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Zooplankton and Micronekton in Cyclones and Anticyclones in the Northeast Gulf of Mexico

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Two cruises were made to the northeast Gulf of Mexico in October 1996 and August 1997. The main objectives of the cruises were to survey cetacean and seabird populations and describe their hydrographic and biological environments. An additional objective was to characterize cetacean and seabird habitats in terms of food resources. During both cruises a cyclone and an anticyclone were sampled as well as the confluence region between them. Zooplankton and micronekton were sampled both directly with nets and indirectly with a 153-kHz acoustic Doppler current profiler. Within cruises, zooplankton and micronekton biomass was higher in cyclones than in anticyclones. Biomass within the confluence was either highest or intermediate for both cruises. Between cruises, within features, August 1997 biomass was significantly higher than October 1996 biomass.

Direct sampling of zooplankton and micronekton biomass with a variety of towed nets can provide important information on marine ecosystems (Hopkins, 1982; Passarella and Hopkins, 1991). In this study, net sampling was used to provide estimates of the biomass and taxonomic composition of zooplankton and micronekton within the study area. As a supplement to the net sampling program, acoustic measurements of volume backscattering strength (S_v) were made with an acoustic Doppler current profiler (ADCP). Shipboard ADCPs have been used for making indirect measurements of zooplankton and micronekton biomass continuously while the vessel is underway (Ashjian et al., 1994; Zhou et al., 1994; Zimmerman and Biggs, 1999). When both direct and indirect measurements of zooplankton and micronekton are taken over a wide geographic or hydrographic range, differences in biomass can be interpreted as differences in the amount of potential food for higher trophic levels, much the same as regional phytoplankton mapping is used to infer differences in zooplankton biomass. Biological oceanographic sampling with nets and the ADCP were used to test the hypothesis that different hydrographic regimes in the study area have different levels of potential prey, and these prey influence the distributions of predators such as cetaceans and seabirds. The abundance of cephalopods and myctophids, two important prey items found frequently in a wide variety of cetacean and seabird stomachs (Fitch and Brownell, 1968; Perrin et al., 1973; Clarke, 1996; Croxall and Prince, 1996), was used to explore the hypothesized link between higher zooplankton biomass levels and richer cetacean prey resources.

Oceanic cephalopods occupy an unusual niche in the marine ecosystem in that they range in size from planktonic (as paralarvae) to some of the largest nekton (the giant squid *Architeuthis*) (Roper et al., 1984). Both juvenile and adult cephalopods are voracious predators yet are also preyed upon by many marine mammals, fish and seabirds (Clarke, 1977, 1996; Croxall and Prince, 1996). Therefore, cephalopod distribution and abundance may influence the distribution and abundance of their predators. However, adult cephalopods, because of their agility and keen eyesight, are extremely difficult to catch. Consequently, "paralarval" cephalopods were used in this study as the link to adult cephalopods. A paralarval squid is defined by Young and Harman (1989) as a "cephalopod of the first post-hatching growth stage that is pelagic in near-surface waters during the day and that has a distinctly different mode of life from that of older conspecific individuals."

Myctophids (lanternfish, family Myctophidae) were chosen to represent the influence of small midwater fishes on cetacean prey distributions because of their worldwide abundance and high numbers in the net samples. There are 17 genera of myctophids in the Gulf of Mexico (McEachran and Fechhelm, 1998). Most species are vertical migrators, with those in the eastern Gulf of Mexico concentrated in the upper 150 m at night and from 300 to 900 m during the day (Gartner et al., 1987). Myctophids feed on a wide variety of zooplankton and often select their prey opportunistically on the basis of size (Nafpaktitis et al., 1977; Hopkins and Baird, 1985). Myctophids themselves are an important food source for cetaceans, seabirds, game fish, and cephalopods (Nafpaktitis et al., 1977). They dominate the remains of small fishes found in cetacean stomachs, often comprising 89% or higher of the total otoliths (ear bones) recovered (Fitch and Brownell, 1968). An area of high abundance of myctophids may, therefore, indicate a preferred foraging region for cetaceans.

ADCPs are normally used by physical oceanographers to measure the velocity of ocean currents. The ADCP transmits a sound pulse into the water and then awaits the return of sound scattered back by passively drifting particles in the water column. The Doppler shift of this backscattered sound is used to estimate current speed and direction. However, the ADCP also measures the intensity of the backscattered acoustic return, which is proportional to the number and backscattering cross-sections of the particles in a given ensonified volume of water (Medwin and Clay, 1998). Under typical open ocean conditions and with the use of frequencies on the order of 100 kHz, the particles primarily responsible for the backscattering are assumed to be zooplankton and micronekton (Stanton et al., 1994; Wiebe et al., 1997; Medwin and Clay, 1998). Although the ADCP was admittedly not designed as a scientific echosounder (Brierly et al., 1998; Griffiths and Diaz, 1996), ADCPs have been successfully used to estimate the biomass of sound scatterers (Flagg and Smith, 1989; Ashjian et al., 1994; Zhou et al., 1994; Ressler et al., 1998). Currently, acoustic methods are recognized as an important way of studying zooplankton and micronekton (Greene and Wiebe, 1990; Wiebe et al., 1997), and there is precedent for their use in assessments of zooplankton and micronekton stocks in cetacean habitat studies (Macaulay et al., 1995; Beardsley et al., 1996; Croll et al., 1998). In fact, Fiedler et al. (1998) recently described the use of a 153-kHz ADCP to examine spatial and temporal variability in the biomass of potential dolphin prey stocks consisting of zooplankton, micronekton, and squid.

