# WINTER-TIME DISTRIBUTION AND ABUNDANCE OF COPEPOD NAUPLII IN THE NORTHERN GULF OF MEXICO

M. J. DAGG[1], P. B. ORTNER[2], AND F. AL-YAMANI[2]

## ABSTRACT

Copepod nauplii were collected from continental shelf waters in 3 regions of the northern Gulf of Mexico during winters between 1981 and 1984, off Cape San Blas, Florida, off the Mississippi River delta, and off of Galveston, Texas. Some statistically significant ($P < 0.05$) patterns in the abundance and distribution of nauplii were observed: there was significant interannual variability in naupliar concentrations within the region around the Mississippi River delta; naupliar concentrations in the upper 10 m decreased in the onshore-offshore direction in 2 of 4 comparisons; naupliar concentrations in the upper 10 m differed regionally in 2 of 3 comparisons; and naupliar concentration was correlated with chlorophyll concentration in 4 of 5 comparisons.

Maximum concentrations of nauplii (number per $m^3$) within a water column were 2–10 times greater at stations influenced by the Mississippi River plumes than in the other 2 regions. This condition in attributed to vertical stratification imparted to the water column by the inflowing low salinity water from the Mississippi River. We conclude that the physical stratification provides a mechanism for the establishment of high concentrations of nauplii that otherwise would not exist in the winter months on the continental shelf.

Microzooplankton are important diet items for larval fish (Arthur 1976; Gamble et al. 1981; Checkley 1982; Govoni et al. 1983; Houde and Lovdal 1984; Stoecker and Govoni 1984), and gut analyses indicate that copepod nauplii are frequently the dominant prey form found in the larvae of many fish species (Duka and Gordina 1973). Available concentrations of microzooplankton are considered an important determinant of larval survival rates in the ocean because this relationship has been demonstrated in the laboratory (Laurence 1974; Houde 1978) and because field studies have demonstrated a relationship between regions or periods of high microplankton and high larval abundance (Arthur 1977; Lasker 1978). Because survival is enhanced by increased food availability, oceanographic processes that result in increased concentration or production of prey items are important.

The gulf menhaden, *Brevoortia patronus* (Clupeiformes), supports the largest volume fishery in the United States (U.S. Department of Commerce 1983). Spawning occurs in the wintertime, from October to March, in continental shelf waters of the northern Gulf of Mexcio (Fore 1970; Lewis and Rothmayr 1981; Warlen 1988), primarily off of Mississippi and Alabama to the east of the Mississippi River delta, and off of Louisiana to the west of the delta. During February and December 1982, concentrations of menhaden larvae in the region near the Mississippi River delta were greater in plume waters than outside and were much higher at the plume front (Govoni and Hoss[3]). Furthermore, gut contents of these larvae indicated that nauplii were the most abundant prey items.

Much of the continental shelf water of the northern and western Gulf of Mexico is vertically unstratified during the winter, and winter is also the season of minimum primary productivity in these regions, as it is in shelf waters of the northeast and southeast United States. However, coastal waters and nearshore regions influenced by freshwater inputs can be physically stratified during winter when low salinity plumes disperse over higher salinity shelf waters. We postulated that shelf waters influenced by fresh water from the Mississippi River plumes would be regions of increased production and concentration of microzooplankton. The purpose of this paper is to examine this hypothesis by describing the vertical and horizontal distribution and abundance of copepod nauplii in shelf waters of the northern Gulf of

[1]Louisiana Universities Marine Consortium, Chauvin, LA 70344.

[2]Applied Oceanic Marine Laboratory, Ocean Coastal Division, NOAA, 4301 Rickenbacker Causeway, Miami, FL 33149.

[3]Govoni and Hoss. Unpubl data. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

Manuscript accepted December 1987.
FISHERY BULLETIN: VOL. 86, NO. 2, 1987.

Mexico and by comparing these with oceanographic and hydrographic indicators of water column stratification and productivity.

## METHODS

Samples were collected during 5 winter cruises between November and March, during 1981–84, (Table 1). Microplankton samples and hydrographic data were collected from 3 general regions of the northern Gulf of Mexico: off of Galveston, TX, in the region of the Mississippi River delta, and off of Cape San Blas, FL (Fig. 1). Samples were not collected from all 3 regions on each cruise.

Water samples for chlorophyll and nutrient analyses were collected with Niskin bottles. For each chlorophyll analysis, between 25 and 150 mL of seawater was filtered onto a GF/F or GF/C glass fiber filter and homogenized by grinding in 90% aqueous acetone. Fluorescence of the filtrate, brought up to a volume of 10.0 mL, was determined before and after acidification with 2 drops of 10% HCl using a Turner Designs[4] Model 10 fluorometer. Chlorophyll and pheopigment concentrations as chlorophyll equivalents were determined from

$$\text{chlorophyll } (\mu g/L) = \frac{K(f_o - f_a)}{v}$$

$$\text{pheopigment } (\mu g/L) = \frac{K(Rf_a - f_o)}{v}$$

where $K$ is the machine calibration constant, $f_o$ and $f_a$ are the fluorescence readings before and after acidification, $R$ is the acid ratio, and $v$ is the volume of seawater filtered, in mL (Strickland and Parsons 1968).

Samples for nutrient analyses were frozen. Nitrate and nitrite were analyzed according to method number 353.2 described by EPA publication number EPA 600/4-79-020 (Environmental Protection Agency 1979).

Temperature and salinity were measured by several methods. During cruise I, temperature was measured by the temperature sensor on the MOCNESS[5] net, and salinity was measured with a refractometer. During cruises II and III, temperature was measured with expendable bathythermographs (Sippican Instruments). Salinity was measured with a YSI Model 33-S-C-T salinometer on cruise II, and with a Beckman Model RS5-3 salinometer on cruise III. For both of these cruises, bottle samples, analyzed in the laboratory with a Guildline Model 8400A Autosal, were used to check the shipboard salinity measure-

TABLE 1.—Station information, 1981–84.

