Relationships Between Odontocete Distributions and Zooplankton Community Structure Along the Southern Edge of Georges Bank

R. B. Griffin

University of Rhode Island Graduate School of Oceanography Narragansett, Rhode Island 02882, USA

Abstract

From 1 June to 2 July 1993, the National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Marine Mammal Investigation, Woods Hole, MA, undertook a shipboard survey on distributions and abundances of cetacean species on the eastern and southern edges of Georges Bank. During transects of the study area, concurrent physical and biological data were collected to examine characteristics of marine mammal habitat. Zooplankton communities were sampled by double oblique bongo tows. Odontocete sighting rates (animals per hour) and their mean group sizes within 20 km of bongo stations were compared with log_{10} copepod density. Sighting rates of striped (*Stenella coeruleoalba*) and common dolphins (*Delphinus delphis*) increased with decreasing copepod density and increasing copepod diversity. Zooplankton community structure was found useful in understanding oceanographic characteristics of the habitat of odontocete species.

Key words: abundance, dolphins, distribution, Georges Bank, whales, zooplankton

Introduction

Low variance estimates of species abundances and distributions are essential to properly manage or protect species impacted by commercial fisheries. To better effect this goal, a refined understanding of cetacean and other apex predator distributions from an ecosystem/community viewpoint is needed. This approach was recommended by the International Whaling Commission and the International Council for the Exploration of the Sea (IWC, 1992), and studies have suggested that surveys should focus on oceanographic structure, prey species distribution and density dependent habitat selection (Smith *et al.*, 1996).

Marine mammals are best understood as part of an ecosystem. Species distributions are influenced by complex environmental interactions, which exert selective pressure to direct their evolution. Feeding ecology and reproductive behaviors are likely prime factors in the distributions of cetaceans (Gaskin, 1976), and mesoscale oceanographic features affecting prey distributions may be important factors affecting cetacean distribution (Selzer and Payne, 1988). Thus, studies of relationships between the environment, prey species and cetacean species distributions may aid in describing marine mammal habitat.

The distribution of cetacean species have frequently been described in terms of physical oceanographic variables. For example, distributions of many species in the western Atlantic were explained by water depth (CETAP, 1982). White-sided dolphins (Lagenorhynchus acutus) in the northwestern Atlantic Ocean were observed in areas of high topographic relief, low temperature and low salinity, while common dolphins (Delphinus delphis) were found in areas of high sea-floor relief where temperatures were warmer and more saline (Selzer and Payne, 1988). In the eastern tropical Pacific (ETP), the delphinid and sperm whale (*Physeter*) macrocephalus) habitat use was significantly related to sea surface temperature and thermocline topography (Polacheck, 1987; Reilly and Fiedler, 1994). Quality of physical habitat (defined as a cetacean community ordination function of surface temperature, thermocline depth and thermocline thickness) was significantly related to delphinid species abundance estimates (Fiedler and Reilly, 1994).

Prey fish abundance significantly explained variation in cetacean sighting rates in the Northwest Atlantic (Waring, 1995). Similarly, a high level of spatial correlation was found between the occurrence of fish larvae and their zooplankton food source. Seasonal, seaward progression in spawning activity of fish species off Southwest Ireland and larval fish behavior appeared influenced by zooplankton distributions (Doyle and Ryan, 1989). In the North Sea, herring, cod and flatfish recruitment rates were associated with fluctuations in Calanus sp. abundance (Pepin, 1990), and diversity and abundance of herring were shown to be a function of zooplankton concentrations off the Atlantic coast of Nova Scotia (Stone and Jessop, 1992).

Relationships between plankton communities and cetacean distributions have been found in the Georges Bank area of the Northwest Atlantic Ocean (Griffin, 1996). Analyses of Icelandic whale fishery statistics have demonstrated that whales concentrated their feeding along the axis of heaviest zooplankton densities (Foerster and Thompson, 1985). Acoustic detection of relative planktonic biomass in the Mediterranean Sea suggested sperm whales were most abundant in areas with higher plankton densities (Viale, 1991), and work has shown sperm whales were more abundant in areas of high production in the North Atlantic and South Pacific (Gulland, 1974; Jaquet and Whitehead, 1996).

