Indications of habitat use patterns among small cetaceans in the central North Pacific based on fisheries observer data

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ABSTRACT

Biological specimens and environmental data collected by observers monitoring Japanese squid driftnet fishing operations during the summers of 1990 and 1991 in the central North Pacific (37°N-46°N, and 170°E-150°W) were used to explore habitat use patterns among three small cetacean species common to that area: the Dall's porpoise (*Phocoenoides dalli*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) and northern right whale dolphin (*Lissodelphis borealis*). Sex and maturity status were determined for 805 northern right whale dolphins, 421 Pacific white-sided dolphins and 206 Dall's porpoises incidentally taken in 800 observed gillnet sets, allowing sub-taxon comparisons of habitat use patterns. Habitat variables were based on observer records of sea surface temperature (SST), wind velocity and direction, and swell height. Current velocity and direction and SST gradients were also derived. Canonical Correspondence Analysis (CCA) was used to relate the species categories to the habitat conditions recorded for the gillnet operations in which entanglements occurred. The samples collected from the southern, middle and northern latitudes within the overall study area were examined separately to account for northward movement of the fishing fleets across the summer months. SST was the most dominant and consistent feature; northern right whale dolphins occupied the warmest waters, Dall's porpoises the coldest; Pacific white-sided dolphins were found in-between, but more similar to the latter. Wind velocity and swell height also reflected potentially important habitat features. Young-of-the-year northern right whale dolphin showed a preference for the warmest waters observed in the middle latitude band, coincident with that species summer calving mode.

KEYWORDS: DALL'S PORPOISE; NORTHERN RIGHT WHALE DOLPHIN; PACIFIC WHITE-SIDED DOLPHIN; HABITAT; ECOSYSTEMS; BYCATCH; DISTRIBUTION

INTRODUCTION

The vast pelagic environment of the North Pacific provides habitat for a variety of often seen but infrequently studied porpoise and dolphin taxa. The three most common cetacean species in the central North Pacific (Hobbs and Jones, 1993), the northern right whale dolphin (*Lissodelphis borealis*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) and Dall's porpoise (*Phocoenoides dalli*), share broadly overlapping distributions. The Dall's porpoise, principally a cold temperate and sub-arctic species of the North Pacific and adjacent seas, ranges from the Bering Sea south to 41°N in pelagic waters (Morejohn, 1979; Kasuya and Jones, 1984). The Pacific white-sided dolphin occurs across temperate Pacific waters, to latitudes as low or lower than 38°N, and northward to the Bering Sea (Leatherwood *et al*., 1984; Walker *et al*., 1984) and coastal areas of southeast Alaska (Dahlheim and Towell, 1994). The northern right whale dolphin is endemic to the North Pacific, ranging from approximately 30°N to 50°N in the eastern Pacific (Leatherwood and Walker, 1979) and 35°N to 51°N in the western Pacific (Sleptsov, 1961; Nishiwaki, 1967; Kasuya, 1971). Kajimura and Loughlin (1988) reported isolated sightings of northern right whale dolphins as far north as 52°N in the southwestern Aleutian Islands. Aside from descriptions of their relative distributions, little else is known about the relationships among these species and the characteristics of their physical and biological habitats.

Over the past three decades, opportunistic sightings surveys and research effort associated with high seas driftnet fisheries have provided platforms for several studies of life history and population ecology for all three species (Buckland *et al*., 1993; Ferrero and Walker, 1993; 1996; 1999; Hiramatsu, 1993; Miyashita, 1993; Tanaka, 1993; Turnock and Buckland, 1995; Turnock *et al*., 1995). Movement patterns and stock structure of Dall's porpoises and Pacific white-sided dolphins have also been studied (Kasuya and Jones, 1984; Walker and Sinclair, 1990). Despite this, information on habitat use patterns for any of the three species is limited. Consequently, fundamental ecological questions remain unanswered, for example how do the distributions of these three species relate to habitat characteristics, and to what extent do they share or partition habitat? The objective of this paper, is to take an initial step toward answering these questions by using gillnet fisheries observer data to explore habitat use patterns. The relative levels of incidental take of these three species, across differing oceanographic and environmental conditions, provided the basis for comparisons.

Habitat partitioning studies often include diet as one of the dimensions reflecting differences among closely related species. Analyses of dietary data for these three species have not been completed but may eventually provide critical information on habitat partitioning. However, preliminary results suggest very little difference in diet (based on stomach contents analyses) of northern right whale and Pacific white-sided dolphins (Walker and Jones, 1993) while the prey of Dall's porpoises may differ slightly (Crawford, 1981; William A. Walker, pers. comm.). Likewise, anecdotal evidence from sightings data suggests that all three species can be found in proximity to one another and that northern right whale dolphins and Pacific white-sided dolphins are commonly observed in mixed schools

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(Leatherwood and Walker, 1979; Leatherwood *et al*., 1982; 1984). Thus, most available information highlights the apparent similarities among the species rather than suggesting unique characteristics.

Empirical studies of species/habitat relationships have only recently been applied to marine mammals. Moore and DeMaster (1998) compared water depth and surface ice cover conditions associated with sightings of cetaceans in the Alaskan Arctic. Additional analyses of marine mammal habitat use patterns have employed the multivariate ordination technique known as Canonical Correspondence Analysis, CCA (see discussion in Ter Braak, 1986). Reilly and Fiedler (1994) applied CCA to sightings survey abundance data and oceanographic observations to compare habitat preferences among dolphin species in the Eastern Tropical Pacific. More recently, the same approach has been used to explore cetacean habitat partitioning in the California Current (Reilly *et al*., 1997) and in the Western Tropical Indian Ocean (Ballance *et al*., 1997).

