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Distribution and Abundance of Phytoplankton, Zooplankton, Ichthyoplankton, and Micronekton in the Deepwater Gulf of Mexico

DOUGLAS C. BIGGS AND PATRICK H. RESSLER

Expeditions in the 1960s and 1970s are the basis for the general paradigm that standing stocks and productivity of phytoplankton are both low ($<0.1 \text{ mg chl-m}^{-3}$; $<150 \text{ mg C-m}^{-2}\cdot\text{d}^{-1}$) seaward of the shelf-slope break in the Gulf of Mexico. The present review supports this description of the mean (stable) state but also shows “hot spots” in primary production ($>2 \text{ g C-m}^{-2}\cdot\text{d}^{-1}$) occur when/where nutrient availability is locally enhanced seaward of the shelf-slope break. Recent collections with Bongo and MOCNESS nets, midwater trawls, and bioacoustic surveys of the Loop Current and associated cyclonic and anticyclonic eddies in the Gulf of Mexico show that these deepwater “hot spots” have higher stocks of zooplankton and micronekton as well. The local aggregations ranged in size from coarse- to meso- spatial scales (10s to 100s of kilometers) though locations of such “oases” were spatially variable along the continental margin.

Phytoplankton distribution and abundance in Gulf of Mexico (GOM) waters has been reviewed at decadal intervals, first by Björnberg (1971), then by Iverson (in Iverson and Hopkins, 1981), and most recently by Vargo (in Vargo and Hopkins, 1990). However, most of the primary literature these reviewers cited focused on the continental shelf. Moreover, Vargo, in particular, noted that much of the information for his review came from studies conducted prior to 1980. In fact, data collected by expeditions in the 1960s and 1970s remain the basis for the general paradigm that standing stocks and productivity of phytoplankton are both quite low seaward of the shelf-slope break in the GOM ($<0.1 \text{ mg chl-m}^{-3}$; $<150 \text{ mg C-m}^{-2}\cdot\text{d}^{-1}$). In the present review, we will support that description of the mean state but we will also show that research carried out since 1987 indicates “hot spots” in primary production ($>2 \text{ g C-m}^{-2}\cdot\text{d}^{-1}$) occur when/where nutrient availability is locally enhanced, even in deepwater (water depths greater than 300 m). In this review, we summarize the available evidence from the GOM that deepwater “oases” that are temporally persistent (even if they are spatially variable) have higher stocks of zooplankton and micronekton.

DEEPWATER PHYTOPLANKTON: MEAN CONDITION

The GOM is a subtropical ocean basin in which the near-surface circulation is dominated by the anticyclonic flow of the Loop Current (LC). East of 90°W , upper layer flow enters through the Yucatan Channel and leaves through the Florida Straits. Because this current enters from the Caribbean, it acts as a bi-

ological conveyor belt to maintain the exchange of pelagic species between the Caribbean and the GOM (Wiseman and Sturges, 1999). This conveyor does not fertilize downstream plant plankton, however, because LC surface waters are among the most oligotrophic in the world ocean. Nitrate, phosphate, and other essential plant nutrients are usually below the analytical detection limit ($<0.05 \mu\text{M}\cdot\text{l}^{-1}$) in LC inflow water from the surface to depths of 80–90 m. The extinction coefficient, “ k ,” which describes how rapidly irradiance decreases with depth according to the exponential equation $I_z = I_0 \cdot e^{-kz}$, is usually <0.05 in LC surface water. As a consequence, the LC inflow into the GOM is almost swimming pool clear and therefore is deep blue in color.

In the central and western deepwater GOM, the standing stocks and biological productivity of the plant and animal communities living in the upper part of the water column are also in general those that might be expected in a nutrient-limited ecosystem. In the late 1960s, as part of a review of plankton productivity of the world ocean, Soviet scientists characterized the deepwater GOM as very low in standing plankton biomass (Bogdanov et al., 1968), with mean primary productivity of just $100\text{--}150 \text{ mg C-m}^{-2}\cdot\text{d}^{-1}$ (Koblentz-Mishke et al., 1970). A few years later, extensive surveys of phytoplankton chlorophyll and primary production that span the period 1964–71 were summarized by El-Sayed (1972) in atlas format as averages within 2° squares of latitude and longitude. These atlas maps show that surface chlorophyll generally ranges $0.06\text{--}0.32 \text{ mg}\cdot\text{m}^{-3}$ in deepwater central and western GOM. There is usually a subsurface “deep chlorophyll maximum”

(DCM) within which concentrations are 2–3 fold higher, and so the atlas reported that chlorophyll in deep water could reach $21 \text{ mg} \cdot \text{m}^{-2}$ when integrated from the surface to the base of the photic zone. Most values, though, ranged $5\text{--}17 \text{ mg} \cdot \text{m}^{-2}$ where water depth was greater than 2,000 m (El-Sayed, 1972). Low values of primary production ($<0.25 \text{ mg} \cdot \text{C} \cdot \text{m}^{-3} \cdot \text{hr}^{-1}$) are typical for surface waters at the majority of the oceanic stations in this atlas, equivalent to $<10 \text{ mg} \cdot \text{C} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ when integrated from the surface to the base of the photic zone. If there are on average 12 hr of sunlight per day, this rate is equivalent to $<120 \text{ mg} \cdot \text{C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ and so is in good agreement with the characterization by Koblenz-Mishke et al. (1970). Allowing for primary production to proceed 300 d a year in the GOM because of its subtropical climate, this rate of primary productivity is $<36 \text{ g} \cdot \text{C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. As a consequence, the deepwater GOM is usually placed at the low end of the estimated range of $50\text{--}160 \text{ g} \cdot \text{C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ that is generally accepted for the annual gross primary production in open-ocean ecosystems (Smith and Hollibaugh, 1993).

Later studies conducted size fractionation of chlorophyll and primary production in deep water. Early data were summarized by El-Sayed and Turner (1977). They noted that the $<20\text{-}\mu\text{m}$ size fraction accounted for on average 83% of the standing crop and 83% of the total production. These values emphasize the importance of the nanoplankton size fraction in the phytoplankton community and further reinforce the paradigm that low-nutrient surface waters are characteristically dominated by small-size phytoplankton and by blue-green algae like *Trichodesmium*. Vargo and Hopkins (1990) emphasized the importance of this blue-green alga in the deepwater GOM, for when abundant in the top 20 m of the water column, *Trichodesmium* may have photosynthetic rates of tens of milligrams of C per square meter per day (Carpenter, 1983). After the potential importance of phytoplankton even smaller in size than nanoplankton became widely recognized, subsequent researchers working in the GOM and elsewhere have size fractionated chlorophyll and primary production into pico ($<2 \mu\text{m}$) as well as nano ($2\text{--}20 \mu\text{m}$), and net ($>20 \mu\text{m}$) fractions (Al-Abdulkader, 1996; Gonzalez-Rodas, 1999).

When it became known that even low concentrations of trace metals can greatly depress measured rates of gross primary production, biogeochemists advocated the use of trace-metal clean techniques to remeasure primary pro-

Fig. 1. Deepwater locations of recent measurements of primary production, 1987–99, on oceanographic cruises by Texas A&M University (TAMU) and the Universidad Nacional Autonoma de Mexico (UNAM).

duction in oceanic ecosystems (Fitzwater et al., 1982). After 1982, such “clean techniques” were used routinely to remeasure primary production in the GOM. Ferguson and Sunda (1984) reported rates of $0.11 \text{ mg} \cdot \text{C} \cdot \text{m}^{-3} \cdot \text{hr}^{-1}$ for a LC station. Ortnier et al. (1984) measured similar values in the LC and calculated that integrated production rates ($0\text{--}90 \text{ m}$) ranged from $14 \text{ mg} \cdot \text{C} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ (temperature-stratified conditions) to $62 \text{ mg} \cdot \text{C} \cdot \text{m}^{-2} \cdot \text{hr}^{-1}$ (after wind mixing to $110\text{--}120 \text{ m}$). Yoder and Mahood (1983), who measured primary production from the shelf out into deep water during the Southwest Florida Shelf Ecosystems Study, found that production averaged $0.1 \text{ g} \cdot \text{C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ in deep water outside an eddy-induced upwelling area. On average, then, it appeared that remeasurements with the use of clean techniques in the 1980s yielded results that were comparable to those that were obtained during the more extensive surveys of the 1970s.

