

Temporal Variation in Atlantic Spotted Dolphin (*Stenella frontalis*) and Bottlenose Dolphin (*Tursiops truncatus*) Densities on the West Florida Continental Shelf

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Abstract

We surveyed Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) in an area of the west Florida continental shelf (82° to 84.5° W and 26° to 28° N) from November 1998 to December 2001. Objectives were to estimate relative abundances of these two species and test for seasonal and interannual variations in distribution. Monthly surveys were conducted over a three-year period between the coast and the 180 m depth contour. Abundances of Atlantic spotted dolphins and bottlenose dolphins were estimated using the software program *Distance*. Sightings from monthly surveys were pooled by years and by seasons within a year. Significant seasonal variations in Atlantic spotted dolphin densities were repeated across years, with lower abundances during the warm season (June-October), and higher densities during the cool season (November-May). Atlantic spotted dolphin densities significantly decreased during 2000, while bottlenose dolphin density trends were not apparent. These trends continued into 2001, suggesting differential species response to environmental variation may affect changes in cetacean community structure over relatively short temporal scales.

Key Words: seasonality, habitat, density, Gulf of Mexico, Atlantic spotted dolphin, *Stenella frontalis*, bottlenose dolphin, *Tursiops truncatus*

Introduction

Cetacean densities in a region may vary temporally due to a number of causes. Increases or decreases in recruitment or mortality will affect absolute population size. Immigration or emigration in response to environmental or trophic variation may leave population sizes unchanged, while regional densities may display important short-term or seasonal effects.

Risk of shark predation may influence dolphin habitat use (Heithaus, 2001; Heithaus & Dill,

2002). Distribution of foraging dolphins matched the distribution of their food when sharks were absent, yet deviated from the prey distribution when sharks were in high density. Foraging dolphins are more likely to be found in risky habitat than resting dolphins. Pelagic dolphins apparently adapt to increased risk of predation with increases in group size.

Individuals within a species are expected to maximize their net caloric intake per unit time (Emlen, 1966). The degree of selectivity for preferred food items will increase with increasing abundance of available food items. Sub-optimal food items may be preferred when they are relatively more common than an optimal food item. According to the marginal value theorem (Charnov, 1976), an animal foraging in a resource patch should leave the patch when the rate of energy gain falls below the mean rate of gain for the habitat. Patch residence time should increase with increasing patch quality, and it should decrease with increasing habitat quality. Where patch qualities are equal, residence time in a patch should decrease with decreasing distance between patches. Food preferences appear to change in response to environmental changes.

Environmental control was a major contributor in structuring distribution and abundance (Hofmann & Powell, 1998) in northern cod (*Gadus morhua*), cod and haddock (*Melanogrammus aeglefinus*) larvae, the eastern oyster (*Crassostrea virginica*), and Antarctic krill (*Euphausia superba*). Environmental effects manifested at a variety of scales and at multiple trophic levels. In some systems, the response to environmental variability was delayed one to five years before the full effect was observed. Climate change caused contrasting trends in reproductive success of two species of alcids (Kitaysky & Golubova, 2000) in an eight-year study in Tauyskaya Bay (Okhotsk Sea, northwestern Pacific). Recruitment of planktivorous auklets was negatively correlated with sea surface temperature, while reproductive success of

piscivorous puffins was correlated positively with sea surface temperature. Interannual oceanographic change probably impacted reproductive performances by affecting food accessibility to the two species in opposite ways.

Dolphin (family Delphinidae) responses to seasonal environmental variation are diverse. Seasonal movements may occur in response to movement of prey. Studies of the northern resident community of killer whales (*Orcinus orca*) off British Columbia have suggested seasonal ranges, with temporal distributions of some pods associated with the presence of certain salmon species (Nichol & Shackleton, 1996). Seasonal distribution of killer whales around northern Norway was closely related to the distribution of spring-spawning herring (*Clupea harengus*) in the area (Similae & Christensen, 1992). Most of the whales leave the area in January when herring migrate to spawning grounds 700 km south.

Common dolphins (*Delphinus delphis*) in the northwest Atlantic migrated north and onto the shelf in summer (Selzer & Payne, 1988) and south into slope waters in winter. Evidence suggests these movements were in response to prey abundance. In the southern hemisphere, seasonal ranging patterns and density of common dolphins expanded to lower latitudes in winter (Cockcroft & Peddemors, 1990), coincidental with the annual "sardine run." Seasonal migrations of other species have been described where prey movements were not known.