Data reported here were collected in a broad segment of the North Pacific, ranging from approximately 150°W to 170°E and from 37° to 46°N. Oceanographic characteristics of the study area are summarised based on reviews of Uda (1963) and Dodimead *et al*. (1963). The primary habitat feature of the area is the Polar Front Region, located at approximately 45°N at 170°E and curving monotonically southward to approximately 42°N at 150°W. North of the Front, surface waters generally are of relatively low salinity (< 33.0%), with waters south of the front relatively more saline (> 33.8%). A significant feature of vertical structure north of the Front is a persistent halocline at depths of 80-150m. The halocline diminishes in intensity approaching the Front from the north, and is absent to the south. The latitudinal gradient in sea surface temperature (SST) across the Front is much stronger in the western than the eastern part of the study area. For example, at 175°E longitude, SST may increase from < 10°C to > 18°C over a north-to-south latitudinal interval of 4° during summer. At 155°W, summer SST may increase from < 11°C to > 20°C, but over a north-to-south latitudinal range of 10° or more. During summer, vertical temperature profiles north of the Front are dichothermal (*sensu* Uda, 1963). Temperature declines rapidly with depth to a temperature minimum of about 3°C at depths of 50-100m. Temperatures then rise to a secondary maximum of 5°C at approximately 120m, declining very slowly below that point with increasing depth. During winter months, SSTs decline by several degrees C, and mixing processes create isothermal and isohaline profiles in the upper 100m of the water column.

Surface circulation in the study area is dominated by the West Wind Drift north of the Polar Front and by the North Pacific Current to the south (Dodimead *et al*., 1963). The two currents set in parallel from west to east, with waters in the North Pacific Current noticeably warmer that those in the West Wind Drift. In both cases flow velocity diminishes from west to east. At their respective western extremes, the West Wind Drift receives input from the relatively cold Oyashio Current, and the North Pacific Current from the relatively warm Kuroshio Current.

While this study shares a similar objective with other cetacean habitat preference studies, the method differs in two ways. First, rather than using sightings data to measure relative abundance, mortality data were used (incidental kills in high seas driftnets); appropriate sightings data are not available. Second, the results of life history investigations on each of the three marine mammal species (Ferrero and Walker, 1993; 1996; 1999) provided the means to differentiate population components by sex and reproductive status, thus, allowing analysis of habitat use patterns both between and within species.

MATERIALS AND METHODS

Scientific observers stationed onboard Japanese squid driftnet vessels during 1990 and 1991 were trained to collect a standardised suite of data on each driftnet operation monitored (Fitzgerald *et al*., 1993). The data elements included spatial and temporal reference points for the beginning and ending of net sets and net retrievals, the amount of gear fished, target species and bycatch tallies, and simple oceanographic and environmental measures: SST, wind velocity (Beaufort stage), wind direction and swell height.

Driftnet data from the three summer months of the fishing season when observer sampling was greatest were included in these analyses. From 1 June to 30 September, 1990 and 1991, 800 of the driftnet operations monitored in the central North Pacific (37°N to 46°N and 170°E to 150°W) resulted in the catches of northern right whale dolphin, Pacific white-sided dolphin or Dall's porpoise.

Biological data, including species identification, total length and sex, were collected from all marine mammals entangled and brought onboard dead. All entangled animals that were still alive when brought onboard, were released immediately and are not represented in this analysis. Note that observer records did not indicate a species, species group or size bias in the animals released alive. Life history specimens including reproductive organs were collected in cases where the observer had been appropriately trained and assigned marine mammal necropsy duties. Collection protocols, and laboratory examination of reproductive samples for determination of sexual maturity status followed procedures in Perrin *et al.* (1976) and Ferrero and Walker (1993).

The relative distribution and abundance of marine mammal species represented by driftnet catch composition were related to habitat conditions using CCA, specifically the routine contained in the computer program CANOCO version 3.1 (Ter Braak, 1988). CCA fits a unimodal response curve for each column in the species matrix to each of a set of orthogonal axes of the environmental matrix. The technique then seeks the set of orthogonal axes that minimise the width of the unimodal response. It should be noted that a monotonic response is a special case of the unimodal in which the mode is outside the domain of the environmental data so that only one side of the unimodal is fit and symmetry along each axis is a reasonable assumption to limit the number of variables to be fit. The model and algorithm documentation are detailed in Ter Braak (1988), while Reilly and Fiedler (1994) summarised the technique as applied to marine mammals. CCA extracts orthogonal axes of variation in indices of abundance for multiple species collected at multiple locations, with axes constrained to be linear combinations of measured environmental variables. The significance of the species category and environmental data relationship (H_o: $\lambda = 0$) reflected by the first canonical axis was tested using a Monte Carlo randomisation test (1,000 repetitions) incorporated in the CANOCO program.

The CANOCO program requires that data be organised into two matrices: one containing species abundances and the other containing environmental data. The matrices are linked by the sample units, which in this case were represented by each gillnet operation where at least one northern right whale dolphin, Pacific white-sided dolphin or

Dall's porpoise was caught. Differences in the amount of gear set per operation were compensated for by expressing all abundance measures as catch per unit effort (CPUE):

$$CPUE = (C_{x,y}/T_y) \times 1{,}000$$

where C_x is the total catch of species x in set y and T_y is the total number of tans of net fished in set y (a tan is equal to a 50m long by 12m deep panel of gillnet). Since each gillnet operation employed approximately 60km of gillnet, this distance set the lower limit on the scale of environmental features that could be described in the study.

Using the available life history information, both inter- and intraspecific species-environmental relationships were examined. For each of the three species, sex and sexual maturity status were incorporated by classifying each specimen into one of four groups (male or female × sexually mature or immature). A 'young-of-the-year' category was added for northern right whale dolphins and Pacific white-sided dolphins which included only neonates and calves (< 1 year old). Young-of-the-year Dall's porpoises were not encountered. Thus, a total of 14 categories were established.

Where reproductive organs had been collected, the results of laboratory examinations of gonadal tissues determined sub-taxa category assignment with respect to sexual maturity status. However, to maximise the sample, specimens were also classified that had not been necropsied, but for which species identification, length and sex were known. For these cases, species- and sex-specific estimates of average length at sexual maturity (LSM) were used as the grouping criteria. To reduce classification error, specimens with lengths within 5cm of LSM were not included, although less than 5% of all length measurements fell in this interval. Specimens larger than LSM were considered mature; those smaller were classified as immature. The LSM estimates for northern right whale dolphin, Pacific white-sided dolphin and Dall's porpoise were based on the life history investigations of Ferrero and Walker (1993), Ferrero and Walker (1996) and Ferrero and Walker (1999), respectively.

The data analysis was divided into three separate CCA runs using samples collected in the southern (37°N-40°N), middle (40°N-43°N) and northern (43°N-46°N) latitude bands of the study area. The latitudinal stratification coincided with shifts in the fishing area occurring in response to regulatory openings or closings across the summer months (Nagao *et al*., 1993). These shifts created almost entirely distinct fishing grounds as reflected by the location of sampling within the three bands (Fig. 1).