Materials and Methods

Net sampling.—Samples for both zooplankton and micronekton were taken in October 1996 and August 1997. Two types of sampling equipment were used. A 1-m^2 Multiple Opening/Closing Net and Environmental Sampling System (MOCNESS) with a mesh size of 333 μm was used on the second half of the cruise in October 1996 and on the entire August 1997 cruise. The MOCNESS (Wiebe et al., 1976) is commonly used in several sizes that refer to the net's vertical mouth area when towing at a 45° angle to the vertical. The MOCNESS allows up to nine discrete samples to be collected during one tow, sampling either obliquely or horizontally. The MOCNESS collects water temperature, depth, and salinity data and displays them in real time, allowing changes in sampling strategy during the course of a tow, and it monitors net angle and computes volume filtered for each individual net. On the October 1996 cruise, the first net of the 1-m^2 MOCNESS was used to collect one oblique sample to the maximum depth of each tow during all tows; in August 1997, all of the MOCNESS nets were fished during descent, yielding nine depth-discrete samples. The 1-m^2 MOCNESS was towed at speeds of 1.5–2.0 knots (75–100 cm/sec).

On the August 1997 cruise, a 15-foot (4.6-m) Isaacs Kidd midwater trawl (IKMT) with a mouth opening of 14.7 m^2 and a mesh size of 4 mm was also used. The IKMT, which collects only one sample, was towed obliquely. Volume was recorded by a flowmeter suspended in the mouth of the net. Maximum depth of tow was determined by the wire length and wire angle method. Unlike the MOCNESS, the IKMT was towed at 4.0–5.0 knots (200–250 cm/sec). The advantage of this faster towing speed is a reduction in the effects of net avoidance by more actively swimming organisms (e.g., cephalopods and myctophids). Depth-discrete data for zooplankton biomass and cephalopod paralarvae were obtained from the 1-m^2 MOCNESS.

Net towing was done almost exclusively at night because of visual surveys of marine mammals and birds during all daylight hours. The net towing sequence each night consisted of a 1-m^2 MOCNESS tow followed by a 15-foot IKMT tow followed by a 1-m^2 MOCNESS tow or two 15-foot IKMT tows (average duration 77 min, range 46–140 min) bracketing a 1-m^2 MOCNESS tow. The turnaround time between tows averaged about 15–20 min. The average duration of the 1-m^2 MOCNESS tows was 66 min (range 42–90 min).

Locations for all tows depended on the ship's location after daylight-dependent cetacean observations. As a result, sufficient sampling for most statistical procedures in different environmental features was difficult to obtain. The environment of each tow was characterized by its temperature and salinity profile as determined by sensors on the MOCNESS, by expendable bathythermograph (XBT) and/or conductivity-temperature-depth (CTD) sampling during, before, or after each tow, or by sea surface topography derived from the hydrographic data.

Samples were preserved in 10% buffered formalin on the ship. On the October 1996 cruise, 171 samples were collected with the 1-m^2 MOCNESS. On the August 1997 cruise, 177 samples were collected (162 1-m^2 MOCNESS samples and 15 IKMT samples). After a minimum of 2 wk of preservation, the displacement volumes were determined for the 1-m^2 MOCNESS samples. All samples were sorted for paralarval cephalopods. The cephalopods were then identified to the lowest taxonomic category possible.

Myctophids were low in abundance or were not captured at all in many of the 1-m^2 MOCNESS tows. For this reason, only the myctophids from the IKMT tows were studied. Eight IKMT tows from the different environments were chosen: three from the cyclone, three from the confluence, and two from the anticyclone. All of these tows were taken between late evening and early morning during either 7–9 August 1997 (time interval I) or 12–20 August 1997 (time interval II). This reduced the possibility of variation due to temporal factors. The maximum depths of these trawls ranged from 106 m to 354 m. Myctophids were identified to genus by the location of photophores and other luminous tissue on their bodies.

Acoustic sampling.—A 153-kHz narrowband R. D. Instruments ADCP was used to collect acoustic volume backscatter data during both cruises. The ADCP was installed in a "moonpool" in R/V *Gyre*'s hull, with its four acoustic transducers facing downward from the bottom of the ship in a concave configuration at 30° angles. Backscatter data were collected during day and night, both while on-station and while underway except during data backup. The signals from all four beams were averaged every 5 min. These averages were then converted from the "echo intensity" units, recorded by the ADCP's automatic gain control circuitry, into a calibrated measure of S_v with measured system calibration values and hydrographic parameters affecting the speed and absorption of sound in seawater (see R. D. Instruments, 1990; Zimmerman, 1997 for details of this procedure).

