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Sperm Whale (*Physeter macrocephalus*) Habitat in the Gulf of Mexico: Satellite Observed Ocean Color and Altimetry Applied to Small-Scale Variability in Distribution

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Abstract

During the summers of 2004 and 2005, researchers surveyed cetacean presence along the continental slope of the northern Gulf of Mexico. Towed, passive acoustic hydrophones were used to identify locations along the cruise tracks where sperm whales were encountered and not encountered. During both summers, 35 groups of sperm whales (*Physeter macrocephalus*) were encountered at a frequency of about one group every 120 nmi of survey effort. To assess the linkages between surface oceanography and the distribution of sperm whales, surface ocean color from NASA's Moderate Imaging Spectroradiometer (MODIS) and surface dynamic height from NASA's Earth orbital altimeters were evaluated in conjunction with survey data. Most sperm whale groups were found within regions of enhanced sea surface chlorophyll (SSC), particularly 2 wks after the initial development of locally higher SSC anomalies. Results from this study indicate sperm whale distribution in the Gulf of Mexico is linked to surface oceanography at shorter time scales than previously documented.

Key Words: sperm whale, *Physeter macrocephalus,* sea surface chlorophyll, habitat, Gulf of Mexico

Introduction

The distribution and habitat selection of sperm whales (*Physeter macrocephalus*) is generally attributed to their prey availability (Whitehead, 1996; Davis et al., 2002; Jaquet & Gendron, 2002). Most cephalopods, likely the main prey of sperm whales, are terminal spawners that aggregate to reproduce (Clarke, 1996). Since cephalopods mature rapidly and react to productive environmental conditions quickly, their spawning grounds are believed to lie within areas of enhanced biological productivity (Anderson & Rodhouse, 2001).

The biological response to physical oceanography in the Gulf of Mexico is a complicated process. Geographic locations of on-margin, off-margin, and along-margin surface circulation in the Gulf of Mexico are affected through a complex interplay of bathymetry, deepwater flow, surface currents, and the mid-water eddy field (Biggs et al., 2005). Upper layer ocean currents (the surface down to about 800 to 1,000 m) are dominated by the Loop Current, an extension of the Gulf Stream, which enters the Gulf between Cuba and the Yucatan Peninsula, and by Loop Current Eddies (LCEs) that separate from the main flow. These anticyclonic LCEs separate at irregular intervals in time but usually do so between longitudes 88° to 89° W (Leben et al., 2002). LCEs then translate into the western Gulf at speeds of approximately 3 to 6 km/d (Hamilton, 1990) where they may cleave into smaller eddies, sometimes through interaction with cyclonic features (Biggs et al., 1996).

Mid-water and surface eddies are responsible for much of the off-shelf locally high sea surface chlorophyll (SSC), both through upwelling of mid-water nutrients into the euphotic zone as well as by entrainment and advection of high SSC, low salinity, surface water from the coast and shelf into deeper water. During the summer months when winds are generally westerly, Belabbassi et al. (2005) reported that approximately 75% of Mississippi River discharge flowed into the northeastern Gulf. However, Belabbassi et al. judged that most of this wind-driven flow impacted continental shelf environments, whereas oceanic areas farthest removed from river mouths were primarily supplied with nutrients from uplift of midwater and not from Mississippi River discharge.

These physical oceanographic features create ephemeral and dynamic habitat for sperm whales along the continental margin of the northern Gulf of Mexico. Frontal boundaries associated with LCEs and their cyclonic counterparts generate areas of enhanced surface primary productivity, which may also highlight areas of secondary mesopelagic productivity. LCEs are characterized by diameters of 300 to 400 km and rotation periods of 7 to 10 d; however the smaller cyclonic eddies that LCEs often produce have diameters of just 40 to 150 km and longer rotation periods of 10 to 20 d (Hamilton & Lee, 2005). Griffin (1999) found that sperm whales encountered off Georges Bank appeared to associate with the eastern thermal frontal boundary of a warm core, anticyclonic eddy. The same may be true for sperm whales in the Gulf of Mexico.