Ideally, the environmental variables included in CCA should reflect the most characteristic habitat features influencing community structure (Ter Braak, 1988). The best set of environmental variables to describe the small cetacean habitats in this study were unknown. The fishery observers' records, specific to each gillnet set monitored, were used to define values of the best available environmental parameters. These are discussed below.

Sea surface temperature (SST)

Sea surface temperature (SST) was recorded directly by observers from the ship's thermograph at the beginning and end of each retrieval operation. The mean SST value was used if readings were different. The sensors were generally located near the ship's keel, at a depth of about 3-4m. The range of observed SST was 11.0° to 18.8°C.

Delta SST

Delta sea surface temperature (DSST) was the difference in the temperature readings from one end of the net to the other. A large difference in SST across the 60km (maximum) net (e.g. > 4.0°C) was considered an indication that the net crossed a thermal front. The DSST measurements ranged from 0.0-4.7°C.

Current velocity

The current velocity (*CV*) was calculated using the starting and ending times and positions of a chosen buoy marking a net end as:

$$CV = D/t_2\text{-}t_1,$$

where t_1 is the time of buoy deployment and t_2 is the time of buoy retrieval.

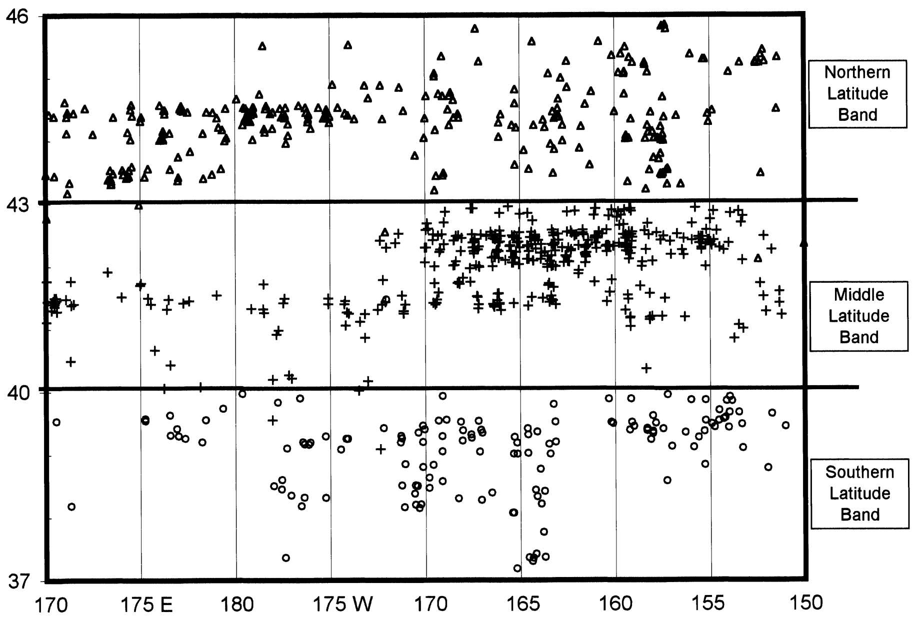


Fig. 1. Locations of Japanese driftnet fishing operations that resulted in one or more observed entanglements of Dall's porpoise (*Phocoenoides dalli*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) or northern right whale dolphin (*Lissodelphis borealis*) during 1990 and 1991. The circles, crosses and triangles represent the sampling locations for the southern, middle and northern latitude data sets, respectively.

The distance travelled by the buoy (D) was calculated as:

$$D = (60 \times (180/\pi) \times \arccos(\sin lat_1) \times \sin lat_2) + (\cos lat_1 \times \cos lat_2 \times \cos(lon_2 - lon_1))$$

where lat_1 is the latitude of the initial position, lat_2 is the latitude of the ending position, lon_1 is the longitude of the initial position and lon_2 is the longitude of the ending position. The variables lat_1, lat_2 and the term ($lon_2 - lon_1$) are expressed in radians.

The drift of that particular buoy was assumed to represent the general velocity of the water mass containing the net. Current velocities up to 6.0 knots were calculated.

Current direction

Current direction was broken into two components (east/west and north/south) because the non-linear measurement from 0-359 degrees would represent a confounded gradient in the CCA (i.e. both ends of the scale, 0 and 359 degrees represented virtually the same wind direction). Instead, since the mean current direction in the study area was eastward, corresponding to the dominant flows of the West Wind Drift and the North Pacific Current (Dodimead *et al*., 1963; Pickard and Emery, 1991), variations from this norm, suggesting possible eddies or counter-currents, were considered potentially important habitat features. The east/west aspect was calculated as the cosine of the angular direction. Strong deviation from an easterly flow would suggest a counter-current. The north/south aspect was characterised, without regard to direction, as the absolute value of the sine of angular direction. This approach assumed that currents flowing northward rated the same importance as currents flowing southward as habitat features.

Wind velocity

Wind velocity was recorded by observers using the Beaufort scale at the beginning of the net retrieval operation and up to four additional times thereafter. When conditions changed during the operation, an average value, rounded to the nearest whole number, was used. Higher wind velocities were considered indicative of local storm activity, which could give rise to greater surface mixing. Observed wind velocities ranged from Beaufort 0 (0-1kt, $<3\text{ms}^{-1}$) to Beaufort 7 (28-33kt, $13.9\text{-}17.1\text{ms}^{-1}$).

Wind direction

Wind direction was broken into north/south and east/west components following the same logic described for current direction. The prevailing winds in the study area were from the west, so that winds from the north, south or east deviating from the norm were considered possible stimuli for enhanced surface mixing. Like current direction, the east/west aspect was calculated as the cosine of the angular direction and the north/south aspect as the absolute value of the sine.

Swell height

Swell height was estimated directly by observers and recorded as distance from trough to crest. It provided an index to storm activity beyond the local area and up to several days earlier. Its local effect would have been an increase in surface mixing. Estimated swell heights ranged from 0-10m.

These definitions resulted in nine environmental parameters (including both the north/south and east/west aspects of parameters 4 and 6) that could be quantified and included in the CCA analyses. Although several were considered potential causes of enhanced surface mixing and higher productivity levels, they were treated as separate parameters to explore possible differences in their relative importance.