S_v was collected in 4-m depth bins and analyzed over a depth range of 10–202 m; 10 m is the upper limit of the data collected, and 202 m was used as the lower limit because the signal to noise ratio decreases appreciably below this depth. Biomass estimates of zooplankton and micronekton were made with an empirical calibration of the acoustic signal from the ADCP with samples of zooplankton and micronekton taken from the 1-m^2 MOCNESS (Flagg and Smith, 1989; Ashjian et al., 1994; Zhou et al., 1994; Zimmerman, 1997; Ressler et al., 1998). For each 1-m^2 MOCNESS tow, the mean S_v measured in a given depth interval during the tow was matched with the measured wet displacement volume biomass from the corresponding depth-discrete net sample. Linear regression of the $\log_{10}$ of MOCNESS displacement volume biomass (in $cc \cdot m^{-3} \times 10^3$) as a function of mean S_v (in dB re m^{-1} $4\pi^{-1}$) was used as a first-order empirical model of predicted mean biomass (PMB) in units of $cc \cdot m^{-3}$.

PMB values have a horizontal resolution of 0.3–1.5 km, depending on ship speed, and a vertical resolution of 4 m. These estimates were integrated over the depth interval 10–50 m to provide integrated PMB values in units of $cc \cdot m^{-2}$. The 50 m lower limit was chosen so that the integration from 10 to 50 m could be used as a proxy for biomass within the mixed layer, the mean depth of which was approximately equal to or less than 50 m on the GulfCet II cruises. The near-surface mixed layer is where the increased upward flux of nutrients that occurs in cyclonic circulation features is thought to be most important relative to anticyclones (Biggs et al., 1988; Biggs, 1992), stimulating increased biological productivity and leading to richer food resources in the cyclones.

The integrated PMB data set was filtered for on-station artifacts and periods of diel vertical migration (for additional details, see Davis et al., 2000). Integrated PMB values were then compared with values of integrated displacement volume biomass from 1-m^2 MOCNESS samples to assess their agreement. Interpolated contour maps of daytime and nighttime integrated PMB were made to show spatial variation with respect to geographic location and hydrographic features for each cruise. Finally, integrated PMB was analyzed as a function of 15 C depth (a proxy for hydrographic feature) to test for significant spatial variation according to environment.

Results

Zooplankton.—The data on tow number, location, depth, biomass, number of cephalopod paralarvae, and environment are listed in Davis et al. (2000). Figure 1A,B shows that integrated zooplankton biomass for the 1-m^2 MOCNESS tows during the October 1996 and August 1997 cruises tended to be lower (smaller circles) in anticyclones than in cyclones. All tow locations are superimposed on sea surface dynamic