Many past studies of cetaceans and their physical habitat have focused on the distribution and abundance of whales in relation to variations in sea surface temperature (Hooker et al., 1999; Baumgartner et al., 2003; Keller et al., 2006) and bathymetry (Hooker et al., 1999; Hastie et al., 2004; Mullin & Fulling, 2004). The development of satellite altimeters that measure sea surface height (SSH) and ocean color sensors that measure SSC resolve yet another layer of the dynamic environment in which whales live. In this paper, habitat data obtained from NASA's Moderate Imaging Spectroradiometer (MODIS) and satellite altimetry are described in relation to two surveys of sperm whale distribution in the northern Gulf of Mexico during the summers of 2004 and 2005.

Materials and Methods

Mesoscale Population Study (MPS) surveys for sperm whales conducted in the northern Gulf of Mexico during June through August of 2004 and 2005 utilized a chartered 46' sloop sailboat, *Summer Breeze*. Surveys focused effort between the 500- and 1,500-m isobaths, an area of high oil and gas platform density as well as anthropogenic activity. Survey details are summarized in Table 1.

Whales were primarily encountered acoustically using stereo-towed hydrophone arrays constructed by Ecologic UK. Hydrophones were monitored every 15 min for 1 min while the sailboat was in survey mode. *Summer Breeze* crew noted presence/absence of sperm whales and other cetaceans at each cruise track location. Survey tracks were charted to achieve the most representative coverage of the study area possible given fuel, time, and weather constraints. Any deviations from survey mode in order to follow an encountered group (tracking mode) or locate a tagged whale were identified in the dataset and not included in the general habitat analysis. Once MPS researchers encountered a group of sperm whales, they followed the group (tracking group) both visually and acoustically for as long as possible or until all individuals in the group were photographed (about 10 to 60 h). The sailboat then moved to another area and resumed its survey. Ranges to whales were measured with a Bushnell 1000 Yard Pro laser range finder (Jochens et al., 2008).

Along Cruise Track Average SSC and SSH Values

Along-cruise track SSC values were extracted from daily-pass Hierarchical Data Files (HDF) from MODIS. SSC values represent composited 3 × 3 pixel boxes surrounding each cruise track location, which provided 9 km^2 spatial resolution.

MODIS HDFs were selected by first visually examining composited images at the GCOOS site (http://modis.marine.usf.edu/weekly/gcoos/gcoos.index.html) for the best cloud-free image. One daily-pass HDF within 3 d of a survey/tracking day was selected for each day of the 2004 and 2005 surveys. Survey/tracking days are referred to as zero days. Six additional HDFs were selected for each day of cruise effort. These images represent a single day approximately 1 wk, 2 wks, 4 wks, and 16 wks before and after each survey day. MODIS HDFs were selected at discrete time lags from survey/tracking days in order to describe dynamic oceanographic effects on sperm whale distribution and approximate time scales on which these oceanographic parameters are relevant. Mesoscale oceanography examined in this paper can change on the order of days and weeks, so the use of composited satellite imagery was minimized.

Satellite altimetry of SSH data were collected and processed by the Real-Time Altimetry Project at the University of Colorado Center for Astrodynamics Research (CCAR). Altimetry data were selected for the same time lags as those of SSC but were 0.25° × 0.25° gridded at CCAR before being processed in this analysis. Eight-day composites, using the day of interest as the median day, were used to temporally average the SSH data (Leben et al., 2002).

In order to assess differences in oceanographic habitat across the northern Gulf, the study area

Table 1. Summary of overall acoustic and visual survey effort during the summers of 2004 and 2005

Year	Dates of field work	Range of continental margin surveyed	Nautical miles surveyed	Groups of sperm whales
2004	20 June - 15 August	90.5° - 84.5° W	2,194	19
2005	13 June - 3 August	94.5° - 85° W	1,969	16

was divided into eastern and western portions at 88.5° W. To the east of this dividing line is the Desoto Canyon and to the west is the Mississippi Canyon. Centered along the dividing line is the approximate outflow of the Mississippi River and the Delta. Geometric mean values of SSC were calculated for locations of whale encounters east and west of 88.5° W.

Statistical Analyses

Each location from the cruise tracks does not necessarily have a corresponding SSC value for each time lag because SSC values could only be extracted for cloud-free locations. To more closely represent a normal distribution, SSC values were converted to a base 10 log scale to calculate geometric means for SSC at each time lag. A log scale was chosen for comparison of SSC values based on the work of Campbell (1995) and Doney et al. (2003) to better represent the lognormal optical variability of the surface ocean. All "mean" SSC values in this paper are geometric means.