Interpretation of CCA plots

For each of the three CCA analyses, a plot was generated to show the relative positions of species categories in ordination space as well as their relationships to the first two orthogonal axes and the environmental parameters. Each species category was given a different symbol and its eigenvalue plotted on Axis 1 and Axis 2. The environmental gradients were represented by vectors from the origin. In general, the longer the vector the greater of the variance represented by the eigenvalues that it could explain. Similarly, the eigenvalues most closely aligned with and farthest out along a particular vector, indicated the strongest relationship between the species and the habitat described by the environmental feature. The degree of similarity between species habitat selection patterns was described by ranges about each eigenvalue based on 'species tolerance values' calculated by CANOCO. These values represent the approximate measures of the species response curves along a particular ordination axis (Smilauer, 1992) and are analogous to the 95% confidence limits for the species loadings as used by Reilly and Fiedler (1994). In short, they define the area of the ordination around each species that reflects the habitat characteristics where that species was caught. Overlapping tolerance ranges, thus, indicate habitats shared by two or more species categories, while discrete tolerance ranges suggest occupation of different habitat types (i.e. habitat partitioning).

RESULTS

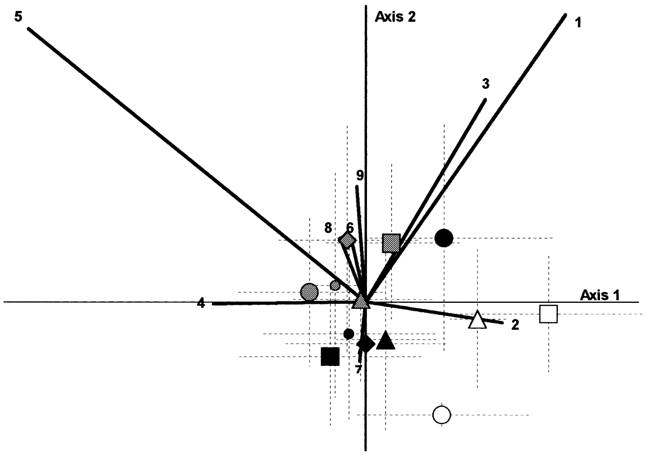
A total of 800 observed fishing operations resulted in catches of one or more of the three small cetacean species, including 143 sets in the southern, 384 in the middle and 273 in the northern latitude bands. These operations resulted in 1,432 incidental catches, comprising of 805 northern right whale dolphins, 421 Pacific white-sided dolphins and 206 Dall's porpoise (Table 1).

Across the three CCA runs, the gradient of SST was the most pronounced environmental feature underlying the placement of species categories, and was highly correlated with one of the first two orthogonal axes. Wind velocity (Beaufort scale) also appeared to be a relevant habitat feature. Wind velocity tended to be more strongly correlated with the first orthogonal axis if SST was correlated with the second axis, and vice versa. To a lesser degree (i.e. based on r-values), swell height and deviations in wind direction to the north or south of the predominant westerlies (i.e. wind N/S) were also relevant, and generally aligned with the gradient in wind velocity. Compared to these environmental parameters, those describing current velocity, current direction or differences in sea surface temperature across the length of a driftnet (DSST) were poorly correlated with either of the first two orthogonal axes and inconsistent in terms of their alignment with the other environmental parameters across latitude in the three CCA runs. Thus, the following descriptions of each ordination plot focus primarily on the relationships between the dominant environmental gradients and the species eigenvalues.

Table 1

Numbers of marine mammals by species, category, latitude band included in each of the three CCA runs analysing dolphin and porpoise species relative abundance (as reflected by incidental catch data) and environmental data collected in high seas driftnets during June-August 1990 and 1991 in the central North Pacific Ocean.

Species	Latitude Band			
	Southern	Middle	Northern	Total
L. borealis				
Mature males	13	63	35	
Immature males	33	116	65	
Mature females	26	137	94	
Immature females	27	102	49	
Young-of-the-year	2	9	34	
Total	101	427	277	805
L. obliquidens				
Mature males	13	21	22	
Immature males	18	41	45	
Mature females	12	19	23	
Immature females	18	38	50	
Young-of-the-year	37	46	18	
Total	98	165	158	421
P. dalli				
Mature males	7	42	17	
Immature males	0	42	20	
Mature females	3	6	15	
Immature females	3	24	27	
Total	13	114	79	206
Grand total	212	706	514	1,432



Species	Male		Female		Young-of-the-year
	Mature	Immature	Mature	Immature	
Dall's porpoise	◇	q	❍	△	
Pacific white-sided dolphin	u	n	l	s	l
Northern right whale dolphin	u	n	l	s	l

Fig. 2. Species ordination diagram for CCA run 1, the southern latitude band (37°N to 40°N), relating species category occurrence along environmental gradients associated with the first two canonical axes. Species tolerance limits are represented by the dashed lines. Vectors representing each environmental vector are indicated by the solid dark lines and labelled as follows: (1) Beaufort wind velocity; (2) swell; (3) wind direction (N/S); (4) wind direction (E/W); (5) sea surface temperature; (6) delta sea surface temperature; (7) current velocity; (8) current direction (N/S); and (9) current direction (E/W).

The southern latitude band

A total of 143 fishing operations were sampled from 37°N to 40°N, and 170°E to 150°W, representing the southern extent of the fishing grounds typical of early summer (i.e. June) (Fig. 1). All species categories except immature male Dall's porpoises were represented in the sample. The percentage of variance explained by Axis 1 and Axis 2 was 31.5% and 22.1%, respectively (Table 2).

Axis 1 showed a strong negative correlation with SST (r = -0.7452) (Table 3). The mature male, immature female and mature female Dall's porpoises occupied positive Axis 1 eigenvalues, suggesting a preference for cooler waters (Fig. 2). Of these, the mature female Dall's porpoises occupied the most extreme position (i.e. coolest waters) along the SST gradient. The opposite side of the SST gradient, corresponding to warm waters, was populated by all categories of northern right whale dolphin. Pacific white-sided dolphins filled in between the other two species, suggesting a range of SST preferences that included both the upper extreme for Dall's porpoise and lower extreme for northern right whale dolphin.