| Station | Date | Time | Depth (m) | Lat. (N) | Long. (W) |
|---|---|---|---|---|---|
| I–1 | 2–13–81 | 0000 | 18 | 29°05′ | 94°07′ |
| I–2 | 2–13–81 | 1200 | 18 | 29°06′ | 94°07′ |
| I–3 | 2–14–81 | 0001 | 90 | 28°04′ | 93°03′ |
| I–4 | 2–14–81 | 1200 | 90 | 28°04′ | 93°03′ |
| I–5 | 2–15–81 | 0000 | 180 | 27°54′ | 92°51′ |
| I–6 | 2–15–81 | 1200 | 180 | 25°54′ | 92°50′ |
| I–7 | 2–16–81 | 0001 | 180 | 28°34′ | 89°37′ |
| I–8 | 2–17–81 | 1200 | 180 | 28°35′ | 89°38′ |
| I–9 | 2–18–81 | 0001 | 90 | 28°50′ | 89°16′ |
| I–10 | 2–18–81 | 1200 | 90 | 28°50′ | 89°16′ |
| I–11 | 2–19–81 | 0000 | 18 | 28°56′ | 89°29′ |
| I–12 | 2–19–81 | 1200 | 18 | 28°56′ | 89°29′ |
| I–13 | 2–20–81 | 0000 | 90 | 29°09′ | 85°56′ |
| I–14 | 2–21–81 | 1200 | 90 | 29°08′ | 85°56′ |
| I–15 | 2–22–81 | 0000 | 180 | 29°28′ | 86°07′ |
| I–16 | 2–22–81 | 1200 | 180 | 29°28′ | 86°07′ |
| I–17 | 2–23–81 | 0001 | 18 | 29°36′ | 85°47′ |
| I–18 | 2–23–81 | 1200 | 18 | 29°35′ | 85°47′ |
| I–19 | 2–24–81 | 0001 | 18 | 30°12′ | 87°06′ |
| II–1 | 12–05–82 | 0700 | 25 | 28°53′ | 89°29′ |
| II–2 | 12–05–82 | 1255 | 62 | 28°53′ | 89°32′ |
| II–3 | 12–05–82 | 1945 | 33 | 28°59′ | 89°34′ |
| II–4 | 12–06–82 | 2120 | 887 | 28°20′ | 89°27′ |
| II–5 | 12–07–82 | 0715 | 885 | 28°20′ | 89°27′ |
| II–6 | 12–07–82 | 1220 | 834 | 28°19′ | 89°25′ |
| II–7 | 12–08–82 | 1820 | 443 | 28°32′ | 89°53′ |
| II–8 | 12–09–82 | 0830 | 402 | 28°34′ | 89°53′ |
| II–9 | 12–09–82 | 1215 | 461 | 28°32′ | 89°53′ |
| II–10 | 12–13–82 | 1245 | 44 | 29°26′ | 85°53′ |
| II–11 | 12–15–82 | 1930 | 19 | 28°54′ | 89°29′ |
| II–12 | 12–16–82 | 0900 | 68 | 28°51′ | 89°32′ |
| III–1 | 11–19–83 | 1200 | 27 | 28°54′ | 89°29′ |
| III–2 | 11–20–83 | 0800 | 35 | 28°47′ | 89°59′ |
| III–3 | 11–20–83 | 1946 | 732 | 28°38′ | 89°00′ |
| III–4 | 11–21–83 | 0555 | 27 | 28°54′ | 89°30′ |
| III–5 | 11–22–83 | 1100 | 48 | 28°51′ | 89°30′ |
| III–6 | 11–23–83 | 0500 | 194 | 28°31′ | 89°37′ |
| III–7 | 11–24–83 | 1030 | 50 | 28°50′ | 89°31′ |
| III–8 | 11–25–83 | 0820 | 45 | 28°55′ | 89°34′ |
| III–9 | 11–25–83 | 1945 | 40 | 28°56′ | 89°36′ |
| III–10 | 11–26–83 | 1200 | 16 | 28°54′ | 89°29′ |
| III–11 | 11–27–83 | 0900 | 9 | 29°02′ | 89°30′ |
| III–12 | 11–28–83 | 0840 | 29 | 28°48′ | 89°57′ |
| III–13 | 11–28–83 | 1250 | 44 | 28°56′ | 89°51′ |
| III–14 | 11–29–83 | 0950 | 24 | 29°03′ | 89°39′ |
| III–15 | 11–30–83 | 0930 | 44 | 28°47′ | 89°58′ |
| III–16 | 12–01–83 | 0800 | 38 | 28°52′ | 89°29′ |
| IV–1 | 3–14–83 | | 53 | 27°58′ | 95°53′ |
| IV–2 | 3–19–83 | | 59 | 28°18′ | 90°41′ |
| V–1 | 2–21–84 | 0850 | 18 | 28°54′ | 90°25′ |
| V–2 | 2–22–84 | 0830 | 18 | 28°54′ | 90°25′ |
| V–3 | 2–23–84 | 0910 | 18 | 28°54′ | 90°25′ |
| V–4 | 3–1–84 | 0835 | 18 | 28°54′ | 90°25′ |
| V–5 | 3–1–84 | 0830 | 18 | 28°54′ | 90°25′ |
| V–6 | 3–3–84 | 0730 | 18 | 28°54′ | 90°25′ |

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

[5]Multiple opening-closing net and environmental sensing system.