In order to avoid the effects of pseudo-replication in the analysis of oceanographic parameters, each tracking group of sperm whales was considered a separate event for the purposes of statistical analysis. A tracking group was defined in the field as those individuals observed (acoustically and visually) to be traveling in the same general direction. Since most individuals in a tracking group were photographed (and later assigned a photo-identity) before the sailboat moved on to a new location away from the group (Jochens et al., 2008), and since groups were encountered on different days, we are satisfied that tracking groups represent unique data points. The average of all SSC and SSH values extracted for a single tracking group at each time lag was taken to represent the habitat occupied by that tracking group when encountered by *Summer Breeze*.

Nonsighting locations included the positions and remote sensing data from the survey mode sections of the dataset. Tracking groups containing at least one previously photo-identified female were considered separately from groups containing only newly identified individuals for part of the analysis. Tracking groups that only contained maturing males were considered bachelor male groups and were also separated between those previously and not previously photo-identified. Males were distinguished from females by larger estimated body lengths (Jaquet, 2006). Time of fluke-ups and presence/absence of defecation in the water were noted by observers who also estimated size of whale cluster, presence/absence of calves, and behavior of individuals (Richter et al., in press).

Correlation coefficients representing the zeroth lag of the covariance function for SSC vs whale encounters were calculated for each tracking group at each time lag. Statistically significant correlations were considered at $p \leq 0.05$ and described in the text.

Results

Sperm Whale Distribution and Abundance

In 2004, *Summer Breeze* covered 2,194 nmi of sea while in survey mode, encountering groups of sperm whales at a rate of 0.009 groups/nmi. About 1,198 of those nmi were covered west of 88.5° W with an encounter rate in this region of 0.011 groups/nmi. East of 88.5° W in the Desoto Canyon and Mississippi Delta region, *Summer Breeze* surveyed approximately 996 nmi of sea, encountering 0.006 groups of whales per nmi.

The overall encounter rate of whales was similar in summer 2005. A total of 1,969 nmi were surveyed in 2005, and 0.008 groups of whales per nmi were encountered. *Summer Breeze* surveyed 1,170 nmi west of 88.5° W, and it encountered groups of whales at a rate of 0.008 groups/nmi. The encounter rate was slightly higher over the 798 nmi surveyed in the east, a rate of 0.009 groups/nmi.

Composition of the northern Gulf sperm whale population was different between summers as shown in Table 2. Median group size decreased from 13.7 in 2004 to 6.8 in 2005. The percentage of the population comprised by calves declined by over 50% between summers 2004 and 2005. Defecation rates were also nearly halved between 2004 and 2005.

Eight mixed groups of re-identified whales were encountered in the western portion of the study area during summer 2004, but just three groups were encountered in the west during 2005. In the eastern portion of the study area, there was relatively little change in the number of groups with re-identified individuals encountered (1 during 2004 and 2 during 2005). Fewer mixed groups containing individuals not previously identified were found in the east than the west, but there was almost no change in the encounter rate of these groups between summers (Table 3).

Bachelor male groups were encountered at about the same rate in 2004 as in 2005 (0.002 groups/nmi compared to 0.003 groups/nmi). A total of 10 bachelor male groups were encountered during the two summers of survey effort, seven of which contained only newly identified individuals. These results are summarized in Table 3.

Table 2. Summary of whale encounter groups; groups of whales refer to single tracking periods when the sailboat followed and photographed a group of whales. Whales were estimated to be calves based on observed body length. Defecation rate refers to the proportion of foraging dives where visual observers noted brown colored water immediately following the fluke-up.

Year	Encounter rate of groups of whales/nmi	# calves (% of total)	Median group size	Defecation rate
2004	0.009	15 (12.7%)	13.7	23.5%
2005	0.008	4 (5.7%)	6.8	14.8%

Table 3. Summary of encountered groups of sperm whales; groups represent single tracking periods. Individuals were identified from photographs taken of their flukes and marked as either mixed groups or bachelor male groups by visual observers.