Axis 2 was most strongly correlated with wind velocity (r = 0.5815). The north/south deviation in wind direction (wind N/S) was closely aligned with wind velocity, but its correlation with Axis 2 was less pronounced (r = 0.4114) (Table 3). Northern right whale dolphin eigenvalues were all positive. With the exception of mature females, all Pacific white-sided dolphin eigenvalues were negative.

The tolerance ranges for all species overlapped those of at least one other species category in all cases. The overlap was typically broad, indicating shared occupation of habitats

Table 2

Ordination results from CCA run 1, the southern latitude band (37°N to 40°N), for dolphin and porpoise species relative abundance (as reflected by incidental catch data) and environmental data (wind speed, swell height, wind direction, sea surface temperature, current velocity and current direction) collected on high seas gillnet vessels during June-August 1990 and 1991 in the central North Pacific Ocean. Species-Environmental Total (Sp-Env) is the total species variation related to the environmental variables. 'Total variation' represents all variation in the species incidental catch data. The P-values are based on a Monte Carlo randomisation test (1,000 repetitions).

	Canonical axes				Sp-Env total	Total variation
	1	2	3	4		
Eigenvalues	0.273	0.192	0.155	0.114	0.734	9.091
P-values	<0.001				<0.001	
Species-environment correlations	0.550	0.483	0.405	0.377		
Cumulative percentage variance						
Species-environment relation	31.5	53.6	71.5	84.7		
Total species data	3.0	5.1	6.8	8.1		

Table 3

Correlation matrix from CCA run 1, the southern latitude band (37°N to 40°N), for dolphin and porpoise species relative abundance (as reflected by incidental catch data) and environmental data collected on high seas gillnet vessels during June-August 1990 and 1991 in the central North Pacific Ocean.

	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENV AX1	ENV AX2	ENV AX3	ENV AX4	BEAU	SWELL	WIND N/S	WIND E/W	SST	DSST	CURR VEL	CURR N/S	CURR E/W
SPEC AX1	1.0000																
SPEC AX2	-0.0263	1.0000															
SPEC AX3	0.0426	-0.0503	1.0000														
SPEC AX4	0.0330	0.0287	0.0007	1.0000													
ENV AX1	0.5504	0.0000	0.0000	0.0001	1.0000												
ENV AX2	0.0000	0.4826	0.0000	0.0000	0.0000	1.0000											
ENV AX3	0.0000	0.0000	0.4053	0.0000	0.0000	0.0000	1.0000										
ENV AX4	0.0000	0.0000	0.0000	0.3766	0.0000	0.0000	0.0000	1.0000									
BEAU	0.2305	0.2806	-0.0791	0.1080	0.4188	0.5815	-0.1951	0.2867	1.0000								
SWELL	0.1651	-0.0203	-0.0828	0.1284	0.3000	-0.0420	-0.2043	0.3410	0.5628	1.0000							
WIND N/S	0.1447	0.1986	0.0820	-0.1216	0.2629	0.4114	0.2023	-0.3228	-0.1084	-0.1020	1.0000						
WIND E/W	-0.1843	-0.0018	-0.1688	0.1761	-0.3348	-0.0037	-0.4165	0.4678	-0.1543	-0.1430	-0.0397	1.0000					
SST	-0.4102	0.2677	-0.0365	-0.0358	-0.7452	0.5546	-0.0901	-0.0950	0.1171	-0.0039	0.0158	0.0832	1.0000				
DSST	-0.0154	0.0559	0.0138	0.0788	-0.0281	0.1159	0.0339	0.2093	-0.1129	-0.1035	0.1813	-0.0672	-0.0437	1.0000			
CURR VEL	-0.0069	-0.0575	0.3502	0.0802	-0.0126	-0.1192	0.8640	0.2129	-0.0650	-0.1036	0.0132	-0.1177	-0.1884	-0.1092	1.0000		
CURR N/S	-0.0258	0.0634	0.0424	0.1920	-0.0469	0.1314	0.1045	0.5099	-0.0629	-0.0884	0.1217	0.1749	0.0976	0.0853	0.0098	1.0000	
CURR E/W	-0.0108	0.1133	0.0072	0.0762	-0.0197	0.2347	0.0177	0.2022	0.0483	0.0459	-0.1111	0.0638	0.1024	0.0691	-0.2186	-0.0180	1.0000

Table 4

Correlation matrix from CCA run 2, the middle latitude band (40°N to 43°N), for dolphin and porpoise species relative abundance (as reflected by incidental catch data) and environmental data collected on high seas gillnet vessels during June-August 1990 and 1991 in the central North Pacific Ocean.

	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENV AX1	ENV AX2	ENV AX3	ENV AX4	BEAU	SWELL	WIND N/S	WIND E/W	SST	DSST	CURR VEL	CURR N/S	CURR E/W
SPEC AX1	1.0000																
SPEC AX2	-0.0108	1.0000															
SPEC AX3	-0.0400	-0.0174	1.0000														
SPEC AX4	0.0103	-0.0478	-0.0504	1.0000													
ENV AX1	0.5354	0.0000	0.0000	0.0000	1.0000												
ENV AX2	0.0000	0.2792	0.0000	0.0000	0.0000	1.0000											
ENV AX3	0.0000	0.0000	0.2537	0.0000	0.0000	0.0000	1.0000										
ENV AX4	0.0000	0.0000	0.0000	0.2194	0.0000	0.0000	0.0000	1.0000									
BEAU	0.0908	0.1625	-0.0416	0.0946	0.1696	0.5821	-0.1641	0.4313	1.0000								
SWELL	0.0680	0.1558	0.0004	0.0548	0.1271	0.5581	0.0016	0.2496	0.5344	1.0000							
WIND N/S	-0.0157	-0.1388	-0.1532	0.0729	-0.0294	-0.4969	-0.6039	0.3322	-0.0802	0.0504	1.0000						
WIND E/W	0.0506	-0.0866	0.1118	0.0108	0.0945	-0.3100	0.4405	0.0492	-0.1733	-0.2281	-0.0930	1.0000					
SST	-0.5133	0.0477	-0.0173	-0.0168	-0.9588	0.1709	-0.0680	-0.0767	-0.0805	-0.0344	0.0126	-0.2055	1.0000				
DSST	-0.0114	0.0836	-0.0223	0.0826	-0.0213	0.2995	-0.0879	0.3764	-0.1107	-0.0196	-0.0074	0.0235	-0.0269	1.0000			
CURR VEL	-0.0726	-0.0360	-0.0036	-0.0772	-0.1335	-0.1291	-0.0141	-0.3516	-0.0572	-0.0583	0.0765	0.0793	0.0382	-0.0487	1.0000		
CURR N/S	0.1498	0.0285	0.0808	-0.0226	0.2798	0.1019	0.3185	-0.1031	-0.0939	-0.0186	0.0415	0.1650	-0.1327	0.0354	-0.0255	1.0000	
CURR E/W	0.1051	0.1111	-0.1110	-0.1359	0.1963	0.3977	-0.4374	-0.6193	0.0369	-0.1062	-0.2400	-0.0411	-0.0309	-0.0199	-0.0849	0.0350	1.0000