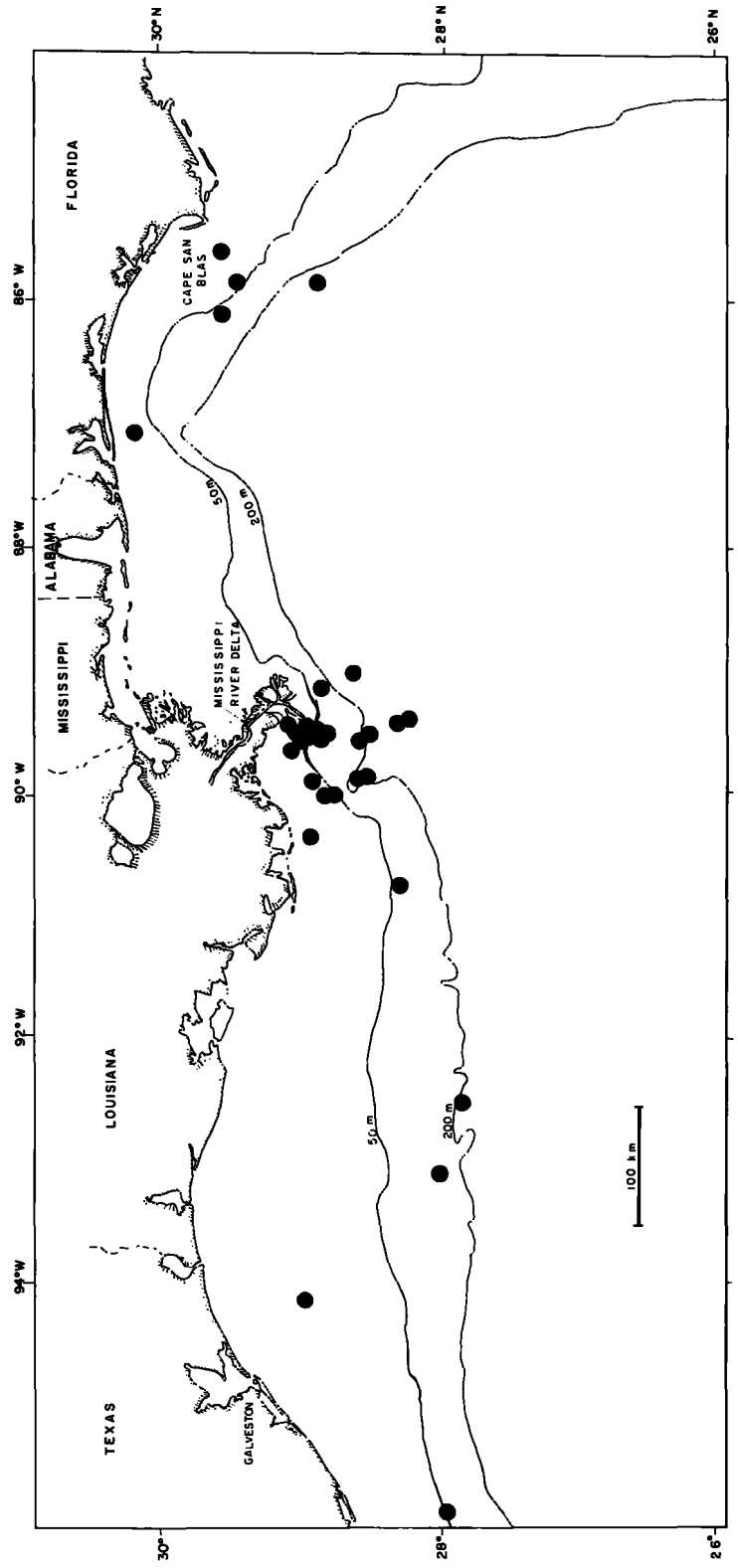


FIGURE 1.—Station Locations.

ments. On cruise IV, a Plessey Model 9040 CTD was used for both temperature and salinity. On cruise V, salinity samples were stored in bottles and analyzed in the laboratory using a Guildline Model 8400A Autosal, and temperature was measured with reversing thermometers.

Microzooplankton were collected using 5 L (cruises I, II, and V) or 30 L (cruises III and IV) Niskin bottles. During cruise I, 1 L samples of untreated water were collected from 3 depths and preserved for later analysis. During subsequent cruises, samples were collected from up to 8 depths; four liters were poured gently through a 20 μm sieve, backwashed with filtered seawater into a sample jar, and preserved in a 5% formalin-seawater solution. In the laboratory, all organisms in each preserved sample were identified and counted. In selected samples, the length and width of the first 50 copepod nauplii were measured using an ocular micrometer. In addition, during cruise I larger nauplii were collected with 0.1 $m^2$ 64 μm mesh nets nested inside the 1 $m^2$ 333 μm mesh nets of a MOCNESS net (Wiebe et al. 1976). Estimates of naupliar abundance from these collections were used separately in the analyses for patterns in distribution and abundance. Lastly, from cruise I, the total number of copepods in the shallow-water samples, total number of copepods from the 333 μm nets, and the zooplankton displacement volume from the 333 μm nets were analyzed for patterns in distribution and abundance.

## RESULTS

Samples from the Mississippi River delta region, collected during 1981 (cruise I), 1982 (cruise II), and 1983 (cruise III), were compared to determine if there was significant interannual variability within a region. Whole water samples and samples retained on 20 μm mesh sieves were pooled for this analysis under the assumption that nauplii in a whole water sample would be retained on a 20 μm mesh screen. The 64 μm net samples were excluded from this analysis. This test was made using average naupliar concentrations in the upper 10 m only; naupliar concentrations were typically lower in deeper waters, and we did not have the same number of deep and shallow stations for each of the 3 sampling years. A 1-way analysis of variance indicated significant variation between years within the Mississippi River delta region ($P < 0.01$). All 3 years were statistically different. These results indicated to us that regional or other spatial comparisons can only be made using samples collected during the same year. Interannual comparisons for other regions were not possible.

Samples were collected from all 3 regions during cruise I. Four tests for regional differences during this cruise were made. First, regions were compared based on naupliar concentrations in the upper 10 m only (Table 2); based on whole water collections $F$ was significant at $P < 0.05$ and based on samples collected with 64 μm mesh nets $F$ was significant at $P < 0.09$. Second, regions were compared based on naupliar concentrations from all depths (Table 2); based on whole water collections $F$ was significant at $P < 0.01$ and based on samples collected with 64 μm mesh nets $F$ was significant at $P < 0.22$. Thus, whole water samples collected on cruise I indicated significant regional differences in naupliar concentration but samples collected with 64 μm mesh nets did not. In addition, there were significant regional differences in the concentrations of total copepods ($P < 0.01$) and in zooplankton displacement volume ($P < 0.05$) during cruise I (data not shown). Regional comparisons were not possible during other cruises because all 3 regions were not sampled in years other than 1981.

Where possible, we also tested for onshore-offshore gradients in naupliar concentrations in the upper 10 m. Stations were categorized according to bottom depth as shallow, <18 m, intermediate, 18–90 m, and deep, >90 m, and comparisons were made between these 3 depth categories. A highly significant onshore-offshore difference existed during cruise I for nauplii collected with the 64 μm MOCNESS nets (Table 3). During cruise III samples were only collected in the Mississippi River delta region but onshore-offshore differences within this region were significant (Table 3). No significant onshore-offshore gradients were observed in naupliar concentrations determined from whole water samples collected from all 3 regions during cruise I, or in nauplii from only the Mississippi River delta region during cruise II (Table 3).

Although regional differences in average concentrations of nauplii were not strong, the vertical distributions were different. For example, several stations at approximately the 50 m isobath are compared in Figure 2. At station IV-1 (Fig. 2a) off the coast of Texas, there was no marked vertical heterogeneity in naupliar concentrations, the maximum concentration was low (23 nauplii/L), and the average concentration was

TABLE 2.—Regional comparisons of naupliar concentrations during cruise I. Samples were collected by 2 methods: whole water samples were collected with Niskin bottles, and 64 μm mesh nets were used to collect the net caught samples.

| Cruise | Depths | Sample type | *n* | Probability of *F* |
|---|---|---|---|---|
| I | upper 10 m | whole water | 28 | < 0.05 |
| I | upper 10 m | 64 μm nets | 126 | < 0.09 |
| I | all depths | whole water | 57 | < 0.01 |
| I | all depths | 64 μm nets | 222 | < 0.22 |

TABLE 3.—Onshore-offshore comparisons of naupliar concentrations from the upper 10 m of each station. Tests for cruise I are based on naupliar concentrations from all 3 regions pooled then separated into 3 depth categories. During cruises II and III, nauplii were only collected from the Mississippi River delta region.

| Cruise | Regions | Sample type | *n* | Probability of *F* |
|---|---|---|---|---|
| I | all | whole water | 28 | < 0.14 |
| I | all | 64 μm nets | 126 | < 0.01 |
| II | Mississippi R. | 20 μm sieve | 28 | < 0.25 |
| III | Mississippi R. | 20 μm sieve | 49 | < 0.01 |

