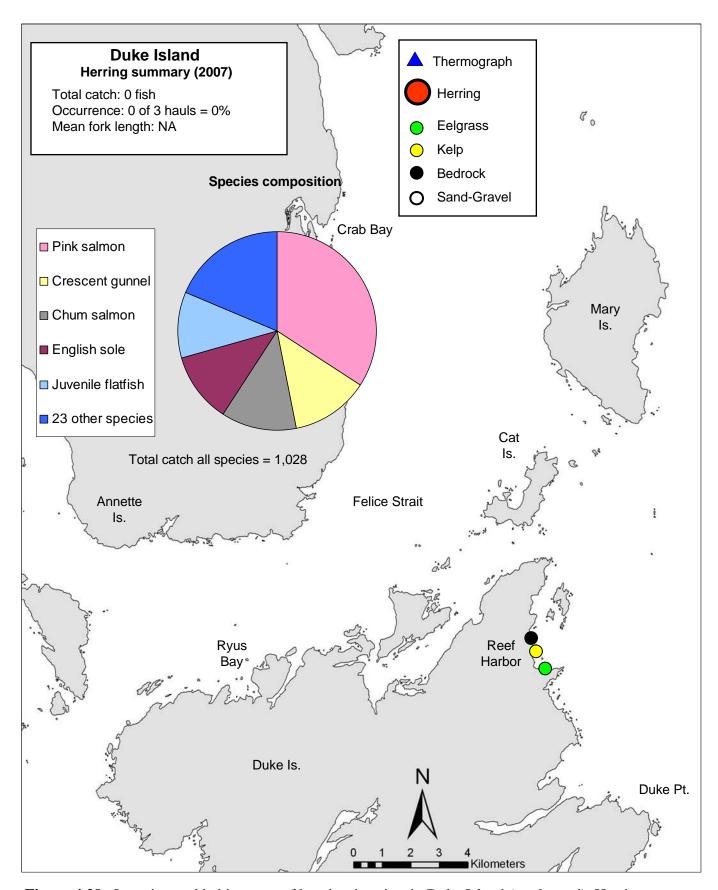


Figure 4.29. Location and habitat type of beach seine sites in Duke Island (see legend). Herring are summarized by total catch, percent occurrence, and mean fork length. Seine catch data (pie graph) represents the percent species composition of 3 seine hauls from 2007.

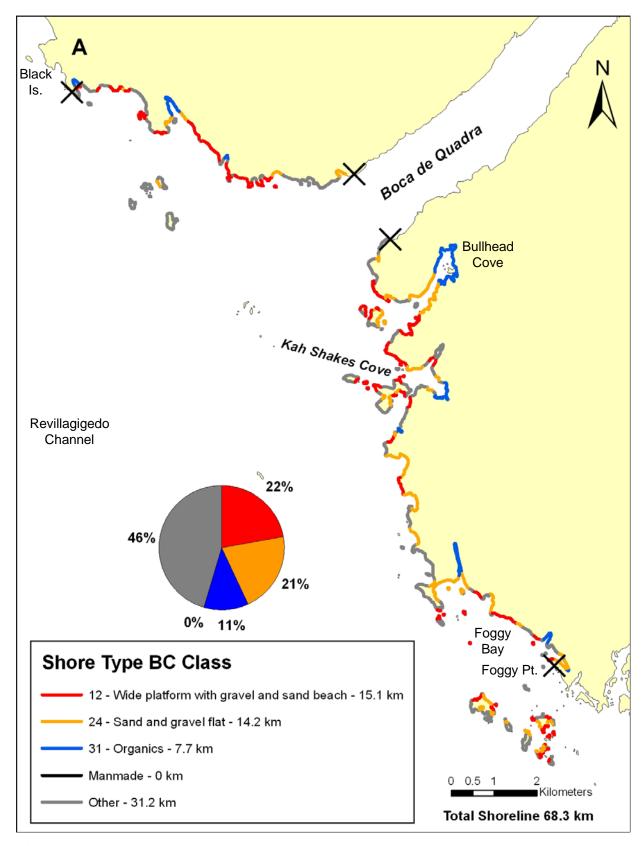


Figure 4.30. Kah Shakes: *ShoreZone* coastal habitat map. Proportion of dominant shore types are delineated in panel A. *ShoreZone* information for Habitat Class, kelps, and seagrasses are currently unavailable. For definitions of *ShoreZone* habitat classifications see Appendix A.

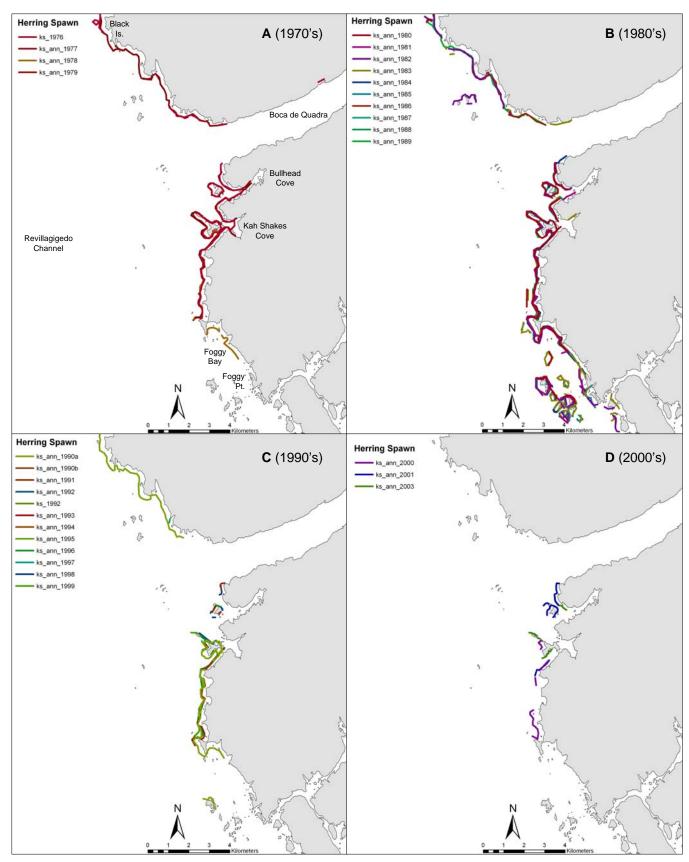


Figure 4.31. Kah Shakes: ADFG records of herring spawn (Pritchett 2007). Panel A shows spawn records for 1970's, panel B for 1980's, panel C for 1990's, and panel D for 2000–2003. Some panels may not have spawn records for each year in a given decade. Refer to each panel's legend for color coded, annual spawn records.

4.48

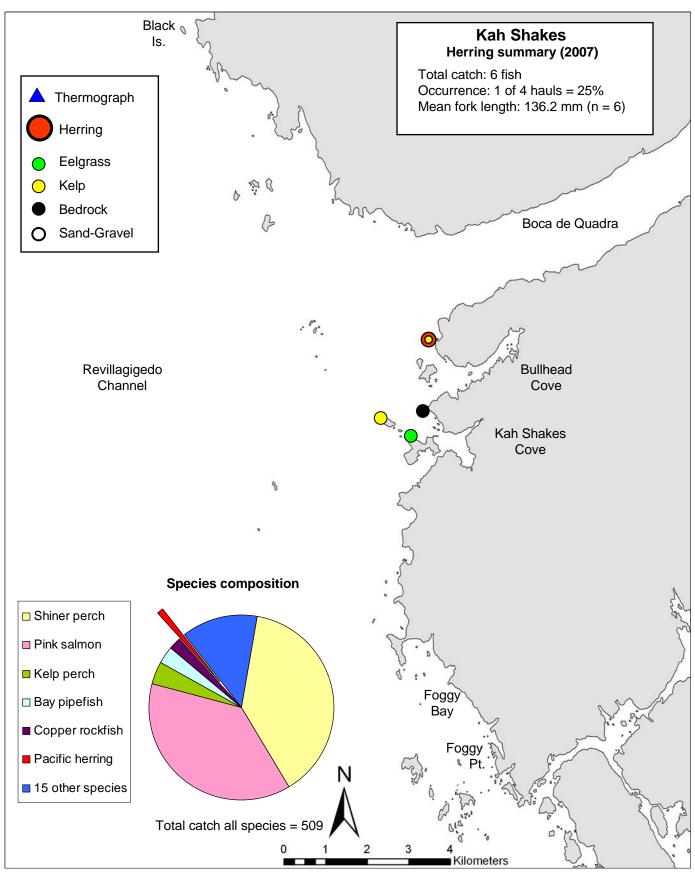


Figure 4.32. Location and habitat type of beach seine sites in Kah Shakes (see legend). Herring are summarized by total catch, percent occurrence, and mean fork length. Seine catch data (pie graph) represents the percent species composition of 1 seine haul from 2007.