	2004 west	2005 west	2004 east	2005 east
Mixed groups with re-identified individuals	8	3	1	2
Mixed groups with newly identified individuals	4	4	2	1
Bachelor male groups with re-identified individuals	1	0	1	1
Bachelor male groups with newly identified individuals	0	2	2	3
Total number of groups encountered	13	9	6	7
Total nmi surveyed	1,198	1,170	996	798

Surface Habitat Characteristics

Figure 1 is a summary composite of SSH and SSC in the northern Gulf of Mexico for each summer. Along the cruise track, mean SSH was similar in both summers. In 2004, the along-track mean SSH was -8.2 cm, and in 2005 it was -7.1 cm. These negative SSH values are diagnostic of the cyclonic side of frontal boundary locations between cyclonic-anticyclonic eddy pairs. Whales were encountered in summer 2004 in areas where SSH ranged between -15.1 and -2.0 cm with a mean SSH of -8.0 dynamic cm. Non-encounter locations covered a much wider range of -23.6 to +1.0 cm but had a similar mean (-7.5 cm). During summer 2005, SSH of whale encounters ranged from -12.6 to +1.2 cm (mean SSH was -4.5 cm). Locations where no whales were encountered in summer 2005 had a SSH range of -25.1 to +1.2 cm (mean was -6.0 cm).

Satellite measurements of SSC made by NASA's SeaWiFS instrument for stations during the Deep Gulf of Mexico Benthos study (DGoMB) provided a baseline of comparison for sperm whale habitat in the northern Gulf of Mexico. Monthly composite imagery of DGoMB stations sampled between 86º W and 90º W and 300 to 2,000 m revealed that geometric mean SSC from 1998 to 2000 was 0.40 mg/m^3 east of 88.5º W. West of 88.5º W, geometric mean SSC was 0.63 mg/m^3 or one third greater than the SSC level measured in the east (Biggs et al., 2008). DGoMB results are similar to MODIS-derived estimates of SSC in 2004 at the locations of whale encounters where mean SSC was 0.53 mg/m^3 east of 88.5º W and 0.69 mg/m^3 west of 88.5º W. In contrast, mean SSC at the locations of whale encounters measured 0.17 mg/m^3 east and only 0.14 mg/m^3 west of 88.5º W in 2005.

Most mixed groups were encountered during both summers in the higher SSC waters of the western study area. In 2004, two thirds of the encountered groups were mixed groups in the west, whereas only one sixth of encountered groups in the east were mixed groups. In 2005, mixed groups in the west comprised two fifths of encountered groups and almost one fifth of encountered groups in the east.

In 2004, there was no significant difference in SSC between areas where groups of whales were encountered than locations where only groups with at least one re-identified whale were encountered. Interestingly, in 2005, locations where groups with re-identified whales were encountered had significantly less SSC than general whale encounter locations at several different time lags. At the 1 wk before and after time lags, locations of re-identified whales were also areas where SSC was significantly lower than non-encounter locations. These data are summarized in Figure 2.

Bachelor male groups increased between summers in both the west and east but generally were found in the east rather than the west. Despite the predominance of bachelor male groups in eastern study area waters where overall SSC was generally lower than in the west, their correlation with SSC was stronger than that of mixed groups (when only locations of whale encounters were considered for