Seasonal movements of delphinids residing in temperate latitudes often are characterized by travel between higher and lower latitudes or by inshore-offshore movement. Atlantic white-sided dolphins (*Lagenorhynchus acutus*) off the northeastern coast of the United States appeared to exhibit some seasonal shifts in distribution and were more common in the central and northern Gulf of Maine during summer months (Northridge et al., 1995; Selzer & Payne, 1988). White-sided dolphins migrated back to Georges Bank and the Great South channel in winter. Along the central east coast of the U.S., bottlenose dolphins (*Tursiops truncatus*) of the coastal migratory stock traveled north in spring and summer, and south from November to March (Barco et al., 1999). Seasonal movements of Pacific white-sided dolphins (*L. obliquidens*) in the eastern North Pacific were apparent between 30°-35° N off southern California, where peak numbers occurred inshore from November through April. Winter abundance of Pacific white-sided dolphins was 20 times greater than summer abundance (Forney & Barlow, 1998). A shipboard survey out to 556 km from the California coast during July to November 1991 found only one Pacific white-sided dolphin in waters beyond 278 km, suggesting the population moved northward in summer, rather than offshore.

Studies of tropical delphinids suggest these species tend to move inshore in autumn and winter, and then offshore during spring and summer (Perrin, 1975). Pantropical spotted dolphin (*Stenella attenuata*), spinner dolphin (*S. longirostris*), and striped dolphin (*S. coeruleoalba*) distributions in the Eastern Tropical Pacific (ETP) tended to be pelagic in summer and more nearshore and southern in winter (Reilly, 1990). Offshore distributions coincided with winter oceanographic conditions favorable to aggregation of prey. Common dolphin distributions in the ETP showed little seasonal change.

Some work has examined seasonal distributions of delphinids in the eastern Gulf of Mexico. Bottlenose dolphins along western Florida were found in relatively higher numbers in channels and bays inshore of barrier islands during summer, but were more abundant in passes and along the Gulf shore in winter (Irvine et al., 1981). Seasonal patterns of this species have not been studied previously in offshore waters of the eastern Gulf of Mexico. Available information on Atlantic spotted dolphin (*Stenella frontalis*) ecology is limited. Most life history work on Atlantic spotted dolphins has been done in the Bahamas (Brunnick, 2000; Dudzinski, 1996; Herzing, 1996a, 1996b; Herzing & Brunnick, 1997; Herzing & Johnson, 1997), but seasonal movements of this species have not been described for the Bahamian population. Analyses of seven years of opportunistic sightings data from the northern Gulf of Mexico (Mills & Rademacher, 1996) suggested Atlantic spotted dolphins were found primarily in the 15-100 m depth range, with densities greatest east of the Mississippi River. While seasonality in distribution was examined, no clear patterns emerged. Recent work (Griffin & Griffin, 2003) showed Atlantic spotted dolphin densities in the eastern Gulf of Mexico are greatest in waters 20-50 m in depth.

Ecological patterns influencing dolphin distributions and abundance are likely complex and multi-layered, operating over a variety of temporal scales. While very few of the movement patterns described above have been linked conclusively or quantitatively with prey, evidence suggests that general patterns in delphinid migrations are likely affected by prey abundance and distribution. Prey ecology is difficult to assess in oceanic cetaceans, yet may be examined through the proxies of oceanographic processes and temporal environmental variation. Environmental variation may be intra-annual (seasonal variation), or inter-annual (resulting from cyclical multi-annual patterns or long-term trends). Interactions between multiple temporal cycles may result in complex regional variations in animal density. Closely related

species may use different prey resources and, thus, exhibit unique responses to ecological variation.

Dolphin surveys were conducted on the west Florida continental shelf to examine Atlantic spotted dolphin and bottlenose dolphin population densities. Data were tested for seasonal and inter-annual variation in density.

Materials and Methods

We conducted monthly shipboard dolphin surveys on the west Florida continental shelf aboard the *R/V Suncoaster* (Florida Institute of Oceanography) for a three-year period (November 1998 through December 2001) in conjunction with oceanographic surveys funded under the Ecology of Harmful Algal Blooms (ECOHAB) program. Surveys included a series of repeatable transects, with 79 oceanographic stations at 9-km interval transect segments (Griffin & Griffin, 2003) in an area bounded by 82° to 84.5° W, 26° to 28° N (Figure 1).

Two cross-shelf transects between the 10-50 m depth, as well as one cross-shelf transect between 10-180 m, were surveyed independently throughout the study period. These three transects were sampled consistently throughout the study period. Additional transects were surveyed during a portion of the study period, including a (1) coastal transect along the 10-m isobath, (2) diagonal transect from 10-50 m depth, and (3) transect along the 50-m isobath. Hydrographic profiles were collected via Conductivity Temperature

Depth Bathythermograph (CTD) at oceanographic stations, and continuous underway surface data of temperature, salinity, and chlorophyll concentration were collected via a flow-through CTD apparatus.