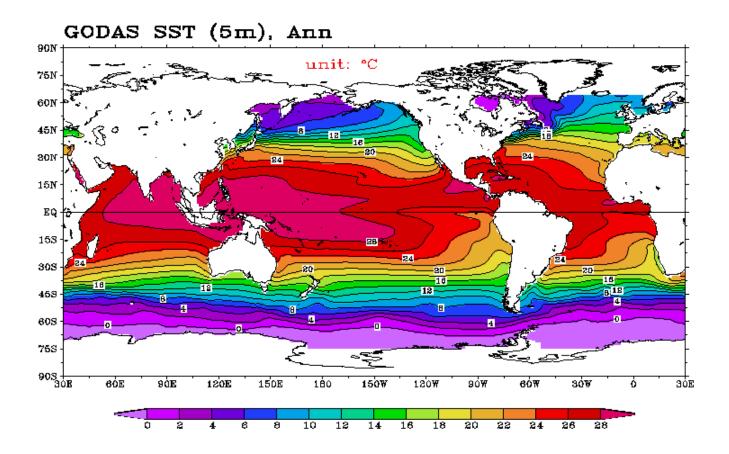
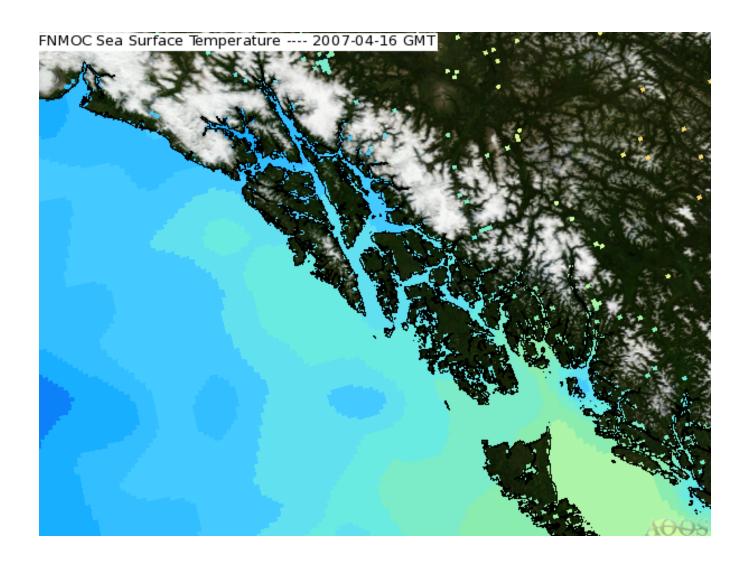


Fig. 4.33. General global sea surface temperature distribution (15).



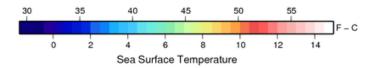


Fig. 4.34. Sea surface temperature in SEAK illustrating the general pattern of warmest waters in the south and coolest toward the north and inside waters (*16*).

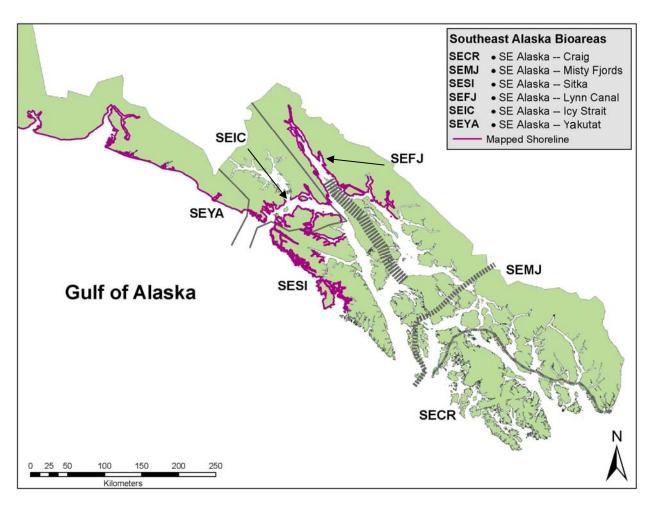


Figure 4.35. *ShoreZone* bioareas for SEAK. Delineation of further bioareas pending completion of habitat mapping but projected with hatched lines.

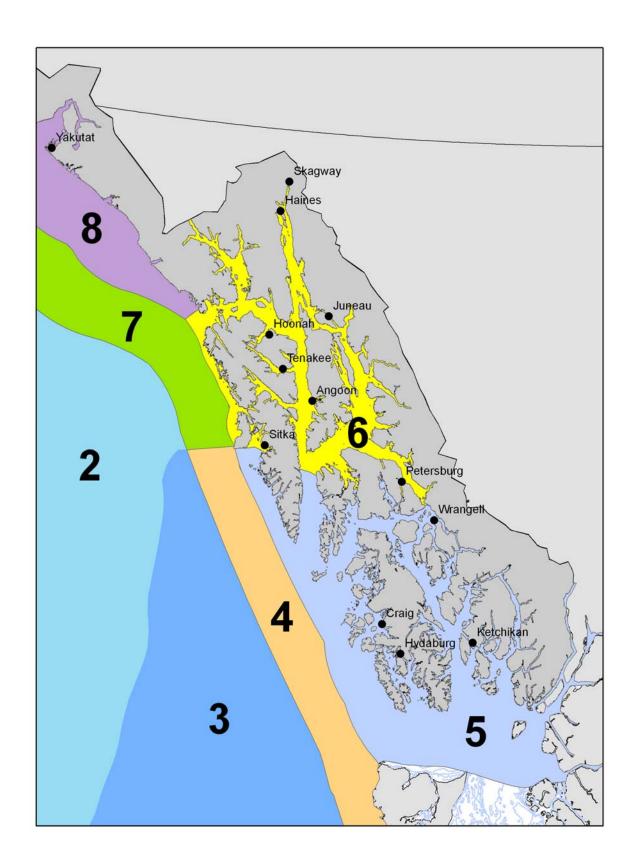


Fig. 4.36. Alaska Marine Ecoregions (Piatt and Springer 2007); North Pacific Current – Alaska Stream Loop (2), eastern Gulf of Alaska transitional (3), eastern Gulf of Alaska slope (4), Prince of Wales shelf and inside waters (5), Chichagof shelf and inside waters (6), northern Gulf of Alaska slope (7), and northern Gulf of Alaska shelf (8).

Chapter 5 Are Lynn Canal herring a discrete population segment (DPS)?