In a recent review of patterns of primary productivity in the GOM, Lohrenz et al. (1999b) provided a plot of locations where ^{14}C primary production measurements have been made in the GOM. Most of these lie over the continental shelf (water depth $<200 \text{ m}$), and the densest spacing is over the inner and middle shelf off the Mississippi–Atchafalaya River. In contrast, Figure 1 shows the location of primary production measurements made in deep water after Vargo’s review by Texas A&M University and by the Universidad Nacional Autonoma de Mexico (UNAM) during the period 1987–1999. All of these measurements were done by trace-metal clean techniques. The 1990 deepwater measurements made in support of the

Nutrient Enriched Coastal Ocean Productivity (NECOP) program were reported by Biggs and Sanchez (1997), and the 1987–88 measurements were discussed by Biggs (1992). Three dozen deepwater measurements made during 1992–94 in support of the Texas–Louisiana Shelf Circulation and Transport Processes Study (LATEX) were reported by Al-Abdulkader (1996) and Gonzalez-Rodas (1999). The primary productivity data from UNAM stations taken in summer 1997 were obtained from Dr. Elva Escobar-Briones (escobri@mar.icmynl.unam.mx).

During LATEX, size fractionation of chlorophyll and primary production was done along cross-margin transects that extended from shallow water to the shelf edge and also at sampling sites along and seaward of the 200-m isobath of the western and central GOM. Ten LATEX cruises from 1992 to 1994 sampled the continental margin in May (1992, 1993, 1994), Aug. (1992, 1993, 1994), Nov. (1992, 1993, 1994), and Feb. (1993 only). Nowlin et al. (1998) summarized the circulation and transport processes; phytoplankton pigment concentrations and species counts were reported by Neuhard (1994) and Bontempi (1995) and also by Al-Abdulkader (1996) and Gonzalez-Rodas (1999). In general, the LATEX results support the findings of El-Sayed and Turner (1977) that pico+nanoplankton make up more than $\frac{3}{4}$ of deepwater cell counts and accounted for $>\frac{3}{4}$ of the primary production. The exception was the “winter” cruise in Feb., when diatoms of the genera *Leptocylindrus* and *Chaetoceros* comprised $>50\%$ of phytoplankton numbers not just in deep water but across the outer, middle, and inner shelf as well.

DEEPWATER PHYTOPLANKTON: SEASONAL CHANGES

Pigment concentration at the surface in the deepwater GOM undergoes a well-defined seasonal cycle that is generally synchronous throughout the region. Müller-Karger et al. (1991) and Melo-Gonzalez et al. (2000) reviewed monthly climatologies of near-surface phytoplankton pigment concentration from multiyear series of coastal zone color scanner (CZCS) images for the period 1978–86. They reported that highest surface concentrations of chlorophyll occur between Dec. and Feb. and lowest values occur between May and July. There is only about 3-fold variation between the lowest ($\sim 0.06 \text{ mg}\cdot\text{m}^{-3}$) and highest ($0.2 \text{ mg}\cdot\text{m}^{-3}$) deepwater surface pigment concentrations, however. Model simulations show that

the single most important factor controlling the seasonal cycle in surface pigment concentration is the depth of the mixed layer (Walsh et al., 1989). Müller-Karger et al. (1991) concluded that, because of this dependence, annual cycles of algal biomass are one or more months out of phase relative to the seasonal cycle of sea surface temperature.

DEEPWATER PHYTOPLANKTON: “HOT SPOTS” FROM ENTRAINMENT OF FRESHWATER

Because essential plant nutrients are limiting, any process that increases the nutrient concentrations available to the phytoplankton in the deepwater GOM will increase primary productivity. That freshwater inputs carry high nutrient loads is well known, but in the GOM, these high nutrient inputs are usually measurable only close in to rivers and estuaries (Lohrenz et al., 1997, 1999a). An exception occurs, however, when surface currents set up off-shelf flow that carries the river water seaward past the shelf-slope break and into deep water (Müller-Karger et al., 1991). Biggs and Mueller-Karger (1994) combined CZCS data with ship data to document that high-chlorophyll “plumes” form in the western GOM when a seaward-moving surface flow confluence is created by deepwater cyclone–anticyclone circulation pairs. Analogous to a pair of anticlockwise-rotating and clockwise-rotating gears, these circulations entrain coastal water from the western and central GOM and draw this offshore when the cyclone (anticlockwise circulation) lies immediately to the north or east of the anticyclone (clockwise circulation).

Both cyclones and anticyclones are meso-scale features that can be detected by the topography of the 15°C isotherm. This isotherm is domed upward in the cyclones and pushed locally deep within the anticyclones. Both types of features can now be located with satellite altimetry as well because GOM cold-core eddies (15°C isotherm domed) have 10–20-cm local depressions in sea surface height, whereas warm-core eddies (15°C isotherm pushed locally deep) have 20–70-cm local elevations in sea surface height (Leben et al., 1993). As one recent example, Figure 2 shows dynamic topography, gridded upper layer geostrophic velocity, surface salinity and surface chlorophyll concentrations over deep water of the north-east GOM in midsummer 1997. Low-salinity Mississippi River water was entrained into the flow confluence created by a gradient of $>80 \text{ dyn cm}$ in geopotential anomaly between between a cyclone located to the north-northeast

Fig. 2. (A) Dynamic topography (cm, 0 m relative to 800 m) of the deepwater GulfCet II focal area, as determined from 107 hydrographic stations made on R/V *Gyre* cruise 97G08. (B) Gridded upper layer geostrophic velocity (0 m relative to 800 m) computed from the dynamic topography data in A. (C) Sea surface salinity map, superimposed on ship track lines of 97G08. (D) Sea surface chlorophyll ($\text{mg}\cdot\text{m}^{-3}$), superimposed on ship track lines. All four figures from Chapter 2 of GulfCet II final report (Davis et al., 2000).

of a LC eddy. Note that low-salinity patches of river water were wrapped anticlockwise around the periphery of the cyclone. A comparison of the salinity and chlorophyll fields shows that surface chlorophyll concentrations in this river water reached $2.0 \text{ mg}\cdot\text{m}^{-3}$ and that, especially in the concentration range $0.1\text{--}0.4 \text{ mg}\cdot\text{m}^{-3}$, the patches of highest surface chlorophyll cor-

respond spatially to the patches of lowest surface salinity.

As a second example, Figure 3 shows sea surface height anomaly, surface salinity, and surface chlorophyll over the same region the next summer, in Aug. 1998. This time, there is no well-developed cyclone–anticyclone modon pair. Rather, it is the clockwise circulation

Fig. 3. (Top) Sea surface height anomaly for water depths >200 m from satellite altimeter data for the NEGOM study area for 29 July 1998 (hindcast data). (Middle) Salinity at ~3 m from thermosalinograph observations on NEGOM cruise N3, 26 July–6 Aug. 1998. (Bottom) Chlorophyll ($\text{mg}\cdot\text{m}^{-3}$) at ~3 m calculated from flow-through fluorescence on NEGOM cruise N3. All from NEGOM annual report, year 2 (Jochens and Nowlin, 1999). Shading indicates patches of low-salinity, high-chlorophyll river water being entrained anticyclonically around the warm slope eddy centered over deepwater in DeSoto Canyon.