Dolphin surveys were conducted by three observers, with two observers "on effort" during each duty rotation. Observers maintained watch from the bow during transit between stations (approximately 30 min), then stopped effort for 20 min while oceanographic data were obtained. Handheld binoculars (7 x 50) were used to sight and identify species when cues or animals were seen. Sighting data collected included time, location, bearing, and an estimation of distance to animals when initially sighted, species, and estimated numbers of adults and calves. We estimated bearing using a 360° course plotter. Observers with prior training and experience in distance approximation visually estimated distances without the use of a range finder. Observer distance estimation skills were tested periodically by comparing estimated distances to buoys with distances obtained by ship's radar. Calves were defined as animals less than or equal to 75% the body length of an associated adult. We deviated from trackline to identify and observe dolphins sighted, when time permitted, and experienced observers assigned species identifications.

Biological and physical data within transect segments were collected to document conditions between oceanographic stations. These data included observations of surface manifestations of biology (e.g., birds, flying fish, schooling fish, cnidarians); descriptors of sea state and sighting conditions; and cargo, fishing, and recreational vessel presence.

Data from three cross-shelf transects were analysed, with 9-km transect segments between oceanographic stations used as the sampling unit. We used the software program *Distance* (Thomas et al., 1998) to estimate abundances of Atlantic spotted dolphins and bottlenose dolphins. Abundance estimates reported here represent a surveyed area of approximately 10,850 km².

Since Atlantic spotted dolphins in this area have been reported from depths of ≥ 16 m (Griffin & Griffin, 2003), we examined transect segments with a mean depth ≥ 20 m. To examine variation between years, monthly sightings data were pooled by year: November 1998 to October 1999 (Year 1), November 1999 to October 2000 (Year 2), and November 2000 to October 2001 (Year 3). To examine variations within a year, sightings were pooled by season within each year, with season defined by the mean underway surface sea temperature (Figure 2). We defined a cool season (C) as November through May and a warm season (W) as June through October.

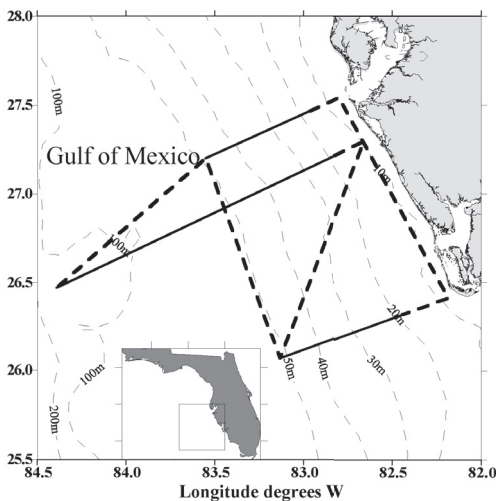


Figure 1. Location of Offshore Cetacean Ecology Program study area in the eastern Gulf of Mexico during 1998-2001; solid lines represent "cross-shelf" ECOHAB synoptic survey trackline, dashed lines represent survey transects not included in these analyses.

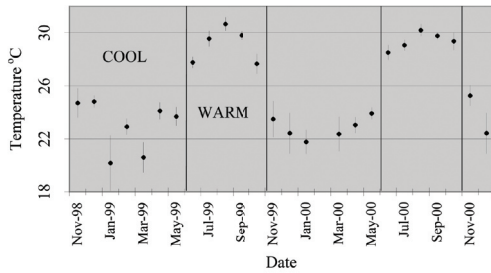


Figure 2. Mean underway surface sea temperature ($^{\circ}\text{C} \pm \text{SD}$) for monthly surveys of marine mammals along ECOHAB synoptic survey trackline during Years 1 and 2 of this study; solid vertical bars define seasonal boundaries.

Truncation distances were selected from examination of data to exclude sightings at extreme distances outside of the normal distribution. Data of both species were truncated at perpendicular distances greater than 750 m during Year 1, and 500 m during Year 2. During Year 3, bottlenose dolphin sightings were truncated at perpendicular distances of 750 m, while Atlantic spotted dolphin sightings were truncated beyond 500 m. Detection function and cluster size were estimated globally by species. Three models were tested—uniform+cosine, half-normal+cosine, and half-normal+hermite polynomial—and Akaike's (1973) Information Criterion was used to select the most parsimonious model. Regressions of observed group size against distance were not significant at an alpha level of 0.15; hence, mean group sizes were calculated as the mean of observed values.

To examine differences in species' densities between seasons and years, we employed a bootstrap procedure used by Forney & Barlow (1998). Using *Distance*, random transects were subsampled with replacement of sampling units, and a series of 1,000 bootstrap estimates were obtained for the three years and six seasons defined for the study. Given density estimates for Years 1-3 (D1, D2, D3), and for warm and cool seasons (W and C) within years (e.g., D1C, D1W, D2C, D2W, D3C, D3W), differences, d , were then calculated between years by subtracting subsequent years from preceding years, and between seasons by subtracting W from C estimates within years. For example, the estimated difference in density between Year 1 and Year 2 was calculated as $D1-D2$, while the estimated difference in density between cool and warm seasons within Year 1 was calculated as $D1C-D1W$. Differences, d^* , between the 1,000 bootstrap density estimates were calculated, and two methods were applied to the d^* set for each comparison to calculate confidence intervals: (1) theoretical 95% confidence interval of d^* (Lo, 1994) and (2) the BCa method described by Efron

& Tibshirani (1993). Density estimates were considered significantly different when 95% CIs of d did not overlap zero.