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Abstract

Pacific herring in Lynn Canal are not a distinct population segment (DPS) as defined by the Endangered Species Act (ESA). Examination of all available data by the biological review team (BRT) did not convince the majority of members that herring in Lynn Canal were markedly discrete from other populations of the same taxon in southeast Alaska (SEAK). No members perceived Lynn Canal herring to be significant with respect to the taxon (although all recognized the importance of herring to the local ecosystem). Available biological data were either incomplete or were too similar to definitively separate herring populations within SEAK, thus the team concluded that the smallest defensible DPS that includes Lynn Canal is SEAK. The southern limit of the DPS, Dixon Entrance, is identified by genetic differences between herring in SEAK and those in British Columbia. The northern border is defined by a physical barrier, mobile open ocean beaches inadequate as spawning and rearing habitat; the oceanward boundary is near Icy Point. Glacier Bay and Lynn Canal are both included in the SEAK DPS. The team did not rule out the possibility that SEAK might be subdivided into smaller DPS units if more detailed data collected in the future thus indicate.

Introduction

Endangered Species Act (ESA)

For the purpose of the ESA, Congress has defined a species as "any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife which interbreeds when mature." Guidance on what constitutes a distinct population segment (DPS) is provided by the joint NMFS-USFWS interagency DPS policy (61 FR 4722, February 7, 1996). In order to be classified as a DPS, a vertebrate population must fulfill two criteria – discreteness and significance. To be considered "distinct," a population, or group of populations, must first be "discrete" from other populations and then "significant" to the taxon (species or subspecies) to which it belongs.

The fundamental species question addressed by the Biological Review Team for this status review was "does the Lynn Canal herring stock comprise a distinct population segment (DPS) as defined under the Endangered Species Act?" The Team's approach to answering this question is described in this chapter. Prior to the commencement of this status review, Pacific herring stocks in Southeast Alaska had not been examined in detail for DPS structure. However,

several herring studies conducted in the North Pacific helped the BRT evaluate population discreteness and significance, shedding light on whether or not Pacific herring in Lynn Canal are a distinct population segment as defined under the ESA.

Evaluation of discreteness

As stated previously, a population segment of a vertebrate species may be considered discrete if it is markedly separated from other populations of the same taxon as a consequence of physical, physiological, ecological, or behavioral factors. Quantitative measures of genetic or morphological discontinuity may also provide evidence of this separation. A population may also be considered discrete if it is delimited by international governmental boundaries, between which exist differences in control of exploitation, management of habitat, conservation status, or regulatory mechanisms that are significant in light of Section 4(a)(1)(D) of the ESA. Because the focus of this status review document is the scientific assessment of population structure, the Biological Review Team focused on the available scientific evidence for population discreteness.

Evaluation of significance

Once a population segment is determined to be discrete under one or more of the above conditions, its biological and ecological significance to the taxon must then be considered. Criteria that can be used to assess whether the discrete population segment is significant include:

- 1. Persistence of the discrete population segment in an ecological setting unusual or unique for the taxon;
- 2. Evidence that loss of the discrete population segment would result in a significant gap in the range of a taxon;
- 3. Evidence that the discrete population segment represents the only surviving natural occurrence of a taxon that may be more abundant elsewhere as an introduced population outside its historic range; or
- 4. Evidence that the discrete population segment differs markedly from other populations of the species in its genetic characteristics.

A discrete population segment needs to satisfy only one of these criteria to be considered significant. However, the list of criteria is not exhaustive; other criteria may be used as deemed appropriate.

DPS decision process by the BRT

The fundamental goal was to determine if Lynn Canal herring are a DPS and if not, to identify the DPS that includes Lynn Canal herring. The ESA discreteness question was examined first. To understand Lynn Canal in its physical and biological context, data review (detailed in Chapters 2 to 4) began at large geospatial scales and moved toward smaller scales, ending with Lynn Canal. After determining that Lynn Canal herring were not discrete, i.e., not markedly different from nearby stocks, the BRT determined the smallest discrete geographic area supported by the data (SEAK) and debated the significance of this area with respect to the taxon.

Structure among Pacific herring at large and small scales

Genetic differences and known herring mobility provided the largest scale evidence of differences among Pacific herring subpopulations (Chapter 2, Fig. 2.2). In particular, the genetic differences between herring in Asia, the Bering Sea, and those in the Gulf of Alaska (Grant and Utter 1984; Kobayashi 1993; O'Connell et al. 1998) are consistent with herring migration ability; the maximum observed yearly net movement of tagged fish ranges from nearly 200 km (SEAK) to 300 km (British Columbia) and the average net movement is about 90 km (Dahlgren 1936; Hay and McKinnell 2002). Thus, genetic drift among populations located thousands of kilometers apart is understandable. Recruitment and biomass data corroborate differences among populations; Bering Sea herring are much different than those along the GOA and in British Columbia (Williams and Quinn 2000). Herring in the northern Gulf of Alaska (Kodiak through Lynn Canal) may be distinct from those further south (Helm Bay near Ketchikan through San Francisco) (Grant and Utter 1984). However, this allozyme study (Grant and Utter 1984) was not designed to discriminate among SEAK stock and a more detailed microsatellite study found a modest genetic difference between herring in SEAK and those from the Queen Charlotte Islands and northern British Columbia (Beacham et al. 2002). (Sample locations in SEAK included Sitka, Seymour Canal, and the vicinity of Kah Shakes, south of Ketchikan.) Evidence for genetic structure in populations east and south of the Alaska Peninsula is relatively weak: genetic differences among populations covering the large geographic area from San Francisco to Kodiak Island are only about 1/10th as large as those between Gulf of Alaska and Bering Sea populations (Grant and Utter 1984; Kobayashi 1993).

The other biological variables available for comparison within SEAK (migration, spawn timing, vertebrae number, recruitment, and size-at-age) provided modest and often conflicting evidence of discreteness among stocks. (See Chapter 3 for a complete discussion and Fig. 5.1 for a summary map.) Geospatial interpretation of these data was generally highly subjective and variable; geospatial coverage was often incomplete. No clear divisions emerged among herring in SEAK when available biological variables were overlain. In this context, we turned our attention to Lynn Canal herring.

Are Lynn Canal herring discrete?

Based on the available evidence, the BRT concluded 6 to 4 that Lynn Canal herring are not discrete; i.e., they are not markedly different from other stocks in SEAK (Fig. 5.1). The boundaries accepted for Lynn Canal are the ADFG management boundaries, ranging from Berners Bay south to Taku Harbor and encompassing Douglas Island and portions of northern Admiralty Island, notably Oliver Inlet where spawning frequently occurs (Fig. 3.2).

Evidence against discreteness

- There are no known genetic differences between Lynn Canal stock and others in SEAK.
 - O Several studies have included herring from SEAK (Grant and Utter 1984; Grant 1986; Kobayashi 1993; Beacham et al. 2002). Lynn Canal herring were included in one of these (an allozyme study) but sampling within SEAK was generally insufficient to draw conclusions.
 - o The microsatellite DNA study by Beacham et al. (2002) was the most detailed genetic analysis; they concluded that SEAK herring differ from herring in British Columbia but did not provide a detailed comparison of samples (Sitka, Kirk Point, Mary Island, and Seymour Canal) within SEAK.