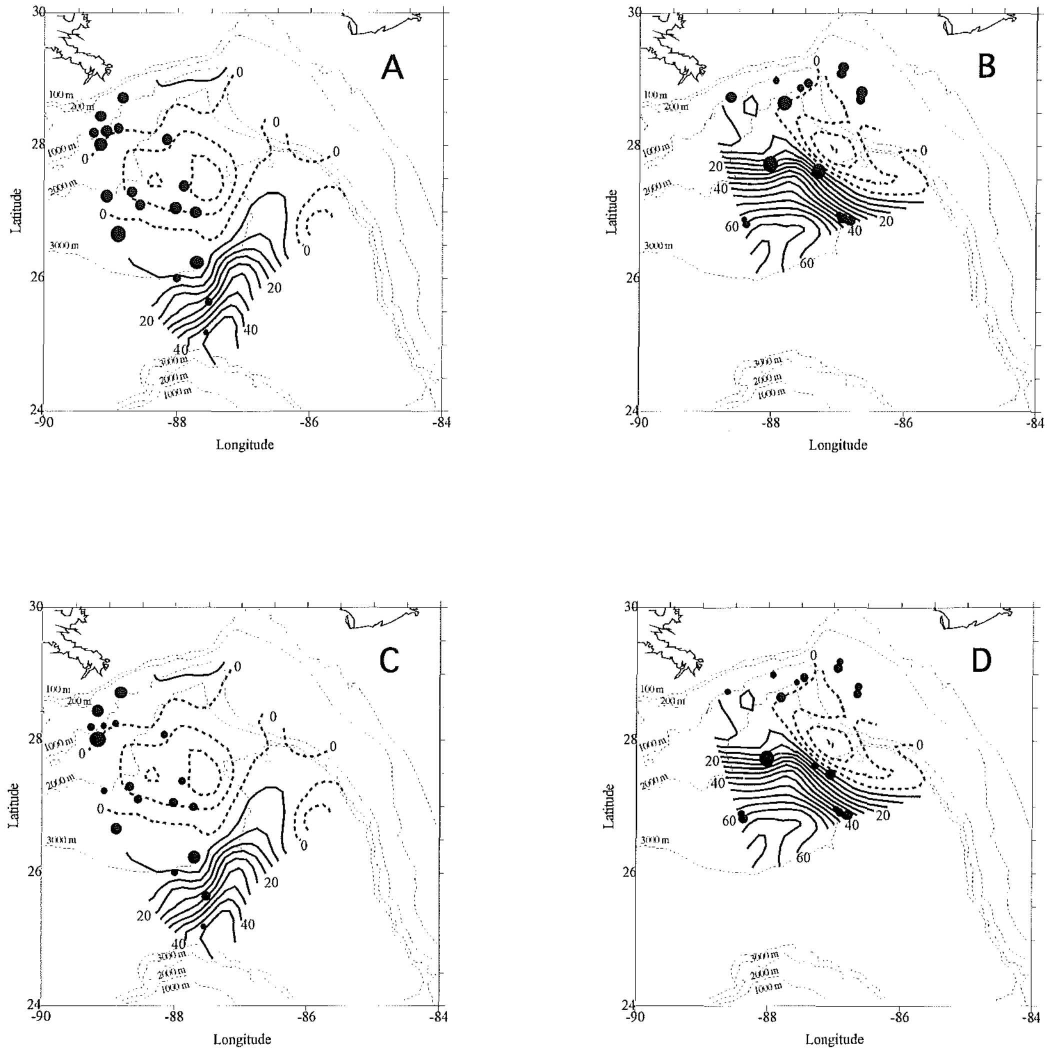

Fig. 1. Integrated zooplankton biomass (cc·m^{-2}) from 1-m^2 MOCNESS samples taken during (A) October 1996 and (B) August 1997 and integrated cephalopod paralarval abundance (no.·m^{-2}) from 1-m^2 MOCNESS samples taken during (C) October 1996 and (D) August 1997. The size of each circle is proportional to the largest value within each plot. Bold solid (positive) and bold dashed (negative) lines are sea surface dynamic height anomaly (DHA, cm) relative to the 100 cm mean. Contour intervals are 5 cm. The cyclone is between 0 and −12 cm, the confluence between 0 and 22 cm, and the anticyclone between 25 and 50 cm.

height anomalies. The zooplankton biomass in the anticyclone in October 1996 was significantly lower than that for the cyclone but not for the confluence tows (Table 1). Zooplankton biomass in the confluence in August 1997 was significantly higher than in either the cyclone or the anticyclone, whereas the cyclone and the anticyclone were not significantly different (Table 2). A comparison of zooplankton biomass by these hydrographic features shows that in all comparisons, the August 1997 values were significantly higher than those from October 1996 (Table 3).

Cephalopod paralarvae.—The most abundant families (and genera) obtained from the 1-m^2 MOCNESS and IKMT tows were Enoploteuthidae (*Abrailia* sp., *Enoploteuthis* sp., and *Abrailiopsis* sp.), Ommastrephidae (*Ommastrephes bartramii, Ornithoteuthis antillarum, Illex* sp., and *Stenoteuthis pteropus*), Pyroteuthidae (*Pyroteuthis margaritifera* and *Pterygioteuthis* sp.), Onychoteu-

TABLE 1. Unpaired t-tests of zooplankton displacement volume and cephalopod paralarval abundance by environment for the October 1996 cruise. Tabled values are probability values with significantly different mean values in parentheses.

Environment	Degrees of freedom	Zooplankton displacement volume (cc·m^{-2})	Cephalopod paralarval abundance (no.·m^{-2})
Anticyclone, confluence	2	0.32	0.62
Anticyclone, cyclone	15	0.002 (2.15, 4.42)	0.39
Confluence, cyclone	15	0.64	0.88

thidae (*Onychoteuthis banksii* and *Onychia carribaea*), and Cranchiidae (*Heliocranchia pfefferi* and *Heliocranchia papillata*). The family Enoploteuthidae was by far the most abundant. However, the rank order of the additional four families varied slightly between the two net types. These five families constituted approximately 94% of all cephalopods collected (a combined total of 1,776 cephalopods) and were the only families used in calculations. In the 1-m^2 MOCNESS samples, the paralarvae were generally concentrated in the upper 130 m.

Figure 1C,D shows that cephalopod numbers per square meter for the 1-m^2 MOCNESS tows during the October 1996 and August 1997 cruises tended to be lower (smaller circles) in anticyclones than in cyclones. A comparison of all 1-m^2 MOCNESS samples from the different environmental regimes having two or more observations for both cruises shows no statistical differences among tows during a given cruise (Tables 1, 2). In the anticyclone and in the cyclone, August 1997 was significantly higher than October 1996 (Table 3).

In addition, a comparison of all 1-m^2 MOCNESS tows from both cruises (36 tows, 333 samples) was made with cephalopod paralarvae (no.·m^{-2}) and zooplankton biomass (cc·m^{-2}). The Spearman rank correlation coefficient was 0.73 ($P < 0.001$).

Myctophids.—Although myctophids from other genera were present, the following four genera dominated the myctophids in the IKMT trawls in every environment: *Benthosema, Ceratoscopelus, Diaphus,* and *Lampanyctus.* Their abundance rankings varied from tow to tow and from environment to environment, although either *Ceratoscopelus* or *Diaphus* was first or second in every tow. Figure 2 shows the locations and integrated myctophid abundance for the chosen IKMT tows. The confluence had the highest integrated myctophid abundance among all three features, both when the environments were looked at separately (average 0.81·m^{-2}; range 0.50–1.34·m^{-2}) and when sets of tows were compared (0.96·m^{-2} and 0.50·m^{-2}). The cyclone margin had the second highest integrated abundance in both cases (separately, average 0.40·m^{-2}, range 0.05–0.81·m^{-2}), by time interval (0.81·m^{-2} and 0.19·m^{-2}), and the anticyclone had the lowest integrated abundance in each case (separately, average 0.17·m^{-2}, range 0.15–0.19·m^{-2}), by time interval (0.15·m^{-2} and 0.19·m^{-2}). Although unpaired *t*-tests showed that the differences were not significant, we feel that this is largely due to the smaller n of the myctophid data. When the genera were pooled by environment, the confluence was the most diverse with 16 genera, the cyclone margin was the

TABLE 2. Unpaired t-tests of zooplankton displacement volume and cephalopod paralarval abundance by environment for the August 1997 cruise. Tabled values are probability values with significantly different mean values in parentheses.