Individual species or discrete biological communities may serve as tracers of water temperature or water mass history. Thermal gradients, structural heterogeneity of the continental shelf, and persistence of hydrographic fronts at continental shelf margins are important factors in zooplankton production (Sabates, et al., 1989), while water temperature and origin of water masses may affect copepod species distributions (Atkinson, et al., 1990). Zooplankton communities were temporally persistent in the near-shore planktonic ecosystem of southern California (Barnett and Jahn, 1987), in the Gulf Stream (Ashjian and Wishner, 1993), and in the North Sea (Williams, et al., 1993). Zooplankton biomass in the North Atlantic has been shown to be lowest in the Gulf Stream and Sargasso Sea, and increasing from the slope water/ Gulf Stream interface to a maximum above the shelf (Allison and Wishner, 1986; Ashjian, et al., 1994; Sherman, et al., 1988).

In this study it is hypothesized that zooplankton community structure can be used as an "indicator" variable in the habitat description of odontocete species. Although odontocetes are not known to utilize zooplankton as a food source, trophic relationships between their prey and the zooplankton community might indirectly influence odontocete foraging movements. Further, zooplankton taxa which are not part of a trophic web leading to Cetacea may still be useful as proxy measures for complicated interactions of hydrography and biology. This paper examines relationships of zooplankton abundance and diversity with odontocete distributions off the northeast coast of the United States and tests the hypothesis that zooplankton abundance and diversity are useful in understanding odontocete habitat utilization.

Methods

From 1 June to 2 July 1993 a United States National Oceanic and Atmospheric Administration, National Marine Fisheries Service (NOAA/NMFS) shipboard cetacean census was conducted along the eastern and southern edges of Georges Bank aboard the NOAA vessel Delaware II (Fig. 1a, b). During transects of the study area from the Scotian Shelf (42.3°N, 65.0°W) to Veatch Canyon (40.0°N, 68.5°W), concurrent physical and biological data were collected to examine characteristics of marine mammal habitat. Cetaceans were sighted using 25×150 power binoculars. Survey protocol involved continuous effort from 0600-1900 hrs (EDST), with two observers scanning through binoculars, and a third observer (serving as data recorder) scanning unaided. Effort continued as sea state and weather conditions permitted.

Transects were designed to frequently traverse the shelf-break in a zig-zag pattern. At the end of each traverse, casts were made to determine hydrographic structure using a conductivity, temperature, depth bathythermograph (CTD), to a depth of 200 m, or to within 10 m of bottom where bottom depth was less than 200 m. Hydrographic data were received and archived on computer instantaneously.

Periodically, zooplankton were sampled simultaneously with the CTD recordings using the double oblique Bongo tow method. These stations were randomly selected at the end of transect lines. In this technique, a double "bongo" frame carrying two



Fig. 1. Sea surface temperature °C (SST) during the survey. Zooplankton sampling sites are designated by circles. Depth contours of 200 m and 1 000 m are shown. Survey trackline is shown within the region considered for these analyses. (A) Composite of SST, 2–8 June 1993. (B) Composite of SST, 23–28 June 1993.

nets, one 303 μ m and one 505 μ m mesh, towed at a speed sufficient to maintain a 30° incline from the verticle of the tow wire, was lowered to 200 m depth and retrieved. Surface temperatures were additionally recorded at 32 of the 36 stations sampled, which covered a variety of habitats (e.g. on-shelf/off-shelf, over canyon/inter-canyon).

In the laboratory, zooplankton samples were split, resulting in sub-samples of approximately 500 organisms. Zooplankton in sub-samples were analyzed for taxa and abundance, and copepods were identified to species level. Zooplankton density (per m³) was computed using abundance data and metered tow volume, and copepod and total organism abundances were log transformed (COPEPLOG) to compensate for potential curvilinearity. For copepods, a Shannon Diversity Index (SHANNON) was calculated from:

$$H' = -\Sigma p_i \ln (p_i)$$

where p_i is the decimal fraction of individuals belonging to the *i*th species and *H'* is the diversity index.