Fig. 4. Annual mean chlorophyll concentration in the Gulf of Mexico ($\text{mg}\cdot\text{m}^{-3}$), composited using all available SeaWiFS data Jan. 1998–Dec. 1999. Note “halo” of locally high pigment concentration (light gray color) that outlines the periphery of the Loop Current. SeaWiFS data are courtesy of Orbimage and NASA; data were collected and processed by Frank Müller-Karger and annual mean was composited by Andrew Remsen (both at College of Marine Science, University of South Florida).

around the periphery of a small anticyclone that was located close off the Mississippi River delta that has entrained river waters eastward along its edge. In the periphery of the anticyclone, patches of low-salinity, high-chlorophyll waters got transported from the inner shelf eastward across the continental margin to deepwater depths >500 m (see also Müller-Karger, 2000). Note that the two irregular-shaped patches of high chlorophyll (>0.6 $\text{mg}\cdot\text{m}^{-3}$) seaward of the 200-m isobath between 86° and 88°W correspond, spatially, to patches where surface salinity is <31 .

DEEPWATER PHYTOPLANKTON: “HOT SPOTS” FROM CROSS-ISOPYCNAL MIXING

Recent fieldwork has shown these mesoscale oceanographic features have additional impacts upon deepwater plankton and micronekton communities. Locally, high nutrients are also introduced to the surface of deepwater ocean regions at eddy edges where there is enhanced vertical mixing. In fact, the periphery region of high-velocity surface currents that surrounds both the cyclonic and the anticy-

clonic eddies are zones of locally high vertical shear. Lee et al. (1991) have shown that meanders and eddies in the Gulf of Mexico are often marked by local aggregations of phytoplankton, and elevated fish stocks appear to concentrate in such areas (Atkinson and Targett, 1983). The presence of multiple cyclonic and anticyclonic features in the GOM can result in strong frontal gradients between these features.

In the CZCS ocean color climatology from 1978–1986 (Müller-Karger et al., 1991) and in imagery from the current generation ocean color sensor (the Sea Wide-Field Scanner, or SeaWiFS, in orbit since Oct. 1997), the peripheries of the LC and of the anticyclonic LC eddies (LCEs) of diameter 200–300 km that are shed from the LC are often seen to be outlined by surface pigment concentrations that are 2–3-fold higher than the extremely low concentrations (0.04 – 0.06 $\text{mg}\cdot\text{m}^{-3}$) in the interior of these circulations. Figure 4, in which a “halo” of locally high chlorophyll standing stock can be seen to encircle the periphery of the LC in this annual mean composite, is one such ex-

Fig. 5. (Top) Cruise track and station locations for LATEX hydrographic survey H05, April–May 1993. (Bottom) Vertical contours of bottle nitrate ($\mu\text{M}\cdot\text{l}^{-1}$) along 200-m isobath during cruise H05. Dots indicate bottle trip depths. Both from LATEX data report (Jochens et al., 1996).

ample. Two other examples from recent field-work are presented as Figures 5 and 6.

Figure 5 shows a hot spot of anomalously high nitrate concentration in surface waters between 91° and 92°W along the 200-m isobath that was encountered in May 1993. At stations

36, 37, and 38 on LATEX hydrographic survey H05, nitrate concentrations $>0.5 \mu\text{M}\cdot\text{l}^{-1}$ occurred at the surface, just south of a strong surface front where salinity increased from 32.0 to 36.3. This hot spot of nitrate apparently arose from strong vertical shear that developed

Fig. 6. Deepwater hot spots of primary productivity ($>2 \text{ g C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$) occurred on the LATEX continental margin in Aug. 1993 and Nov. 1994 at stations in the northern periphery of LCE-W and LCE-Y. Productivity maps are from Gonzalez-Rodas (1999); triangles show location of the eight or nine primary productivity stations done each cruise. SSH anomaly maps from University of Colorado (<http://www-ccar.colorado.edu/~realtime/gom-historical-ssh/>) are marked with stars to show the location of the highest measured ^{14}C productivity in relation to LCE periphery.

in this frontal zone, for the surface salinity and silicate data and the vertical contours shown in Figure 5 strongly suggest that it was fueled by cross-isopycnal vertical mixing from below rather than from entrainment of freshwater from the Atchafalaya Bay or Mississippi River to the north and east. Farther west along the 200-m isobath, an anticyclone (LCE "V") was interacting with the continental margin. Note as well from Figure 5 that the extremely low nutrient interior of the eddy was apparently drawn onshore between stations 207 and 210.

Al-Abdulkader (1996) measured chlorophyll stocks and primary productivity at station 37 within the hot spot of anomalously high surface nitrate and at station 83 some 140 km to the west along the 200-m isobath and also farther west at station 88 at the deepwater end of LATEX line 4, which reached the northeast periphery of LCE "V." These data show that

near-surface chlorophyll at station 37 ranged from 0.4 to $0.5 \text{ mg} \cdot \text{m}^{-3}$, or 3-fold higher than the concentrations of 0.15 – $0.17 \text{ mg} \cdot \text{m}^{-3}$ at station 83 west of the hot spot. Al-Abdulkader's data show that primary productivity in the upper 50 m of the hot spot ranged from 0.2 to $0.3 \text{ mg C} \cdot \text{m}^{-3} \cdot \text{hr}^{-1}$. Integrated to the 0.2% light depth and assuming that photosynthesis proceeds 12 hr per day in May, this is a production of $220 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$. This is 1.4 times higher than the measured production integrated to the same irradiance level at his station 83 ($158 \text{ mg C} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$). At station 88 in the northeast periphery of LCE "V," locally low salinity surface water was present (33.6 – 33.8 in the upper 10 m). This surface water was low in nitrate, and near-surface chlorophyll concentrations in it were similar to those at station 83, but high silicate levels in the upper 10 m at station 88 indicate this low-salinity cap was

probably entrained Mississippi River outflow. Data from Al-Abdulkader's dissertation show that primary productivity in the low-salinity surface water was locally high ($0.3\text{--}0.4\text{ mg C}\cdot\text{m}^{-3}\cdot\text{hr}^{-1}$) and that, even below this low-salinity layer, productivity averaged $0.16\text{ mg C}\cdot\text{m}^{-3}\cdot\text{hr}^{-1}$ to a depth of 100 m. When integrated to the 0.2% I_0 depth, this is a production of $226\text{ mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, equivalent to that in the nitrate "hot spot."

A recent dissertation by Gonzalez-Rodas (1999) summarized primary productivity measurements on six subsequent LATEX cruises. Figure 6 shows Gonzalez-Rodas' summary of integrated primary productivity for the LATEX continental margin on two of these cruises, in Aug. 1993 and Nov. 1994. Note that hot spots in deepwater primary production ($>2\text{ g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) were present near 27.5°N and 92°W on both cruises. In summer 1993, the northern edge of LCE-W was interacting with the continental margin between 91° and 93°W ; the locally high shear there apparently fueled a region of anomalously high deepwater primary production. This eddy had a diameter of some 250 km, and at the location where the productivity was measured, the geopotential anomaly was about $+20\text{ cm}$ and current speeds were about $60\text{ cm}\cdot\text{s}^{-1}$ (see Gonzalez-Rodas, 1999: table 5). In fall 1994, the northern edge of another anticyclone, LCE-Y, was interacting with the continental margin again between 91° and 92°W . This eddy was even larger in diameter (320 km) and presented a geopotential anomaly of $+36\text{ cm}$ (from Gonzalez-Rodas, 1999: table 5). On four other cruises, LCEs were too far offshore to be sampled and deepwater primary productivity along the LATEX margin averaged $<0.3\text{ g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Gonzalez-Rodas, 1999).

