VERTICAL STRUCTURE OF NEARSHORE PLANKTON OFF SOUTHERN CALIFORNIA: A STORM AND A LARVAL FISH FOOD WEB

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ABSTRACT

Samples of zooplankton and phytoplankton were taken at 5 m depth intervals in the upper 50 m of water off Dana Point, California, in the spring of 1980, just before and just after a local storm. Most of the 43 zooplanktonic taxa, many phytoplanktonic taxa, and chlorophyll were vertically stratified. After the storm, naupliar copepods, chlorophyll, and a few phytoplanktonic taxa were more abundant, and several zooplanktonic taxa were more concentrated in the upper layers. The storm did not decrease the vertical stratification of larval fish food, so the feeding environment after the storm was at least as favorable as that before the storm, but larval fish were less abundant.

Studies in the laboratory have provided data on the kinds and abundances of food which are required for survival and growth of some types of zooplankton found in the surface waters of the Southern California Bight (e.g., Mullin and Brooks 1970; Paffenhöfer 1976) and of the larvae of the anchovy, *Engraulis mordax*, (e.g., Hunter 1976; Lasker et al. 1970) and jack mackerel, *Trachurus symmetricus*, (Devonald 1983). The anchovy has overwhelmingly dominated the larval fish assemblage of the area in recent years (e.g., Gruber et al. 1982). Direct experimentation (Lasker 1975) and indirect comparison of metabolic requirements and observed concentrations of likely food (Mullin and Brooks 1976; Cox et al. 1983) have shown examples of situations where only in layers or patches of anomalously high concentration of food can larval fish or copepods obtain enough nutrition to grow. Field data on vertical distributions indicate that extensive, sharply defined layers with elevated abundances of phytoplankton often exist within the euphotic zone (e.g., Cullen and Eppley 1981, for chlorophyll; Kiefer and Lasker 1975, for *Gymnodinium splendens*; Cullen et al. 1982, for several species).

There is also more indirect evidence of the importance of unusually rich layers of food for the survival and growth of planktonic predators: The greater size of "wild" copepods relative to those raised in the laboratory (Mullin and Brooks 1970),

the limitation of egg production of a copepod population (Checkley 1980b), and the failure of year classes of anchovy when storms or upwelling were thought to disrupt layers of food (Lasker 1981). However, direct field evidence concerning starvation or growth limitation by food of larval anchovy is both limited and contradictory (Arthur 1976; Methot and Kramer 1979; O'Connell 1980).

The population of the large copepod, *Calanus pacificus*, is sometimes concentrated in those layers where autotrophic phytoplankton is most abundant (Mullin and Brooks 1972, 1976). However, there also are cases where no such correlations were found (Mullin and Brooks[2]) or where *Calanus* and other herbivores actively avoided a layer of abundant dinoflagellates (Fiedler 1982), and where feeding in such a layer was depressed relative to other parts of the water column (Fiedler 1982; Huntley 1982). In the present study, we examined the vertical relations between several zooplanktonic taxa and chlorophyll, a measure of the autotrophic, phytoplanktonic biomass. Since the nutrition of zooplankton governs growth and fecundity, the vertical relations between zooplankters and their food can affect the future supply of food for fish if the zooplankton is food-limited.

Small-bodied species of zooplankton (or larval stages of larger species), some large-celled, nonthecate dinoflagellates, and protozoans were of particular interest as representing potential lar-

val fish food. Larger zooplankters represent potential competitors with larval fish for dinoflagellate and protozoan prey, or even potential predators of the larvae themselves.

The vertical distribution of larval anchovy within the euphotic zone is less well known than is that of zooplankton, particularly with respect to the vertical distribution of their food sampled concurrently, because larval fish are so rare that nets with large capacity must be used to capture significant numbers of them. It was partly to provide such data that we conducted the present study concurrently with sampling by National Marine Fisheries Service personnel from a second vessel to determine the vertical distribution of larval fish. Records of water temperature, concentration of chlorophyll, and abundances of phytoplankton at the depth of the chlorophyll maximum were also taken from the second vessel, and are compared with our results below.

We were fortunate, intellectually if not physically, to sample a fixed location before and after passage of a local storm (cf. Lasker 1975), and we therefore tried to examine the potential importance for the food web of turbulent rearrangement of vertical distributions. We looked for changes coincident with the storm in overall abundances and in the intensity and patterns of vertical stratification of many planktonic taxa, and in correlations between the vertical distributions of predators and their potential prey. We then made predictions concerning the implications of these changes for the nutrition of larval fish.

METHODS

From mid-March to mid-April 1980, spawning of anchovy was concentrated in the inner portions of the Southern California Bight, apparently confined by plumes of cool water extending south of Point Conception beyond Santa Catalina and San Clemente Islands (Lasker et al. 1981). Between 29 March and 6 April, we took 13 vertical series of samples at 5 m intervals in the upper 50 m of water at lat. 33°28.5'N, long. 117°46.7'W (CalCOFI station 90.28, 3.5 km offshore from Dana Point, California), where the depth of water was ~350 m, using the pump and hose described by Mullin and Brooks (1976) and Mullin (1979). Almost all of the larval anchovy at this station occurred in the upper 40 m (Pommeranz[3]). Because of the re-

stricted area of the anchovy's spawning at the time, our results may be indicative of conditions experienced by a considerable fraction of the larvae produced in late March-early April in the Bight. The volume of water filtered per quantitative sample of zooplankton was typically 200-300 l; for comparison, the rate at which a 1.5 cm larval anchovy searches water for food is about 5 l/h (Hunter 1972). In addition to quantitative, net-concentrated samples of zooplankton and fiberglass-filter concentrated samples of chlorophyll, we preserved unconcentrated samples of water in 5% v:v Formalin[4] for counts of phytoplankton, and filtered nonquantitative samples of net-caught zooplankters onto fiberglass filters which were then frozen for later analysis of plant pigments in the guts.

One profile was completed during 0900-1400 h and another during 2030-0030 h each 24-h day except from 0000 on 1 April to 0900 on 3 April, when a local storm kept us in port. Profiles 1-6 were "prestorm", 7-13 "poststorm".

Analytical procedures for chlorophyll and net-caught zooplankton followed Mullin and Brooks (1976) and Mullin (1979). All recognizable zooplankters were enumerated. For phytoplankton and protozoans, we prepared a physically integrated sample for each profile by mixing 50 ml of water taken from each of the 11 depths. Fifty ml of this integrated sample were settled for 48 h, and cells were counted using the Utermöhl method. For cells ~20 μm or greater (equivalent spherical diameter), half the settled material was counted at 160× magnification (equivalent to a 25 ml sample); for cells <20 μm, one row across the diameter of the settling chamber was studied at 625× magnification (0.33 ml).

Subsequently, 50 ml aliquots from each depth for each profile were settled at least 24 h and examined. Since the flora was very diverse, we selected a short list of taxa using the following criteria: Cells were clearly identifiable even after preservation in Formalin, present in sufficient numbers to provide reliable data, and (with several exceptions) of interest as possible larval fish food. We believe that all taxa usable as food were satisfactorily preserved and counted. Most of the cells were counted using 160× magnification, usually in an equivalent of a 12.5, 25, or 50 ml sample. *Chaetoceros* spp., *Nitzschia* spp., and *Emiliania* (*Coccolithus*) *huxleyi* were enumerated

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[3]Tilman Pommeranz, Institut für Meereskunde, Kiel, West Germany, pers. commun. 1984.

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

at 250×, usually in one or two rows across the settling chamber (1.13 or 2.3 ml). A precipitate developed in certain samples after several months storage, so profiles 1, 2, 8, and 12 could not be included in the analysis based on discrete depths; profile 13 was also excluded in order to balance the data.