Environment	Degrees of freedom	Zooplankton displacement volume (cc·m^{-2})	Cephalopod paralarval abundance (no.·m^{-2})
Anticyclone, confluence	5	0.005 (7.22, 12.75)	0.19
Anticyclone, cyclone	11	0.14	0.63
Confluence, cyclone	8	0.02 (12.75, 8.8)	0.07

TABLE 3. Unpaired t-tests of zooplankton displacement volume and cephalopod paralarval abundance by cruise within environments. Tabled values are probability values with significantly different mean values in October 1996 and August 1997 in parentheses.

Environment	Degrees of freedom	Zooplankton displacement volume ($cc \cdot m^{-2}$)	Cephalopod paralarval abundance ($no. \cdot m^{-2}$)
Anticyclone	5	0.008	0.05
		(2.15, 2.4)	(0.31, 1.34)
Confluence	2	0.02	0.28
		(4.1, 12.75)	
Cyclone	21	<0.0001	0.002
		(4.4, 8.8)	(0.56, 1.2)

next most diverse with 13 genera, and the anticyclone was the least diverse with 11 genera. Each myctophid genus in the cyclone margin and in the anticyclone was present in the confluence.

PMB.—During both the October 1996 and August 1997 cruises, there was a positive functional relationship between net zooplankton biomass and S_v. Although some authors have questioned whether a simple linear model can fully describe the relationship between these two variables (Stanton et al., 1994, 1998; Wiebe et al., 1996), others have used a linear fit with some success (Flagg and Smith, 1989; Ashjian et al., 1994). Linear regression was used to model the relationship during both cruises in

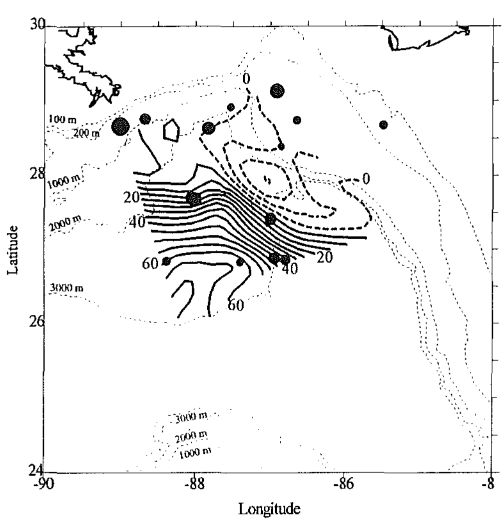

Fig. 2. Integrated myctophid abundance ($no. \cdot m^{-2}$) from the 15-foot Isaacs Kidd midwater trawl tows taken during August 1997. The size of each circle is directly proportional to the largest value within each plot.

this study (Fig. 3A,B). Prior to performing the regression analyses, a logarithmic transformation of the net zooplankton biomass data was required to meet assumptions of normally distributed residuals and homogeneity of variance. Subsequent statistical testing of the October 1996 and August 1997 regression models indicated that they were significantly different in slope (modified *t*-test; Zar, 1974), and therefore a different regression equation was used for each of the cruises to make predictions of PMB.

A comparison of integrated MOCNESS displacement volume and integrated PMB for both October 1996 and August 1997 shows that the regression models make reasonable predictions of the actual biomass sampled with the MOCNESS (Fig. 3C). Although there is scatter about the 1:1 reference line shown on the plot, there is no clear pattern of over- or underestimation by the regression. It is also clear from this comparison that August 1997 biomass values were higher than those obtained in October 1996. This statistically significant difference (ANOVA, $P < 0.0001$) was also shown by the MOCNESS sampling.

To better visualize the spatial patterns in the biomass predictions, integrated PMB from both cruises was gridded (using kriging) and contoured with Surfer, Version 6 (Golden Software, 1997). The impact upon biomass measurements of the vertical migration of zooplankton and micronekton is apparent: integrated PMB 10–50 m was significantly higher at night than during the day during both cruises (ANOVA, $P < 0.0001$; Fig. 4). In October 1996 (Fig. 4A,B), integrated PMB was lowest in the anticyclone, whereas highest values were located in and around the cyclonic feature. The contrast is especially apparent at night, with a "bull's-eye" of high integrated PMB in the center of the cyclonic feature. The follow-