DEEPWATER PHYTOPLANKTON: "HOT SPOTS" FROM MESOSCALE DIVERGENCE

Because the interiors of the anticyclones are areas of convergence, the upper 100 m or so of the water column in both LC and LCEs are areas in which surface waters are infrequently renewed and so they are impoverished in nitrogen and phosphorus nutrients. The interiors of these regions of convergence are generally regarded as biological "ocean deserts." Measurements of chlorophyll standing stocks, primary productivity, and zooplankton standing stocks within an LCE sampled in 1988 are in good agreement with this premise (Biggs, 1992). However, the cyclonic cold-core eddies (local areas of divergence) that are frequently

associated with these anticyclones represent areas of higher biological productivity.

Subsurface sampling of cyclonic GOM eddies from ships showed a highly predictable negative first-order relationship between temperature $<22^\circ\text{C}$ and nitrate concentration. Temperature could thus be used as a proxy for nitrate concentration, and in particular the depth of the 19°C isotherm was a good estimation of the depth of the $10\text{ }\mu\text{M}\cdot\text{I}^{-1}$ nitrate concentration (Biggs et al., 1988). Within one cyclone sampled in 1996, the nitracline was domed 40–60 m shallower than within the LCE that was sampled concurrently (see Zimmerman and Biggs, 1999: fig. 6). Because this doming facilitated a higher flux of new nitrogen into surface waters in cyclone than in anticyclone, the DCM was locally shallower and chlorophyll reached higher maximum concentration in the cyclone than in the LCE. Because this resulted in higher standing stocks of chlorophyll in the upper 100 m in the cyclone, the cyclones are generally regarded as biological "oases," whereas the interior of the LCEs are biological "deserts."

At six hydrographic stations made during a survey of a mesoscale cyclonic eddy that was centered near 26°N and 94°W in Nov. 1987, integrated chlorophyll standing stock averaged $38 \pm 9\text{ mg}\cdot\text{m}^{-2}$ (Biggs et al., 1988), or 2–3 times greater than the mean for the oceanic GOM. Primary productivity averaged $12\text{ mg C}\cdot\text{m}^{-3}\cdot\text{d}^{-1}$ in the upper 10 m, and integrated production to the 1% light level was equal to $250\text{ mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Biggs 1992), or double the mean of $100\text{--}150\text{ mg C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ reported by Koblenz-Mishke et al. (1970). Similarly, Yoder and Mahood (1983) reported that, for stations located seaward of the 200-m isobath off the West Florida Shelf within an area of eddy-induced upwelling, the top of the nitracline domed to depths of just 40–60 m below the surface. They measured the average water column production there at $0.6\text{ g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, whereas for three other stations located outside the eddy-induced upwelling area, production averaged $0.1\text{ g C}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (Yoder and Mahood, 1983). Thus, Yoder and Mahood concluded that subsurface upwelling may enhance deepwater phytoplankton primary production by as much as 6-fold. Subsequent studies of cyclonic gyre formation off the southwest Florida Shelf found that a cold recirculation, approximately 200 km in size, develops off the Dry Tortugas when the LC flow overshoots the entry to the Straits of Florida and that this persists over time scales of about 100 d (Lee et al., 1994). Frantantoni et al. (1998) showed how this

cyclone grows from instabilities along the eastern edge of the LC. This so-called "Tortugas Gyre" formation provides enhanced food supply, retention, and shoreward transports for successful recruitment of locally spawned snapper and grouper larvae in the western and lower Florida Keys.

In summary, the GOM is oligotrophic in general, but mechanisms exist that elevate primary production on smaller space and time scales. These mechanisms serve to increase heterogeneity in what is otherwise classically defined as a "stable" ecosystem. When/where anticyclonic and cyclonic hydrographic features occur over deepwater and especially where they interact with the continental margin, they are expected to play an important role in determining biogeographic patterns and controlling primary productivity.

DEEPWATER ZOOPLANKTON, ICHTHYOPLANKTON, AND MICRONEKTON: MEAN CONDITION

The deepwater GOM has been considered a biologically impoverished ocean for zooplankton, ichthyoplankton, and micronekton because on average the standing stocks of plankton and fish seaward of the shelf break are lower than those found in temperate and higher latitude regions. Soviet-Cuban fisheries investigations in the 1960s reported that zooplankton standing stocks were low across much of the GOM (Bogdanov et al., 1968; Khromov, 1969a), and subsequent reviews by Hopkins have reinforced this perception (Iverson and Hopkins 1981; Vargo and Hopkins, 1990). In fact, in several biologically important ways, the GOM resembles other oligotrophic subtropical oceans. The zooplankton and micronekton fauna of the deepwater GOM are similar in energy content, taxonomic composition, and food habits to those of other low-latitude oceans (Stickney and Torres, 1989; Hopkins and Gartner, 1992; Hopkins et al., 1994, 1996), and the ichthyoplankton fauna of the GOM have been grouped along with those of the western tropical Atlantic Ocean and Caribbean Sea (Richards, 1990).

Relegating secondary production in the GOM to oligotrophic status is nevertheless an oversimplification because the generally low standing stock levels are not uniformly low but are instead punctuated by spatial and temporal variation greater than that found in most other oligotrophic oceans. This variability may be manifested as spatial "hot spots" and temporal peaks in biomass. For example, Khromov (1969a, 1969b) reported that, whereas zoo-

plankton standing stocks in the tropical oligotrophic Caribbean Sea were almost always low and did not exceed 10 ml wet displacement volume (WDV) per 100 m³ in waters offshore of the shelf-slope break, GOM stocks exhibited more seasonal, interannual, and spatial variability, with biomass levels as high as 35 ml WDV per 100 m³ (range <5–35). Also, Hopkins and Lancraft (1984), who compared integrated wet weight biomass of zooplankton and micronekton in three tropical-subtropical locations (Caribbean Sea, GOM, and Pacific Ocean near Hawaii), found that the GOM was the highest in terms of zooplankton and intermediate in rank (above the Caribbean) in terms of micronekton. If gelatinous plankton were included in the micronekton biomass comparison, the GOM then ranked highest of all three locations in both categories. Finally, although studies of GOM biomass do generally reveal low standing stocks (<5 ml·100 m⁻³), reported estimates can vary by a factor of 10 or more from the minima within a given study (Biggs et al., 1988; Richards et al., 1993; Wormuth et al., 2000) to values comparable to standing crops found in upwelling regions of other oceans (14–75 ml·100 m⁻³, as summarized by Austin and Jones, 1974).

The presence of sizable populations of apex predators in the deepwater GOM also contradicts the paradigm of uniformly low secondary production. The larvae and adults of tuna, swordfish, mackerel, and other nekton of importance to commercial and recreational fisheries are found in the deepwater GOM (Vargo and Hopkins, 1990; O'Bannon, 1999). Commercial landings of adult yellowfin tuna alone exceeded 3.7 million pounds (value >\$9 million) in 1998 (National Marine Fisheries Service Annual Commercial Landing Statistics, <http://www.st.nmfs.gov/commercial/landings/annualLandings.html>). The deepwater GOM is also habitat for substantial populations of marine mammals, sea turtles, and seabirds (Mullin et al., 1994; Davis et al., 1998; Weller et al., 2000). In fact, the same cyclones and the frontal zones of both cyclonic and anticyclonic eddies shown to support enriched zooplankton and micronekton biomass (Wormuth et al., 2000) have been identified as deepwater concentrating mechanisms for apex predators such as fish and marine mammals (Lamkin, 1997; Biggs et al., 2000; Davis et al., 2000). In this review, we show that anticyclonic and cyclonic hydrographic features play an important role in determining biogeographic patterns of and controlling secondary productivity in deepwater of the GOM.