- Spawn timing in Lynn Canal does not differ from the timing in other northern SEAK stocks, rather spawn timing appears to partition into an early southern group and a later northern group.
- Comparison of Lynn Canal herring recruitment to other SEAK stocks was not available at the time of the decision and more data are required before recruitment is estimable (Chapter 3).
 - o However, incomplete evidence suggests year class strength in Lynn Canal may be synchronous with that in other SEAK stocks (Fig. 3.9)
- Growth rates in Lynn Canal, based on the limited amount of data at the time of the decision (Rounsefell and Dahlgren 1935; Johnson et al. 1997; Carls et al. 1998; Williams and Quinn 2000), are not different from elsewhere in SEAK. (Subsequent analysis of ADFG data further substantiates this conclusion.)
 - O Variation in median lengths [age 4 herring in 1929; (Rounsefell and Dahlgren 1935)] did not suggest divisions among SEAK herring stocks.
 - o Lynn Canal lengths and weights at age were not unusual [1994 to 1995; (Johnson et al. 1997; Carls et al. 1998)].
 - Analysis of weight-at-age by Williams and Quinn (2000) suggested growth rates in a broad portion of SEAK were similar; however, this analysis did not include Lynn Canal fish.
 - o Given the consistency among the data analyzed to date, marked differences between Lynn Canal herring and other SEAK stock were not expected in the unanalyzed ADFG data set at the time of the BRT decision. Preliminary analysis of 78,971 measurements from the ADFG data set supports the original decision;
 - Current trends in size at age (length) in all SEAK herring stocks is downward and there is no evidence Lynn Canal stock differs from the others.
 - Growth rates do not vary significantly among SEAK herring stocks
- Vertebrae number in Lynn Canal herring is consistent with nearby areas (Rounsefell and Dahlgren 1935).
 - Vertebrae number generally does not provide clear separation within SEAK stocks.
- Lynn Canal herring mix with other SEAK herring in summer feeding areas (Carlson 1980).
 - o However, limited tagging data do not rule out the possibility that stocks remain segregated on spawning grounds.
- Herring occupy nearby waters adjacent to the Lynn Canal area and these populations may be functionally continuous.
 - o Predicted herring fidelity within an area the size of the Lynn Canal management area is about 40%, suggesting considerable exchange with surrounding stocks is plausible. [This estimate is based on the assumption that tagging data averaged over the five managed stocks of herring in British Columbia can be used to predict fidelity in SEAK and is intended only as a rough measure; it is based on central tendancies in the British Columbia data. Scatter in the British Columbia data is high and observed fidelity ranged from about 0 to 100% at this scale (950 km², water only).]

- o The nearest spawning stock, in Port Frederick, is located ~60 km from the Lynn Canal stock, well within net average yearly herring movement [89 km, (Hay et al. 2001; Hay and McKinnell 2002)].
 - Herring can travel considerable distances in short periods of time; e.g., ripe, prespawning herring moved 150 km in 6 d and spent fish moved 350 km in 16 d (Haegele and Schweigert 1985).
- Habitat in Lynn Canal is not markedly different from habitat elsewhere in SEAK.
 - o Measured temperatures are not unique (Chapter 4, Table 4.1)
 - o Expected temperatures are not unique (Chapter 3, Fig. 3.17; Chapter 4, Fig. 4.34)
 - o Measured salinities are not unique (Chapter 4, Table 4.1)
 - o The area is not isolated by features that impede water exchange or act as migration barriers.
 - o There is generally less macroalgae cover in Lynn Canal than elsewhere in SEAK and there are differences in communities between Lynn Canal and other bioareas in SEAK (Chapter 4, Fig. 4.35). However, this does not appear to limit spawning or modify herring behavior; herring are euryhaline, eurythermal, and spawn on a wide variety of substrates (Chapters 2 and 4).
- Lynn Canal herring do not have unusual or elevated polynuclear aromatic hydrocarbon (PAH) contaminant loads (Carls et al. 1998; Carls et al. 1999).
 - o PAH loads in adult herring collected near Shelter Island were low and were not consistent with either petrogenic or pyrogenic contamination.
 - Mean total PAH = 17 ng/g wet weight in ovaries and muscle tissue [the 95% confidence bounds were 15 to 20 ng/g (parts per billion), n = 49 (Carls et al. 1998)].
 - Mean total PAH concentrations were 14 ± 2, 23 ± 3, and 11 ± 4 ng/g wet weight for ovaries or eggs from Shelter Island (Lynn Canal), Cat Island, and Seymour Canal, respectively (the error term is standard error; n = 15, 6, and 4, respectively).
 - Human shoreline development (presumably elevating the relative potential for contaminant discharge and physical disruption), is greatest in the Lynn Canal management area (8%). However Sitka Sound is the second most developed area (6%) and is utilized by the largest and increasing herring biomass in SEAK (Chapter 4, Table 4.2).
 - Note; we cannot eliminate the possibility that shoreline development reduces stock biomass wherever it occurs. Rather, we are suggesting the 2% development difference between Lynn Canal and Sitka habitat disturbance does not explain the very different population loss and growth trajectories at the two locations.

Evidence for discreteness

- Lynn Canal is a consistent spawning area, not contiguous with adjacent spawning areas.
 - o Repeat spawning in a given area suggests utilization by the same fish
 - Caveats:
 - No tagging studies have documented spawning fidelity in SEAK

- The nearest spawning stock, in Port Frederick, is located ~60 km from Lynn Canal stock, well within net average yearly herring movement [89 km, (Hay et al. 2001; Hay and McKinnell 2002)].
- Predicted herring fidelity for the Lynn Canal Management Area is about 40%, implying exchange with surrounding fish is likely.
- o Herring are found year round in this location.
- Temporal changes in biomass are not synchronous with nearby stocks (Figs. 3.8 and 3.13).
 - o Sitka Sound, Hoonah Sound, and Seymour Canal stock biomasses have increased since the 1990s.
 - o Tenakee Inlet stock biomass has fluctuated up and down since the 1990s.
 - o Lynn Canal stock biomass has generally been steady since 1990 (as has that at Hobart Bay / Port Houghton).
 - This suggests that herring do not randomly disperse into areas with lower population density, i.e., there is no evidence that Lynn Canal herring are being repopulated by excesses from nearby, growing populations.
- Persistence of depressed stock abundance
 - o Lynn Canal stock has been depressed since the 1980s.
 - Fishing ended in 1982 (Blankenbeckler and Larson 1987; Pritchett et al. 2008); there are indications that overfishing caused the stock collapse.
 - Other suggested causes are increased marine mammal populations, human shoreline development, waste discharge (e.g., sewage), contaminant discharge, and boat activity.
 - O Typical recolonization time is about 11 y (range 5 to 35 y) for herring in British Columbia (Ware and Tovey 2004).

Are SEAK herring discrete?

Not only was the BRT unable to definitively distinguish Lynn Canal herring from the remainder of SEAK, they could not identify any definitive divisions among SEAK stocks in general. Divisions among regions within SEAK were ambiguous at best (Fig. 5.1). However, SEAK herring can reasonably be distinguished from other Pacific herring to the north with genetic differences (e.g., the Bering Sea) and because the open beaches between SEAK and other northern herring habitat (e.g., Yakutat and Prince William Sound) represent a physical barrier between spawning populations. (These beaches are exposed to ocean surf and thus are not suitable spawning or rearing habitat.) The oceanward boundary for SEAK as defined here is in the vicinity of Icy Point, some 30 km north of Cross Sound and about 200 km south of Yakutat. However, the BRT recognizes this northern boundary cannot be rigorously proven at present and that the DPS may be larger than defined. Glacier Bay and Lynn Canal were both included within the northernmost part of the SEAK DPS. The southern limit of SEAK, Dixon Entrance, is identified by genetic differences between herring in SEAK and those in British Columbia. The team did not rule out the possibility that SEAK might be subdivided into smaller DPS units if more detailed data collected in the future thus indicate.

Evidence for SEAK discreteness

Using ESA questions designed to determine discreteness, the BRT concluded that SEAK herring are discrete. Herring in SEAK are markedly separated from other Pacific herring as a consequence of physical barriers, genetics, and ecological differences.