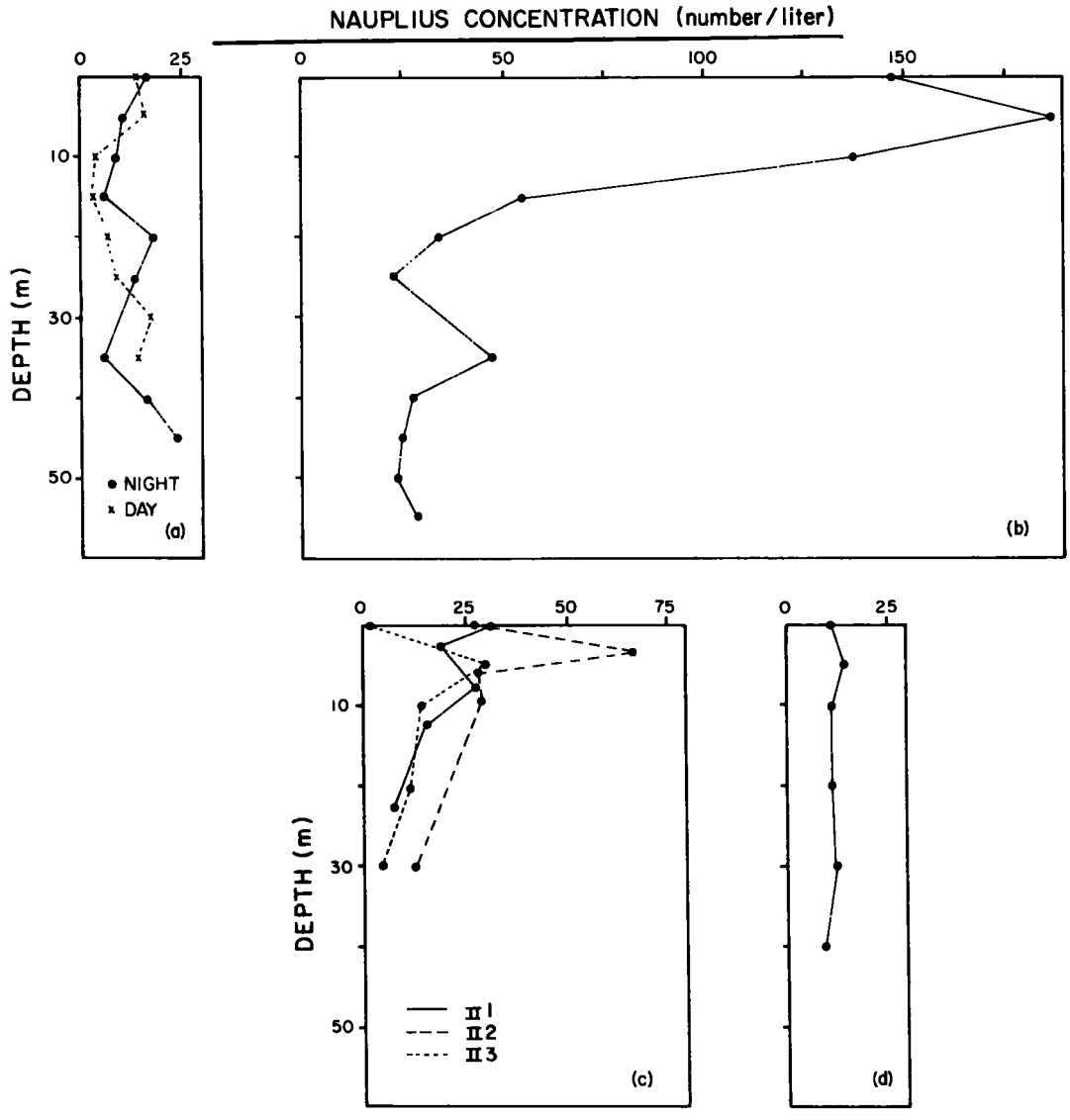


FIGURE 2.—Naupliar concentrations (number/liter) from selected stations near the 50 m isobath on the Texas continental shelf (a, station IV-1), the Louisiana Shelf (b, station IV-2, c, stations II-1, II-2, II-3), and the northwest Florida shelf (d, station II-10).

low (11 nauplii/L). The same pattern was observed off Cape San Blas (Fig. 2d); there was no marked vertical heterogeneity, and the maximum and average concentrations were low, 14 and 12 nauplii/L. In contrast, nauplii at stations near the 50 m isobath in the region near the Mississippi River delta typically showed marked vertical heterogeneity in abundance. At station IV-2 (Fig. 2b), the maximum concentration was 187 nauplii/L and the minimum was 24 nauplii/L. At station II-1, II-2, and II-3 in the Mississippi River delta region (Fig. 2c) naupliar abundances were also vertically heterogenous, although concentrations were lower than at Station IV-2. In general, based on all our vertical profiles (most not shown), regions influenced by the Mississippi River can contain high concentrations of nauplii in the surface layer, while subsurface concentrations are similar to concentrations in the other 2 regions.

Vertical structure in the distribution of nauplii appears to be related to physical structure. At the stations off the coasts of Texas and Florida (Fig. 2a, 2d), temperture and salinity were essentially vertically homogenous (Fig. 3a, 3d) whereas off the Mississippi River delta temperature and