TABLE 1. Chronology of previous reviews of the zooplankton, ichthyoplankton, and micronekton of the Gulf of Mexico.

Year	Author	Synopsis
1954	Galtsoff (editor)	An edited volume containing reviews of GOM zooplankton and micronekton; first major synthesis
1970	Pequegnat and Chace (editors)	Texas A&M University oceanographic studies. Vol. 1; contains reviews of some groups of zooplankton and micronekton; emphasis is on benthic/demersal rather than pelagic taxa
1971	Björnberg and Rass	Reviews of Caribbean and GOM regions by Björnberg (zooplankton) and Rass (deep-sea fish), in UNESCO-FAO proceedings of a 1968 meeting in Curaçao
1973	Hopkins and Briggs	Summary of knowledge of the eastern GOM; contains reviews by Hopkins (zooplankton) and Briggs (nekton)
1981	Iverson and Hopkins	GOM phytoplankton/zooplankton review in Environmental Research Needs in the Gulf of Mexico (GOMEX) symposium proceedings
1990	Darnell and Defenbaugh	GOM environmental overview and history of research, from a special session on the ecology of the Gulf of Mexico published in <i>American Zoologist</i>
1990	Vargo and Hopkins	Hopkins' portion reviewed zooplankton and micronekton + ichthyoplankton. The area of interest was Florida south of the Keys and the deepwater GOM to the west of the Florida coast in MMS's Eastern Planning Area

DEEPWATER ZOOPLANKTON, ICHTHYOPLANKTON, AND MICRONEKTON: PREVIOUS REVIEWS

Several major reviews of GOM zooplankton, ichthyoplankton, and micronekton have been done since the 1950s (Table 1). Their focus and content varied from catalogs of plankton collections yet to be analyzed, to lists of known taxa, to summarized results of studies of specific regions. However, significant portions of the research done in the GOM often have not reached the published literature but instead reside in government or contracting agency technical reports and documents.

The earliest overview was by Galtsoff (1954), who assembled a volume of reviews written by leading government and university specialists about GOM zooplankton and micronekton under the auspices of the U.S. Fish and Wildlife Service. A general review of the state of knowledge of zooplankton was provided by H. B. Moore to supplement specific reviews by other specialists of planktonic foraminifera, cnidarians, ctenophores, salps, chaetognaths, crustaceans, molluscs, and fish. Although some detailed information was available, the general conclusion was that there was still much to be learned about the GOM zooplankton/micronekton community. In fact, Moore concluded that on balance "next to nothing of the zooplankton of the Gulf of Mexico" was known at the time.

Sixteen years later, Pequegnat and Chace

(1970) edited a volume on the biology of the GOM that contained a historical overview, locations, and discussion of investigations of water column sampling with midwater trawls and meter nets by Texas A&M University Department of Oceanography investigators in the 1960s. Although the emphasis of the volume is on benthic/demersal rather than pelagic taxa, some chapters summarized the state of knowledge of particular holoplanktonic groups (penaeid and caridean shrimp, euphausiids, and heteropods) in the deepwater GOM. Around the same time, the proceedings of "A Symposium on Investigations and Resources of the Caribbean Sea and Adjacent Regions" were published and included two reviews of interest. Björnberg (1971) reviewed phytoplankton and zooplankton of the Caribbean and adjacent regions, including the GOM. The state of the knowledge of various taxonomic categories of zooplankton and micronekton was given, including protozoa, medusae, siphonophores, ctenophores, rotifers, polychaetes, nemertines, molluscs, copepods, cladocera, ostracods, mysids, amphipods, isopods, euphausiids, decapods, chaetognaths, hemichordates, urochordates, and cephalochordates. Björnberg concluded that the copepods and chaetognaths were the best studied groups, remarked that much of the study of GOM zooplankton to date had been concentrated in coastal waters and the Florida Current, and fi-

nally noted the need for large-scale, coordinated study of the zooplankton in shelf and oceanic waters of the GOM. In the same volume, Rass reviewed deep-sea fish fauna (members of the micronekton community). Rass provided a list of 203 species from the GOM and estimated that deepwater fish represented about one-third of the total number of fish species in the open GOM.

In a compendium entitled "A Summary of Knowledge of the Eastern Gulf of Mexico," Hopkins (1973) reviewed GOM zooplankton. Work in estuarine and coastal systems had been increasing, but Hopkins noted little work had been published on zooplankton in the oceanic GOM. However, knowledge of eastern GOM physical oceanography had increased considerably, and its potential biological effects were pointed out by Hopkins. The LC and associated upwelling were cited as the most important factors affecting plankton production in the oceanic GOM, whereas in coastal areas, runoff from terrestrial sources and seasonal temperature changes were the most important. Biomass was known to be low in the oligotrophic open GOM and was thought to vary seasonally with the movement of the LC. The use of zooplanktonic indicator species as water mass tracers was mentioned in this review, as well as the ongoing plankton collections that were taking place as part of the EGMEX (Eastern Gulf of Mexico) program. Hopkins' own quantitative studies of biomass and taxonomic composition of zooplankton and micronekton in the eastern central GOM were mentioned as "in progress." Briggs reviewed midwater fishes of the GOM in the same volume, but he noted that the ichthyofauna of waters overlying the continental slope and abyssal plain were still not well known.

In 1981, a review of GOM phytoplankton and zooplankton by Iverson and Hopkins was included in the proceedings of a 1979 symposium on "Environmental Research Needs in the Gulf of Mexico." Hopkins' section on zooplankton reviewed work on the shelf and slope and in the open GOM subsequent to previous reviews of GOM zooplankton, micronekton, and ichthyoplankton. Hopkins noted that, except for published work on zooplankton taxonomy, much of the research done remained in "gray literature" (government reports and theses/dissertations). However, Hopkins featured several major research programs that sampled zooplankton in water depths of 200 m or greater in the review, including Ocean Thermal Energy Conversion (OTEC), a program sponsored by the U.S. Department of En-

ergy (DOE). The zooplankton were studied off Mobile Bay (29°N, 88°W) and off Tampa Bay (27°38'N, 85°34'W). The investigators were able to observe taxonomic composition and biomass levels as a function of depth and time, although the sampling strategy did not allow them to completely resolve diurnal or seasonal trends. Hopkins also summarized his own National Science Foundation-funded trophodynamic study of zooplankton and micronekton in the upper 1,000 m at a station in the eastern central GOM (27°N, 86°W). Diurnal patterns of zooplankton numbers and biomass were studied with trawling, net tows, and bottle sampling. Vertical migration was documented for a "significant portion of the zooplankton and micronekton in the east-central Gulf." Hopkins estimated that the zooplankton biomass at this reference station turned over once every 30–90 d, supported by the relatively low primary production in the oligotrophic open GOM. Some inferences were made about trophic interactions on the basis of the data collected there, and Hopkins included a list of important zooplanktonic and micronektonic predators and prey in the system.

From the studies cited in Hopkins' review for the 1979 symposium, the temporally and spatially patchy nature of the zooplankton and micronekton had become evident. Hopkins emphasized the general lack of basic physiological data for GOM zooplankton, though, which he argued was urgently needed to better understand the flow of energy and/or pollutants through the deepwater ecosystem.