To measure the amount of plant pigments in the guts of selected zooplanktonic taxa, we used an approach similar to that of Mackas and Bohrer (1976). In a darkened room, the frozen contents of each fiberglass filter were washed onto a circle of Nitex mesh (180 μm) and then sucked dry. The mesh disk was transferred to a Petri dish, wetted, and then examined visually using low magnification and low-intensity green light. Organisms were removed singly from each mesh, dipped in filtered seawater, and then sorted into scintillation vials sitting in an ice bath and containing small amounts of 90% reagent grade acetone.

After obtaining enough organisms, we inspected the contents of each vial visually to insure that they were taxonomically homogeneous and to record the number of individuals present. The contents were then homogenized with a motor-driven teflon pestle in a glass grinding vessel to which $MgCO_3$ and acetone were added. The homogenate was transferred by several rinses to a 15 ml screw-cap test tube and the volume was adjusted to 10 ml. All test tubes were stored in a light-tight container in a refrigerator for ~1 h, after which the homogenates were given an additional half hour to extract and to warm to room temperature.

The homogenate from each tube was first mixed and then filtered through a fiberglass filter to remove the $MgCO_3$ and animal tissue/exoskeleton. The amounts of chlorophyll a and phaeopigments in the filtrate were determined fluorometrically (Holm-Hansen et al. 1965) using a Turner Model 111 fluorometer equipped with a high-sensitivity door.

In order to evaluate the method, we collected copepods by oblique net hauls over the Scripps Canyon (~2 km from shore), sorted them, and placed them in filtered seawater to starve for 18-24 h. On other occasions copepods were similarly collected, starved to void their guts, and then allowed to become satiated on mixtures of cultured phytoplankton. All animals were frozen before pigment extraction.

To assess (ex post facto) whether preservation of pigments by freezing was complete, we took oblique net tows (total duration ~2 h) over Scripps Canyon. Each net haul was immediately strained

through pieces of Nitex (<100 μm) netting and then quick-frozen using dry ice. Twelve samples thus obtained were stored in the same freezer as the cruise samples and processed in a similar manner. One sample (T_0) was processed the same day, the other samples at various times thereafter up to 700 d. We were unable to detect a decrease in total pigments over this time period by linear regression, and therefore believe the freezing to be adequate.

The first group of hypotheses we wished to test concerned temporal changes in patterns of vertical distribution. One general procedure was to treat several samples of one kind (e.g., all diurnal samples from a particular depth before the storm) as replicates accounting for variability due to technique and to real patchiness, and then to look for significant differences through an analysis of variance (ANOVA) on log-transformed abundances. Details are in Table 1. This was done for those taxa for which the variances (of log-transformed data) were homogeneous by Bartlett's and/or Cochran's tests (Dixon and Massey 1957). Where the variances were heterogeneous (i.e., $P < 0.01$ of homogeneity), we tested analogous hypotheses through nonparametric tests, as indicated in Table 2. Taxa for which it was necessary to employ the battery of nonparametric tests are indicated by asterisks in the Appendix.

A second group of hypotheses concerned correlations between measured properties, such as the concentration of chlorophyll and the abundance of a particular taxon. These hypotheses were tested by nonparametric correlation or concordance tests; details are in Section C below. We also tested for changes in overall community composition by constructing dendrograms based on rank difference correlation coefficients. All nonparametric tests are from Tate and Clelland (1957).

RESULTS

The overall abundances and vertical distributions of 43 zooplanktonic and 18 phytoplanktonic and protozoan taxa in the upper 50 m are shown in the Appendix, based on median abundances for diurnal and nocturnal profiles, before and after the storm, together with the distributions of chlorophyll. Depending on dietary preferences of the visually feeding larval anchovy (e.g., Arthur 1976), some combination of the diurnal distributions of several taxa represents the "typical" vertical distribution of larval fish food (see Section D below). We will discuss results in the following

TABLE 1.—Three-way analysis of variance on log-transformed abundances (m^{-3}) (see Appendix). To balance the sampling design, the 13th profile for zooplankton and chlorophyll (6 April) was omitted from the analysis. A significance level of $P < 0.01$ was used to compensate for multiple testing of the same hypotheses for many taxa.

Classification of sample	Significance of ANOVA probably indicates:
1. Day vs. night	Taxon migrated dielly from below 50 m into sampled range. Diel variation in avoidance of hose intake would create spurious significance. For very short-lived taxa, strong diel variation in birth, death, or maturation could also cause significant differences.
2. Before vs. after storm	Taxon changed in mean abundance coincident with storm. Cannot distinguish advective from biological causes.
3. Depth	Taxon was nonuniformly distributed 0-50 m in a consistent manner (or avoidance varied with depth).
Interaction 1 × 2	Taxon migrated dielly into sampled range from below 50 m before or after storm, but not both.
Interaction 1 × 3	Taxon had some kind of diel migration. If classification 1 was not significant, migration occurred within upper 50 m. Variation in avoidance both dielly and with depth could create spurious significance.
Interaction 2 × 3	Depth distribution of taxon changed coincident with storm. Change could either result in greater or lesser uniformity with depth or a change in depth of the maximum.
Interaction 1 × 2 × 3	Pattern of diel migration of taxon changed coincident with storm.

TABLE 2.—Questions, hypotheses, and nonparametric statistical tests for taxa with heterogeneous variances (designated by asterisks in Appendix). A significance level of $P < 0.01$ was used to compensate for multiple testing.

Question	Null hypothesis (H_0)	Test and comments
1. What taxa migrated dielly from below 50 m into the sampled range?	No difference in abundance (m^{-2}), day vs. night.	Mann-Whitney U test for difference in median abundances (m^{-2}) of each taxon, day vs. night. Compare to ANOVA classification 1.
2. What taxa migrated dielly within the upper 50 m?	No difference in depth of median animal, day vs. night.	For each taxon for which H_0 1 is accepted, Mann-Whitney U test for difference in depth of median animal, day vs. night. Compare to ANOVA interaction 1 × 3.
3. What taxa changed in abundance coincident with the storm?	No difference in abundance (m^{-2}) before vs. after storm.	For each taxon for which H_0 1 is accepted, Mann-Whitney U test for difference in median abundances (m^{-2}), 29 March-1 April profiles vs. 3-6 April profiles. Compare to ANOVA classification 2.
4. What taxa became more or less uniform in vertical distribution following the storm?	No difference in range of abundances (m^{-3}) 0-50 m.	For each taxon for which H_0 1 is accepted, short-cut F test on ranges in median profiles (Appendix). Compare to ANOVA interaction 2 × 3.
5. Did community structure change coincident with the storm?	No relation between strength of rank correlation between two profiles and timing of these profiles with respect to the storm.	From abundances (m^{-2}) of each taxon in each profile, profiles are grouped by dendrogram based on rank correlation coefficients of abundances.

categories: A. Zooplankton; B. Phytoplankton and protozoa; C. Relations between zooplankton and phytoplankton; and D. Food for larval fish.

Figure 1 shows that the storm was not remarkable in the wind records from San Diego, but was quite apparent in the winds at San Clemente Island and in records of wave height at La Jolla and Oceanside. The generally lower wind speed and greater variability in speed and direction within each day at San Diego than at San Clemente Island are general phenomena (Dorman 1982). The wind at San Diego is probably more typical of the actual wind off Dana Point, while the San Clemente winds are more typical of the offshore condition generating the swell arriving there. Since the energy appearing as wind-induced turbulence increases as the cube of the wind speed, a

doubling of wind speed increases turbulent energy eightfold.