- SEAK herring are isolated to the north by barrier beaches.
 - o Pacific herring do not utilize beaches exposed to ocean surf for spawning.
 - To our knowledge, no spawning has been reported in the relatively unsheltered Gulf of Alaska shoreline between northern SEAK and Yakutat or between Yakutat and Prince William Sound.
 - O The gap between other SEAK habitat and Yakutat is about 200 km (Icy Point to Yakutat). The gap between Yakutat and Zaikof Bay in Prince William Sound is about 400 km, a distance greater than documented maximum annual migration distances [300 km; (Hay and McKinnell 2002)].
- A natural biological boundary between herring populations coincides with the international boundary separating SEAK and British Columbia.
 - o SEAK herring are genetically different from those in British Columbia (Beacham et al. 2002).
 - Parasitism differs among herring north and south of this border (Arthur and Arai 1980), though this is a coarse measure because few sites were sampled, thus this measure yields ambiguous boundary position estimates.
 - o Different biological zones are apparent along the coast, probably a result of both thermal (north-south) and salinity (east-west) gradients (Chapter 4).
- A thermal gradient is clearly evident through British Columbia and SEAK.
 - o Temperatures in SEAK are colder than in British Columbia
 - o SEAK has tidewater glaciers, British Columbia does not, chilling the water and increasing turbidity and possibly nutrients.
 - o SEAK mainland topography is heavily influenced by snowfields and glaciers; this is less prevalent in British Columbia

Are SEAK herring significant with respect to the taxon?

Using the questions posed by the ESA to evaluate significance, the BRT concluded that SEAK herring are significant. The population persists in a unique habitat intermediate between areas further south and further north. Loss of SEAK herring would result in a significant gap in the range of the taxon and SEAK herring are genetically different from herring in British Columbia.

- Does the discrete population persist in habitat unusual or unique for the taxon?
 - Yes, based on the evidence stated for discreteness, SEAK is a unique habitat, intermediate between warmer southern habitat along the eastern Pacific and cooler habitat to the north.
- Would loss of this population segment result in a significant gap in the range of the taxon?
 - O Yes, loss of fish in an area this large will result in a gap in the taxon.
 - The area involved exceeds normal territorial size of herring by more than a factor of 2 and the distance of SEAK from Cross Sound to Dixon Entrance (roughly 500

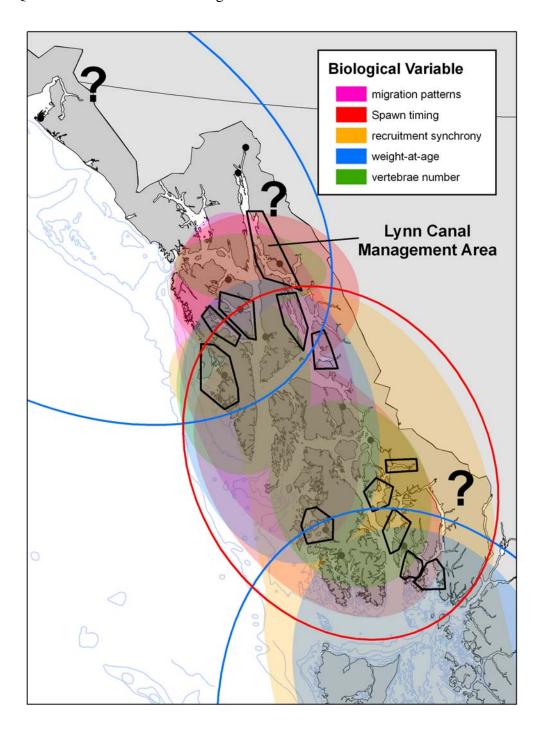
- km) exceeds the presumptive exposed beach barrier distance between Prince William Sound and Yakutat (400 km).
- Does SEAK represent the only surviving natural occurrence of Pacific herring?
 - o No, herring occupy natural habitat around the Pacific Ocean as far south as California in N. America and Korea in Asia and north into the Arctic Ocean, extending nearly to Norway (Chapter 2, Fig. 2.2).
- Do SEAK stock differ genetically from other Pacific herring stock?
 - O Yes and no. Evidence suggests that SEAK stock is different from British Columbia stock (Beacham et al. 2002) but not different from nearby Gulf of Alaska stocks to the north and west (Grant and Utter 1984). One study found evidence of genetic structure within Prince William Sound (Burkey 1986), raising the possibility a more detailed study with modern techniques may reveal differences between these stocks and SEAK stock. However, subsequent study demonstrated that DNA data provide no evidence of stable differentiation among Pacific herring populations within sea basins on spatial scales of up to ~700 km, rather temporal variation was dominant (Seeb et al. 1999).

References

- Arthur, J. R. and H. P. Arai 1980. Studies on the parasites of Pacific herring (*Clupea harengus pallasi* Valenciennes): a preliminary evaluation of parasites as indicators of geographical origin for spawning herring. Can J Zool 58: 521-527.
- Beacham, T. D., J. F. Schweigert, C. MacConnachie, K. D. Le, K. Labaree and K. M. Miller 2002. Population structure of herring (*Clupea pallasi*) in British Columbia determined by microsatellites, with comparisons to southeast Alaska and California, Fisheries and Oceans Canada, Canadian Science Advisory Secretariat.
- Blankenbeckler, D. and R. Larson 1987. Pacific herring (*Clupea harengus pallasi*) harvest statistics, hydroacoustical surveys, age, weight, and length analysis, and spawning ground surveys for southeastern Alaska, 1980-1983. Juneau, Alaska Department of Fish and Game, Division of Commercial Fish. Technical Data Report 202: 121.
- Burkey, C. J. 1986. Population structure of Pacific herring (*Clupea harenqus pallasi*) in Eastern Prince William Sound, Alaska, University of Alaska, Juneau. masters.
- Carls, M. G., G. D. Marty, T. R. Meyers, R. E. Thomas and S. D. Rice 1998. Expression of viral hemorrhagic septicemia virus in prespawning Pacific herring (*Clupea pallasi*) exposed to weathered crude oil. Can J Fish Aquat Sci 55(10): 2300-2309.
- Carls, M. G., S. D. Rice and J. E. Hose 1999. Sensitivity of fish embryos to weathered crude oil: Part I. Low-level exposure during incubation causes malformations, genetic damage, and mortality in larval Pacific herring (*Clupea pallasi*). Environ Toxicol Chem 18(3): 481-493.
- Carlson, H. R. 1980. Seasonal distribution and environment of Pacific herring near Auke Bay, Lynn Canal, southeastern Alaska. Trans Am Fish Soc 109(1): 71-78.
- Dahlgren, E. H. 1936. Further developments in the tagging of the Pacific herring, *Clupea pallasii*. J Conseil 11: 229-247.