In 1987, a special session on the ecology of the GOM was held at the annual meeting of the American Society of Zoologists. In 1990, selected papers from that session were published in an issue of the journal *American Zoologist*. Darnell and Defenbaugh (1990) reviewed the history of environmental research in the GOM, noting that in the 15 yr preceding their review, federal agencies (most notably the Department of the Interior) had spent more than \$75 million in research studies of the northern GOM. As had previous reviewers of the GOM zooplankton/micronekton field of study, these authors reported that much of the results of GOM research remained "locked up in the various technical reports submitted to the sponsoring agencies, and only a small fraction [had] appeared in the professional journal literature." However, although this review provided a list of early historical investigations of the GOM and of major interdisciplinary investigations since 1960, the bulk of these stud-

ies had been targeted to the continental shelf and not to deep water.

In 1990, Vargo and Hopkins provided a review of GOM phytoplankton, zooplankton, and ichthyoplankton in a report to the U.S. Minerals Management Service (MMS). The area of interest was South Florida, mostly south of the Florida Keys but also including the deepwater GOM to the west of the Florida coast (in MMS's Eastern Planning Area). Hopkins' portion of the review included GOM hydrography and circulation relevant to zooplankton, ichthyoplankton, and micronekton populations, as well as tabular data and a discussion regarding the taxonomic dominants and seasonal trends in abundance and biomass in GOM waters deeper than 200 m.

DEEPWATER ZOOPLANKTON, ICHTHYOPLANKTON, AND MICRONEKTON: SYSTEMATICS STUDIES

Many studies of the diverse zooplankton, ichthyoplankton, and micronekton of the GOM have concentrated on the ecology, biology, or systematics of one particular species or group of organisms. Because a table of these works would make the length of this review unnecessarily long, we have archived them chronologically by author with summary description of subject at: http://www-ocean.tamu.edu/~biggs/deepwater_review/.¹ Although the scope of these individual works may be narrow, in ensemble they are very important to an understanding of GOM zooplankton, micronekton, and ichthyoplankton communities. Such research provides the means to identify and enumerate specimens found in collected samples; without knowing "who" is there, we cannot hope to understand the GOM as a system. To understand the flow of energy and nutrients through the deepwater biological system, Hopkins (1982) has argued, knowledge of taxon-specific trophic interactions is often helpful. Thus, we believe this chronology will be of value because these works provide the taxon-specific ecological information needed to interpret studies of biomass and abundance and to allow the identification of species or groups of particular importance.

In brief, the dominant groups of GOM deepwater zooplankton in terms of biomass are holoplanktonic calanoid copepods, euphausiids, and chaetognaths; meroplanktonic larvae are "relatively scarce in the oceanic" zooplankton

community but become more numerous closer to shore (Vargo and Hopkins, 1990). In terms of feeding, the zooplankton community includes herbivorous, detritivorous, and omnivorous members (Hopkins, 1982). The top three groups of deepwater micronekton in order of biomass are scyphomedusae, fish (myctophids and gonostomatids), and crustaceans (decapods and euphausiids) (Hopkins and Lancraft, 1984). Zooplanktonic crustaceans comprise the greater part of the diet of micronektonic midwater fishes (Hopkins and Baird, 1977; Hopkins et al., 1996) and crustaceans (Hopkins et al., 1994), and gelatinous carnivores are also known to be important zooplanktonic predators (Biggs et al., 1984; Vargo and Hopkins, 1990). Further, areas of enriched deepwater zooplankton biomass have been shown to be correlated with increased abundance of squid paralarvae and myctophid fishes (Wormuth et al., 2000). The major components of the deepwater ichthyoplankton community are larval myctophids, gonostomatids, mackerel, tuna, and flyingfishes (Vargo and Hopkins, 1990; Sanvicente-Anorve et al., 1998). The presence of increased abundance of larval fish in areas of enriched zooplankton biomass implies that their diets include zooplankton (Govoni et al., 1989; Lamkin, 1997). However, the available information on the feeding habits of ichthyoplankton is limited, except as the category overlaps with micronekton and zooplankton.

DEEPWATER ZOOPLANKTON, ICHTHYOPLANKTON, AND MICRONEKTON: BIOMASS AND ABUNDANCE

The standing stock biomass of zooplankton, micronekton, and ichthyoplankton in the GOM has been observed to vary in both space and time, but despite numerous studies on the ecology and systematics of particular taxonomic groups, much less work has been done to determine the scales of the variability at the coarse- to mesoscale level and how these determine the patterns in biomass over time. Most of the work has been done by traditional net sampling techniques: a survey of bulk biomass values from the literature reveals up to 10-fold and higher variability in standing stock levels (see Table 2).

Figure 7 includes two maps showing the locations of major collections of plankton biomass data. Despite fairly extensive sampling coverage in many deepwater parts of the GOM over the last 30-odd years, though, there has been no overall summary of the biomass results. There have, however, been numerous

¹ A hard copy can also be obtained by contacting DCB at the address given at the end of this article.

TABLE 2. Chronology of previous estimates of plankton standing stock in the deepwater GOM (biomass as milliliters wet displacement volume per 100 m³).^a

Year	Author	Synopsis	Biomass
1958	Arnold	GOM-wide, upper 10 m, silk mesh in metal tube, horizontal tows	5–6
1958	Arnold	GOM-wide, upper 10 m, all-metal sampler, horizontal tows	11–13
1969 ^b	Khromov	GOM-wide, vertical hauls, upper 100 m, silk Juday meter nets with 38 meshes per inch (0.5-mm aperture); with "inedible forms removed"	<5–35
1973	Hopkins	In review article, mentions biomass estimates for the eastern central GOM that were obtained during EGMEX (eastern Gulf of Mexico) investigations	1–10
1976	Houde et al.	Eastern GOM from multiple years and seasons, upper 200 m, 61-cm-diameter bongo nets with 333- μ m mesh, oblique hauls	2–10
1981	Iverson and Hopkins	Tampa OTEC site in eastern GOM, upper 200 m, 0.75-m open nets with 202- μ m mesh, vertical and oblique hauls; average value reported here	6
1988	Biggs et al.	Western GOM, upper 100 m, open meter nets with 333- μ m mesh, oblique hauls during 2 mo (April and Nov.) of the same year	4–40
1989	Richards et al.	Northeast GOM, upper 200 m, 61-cm-diameter bongo nets with 333- μ m mesh, oblique hauls, data from SEAMAP program	2–12
1991	Grimes and Finucane	Front between Mississippi plume and ocean water, neuston tows, 947- μ m mesh, horizontal tows	1–12
1992	Biggs	Western GOM, upper 200 m, open 70-cm-diameter bongo nets with 333- μ m mesh oblique hauls; range of average day–night values is shown	4–6
1993	Richards et al.	Northeast GOM, upper 200 m, 61-cm-diameter bongo nets with 333- μ m mesh, oblique hauls; data from SEAMAP program	2–33
1997	Biggs et al.	Western GOM, upper 100 m, open meter nets with 333- μ m mesh, oblique hauls	4–9
1997	Lamkin	Upper 200 m, 61-cm-diameter bongo nets with 333- μ m mesh, oblique hauls, data from SEAMAP program; range using averages for the eastern and eastern GOM (respectively) is shown	10–13
1999	Zimmerman and Biggs	Central GOM, various depth intervals in the upper 125 m, 1/4-m ² mouth area MOCNESS with 333- μ m-mesh nets	4–32
2000	Davis et al., Vol. III: data appendix	Northeast GOM during two different years, various depth intervals in the upper 400 m, 1-m ² mouth area MOCNESS with 333- μ m-mesh nets	<0.1–33

^a Notes: Direct comparisons of biomass values are difficult because of differences in gear, sampling technique, and measurement methods. The values above are a sampling of those values reported in wet displacement volume per volume of seawater or similar, with equipment and sampling technique as noted. Volume units were converted as necessary into ml·100 m⁻³. The implicit assumption is that these bulk values are useful in describing the overall biomass of various sizes and kinds of zooplankton, ichthyoplankton, and micronekton in the deepwater GOM.