Following the storm, surface temperatures and the thermal gradient in the upper 30 m were reduced at the sampling location off Dana Point, though the change in thermal gradient was not apparent until more than a day after the storm, and water temperatures at La Jolla were higher after the storm (Fig. 1). Minimal thermal gradients in the upper 30 m were also observed by the second vessel working at Dana Point on the night of 4-5 April. Though there was pronounced day-to-day variation in depths of isotherms, isotherms tended to be shoaler after the storm. For example, the poststorm median depths of 12°, 13°, and 14°C isotherms all were shoaler by 4.7-5.9 m than were the prestorm median depths (Pommeranz foot-
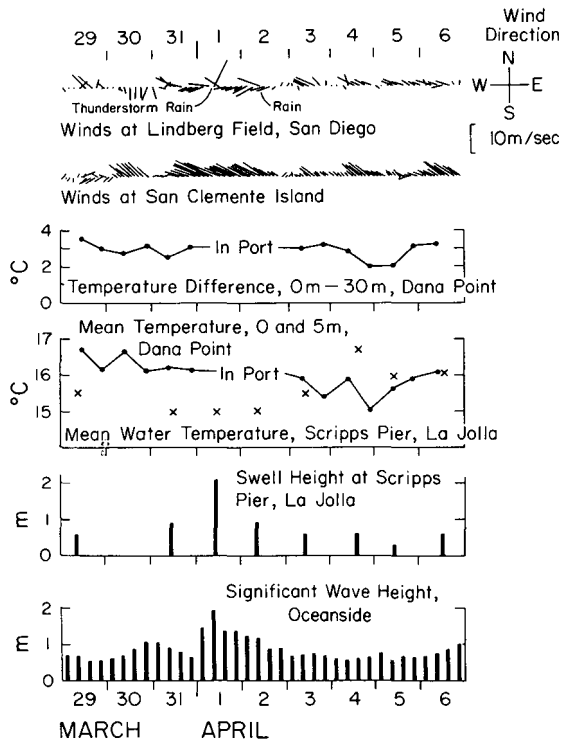
FIGURE 1.—Winds, water temperature, temperature gradient, and wave height at Southern California locations during this study. For temperature, dots are Dana Point, x's are La Jolla. Wind direction is the direction from which the wind is blowing.

note 3), and these differences were each significant by rank sum test ($P \leq 0.05$). This is not what one would expect from simple mixing, in which the nearsurface isotherms should shoal and the deeper isotherms deepen.

A. Zooplanktonic Taxa and Community Structure

We examined statistically the data on zooplankton summarized in the Appendix for answers to several questions concerning temporal changes in the distributions, using the ANOVA or nonparametric tests summarized in Tables 1 and 2. Daytime vertical distributions of many of these taxa off Southern California in late spring and fall are given by Fiedler (1983). As noted in the tables, there are potential ambiguities in the interpretation of even statistically significant results, such as the difficulty in distinguishing diel migration of a zooplanktonic taxon from a diel variation in its capability to avoid capture by the pump. More serious, and applicable to phytoplankton as well as

zooplankton, is the impossibility of distinguishing between 1) biological changes caused directly by the storm (such as vertical redistribution, changes in behavior, or changes in the balance between birth and death of a taxon) and 2) storm-driven advection into the area of water with planktonic populations differing in abundances or behavior from those present prior to the storm, but neither the original nor the replacement populations having themselves changed in these properties. Advection undoubtedly occurred before, during, and after the storm; the issue is whether biologically caused changes associated with the storm occurred as well.

1. Diel Vertical Migrations

Based on results from ANOVA classification 1 (Table 1) or nonparametric Test 1 (Table 2), the taxa migrating into the upper 50 m from deeper water at night were the copepodites and adults of *Pleuromamma* and *Metridia*. These are real migrations, since sampling the water column of the Southern California Bight to greater depths reveals a change in depth of maximal abundance from below 100 m by day to within the upper 50 m at night (Esterly 1912; Enright 1977; Brooks and Mullin 1983). Euphausiid furcilia were also more abundant at night than by day.

Of the remaining zooplanktonic taxa (which did not have significant diel variation in total abundance within the upper 50 m), the populations of female, CV, and CIII *Calanus*, euphausiid calyptopes, and cyphonautes larvae were centered significantly higher at night than by day in the water column. Again, these results are consistent with results of sampling to greater depths in nearby waters (Esterly 1912; Enright and Honegger 1977; Mullin 1979; Brooks and Mullin 1983). Other taxa probably belonging to this category of behavior are adult *Rhincalanus* and *Eucalanus* (numbers too small for reliability). Curiously, when temporal changes are removed from the analysis (ANOVA classification 3 (Table 1)), female and CV *Calanus* and adult *Rhincalanus*, *Eucalanus*, and *Metridia* tend to be uniformly distributed in the upper 50 m.

2. Changes Following the Storm

Several taxa were significantly different in abundance following the passage of the storm [ANOVA classification 2 (Table 1) or nonparametric Test 3 (Table 2)], and most of these were larval

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forms. *Acartia*, *"Paracalanus"*, and "other" nauplii were significantly more abundant in 3-6 April samples than in the prestorm set (Fig. 2), while the abundance of larval fish in our samples decreased, as did that of adult and copepodid *Oithona*. An increase in abundance of appendicularians was almost significant. From the point of view of a larval or young juvenile fish, there were more items of desirable food (copepod nauplii and fewer siblings after the storm. No change was detected in those taxa (adult *Labidocera* and

Corycaeus, chaetognaths) likely to be important zooplanktonic predators on larval anchovy.

Some of these changes appear to be continuations of trends evident before the storm (Fig. 2). However, the fact that larval copepods of several types were more abundant following the storm suggests that the storm directly or indirectly stimulated reproductive activity, though stimulation of hatching of benthic eggs (cf. Uye and Fleminger 1976; Landry 1978) or advection of populations from an area of greater fecundity
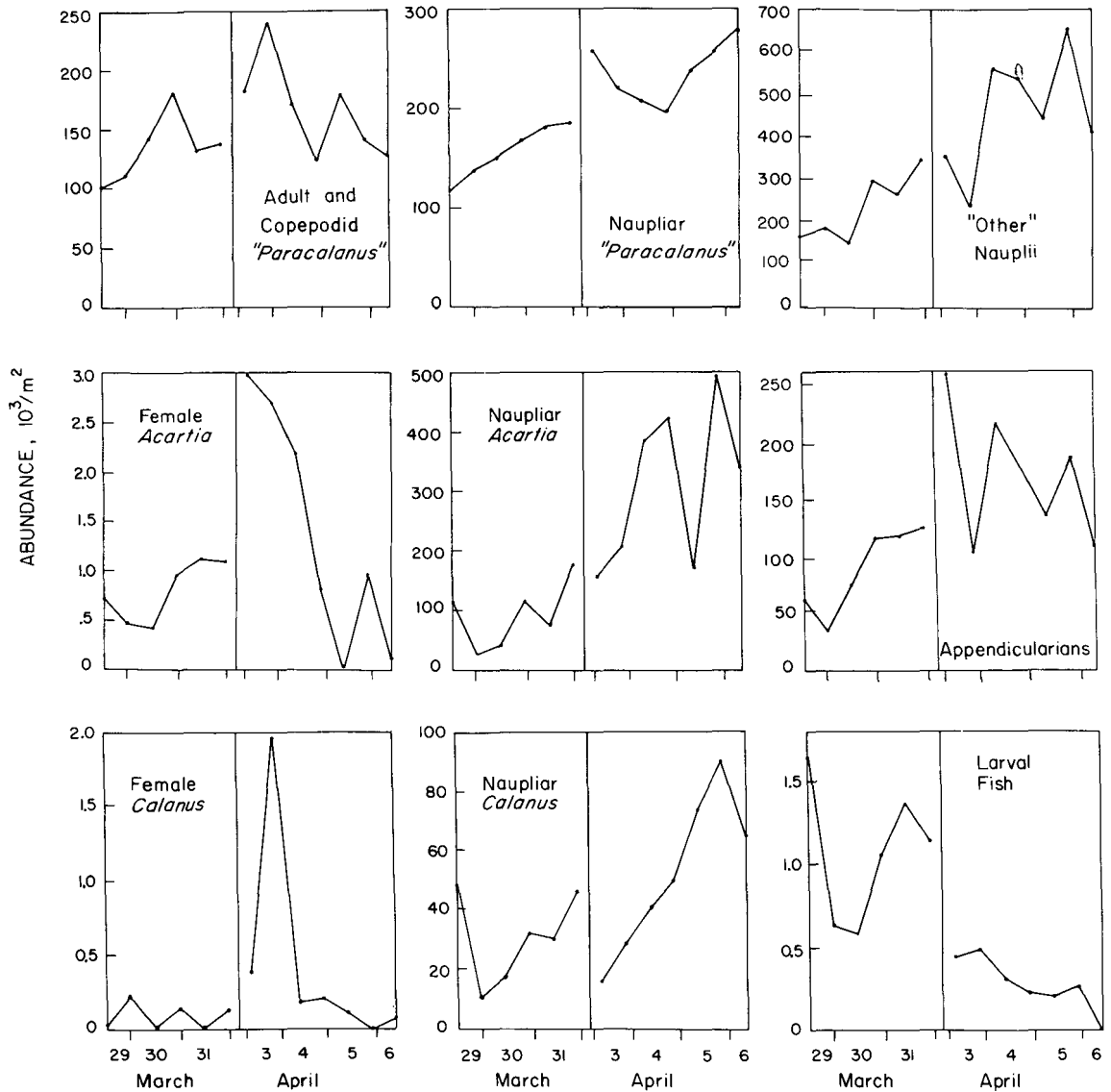