- Grant, W. S. 1986. Biochemical genetic divergence between Atlantic, *Clupea harengus*, and Pacific, *C. pallasi*, herring. Copeia 1986: 714-719.
- Grant, W. S. and F. M. Utter 1984. Biochemical population genetics of Pacific herring (*Clupea pallasi*). Can J Fish Aquat Sci 41(6): 856-864.
- Haegele, C. W. and J. F. Schweigert 1985. Distribution and characteristics of herring spawning grounds and description of spawning behavior. Can J Fish Aquat Sci 42: 39-55.
- Hay, D. E., P. B. McCarter and K. S. Daniel 2001. Tagging of Pacific herring *Clupea pallasi* from 1936-1992: a review with comments on homing, geographic fidelity, and straying. Can J Fish Aquat Sci 58(7): 1356-1370.
- Hay, D. E. and S. M. McKinnell 2002. Tagging along: association among individual Pacific herring (*Clupea pallasi*) revealed by tagging. Can J Fish Aquat Sci 59(12): 1960-1968.
- Johnson, S. W., M. G. Carls, R. P. Stone, C. C. Brodersen and S. D. Rice 1997. Reproductive success of Pacific herring, *Clupea pallasi*, in Prince William Sound, Alaska, six years after the *Exxon Valdez* oil spill. Fish Bull 95(4): 748-761.
- Kobayashi, T. 1993. Biochemical analyses of genetic variability and divergence of populations in Pacific herring. Bull Nat Res Inst Far Seas Fish 30: 1-77.
- O'Connell, M., M. C. Dillon, J. M. Wright, P. Bentzen, S. Merkouris and J. Seeb 1998. Genetic structuring among Alaskan Pacific herring populations identified using microsatellite variation. J Fish Biol 53(1): 150-163.
- Pritchett, M., K. Monagle and D. Harris 2008. Berners Bay area herring research, 2007, Alaska Department of Fish and Game, Division of Commercial Fisheries: 1-10.
- Rounsefell, G. A. and E. H. Dahlgren 1935. Races of herring, *Clupea pallasii*, in southeastern Alaska. Bull Bureau Fish 17.
- Seeb, J., S. E. Merkouris, L. W. Seeb, J. B. Olsen, P. Bentzen and J. M. Wright 1999. Genetic discrimination of Prince William Sound herring populations. Anchorage, AK, Alaska Department of Fish and Game, Genetics Laboratory: 1-111.
- Ware, D. M. and C. Tovey 2004. Pacific herring spawn disappearance and recolonization events, Fisheries and Oceans Canada, Canadian Science Advisory Secretariat: Online at http://www.dfo-mpo.gc.ca/csas/CSAS/DocREC/2004/RES2004_008_E.pdf.
- Williams, E. H. and T. J. Quinn 2000. Pacific herring, *Clupea pallasi*, recruitment in the Bering Sea and northeast Pacific Ocean, I: relationships among different populations. Fish Oceanogr 9(4): 285-299.

Fig. 5.1. Summary of biological information (colored overlays); migration, spawn timing, vertebrae number, recruitment, and weight at age, together with stock management areas (black polygons). The blue ellipses are genetic groupings estimated with allozyme analysis (Grant and Utter 1984); the red ellipse is the SEAK grouping (microsatellite) estimated by Beacham et al. (2002). Question marks indicate missing information.



Appendix A Summary of Pacific herring genetic studies

Robin Waples

Over the last three decades, a number of molecular genetic studies have considerably advanced the understanding of the population structure of herring. Based on the level of differentiation observed at 40 allozyme loci, Grant (Grant 1986) estimated that Pacific herring (*Clupea pallasii*), and Atlantic herring (*C. harengus*) have been isolated since the mid to late Pliocene. This estimated divergence time is consistent with results of a subsequent study based on ribosomal DNA (Domanico et al. 1996).

Within *C. pallasii*, the contrast between populations from Asia and the eastern Bering Sea versus those from the rest of North America provides by far the strongest evidence for population genetic differentiation (Grant and Utter 1984)—with genetic differences about one-tenth as large as those between Pacific and Atlantic herring (Grant 1986). These two studies considered 21 populations from Asia (Korea, Japan, USSR), northeast and southeast Bering Sea, the Gulf of Alaska (including Lynn Canal), and the eastern North Pacific (from Helm Bay to San Francisco). Kobayashi (Kobayashi 1993), based on almost 2400 individuals from 18 populations from the Yellow Sea to California sampled for 25 allozyme loci, and O'Connell et al. (O'Connell et al. 1998), based on 350 herring from 7 locations from Norton Sound to Prince William Sound assayed for 5 microsatellite loci, also identified the Bering Sea – Gulf of Alaska split as representing the major genetic feature within Pacific herring.

Considering only populations east and south of the Alaska Peninsula, evidence for population genetic structure is relatively weak. Both Grant and Utter (Grant and Utter 1984) and Kobayashi (Kobayashi 1993) found that genetic differences among populations covering the large geographic area from San Francisco to Kodiak Island were only about 1/10th as large as those between Gulf of Alaska and Bering Sea populations. Within this large area in the eastern North Pacific, a number of studies have looked at more fine-scale population genetic structure.

In a master's thesis, Burkey (Burkey 1986) evaluated genetic structure within eastern Prince William Sound herring based on 14 allozyme loci and samples taken in 1979 to 1981 from both the winter bait/food and spring sac-roe fisheries. Burkey (Burkey 1986) found no statistically significant allele frequency differences between samples within fisheries, between years within fisheries, or between fisheries. The O'Connell et al. (O'Connell et al. 1998) study cited above included four collections from Prince William Sound, each consisting of 50 fish sampled in one year only. They found little evidence for population structure among the samples from St Matthew's Bay, Fish Bay, and Rocky Bay, but the sample from Port Chalmers was genetically distinct from the other Prince William Sound samples. [There were no obvious differences in size at age among fish sampled by Johnson et al. (Johnson et al. 1997) from these same four locations in the same year,1995; reproductive success was good and did not vary significantly among location.]

In British Columbia, Schweigert and Withler (Schweigert and Withler 1990) used 7 allozyme loci to examine relationships among 12 samples (> 1000 fish total) taken in sac-roe fisheries in 1985 and 1986 from three geographic areas (Strait of Georgia, west coast Vancouver Island, and north coast). Although they found statistically significant heterogeneity of allozyme allele frequencies among the three areas and among regions within the Strait of Georgia, the absolute levels of differentiation were modest. Furthermore, a gene diversity analysis showed that temporal differences between years within collection sites were nearly as large as

differences between sites within years. Schweigert and Withler (Schweigert and Withler 1990) also reported results of restriction enzyme analysis of mtDNA from a much smaller number (31) of individuals collected in 1984. This small study provided no evidence of major population subdivision but had little power to detect subtle differences.

Beacham et al. (Beacham et al. 2002) presented results of a much more ambitious study of variation at 13 microsatellite loci among 20,000 herring taken from spawning aggregations at 83 localities (75 in British Columbia, 5 in SE Alaska, one from Washington (Cherry Point), and two from California). About a third of the locations were sampled in more than one year. In agreement with results reported by previous authors for allozymes, the overall level of differentiation was very low ($F_{ST} = 0.0032^{1}$). Beacham et al. (Beacham et al. 2002) found no evidence of stock structure within a number of the geographic areas they sampled (W. Queen Charlotte Islands, North Coastal, Central Coastal, Johnstone Strait, W. Vancouver Island). Samples from a few locations (Skidegate Inlet and Louscoone Inlet (Q. Charlotte Islands), and Portage Inlet/Esquimault Harbour (Strait of Georgia)) were locally distinctive. Beacham et al. (Beacham et al. 2002) also found evidence for some modest differences between herring from different geographic regions (Johnstone Strait vs other B.C. populations; S.E. Alaska vs Queen Charlotte Islands and Northern B.C.; California vs B.C.). Except for the comparisons involving the samples from Skidegate Inlet and Portage Inlet/Esquimault Harbour, allele frequency differences between temporal samples from the same locality were as larger or larger than those for geographic comparisons between localities.

In a brief unpublished report for WDFW, Bentzen (Bentzen 2004) provided a "Preliminary summary" of analysis of mtDNA sequences from 458 herring from five localities in Puget Sound, including one (Cherry Point) sampled in two years. Samples from Norton Sound, Prince William Sound, British Columbia (Denman/Hornby), and San Francisco Bay were also included as outgroups. The two most common haplotypes were found in all populations. An analysis of molecular variance (AMOVA) found no significant differences among all the samples combined. After lumping some rare haplotypes, however, the analysis was repeated and (barely) statistically significant differences were found among the Puget Sound collections. Including the more geographically distant B.C., Alaskan and Californian samples in the analysis increased the level of differentiation (and the significance level of the heterogeneity test) only slightly. Pairwise tests indicated that the pooled samples from Cherry Point were the most distinctive within Puget Sound.