From the index, a measure of species abundance equitability (J) was computed as:

$$J = H'/H'_{max}$$

where H'_{max} is the value of H' computed with the same number of species, but equal p_i values (Cox, 1985).

The CTD hydrographic data were summarized as 4 variables to quantify thermal structure: 1) maximum temperature above 200 m depth (TEMPMAX), 2) minimum temperature above 200 m depth (TEMPMIN), 3) the difference (°C) between maximum and minimum temperatures (TEMPRANG), 4) water masses classified according to thermal structure (THERCLAS) as; a) thoroughly mixed over the entire water column sampled = 0, b) thermally stratified, with warm water overlying cooler water = +1, and c) thermally stratified, with a warm water mass underlying cooler water = -1. Additional hydrographic data were obtained by shipboard sampling (TEMPSURF), and from satellite images of sea surface temperature. Satellite images were processed such that temperature data were extracted from the images, and contours showing isotherms were computed using a kriging technique.

In addition to plankton and hydrographic variables, fixed geographic variables of bottom depth (m) (BOTM) and latitude (LAT) at station site, were examined for relationships with plankton and odontocete sightings. Longitude was not used as a variable in these analyses.

All recorded odontocete sightings were used, whether recorded during active search effort or sighted while diverting from track to further investigate prior sightings. Sightings were summarized as quantities representing total number of animals within 20 km of bongo stations. These quantities were corrected for effort by dividing total animals seen within 20 km of stations by total number of hours of effort within the block. Block data were used when total effort within a block was 2 hrs or greater. The block size of 20 km was selected as smaller scales were often characterized by less than 1 hr of survey effort.

Standardized species sighting rates were calculated when any odontocete species was found in at least 50% of the survey blocks. These species included the common dolphin (*Delphinus delphis*), striped dolphin (*Stenella coeruleoalba*), Atlantic white-sided dolphin (*Lagenorhynchus acutus*), pilot whales (*Globicephala* spp.), sperm whales (*Physeter macrocephalus*) and beaked whales (*Mesoplodon spp.*). Mean group sizes of species by station were calculated as a function of total animals of a given species sighted, and total number of sightings of that species.

Specific odontocete species were analyzed for abundance and group size relationships with hydrographic conditions and zooplankton variables, when they were sighted within 20 km of 16 or more bongo stations (i.e. half of bongo stations with >2 hrs sighting effort within 20 km of stations). Due to the difficulty of identifying *Globicephala* and Mesoplodon species at sea, they were analyzed on a generic basis. Others were analyzed by species. Pearson's product-moment correlation coefficient method was used (Sokal and Rohlf, 1981), for correlations with environmental parameters.

Results

The research cruise consisted of 2 components: Leg 1, when sighting effort was deployed through 3 June to 11 June 1993 and Leg 2 during 16 June to 30 June 1993. During Leg 1, a warm core ring was positioned along the southeastern edge of Georges Bank. Sighting effort and bongo tows were conducted in cooler waters north of the ring (Fig. 1a). During Leg 2, the warm core ring had moved south, and a second warm core ring occupied the region of cooler water observed during Leg 1. Sighting effort and bongo tows were made in the interface between the southern warm core ring and cooler shelf water (Fig. 1b).

Copepod abundance ranged from 11-1172 per m³, while total zooplankton abundance ranged from 16-1 189 per m³. Copepod diversity (Shannon Index) ranged from 0.02 to 1.43, while equitability of abundance of species (*J*) ranged from 0.02 to 0.86. Surface temperature at bongo sites varied between 6.8° and 22.0°C, while temperatures recorded by the CTD varied between 3.9° and 22.0°C. Depth at sites ranged from 54 to 3 000 m.