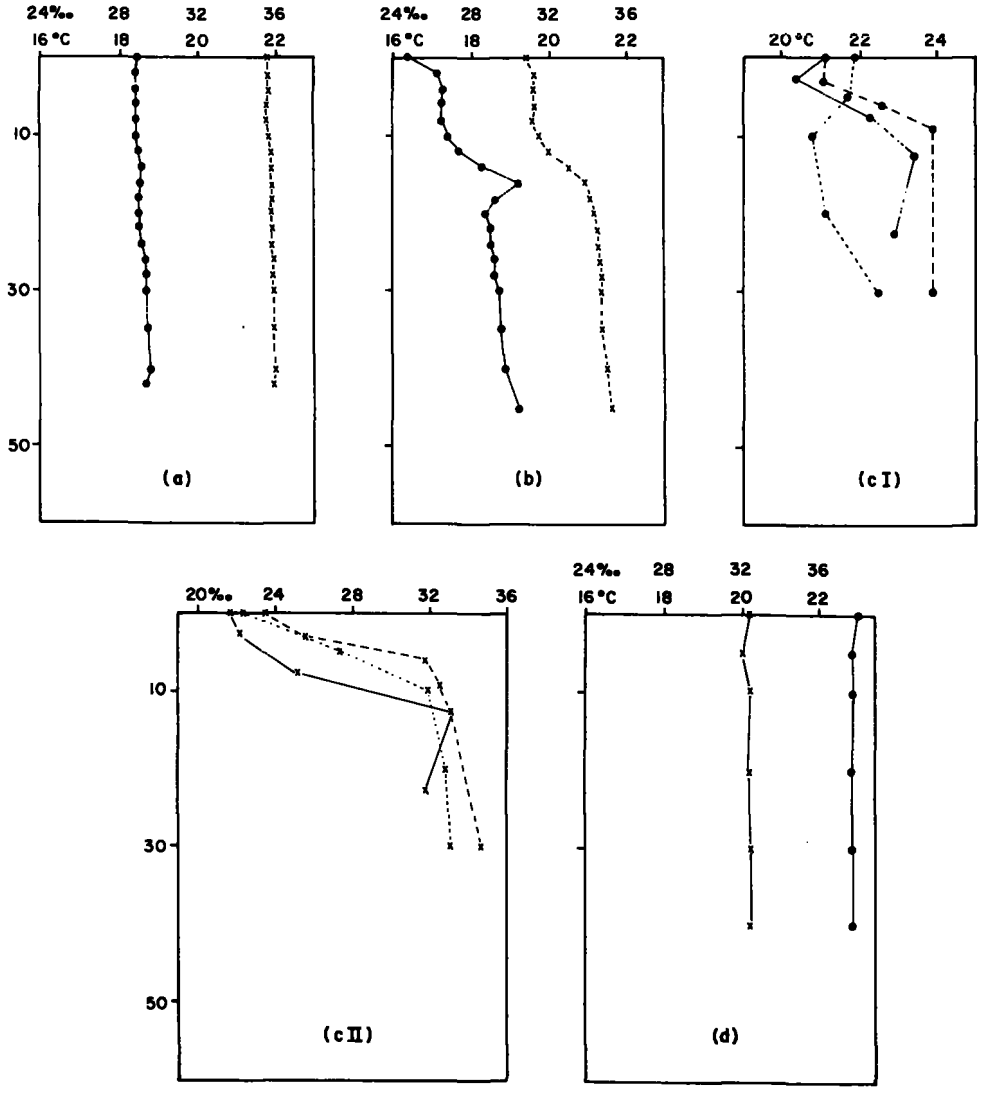


FIGURE 3.—The vertical distribution of temperature (•) and salinity (×) at the stations represented in Figure 2.

salinity were vertically stratified (Fig. 3b, 3c). The same pattern was seen in the chlorophyll a distributions (Fig. 4) and the nitrate distributions (Fig. 5).

Correspondence between chlorophyll a concentration and naupliar abundance was computed; the correlation coefficient for a linear regression of chlorophyll concentration on naupliar abundance for all 5 cruises ($n$ = 269) was 0.39, significant at the 1% level. However, analysis of covariance showed that the relationship between chlorophyll and naupliar concentration was significantly different between cruises, and therefore the data from the 5 cruises should not be pooled. Although a significant relationship between chlorophyll concentration and naupliar concentration typically exists, it is not consistent from cruise to cruise. Regression parameters and correlation coefficients for each cruise are shown in Table 4. Pairwise tests indicate that the slope of the regression for cruise V was significantly different from all the others, cruise IV was differ-

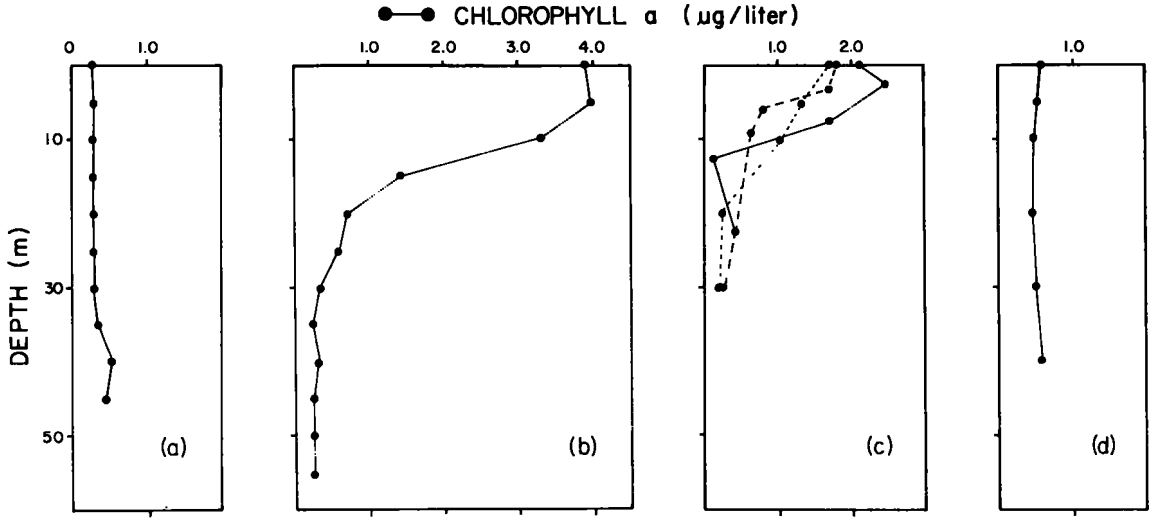


FIGURE 4.—The vertical distribution of chlorophyll a at the stations represented in Figure 2.

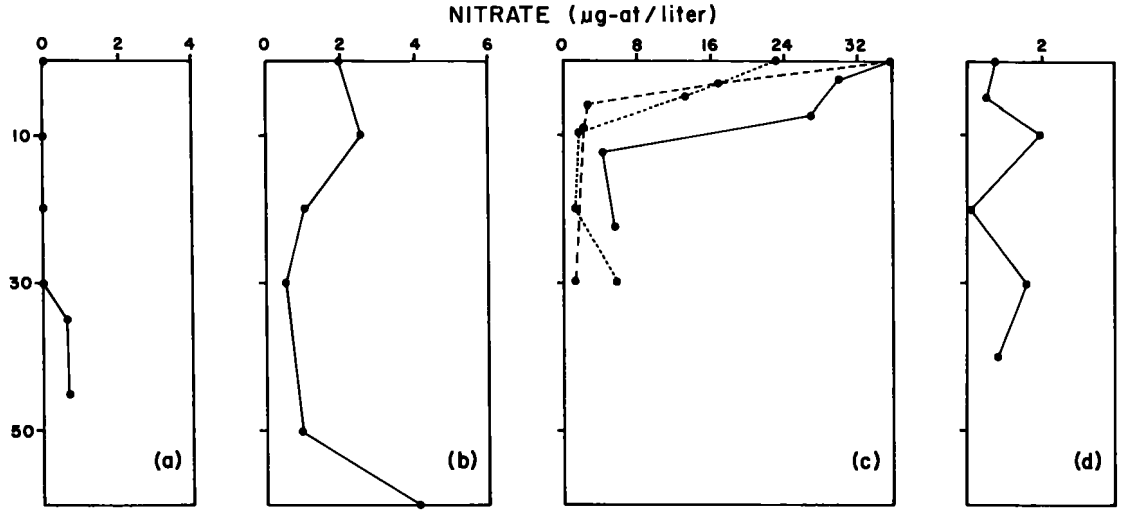


FIGURE 5.—The vertical distribution of nitrate at the stations represented in Figure 2.