FIGURE 2.—Temporal change in total abundance (m^{-2}) of selected zooplanktonic taxa. The vertical line in each panel separates "prestorm" on the left from "poststorm" on the right. *"Paracalanus"* includes some *Clausocalanus* spp.

would give the same result. Given the naupliar life span of a few days, one would expect that, if reproduction were responsible, the ratio of nauplii to adults would continue to increase for the 3 d following the storm (though such a finding would not rule out advection). This is most readily tested for *Acartia* (nauplii/female) and *"Paracalanus"* (nauplii/adults and copepodites), since the older stages remained within the 0-50 m water column day and night (ANOVA classification 1 not significant). The ratio, nauplii/female, for *Acartia* increased dramatically; indeed, so much so that published values of maximal fecundity (50 eggs/female per day, Landry 1978; Uye 1981) are barely sufficient over the 5-d period including the storm (1-5 April) to account for the observed ratio on 6 April, even if no death or metamorphosis of nauplii occurred. This is because female *Acartia*, though unusually abundant immediately after the storm on 3 April, declined dramatically from that time until 6 April (Fig. 2). For *"Paracalanus"*, which has approximately the same maximal fecundity as *Acartia* (Checkley 1980a), the ratio of nauplii to copepodites plus adults was slightly greater on 6 April than during the preceding 2.5 d. Evidence that the capacity of the environment to sustain reproduction of *"Paracalanus"* increased after the storm is presented in Section C below. Hence, the results are qualitatively consistent with the hypothesis that the storm stimulated reproduction, especially in *Acartia;* but other explanations cannot be ruled out. It is noteworthy, however, that no "exotic" taxa appeared after the storm.

Significance of ANOVA interaction 1 × 2 indicated that for two taxa (euphausiid furcilia and CV *Calanus*), the tendency to be more abundant in the upper 50 m at night than by day was more pronounced before the storm. Another migratory taxon—cyphonautes larvae—showed both a change in average depth distribution within the upper 50 m and a change in pattern of diel migration (significance in ANOVA interactions 2 × 3 and 1 × 2 × 3). The nighttime distributions of cyphonautes larvae were similar before and after the storm, but the daytime distribution was shifted to shallower water after the storm; adult *Corycaeus* showed the same (but nonsignificant) tendency, though they did not have a significant diel migration over the whole period (cf., evidence for a reverse migration by this species off Southern California in Fiedler 1983). *Pleuromamma* was virtually absent from the upper 50 m during the day both before and after the storm, but at night

tended to occur shallower within this layer after the storm.

Diel migration was not detected in *Calanus* CII and CIII copepodites (ANOVA interaction 1 × 3 not significant), nor did they change significantly in total abundance after the storm (ANOVA classification 2 not significant). There was, however, a shoaling of the distributions of both stages both day and night after the storm (ANOVA interaction 2 × 3 significant). Larval fish were also shallower in our samples by day after the storm.

The vertical distributions of these three taxa were still stratified after the storm but were shifted with respect to depth. Another potential effect of the storm, which could also result in significance of ANOVA interaction 2 × 3, is homogenization of strongly stratified distributions into more nearly uniform ones. Reduction of the temperature gradient (Fig. 1) reinforces this possibility. The reverse process—an increase in stratification—is possible as a result of biological responses to the physical disturbance. Test 4 is a simple way to examine this question, though it is insufficient to detect some possible complex redistributions. The results of this test were contrary to expectation; only 2 taxa, *Labidocera* nauplii and copepodites, had greater ranges of abundance in the water column before the storm, while 13 taxa had greater ranges after the storm. Included in the latter group were *Acartia* and "other" nauplii, both of which increased in overall abundance after the storm, and all five juvenile copepodid stages of *Calanus*. Thus, as far as the zooplankton is concerned, poststorm stratification was generally more marked than that prestorm. It may be of significance, however, that the two taxa whose prestorm abundances were more strongly stratified than in the poststorm condition were taxa with strong neustonic (nearsurface) affinities (Barnett 1974; Appendix).

Inspection of the data (see Appendix) revealed several other taxa which appeared to have distributional changes of the sorts described above, though these were not significant by the criteria used in the statistical tests. This means that other sources of variability in abundance—notably, horizontal patchiness on the scales of a few kilometers, or vertical internal motions creating high variability at a fixed depth from day to day as water passed the sampling location—were more important than were those patterns of change the statistical tests were chosen to detect.

Finally, we can examine the overall similarities in the zooplanktonic community of the upper 50 m

(as abundances m^{-2}), excluding those taxa which significantly changed in total abundance in this layer from day to night. The weighted-pair dendrogram of Spearman's rank difference correlation coefficients (Fig. 3A) shows an imperfect separation into profiles taken before and after the storm, the first poststorm profile (#7) being more like those before the storm. This is evidence against the hypothesis that physical advection of new populations caused all the poststorm differences, though it is also possible that advection caused by the storm affected our site only after a delay. The storm's apparent effect on the thermal gradient (Fig. 1) was also delayed for some time. Even with some of the migrating taxa excluded, there is a partial separation in the dendrogram of nocturnal from diurnal profiles.

FIGURE 3.—Dendrograms of faunal (A) and floral (B) similarities of the upper 50 m of water off Dana Point, Calif. Faunal assemblages are based on 39 taxa, floral assemblages on 126 taxa (not just those listed in Appendix). "Floral" includes protozoans. All coefficients are significant at $P < 0.001$.

B. Chlorophyll, Phytoplankton, and Protozoa

Because of the mechanisms of feeding used to separate small particles of food from water, there are probably no strict herbivores among the zooplankton we studied, i.e., no animals which ingest living phytoplankton without also ingesting other

particulate organic matter. Nevertheless, we used the distribution of chlorophyll (see Appendix) as the measure of the distribution of food for particle-grazing species; in the euphotic zone of the Southern California Bight, the concentration of chlorophyll is closely correlated with that of particulate organic carbon, with particulate ATP, and (within any one season) with the chlorophyll in particles >5 μm (Mullin and Brooks 1976; Eppley et al. 1977; Mullin 1979).

We had adequate data to answer Questions 1-4 from Table 2 for chlorophyll (= "taxon"). We used the phytoplanktonic and protozoan abundances from the physically integrated samples for all 13 profiles (see Methods) to perform Tests 1, 3, and 5 concerning the whole 50 m water column. We restricted Questions 2 and 4 to the upper 40 m (since these taxa were rare below this depth) and used data from five diurnal and three nocturnal profiles in answering these questions, since only those profiles were suitable for counting (see Methods). Only one of the nocturnal profiles was poststorm. In order to obtain estimates of "within classification" variability and still maintain a balanced design, we reduced the ANOVA to a two-way design, retaining "before vs. after storm" and "depth" as classifications. Thus, diurnal and nocturnal samples were considered replicates (there was no evidence of diel migration in the phytoplanktonic taxa). We again restricted the analysis to the upper 40 m. Variances of log-transformed data for these taxa were all homogeneous in the four profile data set (profiles 5, 6, 9, and 10). Thus we applied the ANOVA to a subset of those profiles suitable for nonparametric tests.