We extracted sea surface height anomaly (SSHa) values found during monthly surveys at a location of 84°W , 27°N , from the Gulf of Mexico Archive maintained by the Naval Research Laboratory at Stennis Space Center. SSHa is the deviation of sea surface height at a location from the mean at that point, after removing tides, and may be positive or negative. Mean monthly salinity values were calculated from underway data. These data were pooled by year and season, and t -tests (Sokal & Rohlf, 1981) were used to examine differences in salinity and SSHa by year and season.

Results

Over 9,000 km of marine mammal survey effort was completed on cross-shelf transects over the three-year period, with 202 on effort dolphin sightings (113 sightings of Atlantic spotted dolphins, 704 animals; 55 bottlenose dolphin sightings, 222 animals; one rough-toothed dolphin (*Steno bredanensis*) sighting, 7 animals; 33 unidentified dolphin sightings, 108 animals, for an overall sighting rate of 0.11 dolphins km^{-1} , or 0.022 sightings km^{-1} . Mean (median, SD) group sizes were 4.0 (2, 4.29) for bottlenose dolphins, 6.2 (5, 5.41) for Atlantic spotted dolphins, and 3.3 (2, 4.14) for unidentified dolphins, respectively. Atlantic spotted dolphin group size ranged from 1 to 48 animals. Group sizes for both bottlenose and unidentified dolphins ranged from 1 to 25 animals.

Annual and seasonal sighting effort (Table 1) within the study area varied. During Years 1 and 2, ten surveys were completed in each year. During Year 3, reduced shiptime funding for the ECOHAB: Florida Project resulted in six surveys completed. Sightings distribution of Atlantic spotted dolphins and bottlenose dolphins differed from each other (Figures 3 & 4). Inter-annual changes in spatial distribution were not apparent for Atlantic spotted dolphins, while bottlenose dolphins' spatial distribution appeared to expand from Year 1 to Years 2 and 3.

A trend for an increase in Atlantic spotted dolphin density and a decrease in bottlenose dolphin density between years was apparent (Figure 5). Trends for density and abundance estimates between seasons and years were significant for Atlantic spotted dolphins (Tables 2 & 3; 95% CI). Atlantic spotted dolphin densities in the study area decreased in the warm season relative to the cool season in Years 1 and 2. Alternating cool and warm seasons were characterized by significantly higher or lower densities ($p < 0.05$), respectively. This trend was not significant during Year 3. Atlantic spotted dolphin

Table 1. Offshore Cetacean Ecology Program marine mammal survey effort (months and km) along cross-shelf transects in the eastern Gulf of Mexico during 1998-2001, by year and season; Year 1 = November 1998 to October 1999, Year 2 = November 1999 to October 2000, and Year 3 = November 2000 to October 2001; C = November to May; W = June to October.

Year	Season	Months surveyed	Effort (km)
1	C	7	2,491
1	W	3	755
2	C	6	2,128
2	W	4	1,561
3	C	2	978
3	W	4	1,441

densities also differed significantly between years, with densities in Years 2 and 3 significantly less than Year 1 densities. Densities during the second and third years of the study were not significantly different. We only had one verified sighting of bottlenose dolphins during the warm season of Year 1, precluding bootstrap comparison of seasonal estimates within this year. Estimates of bottlenose dolphin densities did not vary between seasons during Years 2 and 3. Similarly, densities did not significantly vary between years. Atlantic spotted dolphin densities were significantly greater than bottlenose dolphin densities during the first and second years of the study, and statistically equivalent during the third year.

Proportion of calves in monthly surveys varied significantly between years for both species. Mean proportion of calves among total Atlantic spotted dolphins sighted was greatest during the second year (0.05 Year 1 vs 0.11 Year 2, $p = 0.03$). Similarly, mean proportion of total bottlenose dolphin calves sighted was higher during the second year (0.02 Year 1 vs 0.06 Year 2, $p = 0.01$).

Mean surface salinity during Year 2 of the study (36.132 PSU) was significantly greater than salinity during Year 1 (35.257 PSU; t -test: $t = 6.527$, $p < 0.001$). Mean underway surface sea temperature did not vary significantly between years (t -test: $t = 0.099$, $p = 0.46$). SSHa differed significantly between years (paired t -test: $t = 4.58$, $p < 0.001$), but not seasons ($p > 0.5$). Mean SSHa for November 1998-October 1999 was +3 cm, compared to +10 cm for November 1999-October 2000.