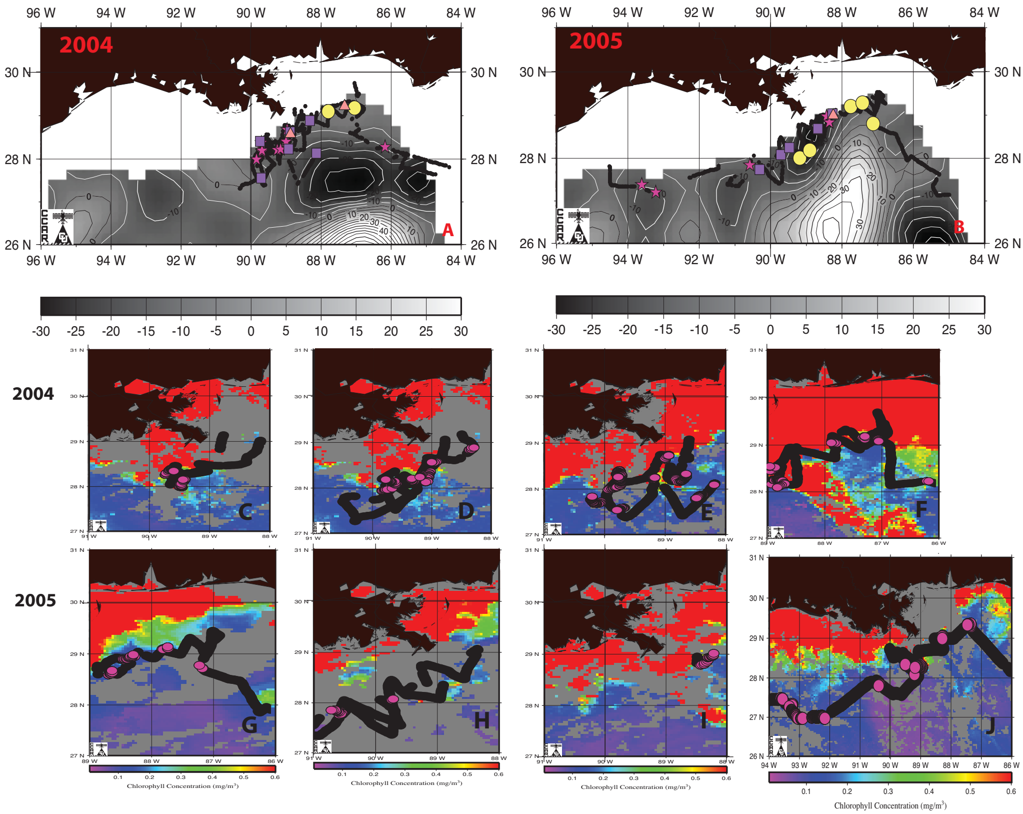

Figure 1. Spatial distribution of groups of whales in summers 2004 and 2005; the SSH composite plots are from the midpoint in time of each cruise. Positive SSH is denoted by solid contour lines and negative SSH by dashed contours. Black points indicate survey effort where no whales were encountered. Pink stars indicate mixed groups containing individuals previously photo-identified, mixed groups containing individuals not previously encountered are indicated by purple squares, male groups with re-identified individuals are indicated by orange triangles, and yellow circles indicate male groups with only new individuals. SSC plots are 8-d composites from the midpoint of each survey leg. Black dots indicate survey effort where no whales were encountered, while pink points denote the path of *Summer Breeze* while tracking whales. Panels C through F represent legs 1 through 4 of 2004 and Panels G through J represent legs 1 through 4 of 2005.

both summers, groups of male whales were associated with log SSC at a time lag of 1 wk preceding encounters [0.66, $p < 0.01$]).

SSC at both whale encounter and no encounter locations is summarized in Figure 2. When SSC and whale encounters were averaged over both summers, only the SSC 2 wks preceding encounters had a statistically significant positive correlation between log SSC and whale encounters (0.13, $p = 0.05$).

Discussion

Oceanographic variation between summers permits several observations about sperm whale distribution in the northern Gulf of Mexico. First, sperm whale habitat utilization in the Gulf, particularly among groups of bachelor males, is closely linked to surface primary productivity on time scales of 1 to 2 wks and spatial scales at least as small as those resolved in this study (9 km^2). This link was supported by the correlation of encounter rate to SSC as well as several changes to group characteristics. Defecation rates fell by about 50% between 2004 and 2005, indicating reduced foraging success of sperm whale groups in 2005 (see Whitehead, 1996, for an explanation of the link between foraging success and defecation rates). The median group size and the number of counted calves in 2005 was also about half that of those in 2004. Determining the smallest scales over which sperm whales respond to theses changes in environmental conditions will help researchers explain which physical and biological oceanographic features influence sperm whale ecology.