Log transformed zooplankton abundances and measures of zooplankton diversity were significantly correlated with both fixed (e.g. latitude, bathymetry) and transient (e.g. temperature) physical variables (Table 1). Copepod abundances were greater in northern regions of the survey, and abundance decreased in deeper waters. Warmer water temperatures were correlated with lower copepod abundances, and copepod numbers were elevated in areas where warm water was found beneath cool water. It is noted that hydrographic conditions of warm water underlying cool water suggest the presence of a sub-surface thermal front. Diversity in the copepod community was highest in southern, offshore regions with warmer water temperatures.

Sighting rates (animals per hr) for delphinids and non-delphinid odontocetes were correlated with biological or physical variables (Table 2). Nondelphinid odontocetes tended to be sighted more frequently in warmer waters, in the vicinity of subsurface thermal fronts. Delphinids were more likely to be found in southern areas with warmer water, and off the shelf. Unlike non-delphinid odontocetes, delphinid abundances were significantly negatively correlated with zooplankton abundance, and positively correlated with copepod diversity.

Approximately 35% of tested relationships between species and environment were significant (Table 3), and most significant tests described relationships of common and striped dolphins with the environment. Common dolphins and striped dolphins were found in deeper, relatively warm water in regions where copepod diversity was high and abundances were low. Abundances were

cept BOIM, LAI, IEMPSURF, where $n = 34$.				
Variable	Coefficient	Р		
	\log_{10} (Copepods per m^3)			
BOTM	-0.5086	0.002		
TEMPSURF	-0.6757	0.0001		
TEMPMAX	-0.8000	0.0001		
TEMPMIN	-0.6644	0.0001		
TEMPRANG	-0.5687	0.0006		
LAT	0.5220	0.002		
THERCLAS	-0.6373	0.0001		
(Shannon's Diversity Index			
BOTM	0.3692	0.03		
TEMPSURF	0.8724	0.0001		
TEMPMAX	0.8856	0.0001		
TEMPMIN	0.7545	0.0001		
TEMPRANG	0.6096	0.0002		
LAT	-0.7996	0.0001		
THERCLAS	0.7584	0.0001		

TABLE 1. Pearson's product-moment correlations of physical parameters with zooplankton parameters. (See text for description of abbreviated variables). n = 33; except BOTM, LAT, TEMPSURF, where n = 34.

TABLE 2. Correlations of physical and zooplankton parameters with effort number of animals sighted per hour within 20 km of bongo stations. (See text for description of abbreviated variables). n = 30 for variables except for TEMPSURF, BOTM and LAT, where n = 31.

14	D			
/ Delahinida	Γ			
Delphinids				
0.5856	0.0004			
-0.6039	0.0003			
0.4036	0.02			
0.3159	0.08			
0.4958	0.005			
0.3186	0.08			
0.4774	0.005			
-0.4647	0.009			
-0.4498	0.01			
0.5346	0.002			
0.5489	0.002			
Non-delphinid odontocetes				
0.0718	0.70			
0.0087	0.96			
-0.3496	0.05			
-0.4857	0.006			
-0.2764	0.13			
-0.5696	0.0008			
0.1534	0.41			
0.1684	0.37			
0.1355	0.48			
-0.3259	0.08			
-0.2523	0.18			
	<i>r</i> Delphinids 0.5856 -0.6039 0.4036 0.3159 0.4958 0.3186 0.4774 -0.4647 -0.4647 -0.4647 -0.4498 0.5346 0.5346 0.5489 elphinid odontocetes 0.0718 0.0087 -0.3496 -0.4857 -0.2764 -0.2764 -0.5696 0.1534 0.1684 0.1355 -0.3259 -0.2523			

negatively correlated with latitude for both striped (r = 0.5272, P = 0.003) and common dolphins (r = -0.5219, P = 0.003). Sperm whale numbers were greatest in deeper water, but were not correlated with physical variables or copepod abundances. Beaked whale sightings were associated with relatively warm surface temperatures in the vicinity of sub-surface thermal fronts, but were not correlated with copepod abundance. White-sided dolphins were sighted in regions of relatively cool surface water with low maximum temperatures in the upper 200 m of the water column. Pilot whales did not exhibit significant correlations with any measured physical or biological variables.