TABLE 4.—Parameters and coefficients for linear regressions of chlorophyll concentration on nauplius concentration for each cruise. $Y = a + b(X)$ where $Y$ = naupliar concentration as number per liter, and $X$ = chlorophyll concentration as μg per liter. Significance level tested is 0.01.

| Cruise | $n$ | Intercept | Slope | Significance of slope | $r^2$ | Significance of correlation |
|---|---|---|---|---|---|---|
| I | 57 | 12.9 | 9.7 | <0.01 | 0.40 | <0.01 |
| II | 70 | 5.4 | 15.4 | <0.01 | 0.53 | <0.01 |
| III | 80 | 3.7 | 9.2 | <0.01 | 0.34 | <0.01 |
| IV | 20 | 6.9 | 39.4 | <0.01 | 0.94 | <0.01 |
| V | 42 | 26.1 | 1.1 | NS | 0.04 | NS |

ent from all others, cruise II was different from all the others, and cruises I and III were not different from each other but different from cruises II, IV, and V. The slopes of all relationships except cruise V were significantly different from zero.

The size-frequency distribution of nauplii did not vary in any systematic manner (Fig. 6). For example, at station IV-1, the bulk of the nauplii were between 20 and 100 μm at all depths sampled during both the daytime and nighttime periods. The size-frequency distribution was essentially identical at station IV-2, off Louisiana (data not shown).

At some stations, copepodid stages <600 μm in length (50–200 μm in width) were counted in addition to nauplii because they are potential prey items for menhaden larvae. Copepodites were usually not as abundant as nauplii, especially at stations with high naupliar abundances. On occasion, they were as abundant or, at specific depths, more abundant than the nauplii (Table 5). The ratio of nauplii to copepodites varied widely, between 16.3 and 0.3, so it is not possible to assign a constant factor to naupliar abundances to estimate the increase in available prey attributable to copepodid stages.

Other microzooplankton were usually not as abundant as nauplii or copepods. In our samples, various forms of eggs reached a maximum density of 6 eggs/L (cruise III station 6 at 3 m, data not shown). Pelecypod larvae at one station (III-11) were abundant, reaching a maximum of 29 larvae/L at 4 m, compared with 22 nauplii, 7 copepodites, and 2 eggs/L in the same sample. Only on this one occasion were organisms other than copepodites or nauplii the dominant form of microzooplankton.

TABLE 5.—Abundance (number/liter) of other microzooplankton in addition to nauplii at selected stations during cruise III.

| Station | Depth (m) | Nauplii | Copepodids <600 μm | Copepodids >600 μm | Larvaceans | Eggs | Other |
|---|---|---|---|---|---|---|---|
| III–3 | 6 | 17.3 | 7.5 | 1.0 | 7.8 | 0.5 | 1.8 |
| | 9 | 29.3 | 12.0 | 0.5 | 11.0 | 0 | 1.8 |
| | 12 | 17.5 | 8.0 | 1.0 | 6.8 | 1.5 | 2.3 |
| | 20 | 7.8 | 2.8 | 0 | 1.0 | 2.0 | 0.5 |
| III–7 | 0 | 24.0 | 6.3 | 4.0 | 0 | 1.0 | 1.0 |
| | 3 | 15.3 | 12.3 | 1.0 | 0 | 0.3 | 1.3 |
| | 5 | 3.0 | 5.0 | 1.0 | 0 | 0.8 | 0.3 |
| | 13 | 4.8 | 5.8 | 0.3 | 0 | 0 | 0.5 |
| | 22 | 2.0 | 1.0 | 0.3 | 0 | 0 | 0 |
| III–14 | 0 | 15.8 | 12.0 | 1.3 | 0 | 1.3 | 2.0 |
| | 5 | 44.8 | 3.8 | 0.3 | 0.5 | 3.0 | 4.0 |
| | 10 | 40.0 | 6.8 | 0.8 | 1.3 | 4.3 | 0.3 |
| | 15 | 11.5 | 8.0 | 3.8 | 1.0 | 1.8 | 0.3 |
| | 20 | 12.0 | 35.0 | 6.8 | 0.3 | 0.3 | 0.8 |
| III–16 | 0 | 15.8 | 25.3 | 5.0 | 0 | 0 | 12.8 |
| | 6 | 8.0 | 16.0 | 2.3 | 0 | 1.0 | 2.5 |
| | 9 | 30.0 | 14.0 | 2.0 | 0 | 0.3 | 2.5 |
| | 12 | 29.0 | 13.3 | 0.5 | 0 | 0.8 | 1.3 |
| | 15 | 17.0 | 12.5 | 1.0 | 0 | 0.8 | 0.5 |
| | 25 | 31.8 | 12.8 | 0.8 | 0 | 0 | 5.0 |