Small et al. (Small et al. 2005) used data for 12 microsatellite loci to examine genetic variation in samples of over 1000 herrring from five sites in Puget Sound, one in southern Strait of Georgia, and one in California. An AMOVA found significant evidence for population structure, with variance associated with geography about twice as large as that associated with temporal samples from the same locality. Geographic differences were primarily due to two populations (Cherry Point and Squaxin Pass) for which temporal samples showed a consistent pattern of genetic differentiation. In Cherry Point, the isolating mechanism appears to be an unusually late spawn timing, whereas it was hypothesized that physical isolation was responsible for the relative distinctiveness of samples from Squaxin Pass. In a subsequent master's study, Mitchell (2006) examined temporal patterns of population structure with 12 microsatellite DNA loci over the years 1999-2005 in many of the same populations surveyed by Small et al (2005). Herring samples from Cherry Point remained genetically differentiated over this time period;

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 $^{^{1}}$ F_{ST} takes values between 0 and 1 and indicates the fraction of overall genetic variance that is due to differences among samples.

however, no significant genetic differences were found between Squaxin Pass and other Puget Sound samples in 2005, with the exception of Cherry Point (Mitchell 2006).

No studies focused specifically on herring from Southeast Alaska, although samples from that area were included in studies by Grant and Utter (Grant and Utter 1984), Kobayashi (Kobayashi 1993), and Beacham et al. (Beacham et al. 2002). As noted above, Beacham et al. (Beacham et al. 2002) found evidence for modest differences between herring sampled from S.E. Alaska and those from the Queen Charlotte Islands and Northern B.C. The Grant and Utter (Grant and Utter 1984) study is the only one to report data for Lynn Canal herring; they did not comment on this sample specifically, and a review of their results does not suggest anything particularly distinctive about Lynn Canal herring.

Discussion

Collectively, results summarized above have demonstrated the following points:

- Atlantic and Pacific herring are characterized by genetic differences that are consistent with a separation of a few million years.
- Within Pacific herring, by far the largest genetic distinction is found between populations from Asia and the Bering Sea versus the rest of North America. With the exception of some differentiated populations from the Alaskan Peninsula, genetic differences among localities within these two major lineages are smaller by an order of magnitude or more.
- Among herring from the Alaska Peninsula to California, some very modest evidence of population structure exists. Herring from some geographic areas can be distinguished in a statistical sense from herring from other areas.
- Some studies included temporal replication of samples from specific areas; in some cases allele frequency differences between years were as large or larger than those between localities. In other cases, (e.g., Cherry Point and perhaps Squaxin Pass) these replicated samples provide consistent evidence for population subdivision. Physical or behavioral isolation may explain consistent genetic differences. There is good evidence, therefore, that some populations in some geographic areas are locally distinctive genetically, albeit on a scale that is modest compared to the differences found between the two major lineages of Pacific herring.

Gustafson et al. (Gustafson et al. 2006) included a useful discussion of some factors that influence how one should interpret genetic data for Pacific herring, or for any species with very large population sizes. Some of those points are summarized here. At presumably neutral markers such as those discussed here, population genetic differentiation (as measured by indices such as F_{ST}) is a function of the product of the effective population size (N_e) and the migration rate (m = fraction of the population that migrates each generation). Based on Wright's (Wright 1978) commonly used (albeit very rough) approximation that at equilibrium, $F_{ST} = 1/(1+4N_e m)$, the $F_{ST} = 0.0032$ reported by Beacham et al. (Beacham et al. 2002) for NE Pacific herring implies $N_e m \sim 78$ migrant individuals per generations. In a small population, that could represent a high migration rate (m), but in a population with 10^6 individuals it equates to $m = 7.8 \times 10^{-5}$ – that is, less than one individual in ten thousand is a migrant each generation. Because of the inverse relationship between F_{ST} and $N_e m$ and the numerous assumptions underlying Wright's formula, robust estimation of migration parameters associated with low F_{ST} values is very difficult (Waples 1998; Whitlock and McCauley 1999), so any quantitative estimates should be treated with caution. Nevertheless, the point remains that in very large populations, very low

levels of genetic differentiation could be associated with migration rates that have little influence in shaping the demographic parameters of the population. That is, large populations might be demographically independent but have only very modest levels of population genetic differentiation. Whether this scenario represents one in which it is reasonable to identify different 'populations' is not a question that has a single, scientifically correct answer; rather, the conclusions one draws for any practical application should be guided by the conservation/management goals one is trying to achieve and the concept of 'population' that is most suitable to that application (Waples and Gaggiotti 2006).

References

- Beacham, T. D., J. F. Schweigert, C. MacConnachie, K. D. Le, K. Labaree and K. M. Miller 2002. Population structure of herring (*Clupea pallasi*) in British Columbia determined by microsatellites, with comparisons to southeast Alaska and California, Fisheries and Oceans Canada, Canadian Science Advisory Secretariat.
- Bentzen, P. 2004. Analysis of mtDNA polymorphism in Puget Sound herring: A preliminary summary provided for WDFW. March 13, 2004, memorandum. Portland, OR, National Marine Fisheries Service, Protected Resources Division.
- Burkey, C. J. 1986. Population structure of Pacific herring (*Clupea harenqus pallasi*) in Eastern Prince William Sound, Alaska, University of Alaska, Juneau. masters.
- Domanico, M. J., R. B. Phillips and J. F. Schweigert 1996. Sequence variation in ribosomal DNA of Pacific (*Clupea pallasi*) and Atlantic herring (*Clupea harengus*). Can J Fish Aquat Sci 53: 2418-2423.
- Grant, W. S. 1986. Biochemical genetic divergence between Atlantic, *Clupea harengus*, and Pacific, *C. pallasi*, herring. Copeia 1986: 714-719.
- Grant, W. S. and F. M. Utter 1984. Biochemical population genetics of Pacific herring (*Clupea pallasi*). Can J Fish Aquat Sci 41(6): 856-864.
- Gustafson, R. G., J. Drake, M. J. Ford, J. M. Myers, E. E. Holmes and R. S. Waples 2006. Status review of Cherry Point Pacific herring (*Clupea pallasii*) and updated status review of the Georgia Basin Pacific herring distinct population segment under the Endangered Species Act. Seattle, WA, Northwest Fisheries Science Center: 182.
- Johnson, S. W., M. G. Carls, R. P. Stone, C. C. Brodersen and S. D. Rice 1997. Reproductive success of Pacific herring, *Clupea pallasi*, in Prince William Sound, Alaska, six years after the *Exxon Valdez* oil spill. Fish Bull 95(4): 748-761.
- Kobayashi, T. 1993. Biochemical analyses of genetic variability and divergence of populations in Pacific herring. Bull Nat Res Inst Far Seas Fish 30: 1-77.
- Mitchell, D. M. 2006. Biocomplexity and metapopulation dynamics of Pacific herring (*Clupea pallasii*) in Puget Sound, Washington. Seattle, University of Washington. Masters: 75.
- O'Connell, M., M. C. Dillon, J. M. Wright, P. Bentzen, S. Merkouris and J. Seeb 1998. Genetic structuring among Alaskan Pacific herring populations identified using microsatellite variation. J Fish Biol 53(1): 150-163.
- Schweigert, J. F. and R. E. Withler 1990. Genetic differentiation of Pacific herring based on enzyme electrophoresis and mitochondrial DNA analysis. Am Fish Soc Symp 7: 459-469.
- Small, M. P., J. L. Loxterman, A. E. Frye, J. F. Von Bargen, C. Bowman and S. F. Young 2005. Temporal and spatial genetic structure among some Pacific herring populations in Puget Sound and the southern Strait of Georgia. Trans Am Fish Soc 134(5): 1329-1341.