Delphinid group sizes were significantly correlated with many variables (Table 4), and groups were larger in warmer waters with greater vertical temperature range. Group size also decreased with decreasing copepod densities and increasing copepod diversity. Non-delphinid odontocete groups were larger in warmer water, but were not related to copepod densities. Only common dolphin group sizes showed significant relationships with copepod density and diversity (Table 5). Mean group sizes were greater when copepod densities were low and diversity high.

Discussion

In these analyses, over 100 correlations have been examined. Theoretically, with an alpha of 0.05, approximately 5 tests showing significant correlations will be in error. In these data

TABLE 3. Correlations of zooplankton and physical parameters with effort as number of animals sighted per hour within 20 km of bongo stations, by species, where species were sighted within 20 km of at least 16 stations. (See text for description of abbreviated variables). n = 30 for variables except for TEMPSURF and BOTM where n = 31.

Variable	r	Р	Variable	r	Р
	Common Dolphins			Beaked Whales	
COPEPLOG	-0 5549	0.002	COPEPLOG	0.1669	0.38
SHANNON	0.5596	0.002	SHANNON	-0.2725	0.15
I	0.5596	0.001	J	-0.1731	0.36
	0.4800	0.001	TEMPSURF	-0.4317	0.01
TEMPMAX	0.5075	0.005	TEMPMAX	-0.3004	0.10
TEMPRANG	0.3241	0.08	TEMPRANG	0.0452	0.81
ROTM	0.5474	0.001	BOTM	0.0071	0.97
THERCLAS	0.4526	0.01	THERCLAS	-0.4534	0.01
	Striped Dolphins		Wh	ite-sided Dolphins	
COPEPLOG	-0.4214	0.02	COPEPLOG	0.2028	0.28
SHANNON	0.4714	0.009	SHANNON	-0.3078	0.10
J	0.4964	0.005	J	-0.2243	0.23
TEMPSURF	0.2583	0.15	TEMPSURF	-0.5545	0.001
TEMPMAX	0.4136	0.02	TEMPMAX	-0.3512	0.05
TEMPRANG	0.4286	0.02	TEMPRANG	-0.0571	0.76
BOTM	0.5840	0.0004	BOTM	0.1192	0.52
THERCLAS	0.2344	0.20	THERCLAS	-0.0960	0.61
	Sperm Whales			Pilot Whales	
COPEPLOG	0.1031	0.59	COPEPLOG	0.3195	0.09
SHANNON	-0.1519	0.42	SHANNON	-0.2475	0.19
J	-0.1307	0.49	J	-0.3053	0.10
TEMPSURF	-0.1069	0.56	TEMPSURF	0.0632	0.73
TEMPMAX	0.0760	0.68	TEMPMAX	-0.1181	0.53
TEMPRANG	0.2975	0.10	TEMPRANG	-0.0645	0.73
BOTM	0.5346	0.002	BOTM	-0.3337	0.06
THERCLAS	-0.2160	0.24	THERCLAS	-0.2963	0.11

52 correlations were significant at alpha = 0.05. Care should be taken in interpreting results of multiple correlations.

The positive correlation of delphinid sighting rate with bottom depth (Table 2) suggests delphinids sighted during this survey were primarily inhabitants of shelf-break or deeper waters. The Cetacean and Turtle Assessment Program described whitesided dolphins as shelf inhabitants, while slope and pelagic cetaceans included the sperm whale, beaked whale, pilot whale, Risso's dolphin (*Grampus* griseus), bottlenose dolphin (*Tursiops truncatus*), common dolphin, and striped dolphin (CETAP, 1982). In this study, the sperm whale, common dolphin and striped dolphin sighting rates were positively correlated with bottom depth, while whitesided dolphin sighting rates were negatively correlated with depth.