The concentration of chlorophyll per m^2 did not change from day to night (H_0 1 accepted), nor did the vertical distribution of chlorophyll within the upper 50 m change from day to night (H_0 2 accepted). The median chlorophyll concentration (m^{-2}) was greater after the storm, but not significantly so by Test 3. Vertical profiles of in vivo fluorescence of chlorophyll and samples of phytoplankton from the fluorescence maximum layer (cf. Kiefer and Lasker 1975; Cullen et al. 1982) were taken from the second ship working concurrently at Dana Point. Comparison of the integrated fluorescence profiles indicated that this measure of chlorophyll increased significantly after the storm ($P < 0.01$ by a variant of Test 3).

Inspection of the data (see Appendix) indicated a shoaling of the chlorophyll maximum layer after the storm, and this was significant by a Mann-Whitney U test for differences in depth of occur-

rence of the median value before vs. after the storm. This tendency was also shown by isotherms (see above). The range of concentrations of chlorophyll in the water column tended to increase, meaning that chlorophyll maxima were accentuated after the storm, though hypothesis 4, based on the median profiles, was not rejected ($0.01 < P < 0.025$).

No phytoplanktonic or protozoan taxa we examined migrated dielly into and out of the upper 50 m nor did any taxon migrate dielly within the upper 40 m. The two-way ANOVA of four profiles detected significant decreases in poststorm abundances of the diatoms *Nitzschia* spp., *Bacteriastrum* spp., *Rh. alata*, and *Rh. fragilissima*; all but the last of these decreases were also significant by nonparametric Test 3 applied to the full 13-member set of integrated profiles. This latter test also revealed a significant decrease in poststorm abundance of another diatom, *S. costatum*. Only the dinoflagellate, *Prorocentrum*, was more abundant after the storm by the ANOVA test. When the data set of 13 integrated profiles was examined by nonparametric Test 3, significant increases were also detected in the poststorm abundance of *Lohmanniella* (a potential larval fish food) and *Ceratium* spp. Neither *Gymnodinium splendens* nor *Cochlodinium catenatum* (two potential food items for larval anchovy) changed significantly in abundance in samples taken at the depth of the fluorescence maximum layer from the second vessel. The large diatom category, *Chaetoceros* spp., did not change in total abundance, but the species comprising this category changed at the time of the storm; in particular, *Ch. constrictus* was the dominant member of the genus after the storm, but was not encountered in the prestorm samples.

From the ANOVA, no phytoplanktonic taxa had poststorm vertical distributions different from their prestorm ones, when the criterion of $P \le 0.01$ was used for significance, and only *Rh. alata* and *Prorocentrum* had significant changes as defined by $P \le 0.05$. Hence, as far as we could tell from the four profiles which were usable in the ANOVA, the storm had much less effect in changing the vertical distributions of specific phytoplankters (and protozoans) than it did for zooplankton. This conclusion is, however, suspect (see below).

Nonparametric Test 4, for which eight profiles were usable, indicated that the poststorm range of abundances in the upper 40 m was greater than the prestorm range for five of the dinoflagellate taxa, *Mesodinium rubrum*, and *Lohmanniella*, while *Nitzschia*, *Rh. fragilissima*, and *S. costatum*

had significantly smaller poststorm ranges. These eight profiles strongly suggested poststorm shoaling of the vertical distributions of the potential food species, *C. catenatum*, *G. splendens*, and *Laboea*, but the data sets were too small to establish statistical significance at $P \le 0.01$.

The general changes associated with the storm were therefore decreases in the abundances and in the degree of stratification of some diatoms, and increases in abundances and degree of stratification of some dinoflagellates and protozoans. However, significant changes in the pattern of stratification with depth were more difficult to detect because of the reduced data sets, except for the shoaling of the distribution of chlorophyll.

The floral composition of the profiles permitted a clear separation into prestorm and poststorm assemblages, with the exception of the last prestorm profile, which was quite different from the others (Fig. 3B). This result was different from the analysis of zooplankton (Fig. 3A), where the first poststorm profile was unexpectedly grouped with prestorm profiles. Both results, however, indicate that the compositional changes associated with the storm were gradual rather than abrupt. Unlike the faunal assemblages, the floral grouping showed no tendency to separate day from night. The difference in correlation coefficients between dendrograms A and B probably reflects the fact that quite different numbers of taxa were counted, and that samples were counted by different techniques, rather than any fundamental distinction between phytoplanktonic and zooplanktonic assemblages.

C. Relations Between Zooplankton and Phytoplanktonic Biomass

If positive correlations between the abundances of particle-grazing zooplanktonic taxa and chlorophyll existed before the storm, it is reasonable to hypothesize that such correlations would be weaker or nonexistent after the storm due to turbulent disruption of associations.

We examined the following taxa of zooplankton in this regard, sometimes combining categories from the Appendix: Naupliar *Acartia*, naupliar *Calanus*, naupliar *"Paracalanus"*, copepodid and adult *Acartia*, CI-CIV *Calanus*, CV and female *Calanus* (nocturnal only), copepodid and adult *"Paracalanus"*, adult *Metridia* (nocturnal only), adult *Pleuromamma* (nocturnal only), and the appendicularians. We grouped data into four sets of profiles: three diurnal, prestorm; three noc-

turnal, prestorm; three diurnal, poststorm (excluding the 6 April profile); and three nocturnal, poststorm. In order to give each profile within a set equal weight and to restrict attention to vertical relations, we arranged data from each profile in order of increasing concentration of chlorophyll; next ranked the samples in order of increasing abundance of the taxon of interest; then calculated the Kendall's tau coefficient as a measure of correlation between that taxon and chlorophyll within each profile; and finally calculated the coefficient of concordance between the rearranged ranks of the taxon in the three profiles of a set as a measure of agreement on a common tendency (see Mullin and Brooks 1972). We then defined a persistent relation between a taxon and chlorophyll in one full set of profiles as requiring a significant ($P \leq 0.05$) concordance between the individual profiles of the set, tau coefficients of all profiles of the same sign (positive or negative), and at least one of the tau coefficients significant ($P \leq 0.05$).

No persistently negative relations were found between any taxon and chlorophyll in any set of profiles. In the diurnal, prestorm set, naupliar *Acartia*, naupliar *Calanus*, copepodid and adult *Acartia*, and appendicularians were all positively related to chlorophyll, and CI-CIV *Calanus* tended in this direction. These relations all vanished at night by our criteria, though naupliar *Calanus* tended to retain a positive association. After the storm, the strength of the diurnal, positive relations of naupliar *Acartia,* copepodid and adult *Acartia*, CI-CIV *Calanus*, and appendicularians increased, and naupliar *"Paracalanus"* also had a positive relation. At night after the storm, all taxa except naupliar *"Paracalanus"*, CV and adult *Calanus*, *Metridia*, and *Pleuromamma* had positive relations with chlorophyll. Thus, contrary to expectations, after the storm there were more positive relations between these particle-grazing taxa and the concentration of their food, measured as chlorophyll.

We reached a similar conclusion for the ciliates, *Laboea* and *Lohmanniella*; neither were persistently related to the vertical distribution of chlorophyll before the storm, but both were positively related after the storm by our criteria. Since fewer profiles for these protozoans were counted, we did not separate night from day in searching for the correlations.