Documented prey of Atlantic spotted dolphins include species of flying fish (Exocoetidae; Richard & Barbeau, 1994), a family of fish we saw in greater abundance in the region during warm season months ($t = 8.36$, $p < 0.001$) when Atlantic spotted dolphin densities were lowest.

Flying fish were observed in a mean of 75% of 9-km transect segments during the warm season months, and were seen a mean of 14% of transect segments during cool months.

Discussion

Seasonal Variation

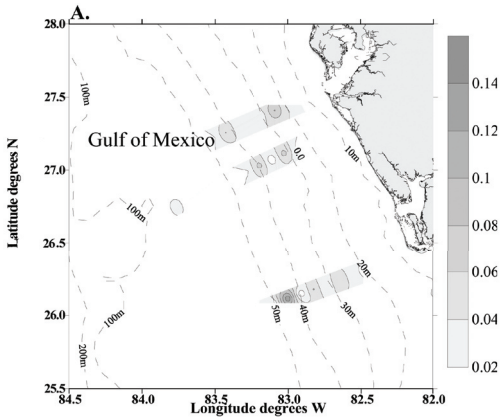
The significant seasonal variation reported here for Atlantic spotted dolphin densities was repeated over two years of survey effort and was indicated in the third year. The lack of seasonal significance for Year 3 may reflect the reduction in cool season effort and the resulting asymmetry of effort between seasons in that year. Surveys of these populations have continued aboard smaller vessels and will permit continued analyses of seasonal trends in local abundance.

Potential seasonal sources of environmental variability included water temperature fluctuations, oceanographic variation (e.g., changes in current pattern or hydrographic profile), and prey migration. While water temperature varied by season (Figure 2), the continued presence of Atlantic spotted dolphins during warm seasons suggests warmer temperatures were within their physiological tolerances. Seasonal oceanographic variation and its effect on continental shelf prey densities were the most likely causes of the observed intra-annual variation in Atlantic spotted dolphin densities.

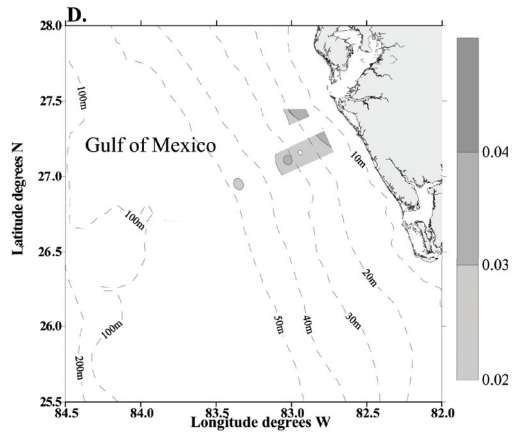
Seasonal modulation of the west Florida continental shelf circulation is driven by a seasonally varying shelf-wide baroclinic structure (Weisberg et al., 1996). At synoptic time scales, water mass movement is primarily wind-forced. Recurrent changes in oceanographic patterns generate serial movements of prey.

Reduced abundance of flying fish in the region during winter reflected a response of one known prey species to hydrographic differences. Increased abundance of Atlantic spotted dolphins during winter relative to summer suggested ranging patterns of this dolphin species responds to preferred prey species other than flying fish. Additional Atlantic spotted dolphin prey reported in the literature include small to large cephalopods, the loliginid squid (*Loligo plei*), small clupeid and carangid fishes, halfbeaks (Exocoetidae), flounder (Bothidae), lizardfish (Synodontidae), wrass (Labridae), blenny (Tripterygiidae), clinids (Clinidae), and conger (Congridae) (dos Santos & Haimovici, 2001; Fertl & Würsig, 1995; Herzog, 1996b; Perrin et al., 1994).

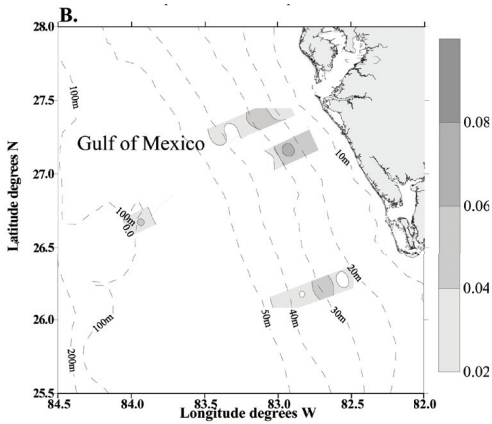
An earlier study examined seasonality in Atlantic spotted dolphins in the Gulf of Mexico (Mills & Rademacher, 1966). Analyses summarized seven years of opportunistic surveys