despite the general tendencies noted above. However, each of the three Dall's porpoise categories tolerance ranges were completely separate from two or more northern right whale dolphin species categories on the opposite side of the SST gradient. The mature categories of Dall's porpoise were the most isolated, with no habitat characteristics in common with the mature or neonatal categories of northern right whale dolphin. In addition, the mature female Dall's porpoises were completely partitioned from all other categories along Axis 2, suggesting they were sampled in calmer sea conditions (i.e. where low wind velocities were recorded) in areas with prevailing westerly winds.

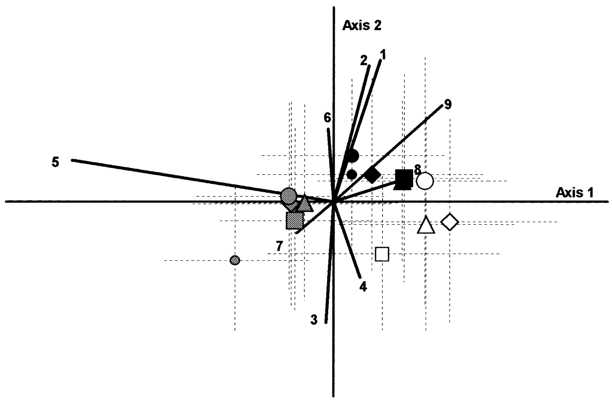
The middle latitude band

The fishery moved northward in July to a band extending from 41°N to 43°N east of 170°W and from 41°N to 42°N west of 170°W (Fig. 1). Of the 384 operations sampled, only six occurred in areas fished the previous month. All 14 species categories were present. The first and second canonical axes explained 46.7% and 13.8% of the variance in the species-environment relation (Table 5).

As in the southern latitude band (Fig. 2), the dominant environmental gradient in the second run was SST, negatively correlated with Axis 1 (r = -0.9588) (Fig. 3, Table 4). The juxtaposition of species categories along the SST gradient was also consistent with the results from the southern latitude band, with Dall's porpoise occupying the coolest waters, northern right whale dolphins in the warmest waters and Pacific white-sided dolphins in-between.

The proximity of Dall's porpoise and Pacific white-sided dolphin species categories, all of which scored positive eigenvalues for both canonical axes 1 and 2, were more pronounced than in the previous run, again indicating a tendency toward occupation of similar habitats. Conversely, the northern right whale dolphin species categories were more isolated, particularly along Axis 1 (correlated with the SST gradient). The neonate northern right whale dolphin category occupied the most extreme position on the SST gradient, in the warmest waters encountered in the middle latitude band. In regard to species tolerance ranges, overlap was evident among most species except in the case of the neonate northern right whale dolphin. In its extreme position on the 'warm side' of the SST gradient, this category shared no habitat characteristics with three of the four Dall's porpoise categories (immature males and females and mature females).

Axis 2 was positively correlated with wind velocity (r = 0.5821) and swell height (r = 0.5581). Conversely, Axis 2 was negatively correlated with wind N/S direction (r = -0.4969) (Table 4). Taken together, these correlations suggest that high positive values along Axis 2 represent rougher sea conditions with winds deviating from the dominant westerly pattern. The Pacific white-sided dolphin categories, for instance, appeared to occupy areas with slightly more extreme sea conditions, although their tolerance ranges overlapped those of nearly all other categories. Most notably, however, was the location of the neonate northern right whale dolphin category, oriented toward the 'calmer' side of the sea condition gradient coincident with Axis 2.



Species	Male		Female		Young-of-the-year
	Mature	Immature	Mature	Immature	
Dall's porpoise	◇	q	❍	△	
Pacific white-sided dolphin	u	n	l	s	l
Northern right whale dolphin	u	n	l	s	l

Fig. 3. Species ordination diagram for CCA run 2, the middle latitude band (40°N to 43°N), relating species category occurrence along environmental gradients associated with the first two canonical axes. Species tolerance limits and environmental vectors are indicated as in Fig. 2.

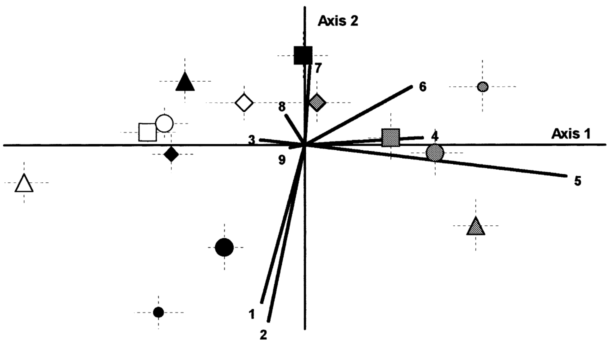
The northern latitude band

The fishery reached its northern limit in August, extending nearly to 46°N east of 170°W, and to 45°N west of 170°W (Fig. 1). Only three of the 273 operations in this sample occurred in the area represented in the middle latitude band. All 14 species categories were contained in the sample.

Table 5

Ordination results from CCA run 2, the middle latitude band (40°N to 43°N), for dolphin and porpoise species relative abundance (as reflected by incidental catch data) and environmental data (wind speed, swell height, wind direction, sea surface temperature, current velocity and current direction) collected on high seas gillnet vessels during June-August 1990 and 1991 in the central North Pacific Ocean. Species-Environmental Total (Sp-Env) is the total species variation related to the environmental variables. 'Total variation' represents all variation in the species incidental catch data. The P-values are based on a Monte Carlo randomisation test (1,000 repetitions).