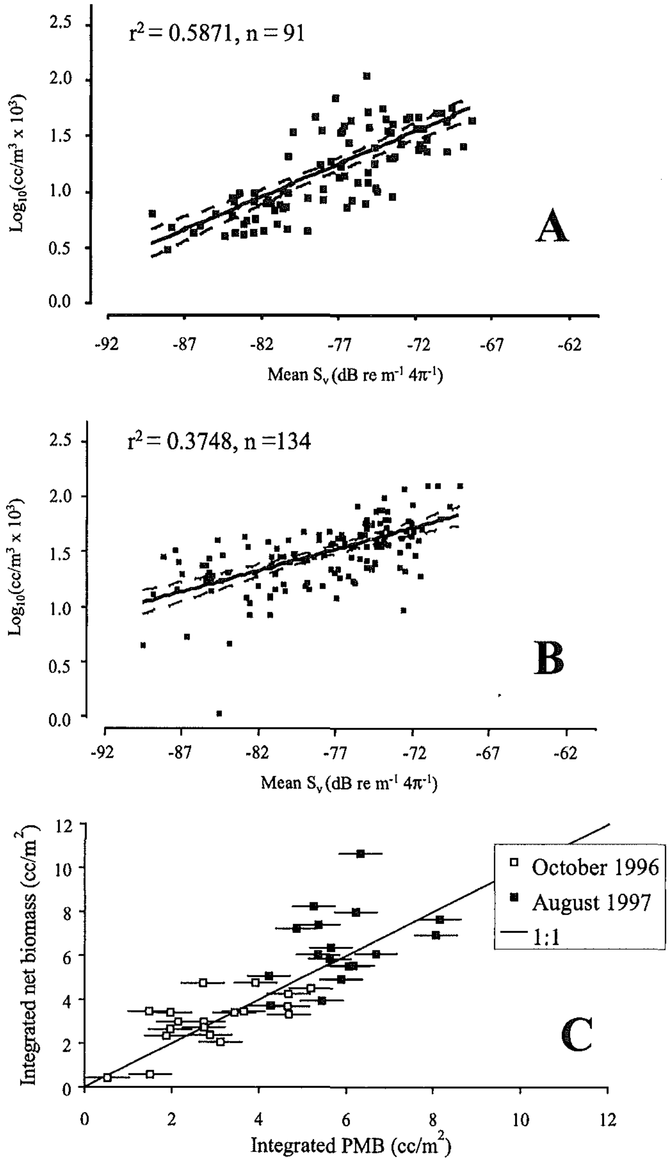

Fig. 3. (A) and (B) Regressions of MOCNESS wet displacement volume biomass on S_v from the ADCP for October 1996 and August 1997, respectively. (C) A comparison of integrated biomass estimates from the MOCNESS and PMB (error bars are 95% prediction intervals).

ing year (August 1997; Fig. 4C,D), the contoured data showed that, although overall biomass levels were higher than the previous October, again the lowest integrated PMB values were located in the anticyclone and highest values were found in and around the cyclone. When integrated PMB is analyzed as a function of 15 C depth at corresponding hydrographic stations (Fig. 5), the spatial variation with environment is evident. The depth of the 15 C isotherm can be used as a proxy for hydrographic regime because it is well correlated with the hydrographic circulation features: the depth of the isotherm is shallowest in the cyclones (<170 m), intermediate in the confluence and other areas along the continental margin (170–250 m), and deep in the anticyclones (>250 m) (Davis et al., 2000). ANOVA testing indicated that the integrated PMB varied significantly across feature classification during day and night, during both October 1996 and August 1997 ($P < 0.0001$), with PMB