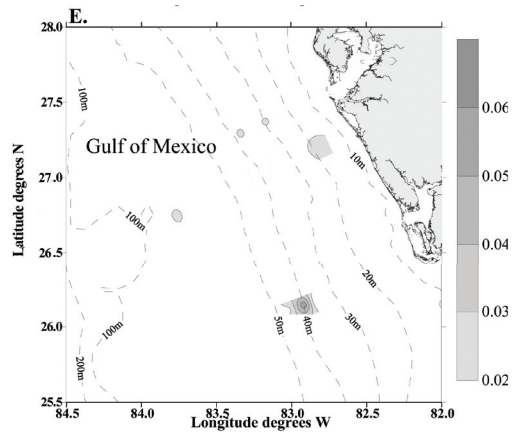
A. Atlantic spotted dolphins – Year 1



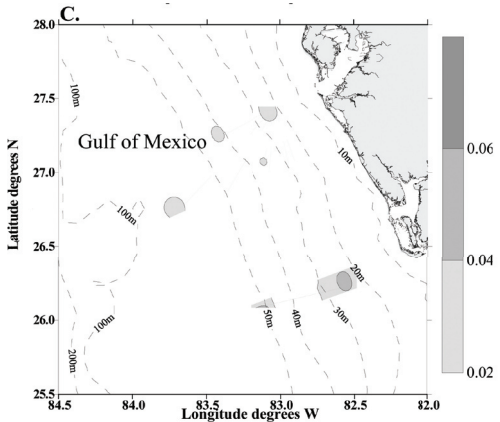
D. Bottlenose dolphins – Year 1



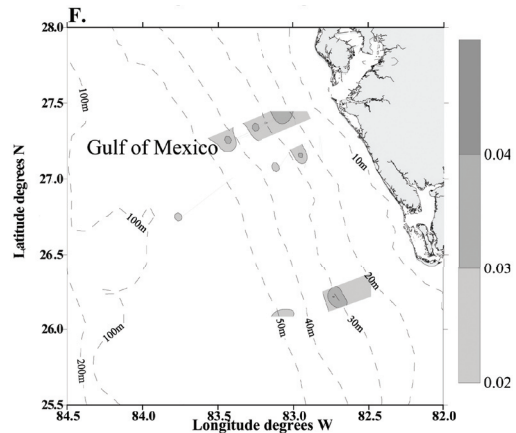
B. Atlantic spotted dolphins – Year 2



E. Bottlenose dolphins – Year 2



C. Atlantic spotted dolphins – Year 3



F. Bottlenose dolphins – Year 3

Figure 3 (A-F). Sightings of cetaceans by species km⁻¹ in transect segments surveyed three or more times per year, for Year 1 (November 1998–October 1999), Year 2 (November 1999–October 2000), and Year 3 (November 2000–October 2001) on the West Florida Continental Shelf

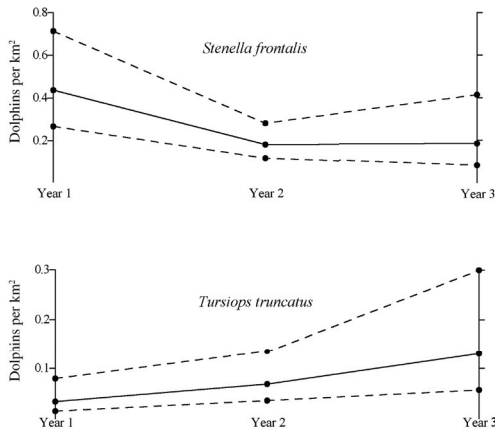


Figure 4. Atlantic spotted dolphin and bottlenose dolphin densities by year, with 95% confidence intervals; solid and dashed lines are included to describe trends.

throughout the Gulf of Mexico, primarily concentrated in the northern Gulf. Season definitions (winter, spring, summer, fall) were not comparable with our study, effort was not uniform between areas of the Gulf, and surveys were not conducted on a monthly basis. Winter sighting rates per unit effort did not differ significantly between waters shallower than 150 m and waters deeper than 150 m (0.19 sightings per h⁻¹, $p > 0.05$), while sightings per unit effort were significantly lower in

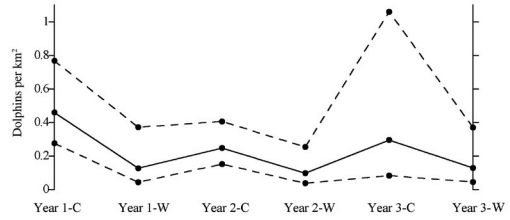


Figure 5. Atlantic spotted dolphin densities by year (Year 1-3) and season (C = November-May; W = June-October), with 95% confidence intervals; solid and dashed lines are included to describe trends.

winter (December-February) than summer (June-August). Data did not support an inshore/offshore migration hypothesis, and the authors suggested Atlantic spotted dolphins in the Gulf of Mexico migrated south alongshore to warmer waters in winter. Our data clearly show reduced densities during the warm season on the west Florida continental shelf (Tables 2 & 3), contrasting with the earlier study.