	Canonical axes				Sp-Env total	Total variation
	1	2	3	4		
Eigenvalues	0.238	0.054	0.038	0.028	0.358	8.760
P-values	<0.001				<0.001	
Species-environment correlations	0.535	0.279	0.254	0.219		
Cumulative percentage variance						
Species-environment relation	60.5	74.3	83.8	91.0		
Total species data	2.7	3.3	3.8	4.1		



Species	Male		Female		Young-of-the-year
	Mature	Immature	Mature	Immature	
Dall's porpoise	◇	q	❍	△	
Pacific white-sided dolphin	u	n	l	s	l
Northern right whale dolphin	u	n	l	s	l

Fig. 4. Species ordination diagram for CCA run 3, the northern latitude band (43°N to 46°N), relating species category occurrence along environmental gradients associated with the first two canonical axes. Species tolerance limits and environmental vectors are indicated as in Fig. 2.

The first two canonical axes explained 49.4% and 15.9% of the variance in the species-environment relation (Fig. 4, Table 6). Axis 1 was highly correlated with positive values of SST ($r = 0.8679$) (Table 7). Once again, all categories of northern right whale dolphin were located in areas corresponding to higher water temperatures along the SST gradient. The Dall's porpoise categories were located on the 'lower temperature' side of the SST gradient similar to the pattern seen in the two previous areas. However, unlike in the two previous areas, two of the Pacific white-sided dolphin categories were interspersed with those of the Dall's porpoise (immature male and mature female).

Axis 2 was negatively correlated with swell height ($r = -0.7666$) and wind velocity ($r = -0.6845$) and positively correlated with current velocity. Along Axis 2, neonatal and mature female Pacific white-sided dolphins again occupied the most extreme locations representing the highest wind velocity and swell conditions observed in the northern band of the study area.

Unlike in either of the previous areas (Figs 2 and 3), the tolerance ranges around nearly all species categories were small, with no overlap between those ranges in all cases except for one cluster containing mature male and female Dall's porpoises and immature male Pacific white-sided dolphins.

DISCUSSION

Canonical Correspondence Analysis offered substantial power to reduce the dimensions of a large multivariate dataset with direct application to habitat relationships in the marine environment. It was recognised that caution has been expressed in the application of CCA to 'noisy' datasets because it can produce distorted images of community structure (McCune, 1997). It is believed that the results in this study are robust to those concerns for two reasons. First, the objective related only to the description of species responses to observed environmental variables which McCune (1997) identifies as an appropriate use of CCA. Second, interpretation of the ordinations was constrained to only broadest observed relationships between the species categories and the dominant environmental variables.

Even so, in preliminary CCA runs it was noted that the results were sensitive to the inclusion of certain data, particularly date and latitude. Preliminary CCA runs including those variables produced uninformative results, driven by the fact that management regulations had established a northward movement of fishing across the summer. The location of species categories simply reflected the relative numbers of each species caught over that time/space gradient, not the underlying environmental conditions. Hence, the decision to stratify by latitude and perform three separate analyses.

The mortality data compared favourably to studies based on marine mammal sightings as a means of explaining variance in species-environmental relationships (e.g. Reilly and Fiedler, 1994). The technique, therefore, may be useful where either of these two common sources of marine mammal distributional data (mortality or sightings data) are available, so long as the mortality data reflects the relative abundance of subject animals in the study area (Ferrero and Walker, 1993). However, the collection of concurrent data on habitat features should be improved beyond those used in this study when possible, particularly with respect to the range of oceanographic and environmental variables considered.

Although the driftnet fisheries data available for the multivariate analyses lacked the detail necessary to describe oceanographic habitats in specific technical terms, they were sufficient to represent contrasts in environmental conditions and provide a basis for detecting habitat selection patterns.

Table 6

Ordination results from CCA run 3, the northern latitude band (43°N to 46°N), for dolphin and porpoise species relative abundance (as reflected by incidental catch data) and environmental data (wind speed, swell height, wind direction, sea surface temperature, current velocity and current direction) collected on high seas gillnet vessels during June-August 1990 and 1991 in the central North Pacific Ocean. Species - Environmental Total (Sp-Env) is the total species variation related to the environmental variables. 'Total variation' represents all variation in the species incidental catch data. The *P*-values are based on a Monte Carlo randomisation test (1,000 repetitions).

	Canonical axes				Sp-Env total	Total variation
	1	2	3	4		
Eigenvalues	0.202	0.065	0.055	0.033	0.355	7.881
P-values	<0.001				<0.001	
Species-environment correlations	0.504	0.342	0.297	0.226		
Cumulative percentage variance						
Species-environment relation	49.4	65.3	78.7	86.8		
Total species data	2.6	3.4	4.1	4.5		

Table 7

Correlation matrix from CCA run 3, the northern latitude band (43°N to 46°N), for dolphin and porpoise species relative abundance (as reflected by incidental catch data) and environmental data collected on high seas gillnet vessels during June-August 1990 and 1991 in the central North Pacific Ocean.