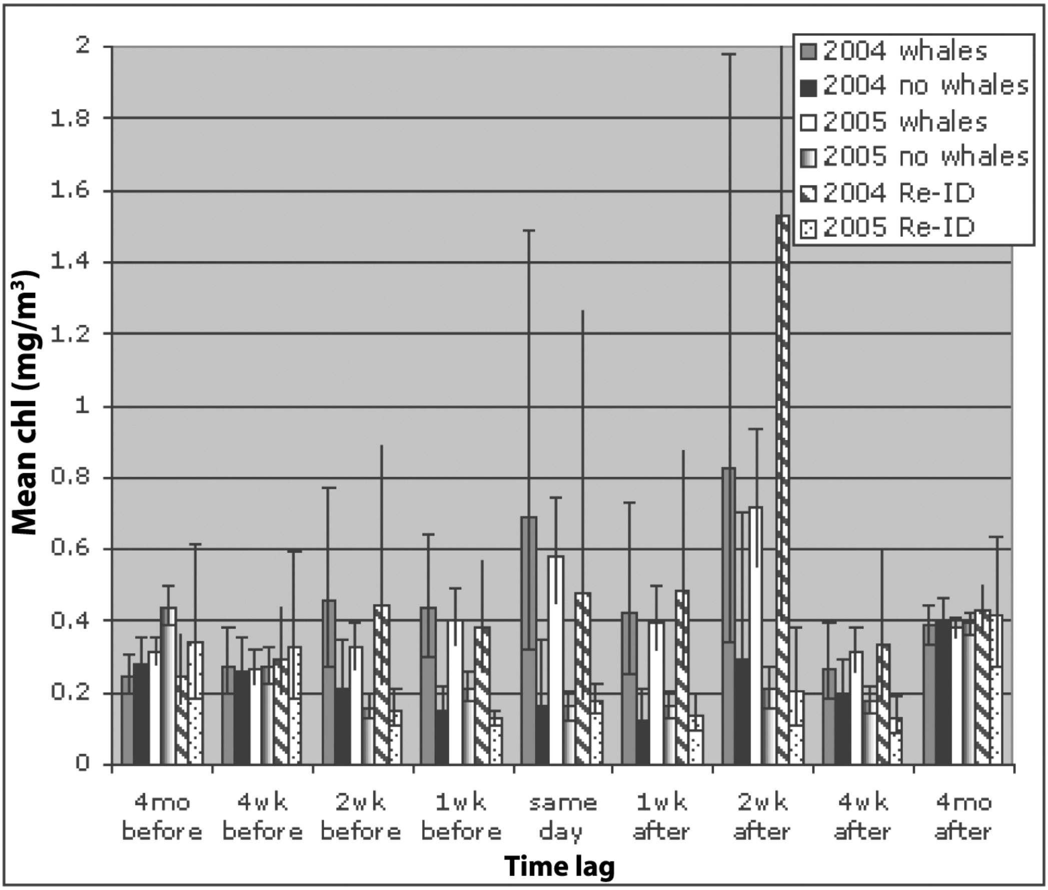

Figure 2. Geometric mean SSC before, during, and after sperm whale surveys in summers 2004 and 2005

Second, mixed groups of females and bachelor groups of males are geographically segregated in the Gulf of Mexico. The boundary where overlap between gender groups occurs lies within a region offshore of the Mississippi Delta where intense physical processes take place. Geographic segregation is the rule between mature males and mixed groups of females and juveniles and is present on a global basis (males inhabiting polar regions and female groups the equatorial and subtropical regions) as well as on a regional basis within temperate zones (Best, 1979; Rice, 1989; Lettevall et al., 2002). Given that groups of males were encountered in areas of generally higher SSC within a region of lower SSC than the groups of females suggests that these whales may be selecting habitat based not on quantity of productivity but on the structure and character of the biological activity. Doniol-Valcroze et al. (2007), using whale sightings and satellite images from 1996 to 2000 in the Gulf of St. Lawrence, showed physical structuring of prey to be important for large balaenopterid whales. They found that rorquals associated within close proximity to thermal frontal boundaries. Enhanced primary productivity generated by frontal boundaries did not explain the whales' association with frontal areas since frontal upwelling can vary spatially over a few days, yet whales were associating with fronts over single days. Instead, the authors emphasized that prey species for balaenopterids aggregate along the edges of frontal upwelling zones, which creates a more efficient foraging situation for the whales. It is possible that in the northern Gulf of Mexico, when LCEs and cyclones spin into the Mississippi Delta and Desoto Canyon regions, they create pockets of concentrated secondary mesopelagic productivity where males can forage in a manner efficient enough to meet their individual energetic needs.