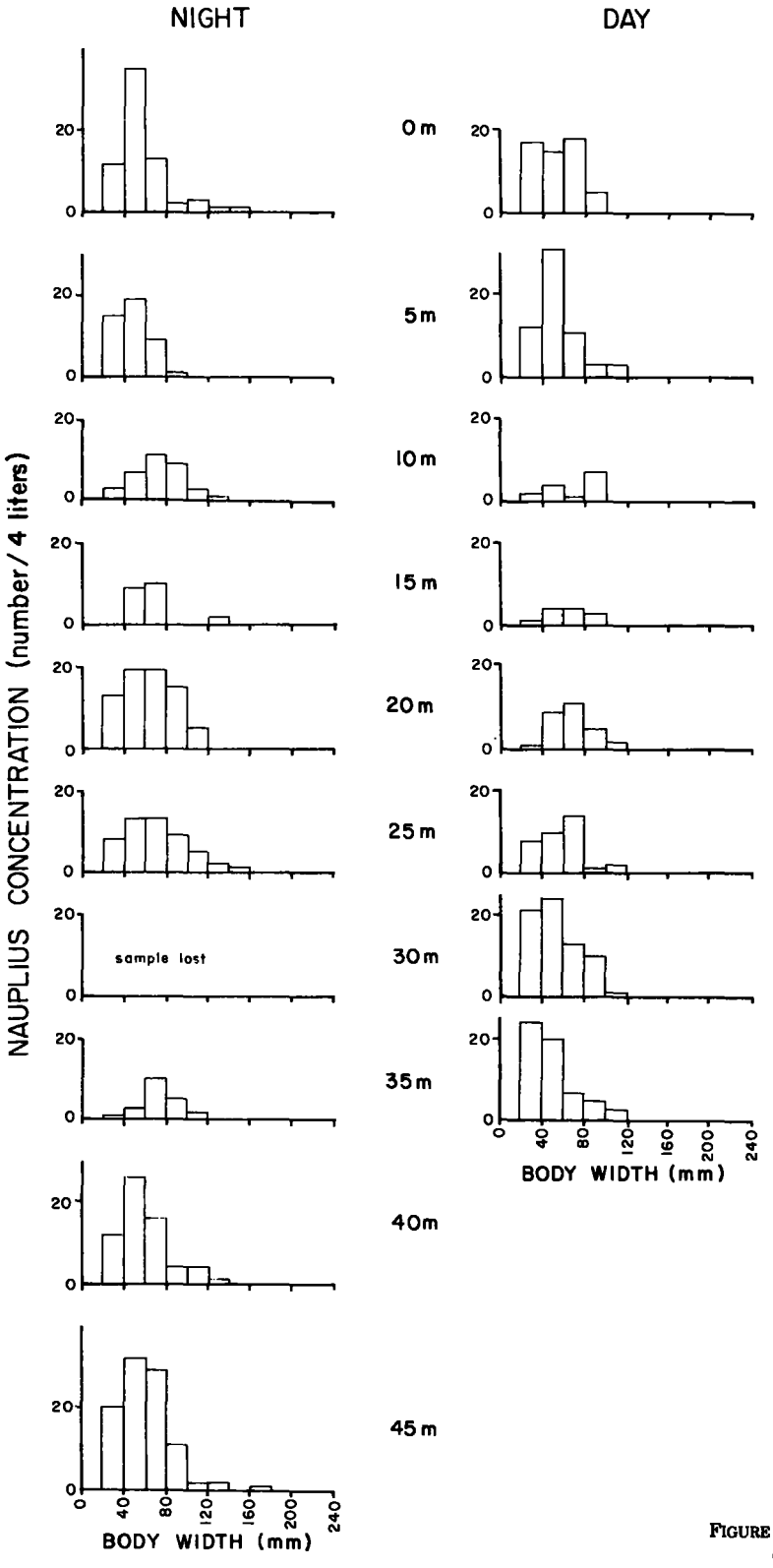


FIGURE 6.—The size-frequency distribution of nauplii from station IV-1.

## DISCUSSION

Menhaden larvae between 3 and 20 mm long collected during wintertime from 3 regions in the northern Gulf of Mexico contained a variety of diet items, including dinoflagellates, tintinnids, copepod eggs, nauplii, copepodids, juvenile pelecypods, and pteropods (Govoni et al. 1983, 1985). Dinoflagellates and tintinnids constituted the main diet items of larvae <5.0 mm long but were replaced by copepod nauplii, then copepodids and small adult copepods as larvae grew larger.

In another study, Stoecker and Govoni (1984) found that copepod nauplii were the dominant items in the diet of menhaden larvae 7.0–9.0 mm long, although only 12 fish were examined. Later studies, however, have verified that nauplii are the dominant items in the diet of a wide size range of larval menhaden collected in the boundary between the plume of the Mississippi River and oceanic waters (Govoni and Hoss fn. 3)

The maximum width of food items in menhaden larvae <5 mm long was about 200 μm (Govoni et al. 1983). This width increased up to about 400 μm for larvae 10 mm long. In another study (Stoecker and Govoni 1984) maximum prey size was calculated in a different manner; the average width of the largest prey type was used. With this index the estimated maximum width of prey items was 50 μm for larvae <5 mm long and about 140 μm for larvae 9–11 mm long. In our study, most of the nauplii were between 40 and 80 μm body width, and most of the copepodites were between 50 and 200 μm body width. These copepod developmental stages were in the size range of diet items typically found in guts of intermediate size (7–11 mm) larvae of the gulf menhaden and we believe our samples are reasonably representative of the prey concentrations available to these larvae. Other prey items for larvae in this size range were common only on rare occasions.

The importance of high prey concentrations to successful feeding and survival of fish larvae has frequently been noted (Hunter 1981). Concentrations required to give high survival in laboratory experiments are seldom found in the ocean but careful attention to culture techniques can result in reasonably high survival at prey densities that are close to or overlap the maximum natural concentrations (Houde 1978). At stations near the river delta that are strongly affected by the river plumes, maximum concentrations of nauplii were typically in the range of 20–50 nauplii/L. At stations farther down plume, away from the delta, maximum naupliar concentrations were higher, up to 187 nauplii/L at station IV-2 for example. It is not clear whether this is a seasonal pattern, a pattern due to the down-plume development of the food web, or a pattern attributable to some other factors. However, the concentrations observed in waters with salinities lowered by the river plumes are mostly within the range of 10–100 nauplii/L that is frequently reported for oceanic and coastal waters for microzooplankton, or the 50–100 nauplii/L range for coastal and estuarine areas (see Houde 1978; Hunter 1981 for summaries). The addition of copepodite stages and other potential prey items to the naupliar abundances in this study would increase the estimates of available prey somewhat but usually not more than 20%. At least during the wintertime, the waters surrounding the Mississippi River delta do not appear to contain exceptionally high concentrations of copepod nauplii, compared to other coastal and estuarine areas.

The vertical distribution of nauplii was frequently similar to that of chlorophyll. Regressions of naupliar concentration on chlorophyll concentration were significant for 4 of the 5 cruises although not the same in each case. Assuming chlorophyll is a reasonable indicator of phytoplankton abundance and thus food abundance for nauplii, then nauplii appear to be aggregated at the depth of highest food availability. Year to year variability in the relationship indicates that other factors are also important in determining the abundance and distribution of nauplii. Because eggs released from adult female copepods would sink out of the surface water before hatching, it is probable that active swimming by nauplii plays a part in the aggregation process, perhaps enchanced by physical convergence processes.

In our study we noted that there were interannual differences in naupliar concentrations, there were sometimes significant regional differences, and there were sometimes significant onshore-offshore differences. Although we anticipated finding higher concentrations of nauplii in the region near the Mississippi River delta, this pattern was not always observed. This finding might indicate that there is not an important difference between the 3 regions as far as larval food availability is concerned. Alternatively, it might indicate that there are subregions within the larger Mississippi River delta region that contain a food environment for fish larvae that allows for enhanced survival and growth, but that we failed

to clearly identify and segregate these regions. The overall region did not always appear significantly better than the other regions because only parts of it are better.