Such correlations can also show seasonal variability; for example, Fiedler (1983) found strongly positive correlations between the vertical distributions of chlorophyll, *Paracalanus*, and *Penilia avirostris* (a cladoceran) in October, but strongly negative correlations between these zooplankters and chlorophyll in May; *Ctenocalanus vanus* showed a seasonal reversal of its relation to chlorophyll in the opposite direction.

In spite of the increased correlation after the storm between particle-grazers and their food, there is some evidence that the poststorm grazing pressure on phytoplankton was less than that prestorm. The ratio of chlorophyll to phaeopigments in the water column is an indicator of the ratio of living phytoplankton to the fecal material of grazers, and hence is inversely related to the grazing pressure per unit phytoplanktonic crop (Lorenzen 1967). The chlorophyll/phaeopigment ratio was significantly greater ($P < 0.05$ by rank sum test) after the storm, indicating a reduction in grazing relative to the available crop.

We derived a second indicator of the effect of the storm on relations between phytoplankton and zooplankton from a study of egg production of the copepod, *Paracalanus parvus*, and chlorophyll and particulate nitrogen in the Southern California Bight (Checkley 1980b). Checkley found that the nitrogen in phytoplankton was the best measure of fecundity-stimulating food, that about half the chlorophyll retained on a fiberglass filter was in particles >5 μm, and that the weight ratio of nitrogen in phytoplankton to chlorophyll was 12. From these relations, the egg production of *Paracalanus* is food-limited where the concentration of total chlorophyll is below 1.3 μg/l. By this standard, only 18% of the upper 50 m contained sufficient food for maximal egg production prior to the storm, while 34% of the water column met this criterion afterwards.

This conclusion is likely to be qualitatively correct unless the size distribution of phytoplankton was altered markedly by the storm, or the breadth of the copepods' diet with respect to nonphytoplankton was changed. Neither of these sources of error is particularly likely, since the ratio of >5 μm to total chlorophyll agrees with earlier results in the Bight (Mullin and Brooks 1976) and since the range of the data from which Checkley deduced the importance of chlorophyll in regulating egg production included all but one of the concentrations of chlorophyll we measured.

Further, the vertical distribution of adult and copepodid *"Paracalanus"* was positively correlated with that of chlorophyll after the storm and at night (see above). If this finding applies to female *"Paracalanus"* by themselves, a consider-

ably greater fraction of total reproduction occurred at maximal (i.e., nonfood-limited) rates after the storm.

A similar quantitative example of augmentation of zooplanktonic nutrition related to the storm can be calculated for CIV-adult *Calanus*, though the vertical distribution of these stages was not well correlated with that of chlorophyll. In June 1980, Cox et al. (1983) estimated the carbon budget of *Calanus* at various stations and depths in the Southern California Bight, and concluded that gain in biomass of these copepods was possible where the concentration of chlorophyll exceeded 0.9 $\mu g/l$. By this standard, the fraction of the upper 50 m where some growth was possible (nighttime only, because of diel migration) was 36% before and 58% after the storm.

A third test of the significance of vertical distributions and the effect of the storm on them was based on the plant pigments in the guts of the large copepods caught at various times and depths. The measurement of fluorescence of gut contents can be used as a quantitative estimate of the rate of ingestion of plant material if the breakdown of pigment, the gut passage time, and the background fluorescence due to an animal's own pigmentation are known (Mackas and Bohrer 1976). We chose to ask two simpler questions based on changes in fluorescence: 1) Were the total gut pigments (chlorophyll + phaeopigments) of copepods caught at specific depths correlated with the concentration of chlorophyll measured at the same depths, before or after the storm or both? 2) Did the amount of gut fluorescence of a taxon, independent of specific depths, change coincident with the storm? The first question addresses the issue of whether the copepods can be shown to have fuller guts at depths where phytoplanktonic food (as measured by chlorophyll) is more concentrated. If copepods move frequently from the depths at which they feed, such correlations would be difficult to establish (cf. Dagg and Wyman 1983). The second question is the more general one of whether the copepods were better nourished after the storm.

We tested data concerning female *Acartia*, female and CV *Calanus*, female *Metridia*, and female *Pleuromamma* in this regard, with 6-28 pre- or poststorm data points per taxon. Of these taxa, only *Acartia's* abundance was significantly positively associated with the vertical distribution of chlorophyll (see above).

The gut pigment per *Acartia* showed no relation to the ambient concentration of chlorophyll, however, while that of *Pleuromamma* was positively correlated with chlorophyll. In no case was the poststorm correlation (tau coefficient) between gut fluorescence and chlorophyll stronger than that prestorm. Hence, we could not show that for these taxa the distribution of degree of satiety became more strongly associated with the vertical distribution of chlorophyll after the storm, even though the range of chlorophyll concentrations available in the upper 50 m had increased.

Nor for any of these taxa was the poststorm amount of gut fluorescence significantly greater than that prestorm. Based on comparison between field-caught female *Acartia* and *Calanus*, and these same taxa fed to excess or starved in the laboratory, we conclude that both these populations were well fed in general both before and after the storm, and animals had plant food in their guts at all depths sampled. Hence, we could not demonstrate a change in nutritional status of the taxa as a result of the storm, even though the overall concentration of chlorophyll increased. All these taxa have been shown to feed on nauplii as well as phytoplankton (e.g., Haq 1967; Lonsdale et al. 1979; Landry 1981), but we could not test whether their nutrition from animal sources had improved coincident with the increase in abundance of nauplii following the storm.

D. Abundance and Vertical Distribution of Food for Larval Fish

Because larval fish are visual predators, it is the diurnal distributions of potential prey which are particularly relevant. Different species select (or are physically able to ingest) different prey, and of course different types of prey differ in their catchability, digestibility, and nutritive value. We will consider the distributions of food for two prototypical larvae representing extremes in a continuum of actual types. One is a small-mouthed larva which we will call "anchovy-like", based on Berner (1959), Lasker et al. (1970), O'Connell and Raymond (1970), Arthur (1976), and Lasker and Zweifel (1978). For these larvae, "large" prey consists of all copepod nauplii and lamellibranch and cyphonautes larvae (Appendix); "small" prey consists of all ciliates and all nonthecate, large dinoflagellates. Laboratory studies suggest the critical concentrations for both good survival and rapid growth are $\geq 5 \times 10^3$ large or $\geq 5 \times 10^4$ small prey l^{-1}, or an equivalent combination.

The other prototypical larva has a larger mouth and is more active; based on Arthur (1976), Hunter

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and Kimbrell (1980), Lipskaya (1982), and De- vonald (1983), this larva is "mackerel-like" (though *Scomber* and *Trachurus*, especially the latter, tend to spawn farther offshore than our sampling location). This larva requires a much lower concentration of "large" prey, 50 1^{-1}, and a large number of zooplanktonic taxa are potential food: all copepod nauplii; lamellibranch and cyphonautes larvae; *Acartia, Labidocera, Met- ridia,* and *Pleuromamma* immature copepodites; *"Paracalanus", Oithona, Euterpina, Corycaeus, Oncaea,* and *Microsetella* copepodites and adults; euphausiid nauplii and calyptopes; CI, CII, and CIII *Calanus*; "other copepods"; cladocerans; and (see Lipskaya 1982) appendicularians. Nauplii and lamellibranch and cyphonautes larvae are considered small prey, the remainder being large. This spectrum of prey is also appropriate for young postlarval anchovy.

Figure 4 shows the prestorm and poststorm diurnal vertical distributions of food for the two prototypical larval types, in terms of the equiva- lent "large prey" for each; the figure legend gives the conversion factors used. In no instance was the

laboratory-determined critical concentration of prey exceeded. We do not believe that this conclu- sion is due to destruction of prey during preserva- tion.

We tested hypotheses concerning the vertical stratification and the effect of the storm on dis- tributions of prey by two-way ANOVAs on log- transformed abundances from the diurnal profiles (3, 5, 7, and 9) similar to those used for phyto- planktonic taxa (Section B above), since variances were homogeneous by Barlett's test. We used our data on the diurnal abundances of total larval fish to examine correlations with the food of "anchovy-like" larvae by means of the tau coeffi- cient for these profiles.