- Waples, R. S. 1998. Separating the wheat from the chaff: patterns of genetic differentiation in high gene flow species. J Hered 89(5): 438-450.
- Waples, R. S. and O. Gaggiotti 2006. What is a population? An empirical evaluation of some genetic methods for identifying the number of gene pools and their degree of connectivity. Mol Ecol 15: 1419-1439.
- Whitlock, M. C. and D. E. McCauley 1999. Indirect measures of gene flow and migration: FST doesn't equal 1/(4Nm+1). Heredity 82: 117-125.
- Wright, S. 1978. Evolution and the genetics of populations. Chicago, University of Chicago Press.

Appendix B Analysis of ADFG age-length-weight data

Data

- Were supplied by ADFG.
- Data structure is complex
 - o e.g., many collection sites, times, collection methods, variable levels of fish maturity, age, gender.

Data restrictions

- Analysis was restricted to fish length
 - o This avoids probable mass changes before, during, and after spawning
- Data were restricted to months of spawn (March, April, May)
 - o The majority of the data were collected in either March-April or April May
 - o Distribution of these collection times corresponded exactly to sites classified as either relatively early or relative late spawners in southeastern Alaska (Fig. 3.14).
- Data were restricted to collections at active spawning.
 - o This ensured that measured fish were spawners at or near capture sites, not transients
 - o This should minimize variance in fish condition at the time of measurement
- Data were restricted to records where fish ages were determined (the vast majority of the data) and where age>2.
- Several likely errors were detected (length of mature fish <50 mm); these data were excluded

Results

Number of samples

stock	n	months	onths years	
Sitka	18294	Mar – Apr	1983 - 2007	19
Lynn Canal	2395	Apr – May	1983 - 2007	7
Craig	7169	Mar – Apr	1981 - 2007	15
Ernest Sound	3319	Apr	1988 - 2007	10
Hobart-Houghton	5777	Apr – May	1995 - 2007	12
Hoonah Sound	5533	Apr – May	1981 - 2007	13
Kah Shakes	11091	Mar – Apr	1997 – 2006	21
Seymour Canal	13153	Apr – May	1997 – 2007	24
West Behm	7189	Apr	1995 - 2007	13
Tenakee	5051	Apr – May	1983 - 2007	13
total	78971			

• Initial results, 3-factor ANOVA (year \times age \times sex)

year 0.0001 sig age 0.0001 sig

```
sex 0.5555 not sig
year*age 0.0001 sig
year*sex 0.4743 not sig
age*sex 0.8598 not sig
year*age*sex 0.7525 not sig
```

• preliminary conclusion: gender is not important, drop this parameter from the model

Size at age trend analysis

- Purpose: compare trends in length at age
- Method
 - o calculate deviations from mean length (mean by stock, age) (Fig. B.1)
 - o summarize by plotting mean deviates vs year where age>2 and age<8.
 - Age was restricted because relatively few fish were present in older year classes (the minimum n = 30 in the final analysis)
 - o Cubic splines (of mean time series) were the best general description of trends
- Results
 - o Stocks are grouped by geographic adjacency (Fig. B.2)
 - o Size at age is currently declining at all sites
 - o An increase in size at age was evident in the 1980s or 1990s at some sites
 - o Trends in Lynn Canal herring were about the same as those in Seymour Canal

Growth rate

- Purpose: compare growth rates among SEAK herring stock
- Model
 - o Regress In(length) on In(year base year) by stock and cohort (power model)
 - \circ Cohort = observation year (fish age 3)
 - o Base year = cohort 1
 - o Growth rate was not estimated for cohorts where the number of measurements was not ≥ 15 in at least 3 y.

Results

- o The number of growth rate estimates for each stock ranged from 3 to 24 (see Fig. B.1 and Table B.1).
- o Lynn Canal had the fewest estimates.
- o Mean growth rates ranged from 0.107 to 0.142 [ln(mm)/ln(year)] and were not significantly different among stocks (P = 0.577).
 - Two-factor ANOVA (stock × cohort) was disconnected (growth of all cohorts was not estimable in all stocks), thus the model could only be run without an interaction term.
 - Growth rate differences among cohorts were significant (P < 0.001).
 - The same conclusion, that growth rate does not vary significantly among stocks (P = 0.223), is reached when the analysis is restricted to cohorts where growth rates in Lynn Canal were estimable (1983, 1995, and 1996).

Table B.1. Mean cohort growth rates by stock [ln(mm)/ln(year)].

		mean	95% confidence		
stock	n	rate	bounds		
Sitka	18	0.127	0.114	0.139	
Lynn Canal	3	0.142	0.098	0.186	
Craig	12	0.115	0.100	0.130	
Ernest Sound	9	0.110	0.087	0.133	
Hobart-Houghton	12	0.107	0.079	0.135	
Hoonah	10	0.114	0.097	0.130	
Kah Shakes	19	0.134	0.117	0.151	
Seymour Canal	24	0.136	0.121	0.151	
West Behm	14	0.107	0.090	0.124	
Tenakee	12	0.123	0.103	0.143	

Fig. B.1. Example length data, summarized with means by age class and overlain with deviation in length (estimated across age classes 3 through 8).

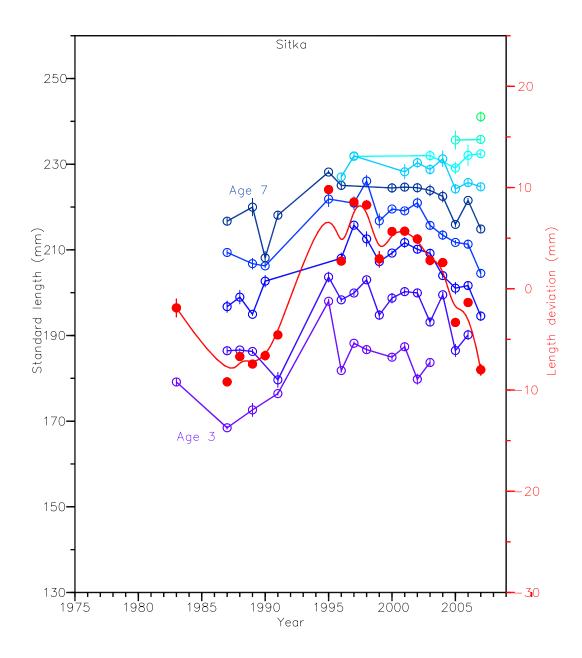


Fig. B.2. Smoothed mean (±SE) trends in length at age in SEAK herring stocks.

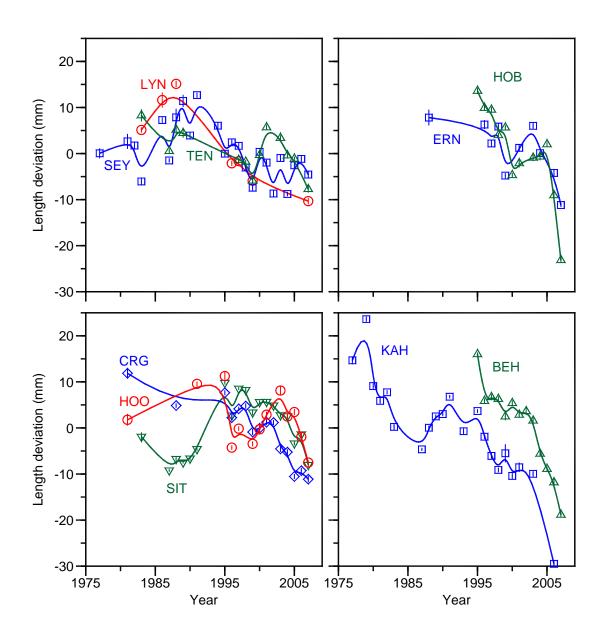


Fig. B.3. Cohort growth in northern SEAK (power model). Individual cohorts are distinguished by color, symbol shape, and symbol fill. Symbol sizes correspond to the number of measurements (the largest indicate >100, the smallest ≤ 10).