Groups of females and juveniles comprised of several individuals may prefer more broadly dispersed regions of secondary productivity. Whitehead (1996) suggested that groups of female sperm whales likely use migration as their primary strategy for survival in times of low productivity. Researchers may have observed this tendency in 2005. Mixed groups of females were encountered at a rate of 0.007/nmi in 2004 but at a rate of 0.005/nmi in 2005. In contrast, the bachelor male group encounter rate increased from 0.002/nmi in 2004 to 0.003/nmi in 2005, which suggests that groups of females moved out of this study area in 2005.

The preference displayed by mixed groups of females for a more westerly habitat within the study area may also be due to their propensity to migrate. The northwestern continental slope of the Gulf offers a suitable habitat for regional migration since whales can follow LCEs and their resultant cyclones as they drift westward. Mixed groups in the northern Gulf can forage along the boundary of an especially productive LCE, slowly tracking its rotation and generally westerly translation. Alternatively, after exploiting one eddy's resources, a group could migrate further west following the smaller, more productive upwelling environments created by LCEs in the form of cyclonic eddies. Both of these features continually flow westward from the Mississippi Delta region, the rough dividing line between mixed groups of females and juveniles and bachelor male groups.

It is interesting to note that whales in the western study area were encountered in 2005 in areas where mean SSC was reduced only by 80% from 2004. In the east, areas where whales were encountered were only reduced in SSC by 68% from 2004 eastern encounter locations. It seems that in the east, where whales could not so easily follow eddies or migrate between eddies, they generally foraged in areas of reliable productivity. Whales in the west may either have been selecting habitat for the structure rather than quantity of its productivity or simply may have been encountered during stretches of migration that included areas of low productivity.

Another possible explanation that could not be examined in this study is that the threat of predation may have contributed to the structuring of sperm whale distribution in this study and influenced the movements of social units. In the Gulf of Mexico, little is known about one potential predator, the killer whale (*Orcinas orca*). Currently, their population is estimated at just 133 (CV = 0.49), with most of the observations of this species being made south of the Mississippi outflow beyond the 1,000-m isobath (Waring et al., 2004). Wirsing et al. (2008) used three separate case studies of marine mammals to show how the sublethal threats imposed by predation may influence the movements and habitat occupied by marine mammals. In our study, the distribution of sperm whales is marked by a noticeable east-west separation between groups of females and juveniles and bachelor male individuals. The male individuals were more closely correlated to high SSC values, but the female/juvenile groups were associated with productivity over larger spatial scales. The mixed groups of females and juveniles might be more sensitive to the threat of predation on calves, particularly during long foraging dives, but they are better able to defend themselves from attacks given their larger group size compared to that of the bachelor male individuals and groups. More study of the killer whale population and the movements specific to each social unit of sperm whales is needed in order to understand the potentially subtle but important influence predation has on sperm whale ecology in the Gulf.

Lastly, what is apparent from the data is that oceanographic changes between the summers of 2004 and 2005 in the northern Gulf of Mexico had a differential impact on social units within the sperm whale population. In 2004, groups of sperm whales whose members were all newly photographed individuals were encountered in areas of about equal SSC as groups with previously identified individuals. In 2005, however, groups containing individuals never before encountered in the Gulf were found in areas of significantly higher SSC than groups that did contain previously identified individuals. These results suggest that sperm whale groups display different foraging strategies in times of altered or decreased biological productivity, supporting the findings of Whitehead & Rendell (2004). They concluded that cultural inheritance and therefore group membership has an important effect on the foraging success and fitness of individuals in varying environmental conditions.

In order to quantify the spatial and time scales on which mesopelagic secondary productivity is linked to surface primary productivity more *in situ* measurements will need to be made. Satellite measurements can tell us about the surface ocean's primary productivity, but only *in situ* measurements will reveal the quantity and character of the biological response. Collection of surface and mesopelagic zooplankton and nektonic species in conjunction with documentation of sperm whale distribution and photo-identification is necessary. Linking surface primary productivity to mesopelagic secondary and tertiary productivity over the time scales on which these physical and biological processes operate will better allow researchers to manage sperm whale populations and decipher complex marine food webs. Such studies will better allow researchers to anticipate the response of the marine food web to environmental variability and better prepare marine resource managers for the potential impacts of climate change.

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