It is apparent from Figure 4A that "small prey" dominated the food supply for "anchovy-like" lar- vae, even when expressed as its equivalence in terms of large prey. Because this category had not increased significantly after the storm, neither had total prey for these larvae; however, large prey were both more abundant and more strongly stratified.

The food supply of "mackerel-type" larvae was
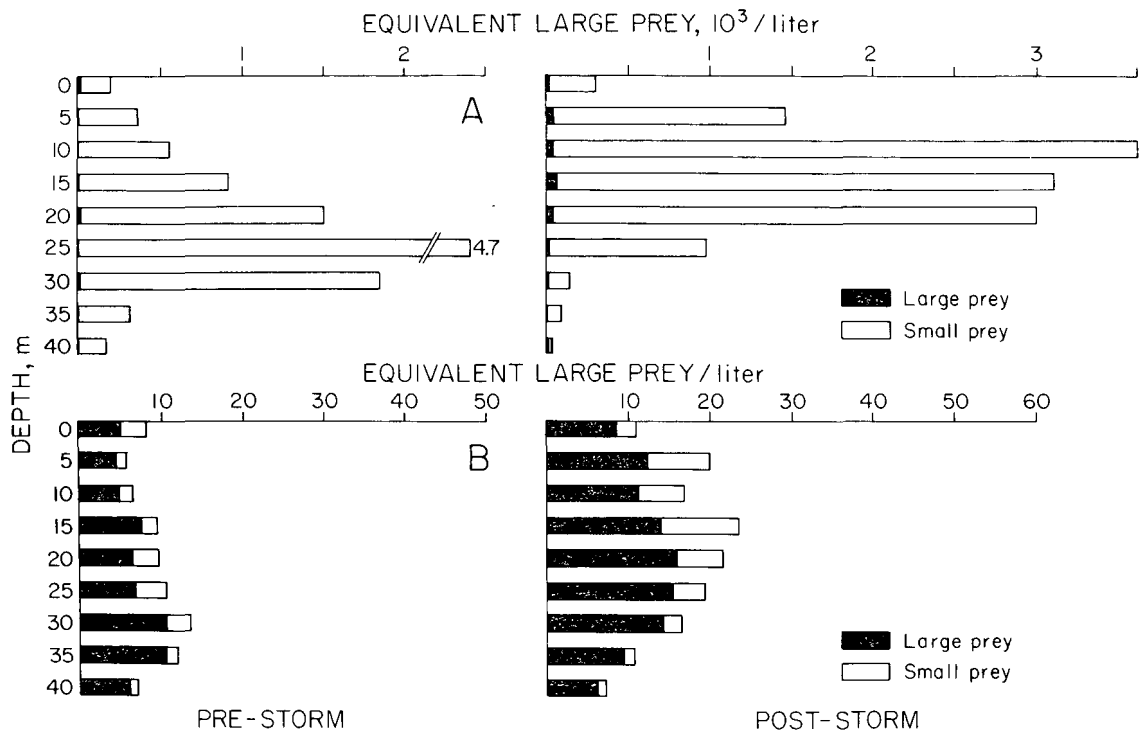

FIGURE 4.—Median vertical, diurnal distributions of larval fish food, as "equivalent large prey", before and after the storm. Taxa comprising categories of prey are listed in text.   A. Prey of "anchovy-like" larvae. Graphed concentrations of small prey are 0.1× actual concentrations.   B. Prey of "mackerel-like" larvae. Graphed concentrations of small prey are 0.2× actual concentrations.

dominated by "large" rather than "small" prey. That these types of zooplankters are less abundant very near surface and below 30 m than at intermediate depths is apparently not unusual in spring (Fiedler 1983:fig. 5). Both types of prey were more abundant after the storm. Total food for both types of larvae tended to be concentrated nearer the surface in the poststorm condition.

Although the numbers of larval fish in our samples are too small, especially after the storm, to provide a strong test of spatial correlation with their food supplies, the tau coefficients of correlation between total larval fish and their food by day were positive in all cases, but somewhat less so after the storm for the nonthecate dinoflagellates and ciliates which dominated the food supply of "anchovy-like" larvae. This was the case even though the poststorm distributions of both larval fish and food were concentrated nearer the surface than were the prestorm distributions.

SUMMARY AND DISCUSSION

We concentrated during this study on the consequences of the vertical distributions of plankton for the production of zooplanktonic food for larval fish, and on the differences in distributions of food experienced by larval fish at one coastal location before and after a small storm. Since advection surely occurred, we do not intend to imply that the same individual larvae experienced both sets of conditions.

Conclusions we believe to be ecologically significant and statistically verified are as follows:

1. The biotic environment was vertically structured.
   a. Of the 28 zooplanktonic taxa for which the ANOVA was appropriate, 22 had a consistently uneven (i.e., stratified) pattern of distribution with depth in the upper 50 m. Of the remaining six taxa, three had regular temporal changes in vertical distribution. Hence, only 3 of the 28 taxa were uniformly distributed both vertically and dielly.
   b. Chlorophyll was stratified in the upper 50 m, and 9 of the 18 phytoplanktonic-protozoan taxa examined had stratified distributions in the upper 40 m; the stratified taxa were notably dinoflagellates and the oligotrich ciliates rather than the diatoms.
   c. Both small prey and total prey for "anchovy-type" larvae were vertically stratified, but prey for "mackerel-type" larvae was not.
   d. Though the abundance of *Acartia* was correlated vertically with that of chlorophyll, its gut fullness was not.
2. Several features were different after the storm.
   a. Several zooplanktonic taxa—notably, various nauplii—were more abundant, while larval fish were less so. *Ceratium, Prorocentrum,* and *Lohmanniella* had increased, while several diatoms had decreased. Evidence suggested a poststorm increase in chlorophyll, but contained ambiguities.
   b. Several zooplanktonic taxa—*Pleuromamma* at night, cyphonautes by day, *Calanus* CII and CIII, larval fish—tended to be concentrated in shallower depths after the storm, as did chlorophyll, but data were insufficient to show that the large-sized phytoplanktonic taxa we studied responded in this way. Food for both types of larval fish was concentrated in shallower water after the storm. The neustonic distribution of *Labidocera* nauplii and copepodites was less pronounced after the storm, but in general the poststorm vertical stratification was at least as great as that prestorm, even though the temperature gradient was lessened. This general conclusion was also true for phytoplankton (except for some diatoms which were less abundant after the storm) and for the sum of forms representing "large food" for "anchovy-like" larvae and "small food" for "mackerel-like" larvae.
3. Relations between predators and prey were different following the storm.
   a. Several taxa maintained or established abundant populations in those parts of the water column where food was most plentiful. However, this was not true for taxa with pronounced diel vertical migrations. The estimated poststorm reproduction of *"Paracalanus"* was less limited by food than was the prestorm reproduction, and *Calanus* could obtain sufficient food for growth in a greater fraction of the water column after the storm; but we could not demonstrate a poststorm increase in gut fullness of large herbivores.
   b. Larval fish, both those categorized as "anchovy-like" and "mackerel-like", also were exposed to augmented concentrations of their respective "large" food items, both immediately and perhaps as a result of en-

hanced growth and reproduction of zooplankton and reduced competition from other larvae. However, the supply of food for larvae was less than that thought necessary for rapid growth and high survival, and the spatial association between total larvae and abundant, small food (dinoflagellates and protozoans) was slightly less strong after the storm; this category of food was not significantly more abundant after the storm.

Lacking information on the planktonic stocks and their distribution, we might have hypothesized that the decrease in abundance of larval fish following the storm (Fig. 2) was due to starvation because the storm-induced turbulence homogenized the vertical distributions of food. The results shown in Figure 4 make this hypothesis untenable.