On the continental shelf in the Gulf of Mexico, as in other shelf regions of the United States, the typical pattern is for the water to be vertically well-mixed during the wintertime (Parker 1968). Autumn cooling breaks down the thermal stratification that has existed throughout the summer and allows the isothermal water column to be easily mixed. The major exception to this general pattern in the Gulf of Mexico is the shelf region influenced by the large volume of freshwater runoff from the Mississippi River. During this period, the freshwater influx is of sufficiently large volume (average flow for December to March in 1975 through 1979 was 17,290 $m^3$/second (U.S. Army Engineer District, New Orleans Corps of Engineers, 1980)) to physically stratify the shelf waters hundreds of km downstream from the delta. We suggest that this salinity-induced stratification is a vital component of the recruitment success of Gulf menhaden because it provides an environment in which prey aggregations can occur. It has been suggested that vertical stratification by other small-scale physical phenomena (e.g., Langmuir circulation) allows significant patchiness of prey items to exist (Lasker 1975). This patchiness provides small regions of comparatively high food concentrations for fish larvae, and results in improved feeding success. In this study, copepod nauplii were aggregated vertically at stations with physical stratification and were nearly homogenously distributed at stations lacking physical stratification. Maximum naupliar concentrations (no. per $m^3$) at stratified stations were typically 2–10 times greater than at non-stratified stations.

In conclusion, we believe that the large freshwater inflow of the Mississippi River during the wintertime spawning period of the Gulf menhaden contributes to the feeding success and survival of larval fish by providing physical stratification which in turn results in a vertical stratification of phytoplankton and microzooplankton in layers or patches of relatively high concentrations.

## ACKNOWLEDGMENTS

Part of this work was done in cooperation with personnel from the National Marine Fisheries Service at Beaufort, NC and at Pascagoula, MS. In particular, we would like to thank D. Hoss for providing time and space in his field programs, and J. Govoni for discussion of several portions of the manuscript. S. Cummings, L. Hill, E. Walser, J. White, J. Turner, P. Morgan, C. Neill, and E. Turner assisted in collecting and analyzing samples. Part of this work was done in cooperation with D. Checkley and A. Amos at the University of Texas; their contributions are greatly appreciated. Thanks also to the captains and crews of the F.R.V. *Oregon II*, the RV *Longhorn*, and the *R. J. Russell*. This work was supported by the Louisiana Universities Marine Consortium, by NSF Grant OCE-8119848, and by the Ocean Assessment Division, National Ocean Services, NOAA.

## LITERATURE CITED

ARTHUR, D. K.
1976. Food and feeding of larvae of three fishes occurring in the California Current, *Sardinops sagax*, *Engraulis mordax*, and *Trachurus symmetricus*. Fish. Bull., U.S. 74:517–530.
1977. Distributions, size, and abundance of microcopepods in the California Current system and their possible influence on survival of marine teleost larvae. Fish. Bull., U.S. 75:601–611.

CHECKLEY, D. M., JR.
1982. Selective feeding by Atlantic herring (*Clupea harengus*) larvae on zooplankton in natural assemblages. Mar. Ecol. Prog. Ser. 9:245–253.

DUKA, I. A., AND A. D. GORDINA.
1973. Abundance of ichthyoplankton and feeding of fish larvae in the western Mediterranean and adjacent areas of the Atlantic Ocean. Hydrobiol. J. 9:54–59.

ENVIRONMENTAL PROTECTION AGENCY.
1979. Methods of chemical analysis of water and wastes. Nitrogen, nitrate-nitrate. U.S. Environ. Prot. Agency, Cincinnati, OH 45268.

FORE, P. L.
1970. Oceanic distribution of eggs and larvae of the Gulf menhaden. Rep. Bur. Comm. Fish. Biol. Lab., Beaufort, NC, Fish. Wildl. Serv. Circ. 341.

GAMBLE, J. C., P. MACLACHLAN, N. T. NICHOLL, AND I. G. BAXTER.
1981. Growth and feeding of Atlantic herring larvae reared in large plastic enclosures. Rapp. P.-v. Réun. Cons. int. Explor. Mer 178:121–134.

GOVONI, J. J., A. J. CHESTER, D. E. HOSS, AND P. B. ORTNER.
1985. An observation of episodic feeding and growth of larvae *Leiostomus xanthrus* in the northern Gulf of Mexico. J. Plankton Res. 7:137–146.

GOVONI, J. J., D. E. HOSS, AND A. J. CHESTER.
1983. Comparative feeding of three species of larval fishes in the northern Gulf of Mexico: *Brevoortia patronus*, *Leiostomus xanthrus*, and *Micropogonias undulatus*. Mar. Ecol. Prog. Ser. 13:189–199.

HOUDE, E. D.
1978. Critical food concentrations for larvae of three species of subtropical marine fishes. Bull. Mar. Sci. 28:395–411.

HOUDE, E. D., AND J. A. LOVDAL.
1984. Seasonality of occurrence, foods and food preferences of ichthyoplankton in Biscayne Bay, Florida. Estuarine Coastal Shelf Sci. 18:403–419.

HUNTER, J. R.
1981. Feeding ecology and predation of marine fish larvae. *In* R. Lasker (editor), Marine fish larvae. Morphology, ecology, and relation to fisheries, p. 34–77. Univ. Wash. Press, Seattle.

LAURENCE, G. C.
1974. Growth and survival of haddock (*Melanogrammus aeglefinus*) larvae in relation to planktonic prey concentration. J. Fish. Res. Board Can. 31:1414–1419.

LASKER, R.
1975. Field criteria for survival of anchovy larvae: The relation between inshore chlorophyll maximum layers and successful first feeding. Fish. Bull., U.S. 73:453–462.
1978. The relation between oceanographic conditions and larval anchovy food in the California Current: Identification of factors contributing to recruitment failure. Rapp. P.-v. Réun. Cons. int. Explor. Mer 173:212–230.

LEWIS, R. M., AND C. M. ROTHMAYR.
1981. Spawning and sexual maturity of gulf menhaden, *Brevoortia patronus*. Fish. Bull., U.S. 78:947–951.

PARKER, C. A.
1968. The effect of a cold air outbreak on the continental shelf waters of the northwestern Gulf of Mexico. Tech. Rep. 68-3T, 89 p. Off. Nav. Res.

STOECKER, D. K., AND J. J. GOVONI.
1984. Food selection by young larval gulf menhaden (*Brevoortia patronus*). Mar. Biol. 80:299–306.

STRICKLAND, J. D. H., AND T. R. PARSONS.
1968. A practical handbook of seawater analysis. Bull. Fish. Res. Board Can. 167, p. 201–203.

U.S. DEPARTMENT OF COMMERCE.
1983. Fisheries Statistics for the United States, 1982.

U.S. ARMY ENGINEER DISTRICT, NEW ORLEANS CORPS OF ENGINEERS.
1980. Stages and discharges of the Mississippi River and its tributaries and other watersheds in the New Orleans District, 1975–1979.

WARLEN, S. M.
1988. Age and growth of larval menhaden, *Brevoortia patronus*, in the northern Gulf of Mexico. Fish. Bull., U.S. 86:77–90.

WIEBE, P. H., K. H. BURT, S. H. BOYD, AND A. W. MORTON.
1976. A multiple opening/closing net and environmental sensing system for sampling zooplankton. J. Mar. Res. 34:313–326.