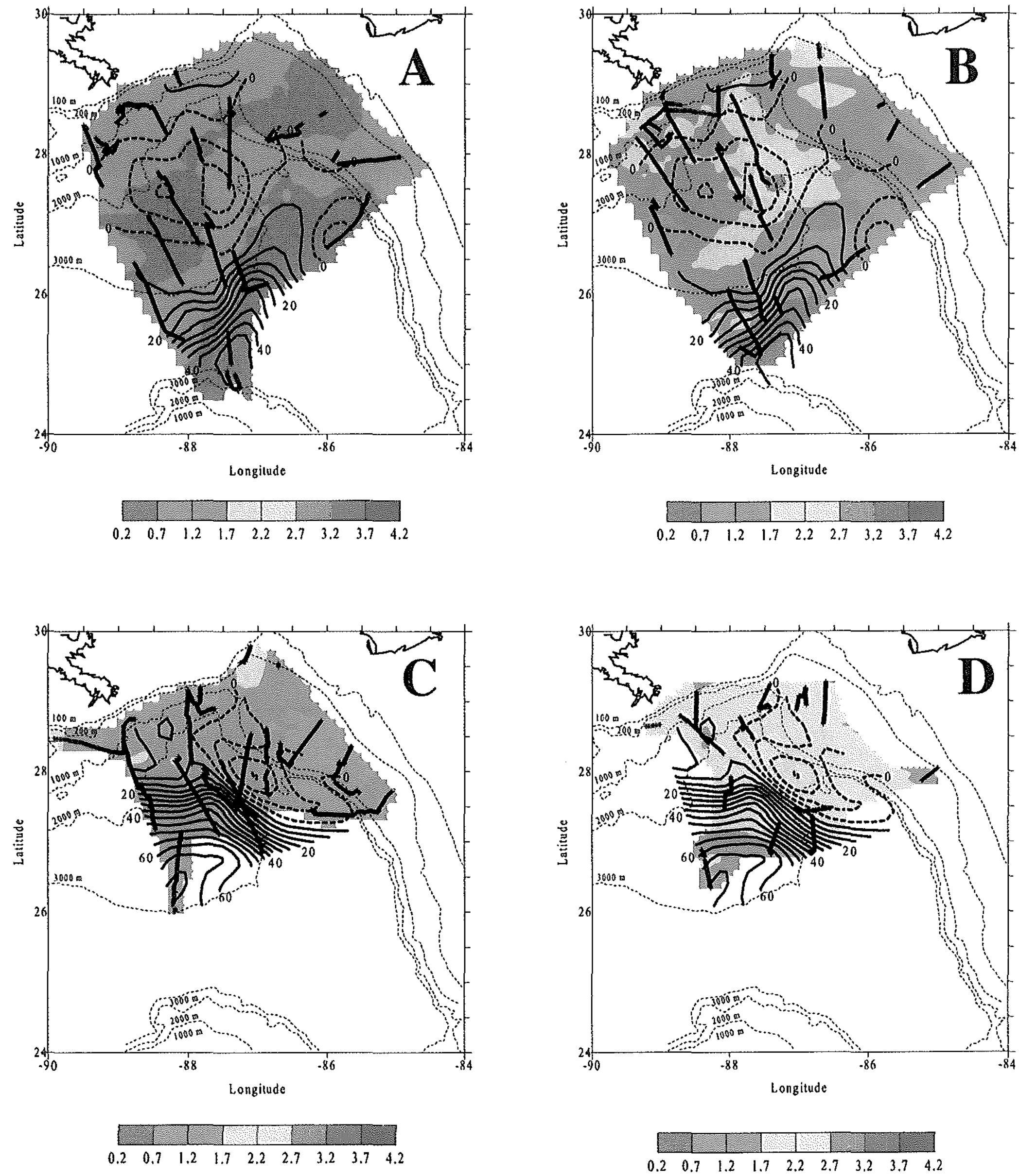

Fig. 4. Gridded and color-contoured distributions of integrated acoustic PMB (cc/m^2) for October 1996 (A) day and (B) night and August 1997 (C) day and (D) night. Dynamic height anomaly (0–800 m, dyn cm) is shown by dashed (positive anomaly) and solid (negative anomaly) contour lines. The heavy dark lines indicate locations of integrated PMB data used for contouring.

in the cyclones and confluence/other margin areas significantly higher than in the anticyclones (Bonferroni *t*-tests, $P < 0.01$).

Discussion

Zooplankton.—There are obvious hydrographic and seasonal differences in integrated zooplankton biomass. The cyclone and confluence regions had higher biomass compared with the anticyclone, regardless of season. August 1997 values were significantly higher than those for October 1996, regardless of hydrographic regime. These differences are statistically significant and may have important ramifications for the distribution and abundance of cetaceans and seabirds. We feel that these higher values are the result of the upward doming of nutri-

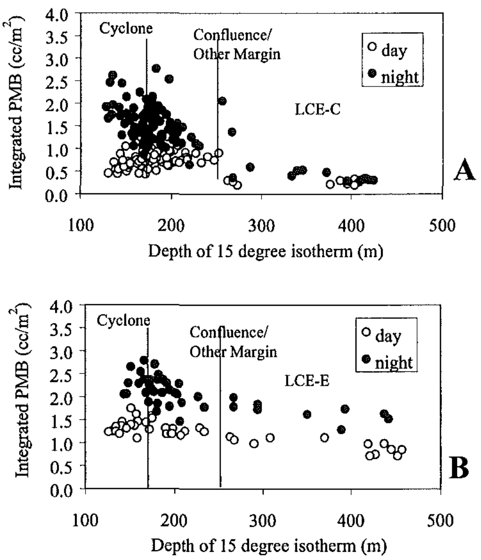

Fig. 5. (A) and (B) Integrated PMB in three different hydrographic regimes during October 1996 and August 1997, respectively. PMB was significantly higher in August 1997 than October 1996, higher at night than in the day, and higher in the cyclone and confluence/other margin areas than in the anticyclones.

ent-rich water toward the base of the mixed layer (Biggs et al., 2000), not a physical concentration of zooplankton as passively drifting particles. We hypothesize that this nutrient input enhances phytoplankton biomass (Biggs and Muller-Karger, 1994) and primary productivity which, in turn, supports increased biomass of zooplankton and enhanced secondary production, as was shown by Wormuth (1985) for some Gulf Stream cold-core species. This contrast between anticyclones and cyclones is similar to the contrast observed between the Sargasso Sea water and that inside of Gulf Stream cold-core cyclonic rings (The Ring Group, 1981), even though the formation process of these features is different.

Cephalopod paralarvae.—According to Clarke (1996), 28 cephalopod families are represented in the diet of cetaceans, and cephalopods are the main food constituent of 28 odontocetes. Clarke also found that although the ommastrephids, and cranchiids are preferred, onychoteuthids and enoploteuthids also form a large portion of cetacean diets. Furthermore, Croxall and Prince (1996) determined that seabirds (terns and petrels) fed on ommastrephids and onychoteuthids, and cranchiids, enoploteuthids, and lycoteuthids also formed an important part of their diets. More importantly, they found that the principal component of the food of petrels was the juvenile stages of these families. All of these cephalopod families were found in our trawl samples. A cephalopod species composition study conducted by Passarella and Hopkins (1991) in the eastern Gulf of Mexico (in the vicinity of 27°N, 86°W) revealed that the order Teuthoidea, specifically the families Enoploteuthidae and Cranchiidae, dominate in these waters. Our results reveal similar patterns of abundance. Furthermore, our samples illustrate that the paralarvae were concentrated in the upper 130 m of the water column in accordance with the vertical distributions of paralarvae as reviewed by Sweeney et al. (1992). Although no significant difference existed among tows during the two cruises, regardless of environmental regime, paralarvae numbers were higher in the cyclonic and confluence regimes, making these areas preferable as feeding habitats for cetaceans as well as seabirds.