Interannual Variation

Our results suggest environmental variations may affect changes in species composition or relative proportions in a region on relatively brief time scales. The significant decrease in Atlantic spotted dolphin densities between years, and the trend for an increase in bottlenose dolphin densities

Table 2. Estimated densities (animals km⁻²) and abundance of Atlantic spotted dolphins and bottlenose dolphins in the study area (~14430 km²), with 95% confidence intervals (CI); Year 1 = November 1998-October 1999, Year 2 = November 1999-October 2000, and Year 3 = November 2000-October 2001; Season C = November-May, and Season W = June-October; dolphin abundances were estimated for the portion of study area > 20 m depth (~10,850 km²).

Species	Year/Season	Number of sightings	Density	95% CI	Abundance	95% CI
Atlantic spotted dolphins	Year 1	48	0.437	0.267-0.714	4740	2,899-7,749
	Season C	39	0.460	0.276-0.768	4992	2,992-8,328
	Season W	9	0.127	0.044-0.372	1384	474-4,040
	Year 2	36	0.182	0.118-0.282	1976	1,277-3,058
	Season C	25	0.248	0.152-0.406	2690	1,644-4,401
	Season W	11	0.098	0.038-0.254	1068	414-2,753
	Year 3	12	0.184	0.082-0.414	1999	889-4,493
	Season C	5	0.296	0.083-1.06	3215	900-11,481
	Season W	7	0.129	0.045-0.370	1396	485-4,016
Bottlenose dolphins	Year 1	12	0.034	0.015-0.080	371	158-872
	Season C	11	0.031	0.013-0.071	663	287-1,531
	Season W	1	---	---	---	---
	Year 2	20	0.069	0.036-0.135	752	386-1,465
	Season C	12	0.081	0.033-0.201	883	357-2,180
	Season W	8	0.058	0.019-0.173	628	210-1,879
	Year 3	17	0.130	0.057-0.300	2823	1,226-6,499
	Season C	9	0.214	0.065-0.703	4639	1,412-15,240
	Season W	8	0.074	0.030-0.185	1613	647-4,020

Table 3. Results of bootstrap tests of differences in density between years (Years 1-3) and seasons (C, W), within species (Atlantic spotted dolphins, bottlenose dolphins), and within years between species (Sf X Tt)

Comparison	d	Percentile		BCa method	
		95% CI(d)	p value	95% CI(d)	p value
<i>Atlantic spotted dolphins</i>					
Year 1-Year 2	0.255	-0.048-0.532	<0.13	0.031-0.731	<0.02
Year 2-Year 3	0.002	-0.150-0.222	<0.65	-0.267-0.131	<0.63
Year 1-Year 3	0.253	-0.019-0.576	<0.07	0.005-0.633	<0.05
Year 1C-Year 1W	0.332	0.019-0.745	<0.04	0.035-0.784	<0.03
Year 2C-Year 2W	0.150	0.024-0.444	<0.03	-0.032-0.332	<0.18
Year 3C-Year 3W	0.168	-0.178-0.572	<0.59	-0.096-0.853	<0.22
<i>Bottlenose dolphins</i>					
Year 1-Year 2	0.035	-0.130-0.038	<0.31	-0.117-0.049	<0.42
Year 2-Year 3	0.061	-0.222-0.072	<0.40	-0.229-0.070	<0.38
Year 1-Year 3	0.096	-0.258-0.006	<0.08	-0.255-0.007	<0.08
Year 2C-Year 2W	0.023	-0.082-0.188	<0.59	-0.098-0.167	<0.75
Year 3C-Year 3W	0.139	-0.084-0.561	<0.32	-0.081-0.576	<0.28
Year 1 Sf X Tt	0.403	-0.687-0.142	<0.001	-0.788-0.193	<0.001
Year 2 Sf X Tt	0.113	-0.270-0.005	<0.04	-0.260-0.017	<0.07
Year 3 Sf X Tt	0.054	-0.213-0.164	<0.90	-0.298-0.097	<0.40

between years support this hypothesis. Ongoing fieldwork during 2002-2004 continues to suggest reduced Atlantic spotted dolphin densities.

Inter-annual changes in dolphin densities likely were not caused by changes in dolphin mortality or recruitment. Occasional Atlantic spotted dolphin strandings have been recorded in this area in the past, yet no unusual mortality events in the eastern Gulf of Mexico were reported for this species during the study. It should be noted, however, that mortality increases may not be reflected in increased coastal stranding of marine mammals. Onshore deposition of cetacean carcasses originating offshore may be affected by various factors, including predation, scavenging, and predominant winds. Two recent bottlenose dolphin die-offs in the panhandle region of Florida were not reflected in population estimates for that species in the eastern Gulf of Mexico. The proportion of calves in total sightings of both species significantly increased during Year 2, yet this trend was counter to Atlantic spotted dolphins' abundance estimates and does not fully account for the trend of an increase in bottlenose dolphin densities during Year 2.