	SPEC AX1	SPEC AX2	SPEC AX3	SPEC AX4	ENV AX1	ENV AX2	ENV AX3	ENV AX4	BEAU	SWELL	WIND N/S	WIND E/W	SST	DSST	CURR VEL	CURR N/S	CURR E/W
SPEC AX1	1.0000																
SPEC AX2	0.0265	1.0000															
SPEC AX3	-0.0323	-0.0298	1.0000														
SPEC AX4	0.0320	0.0235	-0.0892	1.0000													
ENV AX1	0.5043	0.0000	0.0000	0.0000	1.0000												
ENV AX2	0.0000	0.3419	0.0000	0.0000	0.0000	1.0000											
ENV AX3	0.0000	0.0000	0.2968	0.0000	0.0000	0.0000	1.0000										
ENV AX4	0.0000	0.0000	0.0000	0.2259	0.0000	0.0000	0.0000	1.0000									
BEAU	-0.0724	-0.2340	0.0917	0.0438	-0.1436	-0.6845	0.0309	0.1942	1.0000								
SWELL	-0.0594	-0.2621	-0.0520	0.0642	-0.1178	-0.7666	-0.1753	0.2842	0.5737	1.0000							
WIND N/S	-0.0732	0.0067	-0.1832	0.0063	-0.1451	0.0195	-0.6171	0.0279	0.0377	-0.0570	1.0000						
WIND E/W	0.1965	0.0100	0.0079	-0.1498	0.3897	0.0294	0.0265	-0.6631	-0.2322	-0.2568	-0.1052	1.0000					
SST	0.4376	-0.0469	-0.0430	0.0436	0.8679	-0.1371	-0.1447	0.1930	-0.0257	-0.0391	-0.1309	0.1425	1.0000				
DSST	0.1792	0.0868	0.0364	-0.0452	0.3554	0.2238	0.1126	-0.2004	-0.0612	0.0009	-0.0615	0.0778	0.0547	1.0000			
CURR VEL	0.0090	0.1167	0.0156	0.1198	0.0179	0.3415	0.0526	0.5303	0.1370	0.0479	-0.0740	-0.0070	0.0105	-0.0174	1.0000		
CURR N/S	-0.0308	0.0443	-0.1223	-0.1057	-0.0611	0.1297	-0.4120	-0.4678	-0.1621	-0.1628	-0.0798	0.0237	0.1558	-0.0734	-0.0402	1.0000	
CURR E/W	-0.0230	-0.0042	0.0609	0.0666	-0.0455	-0.0123	0.2051	0.2948	0.0844	0.0018	-0.2323	-0.0809	0.1423	0.0900	0.1407	0.0294	1.0000

Differences in habitat selection preferences were suggested both between species and among species constituents. Not surprisingly, the most influential environmental gradient reflected in inter-species placement in ordination space was SST. Yatsu *et al.* (1993) reported temperature related differences in catch per unit effort among several fish and cephalopods caught in the Japanese squid driftnet fishery. Likewise, efforts to model the North Pacific transition zone and identify associations among taxa (MBC Applied Environmental Sciences) incorporated stratification by temperature.

Environmental variables other than SST were included as possible indicators of meso-scale habitat features, namely fronts (DSST), eddies (current velocity and direction) and atmospherically induced areas of increased surface mixing. The importance of either fronts or eddies using the indicators appeared to be low, explaining little of the variance in the species-environment relation. In contrast, consistent correlations between both wind velocity and swell height with Axis 2 were apparent. While this suggests that local mixing of surface waters may be an important habitat feature, it is noted that the ability to characterise other complex features like fronts and eddies was probably very low, and that they may still represent important features. Furthermore, since nearly all driftnet sets were oriented east/west, the analyses suffered a low probability of detecting latitudinal temperature gradients. For the purposes of these exploratory analyses, therefore, SST and surface layer mixing, regardless of their cause, are suggested to be among the habitat features of relevance to small cetaceans in the area studied.

Comparing the results of the three CCA runs, some patterns were consistent, while others were more ephemeral. Clearly, the most robust pattern related to SST preference. Northern right whale dolphins consistently occupied the warm water extremes, while fidelity to cooler waters was characteristic of Dall's porpoise. Pacific white-sided dolphin SST preferences were the broadest of the three species, although they were more allied with those of Dall's porpoise than northern right whale dolphin.

In the southern latitude band, Dall's porpoise were present only in low numbers, well separated from the other species categories in the ordination plots. This portion of the study area may have simply represented the southern fringe of Dall's porpoise habitat, but it was within the core range of the other two species. As the fishery advanced northward in succeeding months, the separation of the Dall's porpoise categories disappeared, and greater isolation of northern right whale dolphin categories took its place. This may have reflected the more southerly distribution of northern right whale dolphin and its more pronounced selection of warmer water habitats at higher latitudes near the fringes of its range.

In addition, northern right whale dolphin habitat preferences may relate to their reproductive activity at the time of sampling. Ferrero and Walker (1993) described a distinct calving mode for the northern right whale dolphin in June and July, in areas corresponding to the southern and middle portions of the study area. Neither of the other two species showed any indications of parturition at that time, in those areas. The northern right whale dolphin neonatal component was well separated from the other species categories in the southern latitude band ordination and positioned in the warmest and perhaps calmest waters. Failure of the northern right whale dolphin mature female category to mirror the same pattern may be an artefact of the sample categorisation process which only reflected sexual maturity, not reproductive activity. Since northern right whale dolphins are not annual breeders (Ferrero and Walker, 1993), the mature female category contains both reproductively active and inactive individuals, of which the latter may not express the same habitat preferences as parturient females and calves. The reproductively active northern right whale dolphin females may, therefore, select habitats in summer that are specific to calving.

A marked contrast among the three CCA runs was in the lack of overlap between species tolerance ranges in the northern latitude band. One possible explanation for the difference may relate to the location of sampling and the diversity of habitats available for selection in those locations. At the southern and middle latitudes, sampling occurred in the North Pacific transition zone, south of the Polar Front Region (Uda, 1963; Pearcy, 1991; Roden, 1991). By comparison, in the northern latitude run, the fishery was probably positioned in the sub-arctic water mass, where habitats, described by combinations of environmental parameters, were more varied. It is unknown, however, whether the lower incidence of tolerance ranges there reflected more focused selection of habitats or an artefact of having more possible combinations of habitat types available, over which to distribute the species data.

These data are potentially useful in the context of conservation and management for the subject species. In addition, this approach may be applicable to evaluations of habitat preferences in other poorly known pelagic odontocetes, thereby contributing to conservation and management insights in the latter cases as well. Habitat characteristics define the ultimate potential distribution of a species, providing the basis against which the present numbers or range of any species or stock can be compared and allowing conclusions about conservation status of the species or stock. Quantitatively documented relationships of species and habitat permit meaningful predictions of trends in stock size or distribution in response to observed trends in physical habitat characters. It follows that observed changes in habitat quality can be interpreted with regard to conservation consequences for resident stocks. Similarly, spatial variation in habitat characteristics, within the extremes of tolerance for resident stocks, are of value in understanding within-species spatial variance in stock structure, with obvious benefit to conservation and management concerns. Obtaining good information on relationships of marine mammal species and habitat characteristics in the pelagic realm will remain logistically challenging and highly costly for the foreseeable future. Utilisation of unorthodox opportunities for data acquisition, such as this paper, will remain important for understanding habitat use in marine mammals as long as challenges and costs of pelagic research remain high.

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