Myctophids.—The patterns suggested by the limited myctophid data are that the confluence appears to host the highest abundance of myctophids. If these patterns are correct, predator species such as cetaceans would be more likely to find myctophid prey in the confluences. The trend toward greater diversity of myctophids in the confluence may not affect opportunistically feeding cetaceans. The individual species of myctophids, however, vary considerably in maximum size (Nafpaktitis et al., 1977). The size, ease of detection, and energy content of certain myctophid species may influence cetacean distributions, with the cetaceans congregating where high numbers of the largest myctophid species occur.

PMB.—The acoustic sampling was intended to provide a semicontinuous, along-track index of the zooplankton and micronekton biomass sampled at single locations by the 1-m² MOCNESS. As with the MOCNESS measurements, integrated PMB was significantly greater in August 1997 than October 1996, implying seasonal and/or interannual variability in zooplankton and micronekton biomass. Integrated PMB also varied significantly by diel period (higher at night than daytime), likely as a result of diel vertical migration. Most importantly in terms of cetacean and seabird distributions, cyclonic features and surrounding areas were clearly richer in integrated PMB than the anticyclones by night and by day during both cruises, providing support to the hypothesis that these areas may indeed be persistently favorable habitat in terms of prey for these predators.

The difference in the relationship between ADCP-measured S_v and net-collected biomass implies a difference in the zooplankton and micronekton communities between the two cruises. Perhaps different abundances of particular organisms and/or different taxa were responsible (Wiebe et al., 1997), although this possibility cannot be confirmed until a more detailed taxonomic analysis of the zooplankton is completed.

Seasonal/ annual differences.—As mentioned earlier, there was an important difference in the pattern of zooplankton and micronekton biomass between the October 1996 and August 1997 cruises. Both MOCNESS and ADCP sampling demonstrated that the zooplankton and micronekton biomass was generally higher during August 1997 relative to October 1996, suggesting a difference in biological processes in the survey area between cruises. This difference could simply be due to interannual variability in zooplankton stocks, or it could reflect seasonal changes in the zooplankton community. Although during both years there was a cyclone–anticyclone pair in the study area of approximately the same age, other data (not presented here) do show that there may have been some important differences in hydrographic conditions between these cruises; for example, in August 1997, the study area was characterized by the presence of offshore streamers of fresher, higher chlorophyll surface water that were by and large not present in October 1996 (Davis et al., 2000). This perhaps indicated the presence of greater nutrient supply from the shelf and resulting phytoplankton production. Nevertheless, without knowing how long those conditions had existed before the cruises, we can only speculate on whether this might have supported a greater abundance of zooplankton.

Habitat differences.—When plots of MOCNESS biomass, cephalopod paralarvae, myctophids, and the contour plots of integrated PMB from both cruises (day or night) are considered, cyclones in deep water areas appear richer in zooplankton and micronekton biomass relative to the anticyclones. Cetaceans and seabirds are not likely to be feeding directly on the relatively small organisms that make up a large portion of the biomass caught in these samples. However, the larger organisms that cetaceans or seabirds might take as prey would depend upon the abundance of animals at these lower trophic levels for their food. Thus, just as measurements of chlorophyll concentration or primary productivity might be used to evaluate whether a habitat is rich or poor in terms of food resources that translate up the food chain into elevated stocks of zooplankton and micronekton, the biomass of zooplankton and micronekton sampled by the MOCNESS and ADCP might be used to make inferences about the potential of an area for supporting the prey of apex predators. Our results from both MOCNESS and ADCP sampling lend support to the hypothesis that cyclonic circulation features in the Gulf of Mexico might be areas of locally high zooplankton stocks because of increased primary production in the mixed layer supported by the doming of nutrient-rich water within these areas (Biggs et al., 1988). If nutrient-rich midwater is indeed being supplied to the surface and allowing increases in phytoplankton stocks, then zooplankton, fish, and cephalopods may become more abundant as these features persist, thus providing greater food resources to attract higher trophic level predators such as cetaceans and seabirds.

Conclusions

Our results suggest that the amount of prey for cetaceans and seabirds in the northeastern Gulf of Mexico may be consistently greater in the cyclones and confluences (as opposed to the anticyclones), making them preferential areas for cetacean and seabird foraging. As noted by Biggs et al. (2000) and Davis et al. (2000), cetaceans in general and sperm whales in particular were more likely to be found in and around cyclonic features rather than in the anticyclones in the study area. In addition, an analysis in Davis et al. (2000) shows that the distribution of predatory seabirds may also be influenced by mesoscale hydrography; in fact, the integrated PMB estimates described here were found to be among the best predictors of the distributions of several seabird species. Further investigation of the abundance and distribution of cetacean and seabird prey is needed, including targeted larger volume net tows in the features to increase catch rates and sample sizes. Acoustic sampling can be used to cover a much larger area than net sampling with considerably less effort. However, net sampling is required in order to identify potential prey and to evaluate the influence of zooplankton and micronekton taxonomic composition on S_v measurements. Both direct net sampling and indirect acoustic sampling are important

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in describing prey distributions and thus the biological environments of apex predators.

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