Shifts in dolphin ranging patterns to remain in optimal oceanographic habitat are the most likely direct cause of density variations reported for both species. Seasonal and inter-annual environmental variations probably induced shifts in prey distribution and densities in response to oceanographic variation. Although prey data were not collected during this study, environmental variation has been shown to contribute to distribution and abundance of some fish species (Brooks

et al., 2002; Hamilton, 1987; Hofmann & Powell, 1998; Shannon et al., 1989).

Changes in salinity reported here suggest an altered oceanographic regime during the second year. Increased salinity found during Year 2 most likely resulted from a drought that affected Florida during 2000-2001. Lower river discharge, in concert with increased evaporation under dry conditions, generated higher salinity over the inner continental shelf. Salinity is considered a conservative characteristic of water masses, acting as a passive tracer of water mass flows (Pickard & Emery, 1990, p. 52).

The significant increase of SSHa during Year 2 further supports the hypothesis that oceanographic variations affected densities of Atlantic spotted and bottlenose dolphins on the west Florida continental shelf. The increase in sea surface elevation relative to the mean indicates reduced upwelling in Year 2 relative to Year 1. Upwelling of nutrient rich water and higher primary productivity is favored in cyclonic eddies where sea surface height is depressed (Biggs et al., 1988, 2000; Wormuth et al., 2000), while downwelling and reduced primary productivity occurs in anticyclonic eddies where sea surface height is elevated. Reduction in upwelling may affect primary productivity and lead to alteration of the trophic structure in a region. Techniques measuring prey abundance rarely have been utilized in offshore surveys of cetacean abundance. Where prey abundances are not known, physical characteristics, such as SSHa and salinity variation, may aid in the explanation of changes in distribution.

Potential sources of inter-annual environmental variability include anthropogenically induced global warming, random hydrographic variation, or influences of multi-annual oceanographic cycles such as the El Niño Southern Oscillation or the North Atlantic Oscillation. Multi-decadal studies are required to elucidate the influence of multi-annual cycles on cetacean distributions. Anthropogenic causes of migration or alteration of ranging patterns were not evident during the three years of this study. Mean sea surface temperature did not significantly change during the study, suggesting warming was not a factor on this time scale. Further research is needed to determine whether long-term anthropogenically induced environmental change will modify dolphin habitat use.

Knowledge of population abundance is valuable when studying the role and importance of marine mammals as apex predators within ecosystems. Temporal variation in density will impact estimates of species or population abundance when this variation is not considered. Abundance surveys conducted in an area with transient high or low densities may result in over- or underestimates of population size. Survey designs that consider habitat use fluctuations resulting from seasonal and inter-annual environmental variation will generate more reliable estimates of population size and, thus, better enable analyses of population trends. Improved survey methodology is needed to ensure availability of accurate data for use in ecological analyses.

Conclusion

Our finding of seasonality and significant inter-annual variation of Atlantic spotted dolphin densities, and the trend for inter-annual variation in bottlenose dolphin densities, suggests multiple environmental mechanisms were in operation. Seasonal patterns cause intra-annual abundance variation, while multi-annual patterns may cause inter-annual abundance variation. Regional variation in density, as reported here, can impact estimates of species or population abundance when this variation is not considered. Abundance surveys conducted in an area with transitory (high or low) densities may result in over- or underestimates of population size. Surveys that consider seasonal and inter-annual variation in density will generate more precise population estimates. With this information, we can better separate short-term variations in density from long-term trends, thus enabling better survey designs for examining questions of abundance or trophic relationships. Knowledge of population abundance is of great importance when managing or protecting marine species. Survey

design should consider habitat use fluctuations resulting from environmental variation in order to ensure that ecological models and management decisions are based on accurate information.

By completion of studies such as this, we can identify sources of natural or anthropogenically induced environmental variation and, thus, better conserve dolphin species. The eastern Gulf of Mexico currently is under an oil exploration moratorium, and no large-scale cetacean/fisheries interactions have been identified, thus facilitating investigations of effects of environmental change on cetacean densities and habitat use. Studies of the impact of natural environmental variation on habitat use are of added relevance today in light of global warming. Continued research will enable us to identify potential effects (e.g., shifts in ranging patterns, changes in abundance) of this change on current populations.

Acknowledgments

This study was completed through participation in a federally funded ECOHAB (Ecology of Harmful Algal Blooms) study, conducted by the University of South Florida–St. Petersburg (USF). We thank Drs. Gabriel Vargo and Cynthia Heil, who provided us with ship time and underway data, and the many Mote Marine Laboratory interns who aided in our survey effort and data recording. Thanks to Dr. Karin Forney, who provided an *Excel* routine we used for comparisons of differences between years and seasons. We also thank Dr. Randall Wells, Dr. Stefan Harzen, and Victoria Thayer, who reviewed earlier versions of the manuscript and provided helpful comments. This research was funded in part by an anonymous donation to Mote Marine Laboratory in support of the postdoctoral work of R. B. Griffin.

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