Bathymetry indirectly affects cetacean distributions through its effect on current flow, upwelling of nutrients, and subsequent biological production. While bathymetry was an important selective pressure in the early evolutionary development of the Cetacea (Gaskin, 1976), it only varies on geological time scales. To understand variation in odontocete species distributions, we must examine interactions of biology and hydrography. While water temperature *per se* may not be important in determining habitat use, temperature boundaries are dynamic zones and are frequently sites of higher productivity. Cetaceans may actively search for these physical features.

TABLE 4. Pearson's correlations of zooplankton and physical parameters with mean group size of animals sighted within 20 km of bongo stations. (See text for description of abbreviated variables). n = 30 for COPEPLOG, SHANNON and J; n = 31 for TEMPMAX and TEMPRANG; n = 32 for TEMPSURF.

Variable	r	Р
	Delphinids	
COPEPLOG	-0.6310	0.0002
SHANNON	0.6372	0.0002
J	0.6165	0.0003
TEMPSURF	0.5503	0.001
TEMPMAX	0.6086	0.0003
TEMPRANG	0.4148	0.02
Non-d	elphinid odontocetes	
COPEPLOG	0.1782	0.35
SHANNON	-0.2093	0.27
J	-0.1055	0.58
TEMPSURF	-0.3430	0.05
TEMPMAX	-0.3305	0.10
TEMPRANG	0.0361	0.85

TABLE 5. Pearson's correlations of zooplankton parameters with mean group size of selected delphinid species sighted within 20 km of bongo stations (See text for description of abbreviated variables).

Variable	r	Р
Comm	on Dolphins $(n = 20)$	
COPEPLOG	-0.5766	0.008
SHANNON	0.6456	0.002
J	0.6430	0.002
Stripe	ed Dolphins $(n = 16)$	
COPEPLOG	0.0371	0.89
SHANNON	0.0223	0.93
J	0.0408	0.88
Pilo	ot Whales $(n = 25)$	
COPEPLOG	0.1657	0.43
SHANNON	-0.2376	0.25
J	-0.2820	0.17
White-s	ided Dolphins (<i>n</i> = 17	 _)
COPEPLOG	0.1141	0.66
SHANNON	0.2366	0.36
J	0.4466	0.07

Delphinid sighting rates were significantly correlated with both physical and biological parameters (Tables 2, 3). The high degree of correlation between physical and biological data raises the question of which variables were acting as causal factors for delphinid distribution. Prior studies have concentrated on cetacean distributions as a function of water thermal structure and depth (CETAP, 1982; Fiedler and Reilly, 1994).

Copepod densities were greater in regions where thermal fronts were present. High copepod abundances and low diversity in cooler waters surveyed during Leg 1, and low copepod abundance and high diversity in warmer waters surveyed during Leg 2, likely resulted from presence of a warm core ring. Common dolphin and striped dolphin sighting rates were negatively correlated with copepod abundances, and positively correlated with copepod diversity. This finding suggests similar optimum habitat requirements between the two species. In the region of this study, a frontal boundary of approximately 15°C roughly separated cool shelf and slope water from the warmer water of a warmcore ring (Fig. 2). A Chi-Square analysis (Sokal and Rohlf, 1981) revealed striped dolphins were not preferentially distributed on either side of the isotherm (P > 0.10), but 80% of common dolphin sightings were on the cool side of the isotherm.

Although zooplankton data in this study suggested common and striped dolphins might live in similar trophic environments, hydrographic data suggested dissimilar habitats. Further research is needed to discover differences between these species in biotic resource utilization. Studies of distributional patterns of cetaceans should always gather abiotic and biotic data. Sampling zooplankton communities with the double oblique bongo tow method can be done quickly when censusing marine mammal populations and comparing zooplankton community structure with cetacean abundance may be helpful in determining biological parameters affecting cetacean distribution.

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Fig. 2. Spatial location of common dolphin and striped dolphin sightings along the eastern edge of Georges Bank during June 1993, with 10°C, 15°C and 20°C sea surface temperature contours shown. Common dolphins = ×, Striped dolphins = +. Depth contours of 100 m, 200 m, 1 000 m, and 2 000 m are shown.

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