^b Values in this paper were originally reported as g/m³, but a footnote indicated that they were volume values that had been converted to weights by assuming a zooplankton "specific weight" of ~1.

publications and analyses of the amount, composition, and variability of the biomass at particular locations in the deepwater GOM (Commins and Horne, 1979; Flock and Hopkins, 1981; Hopkins, 1982; Hopkins and Lancraft, 1984) and regions (Houde and Chitty, 1976; Houde et al., 1976, 1979; Cummings, 1984; Biggs et al., 1988, 1997; Richards et al., 1989, 1993; Grimes and Finucane, 1991; Biggs, 1992;

Gasca et al., 1995; Zimmerman and Biggs, 1999; Wormuth et al., 2000).

DEEPWATER ZOOPLANKTON, ICHTHYOPLANKTON, AND MICRONEKTON: SPATIAL AND TEMPORAL VARIABILITY

The analyses that are available indicate that whereas overall biomass levels are low, there is

Fig. 7. (A) Deepwater locations of SEAMAP plankton surveys, 1982–98. (B) Deepwater locations of plankton collection stations (excluding SEAMAP), 1958–99.

mesoscale spatial variability in biomass across the GOM. The combined standing stock of zooplankton, micronekton, and ichthyoplankton generally varies with distance from shore (shelf areas are generally enriched as opposed to the deepwater areas: Khromov, 1969a; Iverson and Hopkins, 1981), depth in the water column (highest in the upper 200 m and decreasing with depth: Vargo and Hopkins, 1990), and the proximity to riverine input (enriched areas downstream: Bogdanov et al., 1968; Khromov, 1969a). Regions of upwelling, high current shear, or physical aggregation are “hot spots” that have greater standing stocks (Wormuth, 1982; Vargo and Hopkins, 1990; Lamkin, 1997; Wormuth et al., 2000).

There is also evidence for temporal variability in deepwater stocks, both between years and within a given year. In general, 2–4-fold increases in zooplankton standing stock appear to follow closely in time after changes in local forcing factors (Bogdanov et al., 1968; Khromov, 1969a). These forcing factors may range from changes in river outflow (Dagg et al., 1991) to upwelling due to the passage of deep-water eddies. Variation in overall plankton bio-

mass may also result from turnover of the deepwater zooplankton standing stock, estimated at 30–90 d for zooplankton in the eastern GOM (Iverson and Hopkins, 1981). The biomass in a given depth interval can vary on the time scale of a day by a factor of 2 or more because of diel vertical migration (see Vargo and Hopkins, 1990; see also Biggs et al., 1988; Wormuth et al., 2000). Ichthyoplankton distributions are especially variable, for many taxa exhibit pronounced seasonality and year-to-year variation in abundance. Much of this variation appears tied to length and time of year of spawning (Houde and Chitty, 1976; Dilly et al., 1988; Vargo and Hopkins, 1990).

The OTEC sampling off Mobile and Tampa Bays was reported by various authors (e.g. Lawrence Berkeley Laboratory, 1980a, 1980b, 1980c; Flock and Hopkins, 1981) and summarized by Commins and Horne (1979) as well as by Iverson and Hopkins (1981). In addition to taxonomic and size frequency data, Commins and Horne (1979) reported a peak in zooplankton abundance in Oct. and a minimum in June 1978 at the Tampa site, whereas at the Mobile site abundance was greatest in June and least in Aug. Approximately 98% of the zooplankton were found to occur in the upper 200 m of the water column. Diel vertical migration was evident at both sites.

A very extensive analysis of the zooplankton and micronekton community of the so-called Standard Station in the eastern GOM (27°N, 86°W) has been done by T. L. Hopkins and colleagues (see Hopkins et al., 1996 and references therein). Trends in biomass and abundance over depth and time at this location were elucidated in addition to the ecological information gathered about groups of zooplankton and micronekton found there. Biomass results from these studies were not included in Table 2 because they were usually reported in dry weight units based on length-weight regressions for particular groups of organisms rather than in bulk WDV. However, because spatial variation was not the focus of Hopkins' study, it is unclear whether conclusions drawn from the data collected at this single location are generally applicable to the rest of the GOM.

Probably the most complete and systematic sampling of the standing stocks of zooplankton, micronekton, and ichthyoplankton in the deepwater GOM is being carried out as part of an ongoing state–federal project administered by the Gulf States Marine Fisheries Commission. Known as SEAMAP-Gulf of Mexico (Southeast Area Monitoring and Assessment

Program), the primary goal has been to census the abundance of eggs and ichthyoplankton larvae of commercially important fish stocks. Figure 7A shows the station locations where SEAMAP cruises collected deepwater plankton, primarily with 333- μ m mesh bongo nets and 947- μ m mesh neuston tows according to standard fisheries methods but supplemented with Tucker trawls on more recent cruises. Samples are collected one to three times per year on a $\frac{1}{2} \times \frac{1}{2}^\circ$ grid in different seasons (but the majority of deepwater collections have occurred during April and May). Although many of the samples collected by SEAMAP have been from the continental shelf, so far about 2,100 have been tows in water depth >200 m.

Data reports for the SEAMAP program are produced each year and end up in the gray literature, but aliquots of the plankton collected (both sorted and unsorted) are available for loan. Summaries of sampling locations, biomass values, and environmental data collected at each plankton station are available from the SEAMAP data manager.² So far there has been no summary of the interannual or decadal variability of these data. However, some published studies have used SEAMAP collections from particular regions or over certain periods of time. In 1989, Richards et al. reported that both zooplankton WDV and several taxa of larval fish varied across the LC boundary, being lower in abundance in LC interior than in the periphery or outside. Grimes and Finucane (1991) attributed increased abundance of larval fish caught in SEAMAP neuston tows taken in the front between Mississippi River plume and oceanic waters to enriched primary and secondary production there, as indicated by elevated chlorophyll a and zooplankton WDV. Recently, Lamkin (1997) used 6 yr of SEAMAP data, 1983–88, in an investigation of the frontal zones associated with the northern excursions of the LC. Lamkin found a positive correlation between the abundance of larval nomeid fishes and the location of the northern edge of the LC. In particular, *Cubiceps pauciradiatus* has adult spawning grounds and larval habitats closely related to sharp temperature gradients. Larvae of apex predators like bluefin and yellowfin tuna seem to be most abundant along LC frontal zones and within eddy peripheries, where zooplankton biomass and myctophid

larvae numbers in SEAMAP bongo collections were also elevated (Richards et al., 1989). Adult tuna, as well, can be caught in such frontal zones (Roffer Offshore Fish Finding Service, pers. comm.).

Locations of other studies that produced the biomass estimates listed in Table 2 are plotted in Figure 7B. Work by Houde and Chitty (1976) and Houde et al. (1976) included a study of eastern GOM ichthyoplankton; bulk plankton displacement volumes were reported, but most of the analyses concentrated on shelf waters and on ichthyoplankton composition and stock estimates for species of interest rather than on deepwater biomass. As in most studies, bulk biomass was greater on the shelf than in the deepwater part of the study area. There appeared to be a positive relationship between bulk displacement volume and egg/larval abundance, although the association was not always strong. Also notable is the “distinct seasonality” in the data (especially the eggs and fish larvae, due to seasonal spawning), with highest biomass and numbers of eggs and larvae during the spring–summer versus fall–winter, but these seasonal fluctuations were much more apparent on the shelf than in the deepwater part of the study area.

The studies of Biggs et al. (1988) and Biggs (1992) reported opportunistic sampling during cruises to study LC eddies in the deepwater western GOM. The results provide further evidence that the upper 200 m of LCEs are low in plankton stocks, especially in contrast to LCE periphery. With a $\frac{1}{4}$ -m² Multiple Opening/Closing Net Environmental Sensing System (MOCNESS) (for a description of gear, see Wiebe et al., 1985), Zimmerman and Biggs (1999) collected samples in a transit through a cyclone, a LCE, and the LC itself. This sampling documented higher standing stocks of zooplankton and micronekton in the cyclone than in the LC or the LCE. Recently, Wormuth et al. (2000) reported on extensive 1-m² MOCNESS sampling, which they supplemented with Isaacs–Kidd midwater trawl (IKMT) collections, as a part of the GulfCet II multidisciplinary study of marine mammal, sea turtle, and seabird abundance and distribution. Their trawling carried out in support of this recently completed research program, which was co-sponsored by the U.S. Geological Survey and Minerals Management Service, also documented that cyclones had locally higher standing stocks of zooplankton and nekton than did LCEs.

² See <http://www.gsmfc.org/seamap.html> or write to SEAMAP Data Manager, Southeast Fisheries Science Center, Mississippi Laboratories, Bldg. 1103, Rm. 218, Stennis Space Center, MS 39529.

DEEPWATER ZOOPLANKTON, ICHTHYOPLANKTON,
AND MICRONEKTON: ACOUSTIC SAMPLING

Besides traditional net sampling, acoustic methods are also currently recognized as important ways of studying zooplankton and micronekton (Greene and Wiebe, 1990; Wiebe et al., 1997; Greene et al., 1998). Under typical open ocean conditions and with frequencies on the order of 100 kHz, the particles responsible for acoustic volume backscattering (S_v) are assumed to be zooplankton and micronekton (Clay and Medwin, 1977; Stanton et al., 1994). There are several approaches to making standing stock measurements of zooplankton and micronekton with acoustics (for a survey, see Hersey and Backus, 1962; Greene and Wiebe, 1990; Wiebe and Greene, 1994; Foote and Stanton, 2000). One of the simplest is to use a single-frequency echosounder to measure acoustic backscattering from a volume of water and to then relate this measurement to number or biomass of sound-scattering organisms in that volume as determined by direct sampling with nets.

To date, there have been few acoustic surveys of deepwater zooplankton, micronekton, or ichthyoplankton in the GOM. After the early work of Van Schuyler and Hunger (1967) and Thompson (1971) on acoustic volume backscattering, no studies with special purpose acoustics to measure zooplankton, micronekton, or ichthyoplankton in the deepwater GOM have reached the published literature. However, both moored and vessel-mounted Acoustic Doppler Current Profilers (ADCPs) are routinely used to measure the velocity of near-surface currents, and recently, several volume backscattering studies with ADCPs have been completed and published (Biggs et al., 1997; Zimmerman, 1997; Ressler et al., 1998; Zimmerman and Biggs, 1999; Wormuth et al., 2000). 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 then 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 (Clay and Medwin, 1977; Medwin and Clay, 1998).

Although the ADCP was not designed as a scientific echosounder (Brierly et al., 1998), ADCPs have been successfully used to estimate the concentration of sound scatterers (Flagg

and Smith, 1989; Ashjian et al., 1994; Zhou et al., 1994; Griffiths and Diaz, 1996; Ressler et al., 1998). Some of the studies cited above (Ressler et al., 1998; Wormuth et al., 2000) have employed "sea-truth" sampling of zooplankton and micronekton with a 1-m² mouth area, 333- μ m mesh size MOCNESS. With 1) information about the acoustical properties of the ADCP and relevant hydrographic data, 2) net sampling of sound-scattering zooplankton and micronekton concurrent with ADCP surveys, and 3) some acoustic theory to refine the estimate of what is being measured and how different sizes, abundances, and taxa of zooplankton and micronekton are impacting the signal, it is possible to produce ADCP-derived estimates of standing stock biomass and map zooplankton and micronekton biomass distributions over depth, space, and time (Figure 8).

DEEPWATER ZOOPLANKTON, ICHTHYOPLANKTON,
AND MICRONEKTON: OPTICAL SAMPLING

Near-real-time towed optical surveillance with Optical Plankton Counters (OPCs) and Video Plankton Recorders (VPRs) offers another more recently developed means of surveying zooplankton. Deepwater VPR studies have not been conducted in the GOM, but in other regions VPR observations have been used in concert with net and acoustic sampling to study the coarse-scale abundance and composition of zooplankton populations (Benfield et al., 1996, 1998; Davis et al., 1996). Recently, laser line scan imaging by dual light sheet (DLS) technology has been developed for a towed system at the Center for Ocean Technology at the University of South Florida (USF). Known as the High Resolution Sampler II (HRS-II), this towed system is a comprehensive marine particle analysis system consisting of an environmental suite of off-the-shelf instruments (conductivity-temperature-depth sensor, beam transmissometer, chlorophyll fluorometer, irradiance sensor, and pitch and roll sensors); a particle analysis package consisting of a commercially available OPC and the University of South Florida-designed prototype DLS; and a net verification system consisting of a 20-position, 162- μ m plankton net, rotating cod-end carousel. Collections made with the HRS-II system on the West Florida continental margin have recently been reported by Sutton et al., (2001), and the system engineering was described by Samson et al. (1999, 2000).

Fig. 8. False-color running plot of S_v collected with an ADCP along a north-south transect line from the deep water off the Mississippi River, through a cyclone, and into a Loop Current Eddy (LCE-C) during Oct. 1996 (Davis et al., 2000: fig. 3.14). Red and yellow areas on the plot indicate higher S_v ; blue and purple colors indicate less intense returns. Because local time and location are both changing along the x-axis, such field survey data include temporal variability (higher S_v at night than in the daytime) as well as spatial variability (higher S_v in the cyclone than in the LCE).

DEEPWATER ZOOPLANKTON, ICHTHYOPLANKTON, AND MICRONEKTON: A COMBINED APPROACH FOR 21ST CENTURY SURVEYS

Traditional direct sampling and alternative acoustical and optical techniques are complementary approaches. Net sampling provides taxonomic information that cannot currently be gathered with acoustical or optical techniques; it also provides necessary "sea-truth" information needed to interpret acoustical and optical data. However, acoustics and optics can make nearly continuous measurements over various temporal and spatial scales, providing zooplankton-micronekton-ichthyoplankton data with sufficient resolution to examine temporal and spatial trends in a manner impossible with net sampling at single discrete locations. This capacity is also useful given the growing amount of coarse to mesoscale oceanographic data available from satellites. A combination of net, acoustical, and optical techniques appears to be the optimum way to study spatial and temporal "hot spots" in zooplankton and micronekton standing stock biomass, and such a unification of technologies will lead to better understanding of the interaction of hydrography and ecology in the deepwater GOM.

Time-series animation of altimetry data (<http://www-ccar.colorado.edu/~leben/gulfmex-science/>) now allows eddies to be tracked and shows they are temporally persistent though spatially variable regions of positive or negative sea surface height. To judge "how long?" such eddies need persist in order to become biological hot spots, it seems to us that biologically important time scales are the lifetime of the eddies (5–15 mo), modified by how long it takes for the phytoplankton to take advantage of the increased nutrients (days) and how long this energy takes to translate to higher trophic levels (weeks to months). Hence, we propose that eddies that remain spun up for weeks to months are temporally persistent to the populations of organisms that inhabit them.

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