Even though we did not find concentrations of food exceeding laboratory-determined thresholds for growth, certainly the most important conclusion with respect to the storm from the point of view of a larval fish is that there was as much food available after the storm and that copepod nauplii (which laboratory studies have shown to be desirable prey) increased significantly. In view of this, we predict that the larvae present after the storm were growing faster (or starving more slowly), were in better condition, and were more likely to have food in their guts than those present before the storm, even though the latter were the more numerous. Also, since the available food increased at several depths in the water column, we predict that the occurrences of well-nourished anchovy larvae (if any were present) should be shallower after the storm and less strictly confined to one or two depth strata.

A tendency for larvae to be less closely associated after the storm with layers of abundant dinoflagellates and ciliates might negate this prediction; the nature of the vertical relations should now be examined using the more reliable distributions of larvae determined by a towed opening-closing net. Another condition which would result in failure of our prediction is if the larvae actually rely for nutrition on micropatches of food, such as organic aggregates and an associated assemblage of phytoplankton and microzooplankton (e.g., Alldredge 1976; Silver et al. 1978). Devonald (1983) has suggested this for larvae of jack mackerel, *Trachurus symmetricus,* farther offshore in the Southern California Bight. If this is true, sam-

pling on the scale of hundreds of liters, as we did, would not detect the redistribution of food on the scale most important for larval survival and growth; storm-induced turbulence could have disrupted such micropatches, making the supply of food less rather than more favorable. A large amount of true microscale sampling, such as that done by Owen (1981), would then be required to predict correctly the effect of the storm on the larvae.

ACKNOWLEDGMENTS

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APPENDIX

Vertical Distribution of Taxa

APPENDIX TABLE 1.—Diurnal profiles before storm. * = variances heterogeneous; ANOVA not used.

Depth (m):	0	5	10	15	20	25	30	35	40	45	50
ZOOPLANKTON	median number per cubic meter										
Naupliar *Acartia*	75	407	786	1,533	5,074	1,345	448	78	0	39	49
Naupliar *Labidocera*	11,688	325	75	77	70	67	34	0	0	0	0
*Naupliar *"Paracalanus"*[1]	2,397	3,004	2,000	1,529	1,761	2,941	8,679	3,333	1,418	1,023	1,478
*Naupliar *Calanus*	693	956	597	536	515	1,070	299	107	75	79	33
Naupliar *Rhincalanus*	0	0	0	77	7	252	163	71	7	4	0
*Other nauplii	1,653	1,832	3,283	4,138	7,647	2,809	5,000	2,679	3,060	1,732	1,569
Female *Acartia*	4	22	23	19	21	8	4	0	0	0	0
Male *Acartia*	4	11	19	23	11	0	0	0	0	0	0
Copepodite *Acartia*	12	18	302	284	345	147	0	0	0	0	0
*Adult *Labidocera*	0	0	0	0	0	0	0	0	0	0	0
*Copepodite *Labidocera*	1,571	234	4	0	0	0	0	0	0	0	0
Adult and copepodite *"Paracalanus"*[1]	3,117	2,711	2,239	1,456	1,029	840	3,051	4,783	3,694	2,598	1,814
*Appendicularians	285	1,245	1,214	3,218	1,985	4,622	2,164	856	67	24	25
*Adult and copepodite *Oithona*	0	293	970	1,116	2,746	1,070	1,661	1,739	521	736	1,100
Adult and copepodite *Euterpina*	9	0	71	284	662	602	299	107	0	0	0
Euphausiid nauplii	0	0	11	0	4	0	3	11	16	4	13
*Euphausiid calyptopis	0	0	4	17	14	30	4	23	7	8	5
Euphausiid furcilia	0	0	4	0	4	20	7	31	8	12	14
Chaetognaths	11	163	204	307	121	172	97	43	16	35	31
Female *Calanus*	0	0	0	0	0	0	0	0	0	0	0
Male *Calanus*	0	0	0	0	0	0	0	0	0	0	0
C V *Calanus*	0	0	0	0	0	0	0	0	0	3	0
C IV *Calanus*	0	0	0	0	0	4	4	4	8	0	14
C III *Calanus*	0	0	0	4	0	3	8	14	15	4	5
C II *Calanus*	0	4	0	4	7	8	57	21	0	3	0
C I *Calanus*	0	8	4	0	13	13	57	18	4	0	0
*Adult *Corycaeus*	15	33	79	87	92	97	157	74	92	67	64
*Adult and copepodite *Oncaea*	83	73	38	230	70	168	2,463	2,536	1,679	1,299	1,225
Microsetella	0	4	4	843	1,513	1,271	305	286	65	173	196
Adult *Metridia*	0	0	0	0	0	0	0	0	0	0	0
*Adult *Pleuromamma*	0	0	0	0	0	0	0	0	0	0	0
*Copepodite *Metridia* and *Pleuromamma*	0	0	0	0	0	0	0	12	22	91	163
*Adult *Rhincalanus*	0	0	0	0	0	0	0	0	0	0	0
Copepodite *Rhincalanus*	0	0	0	0	0	0	34	18	15	17	15
*Copepodite *Eucalanus*	0	0	0	0	0	0	0	25	0	0	0
Other copepods	0	0	15	0	0	0	75	11	7	0	3
Fish eggs	43	29	18	8	7	3	0	0	0	0	0
Fish larvae	0	0	30	74	59	57	23	7	0	0	0
Cladocerans (*Evadne*)	50	121	86	· 12	0	4	0	0	0	0	0
Polychaete larvae	0	22	104	92	56	104	78	51	28	22	21
Lamellibranch larvae	0	0	0	0	0	0	0	0	0	104	0
Cyphonautes larvae	0	0	0	0	0	0	52	140	116	30	0
*CHLOROPHYLL	median micrograms per liter										
	0.33	0.36	0.44	0.63	0.97	1.03	2.06	0.77	0.49	0.32	0.28
PHYTOPLANKTON + CILIATES	median number per 100 ml										
Nitzschia spp. S	1,627	946	2,412	1,536	2,326	987	1,369	1,008	261		
Bacteriastrum spp. (chains)	56	86	84	78	78	95	66	54	16		
Chaetoceros spp.	2,488	3,845	4,307	3,246	3,576	1,427	4,270	1,764	413		
Rhizosolenia alata	112	116	90	86	80	35	18	4	2		
Rhizosolenia fragilissima	98	120	156	120	268	53	6	0	8		
Skeletonema costatum	78	56	18	96	76	24	3	88	40		
Ceratium spp.	42	30	24	32	14	11	54	4	0		
Gonyaulax polyedra/polygramma	26	14	16	20	12	15	14	0	0		
Prorocentrum sp. C	0	0	2	4	94	34	0	0	0		
Protoperidinium spp.	26	30	26	20	18	7	22	2	4		
Cochlodinium catenatum	50	56	290	714	1,272	4,065	1,182	148	68		
Gymnodinium splendens	0	0	0	2	0	341	300	0	0		
Torodinium robustum	30	26	20	10	0	16	12	0	0		
Umbilicosphaera sibogae	50	52	42	34	44	0	18	4	0		
Emiliania huxleyi	1,213	1,821	1,822	1,298	1,883	1,928	927	2,489	1,152		
Mesodinium rubrum	8	2	6	8	2	8	4	8	14		
Laboea spp.	30	146	110	74	82	104	124	72	36		
Lohmaniella spp.	68	128	116	94	134	154	218	78	50		

[1] Includes some *Clausocalanus*.

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APPENDIX TABLE 2.—Diurnal profiles after storm.

Depth (m):	0	5	10	15	20	25	30	35	40	45	50
ZOOPLANKTON					median number per cubic meter						
Naupliar *Acartia*	1,834	8,333	10,525	21,954	6,583	1,867	197	153	60	0	57
Naupliar *Labidocera*	1,600	4,679	0	0	0	0	0	0	0	0	0
Naupliar *"Paracalanus"*[1]	2,644	10,114	3,669	5,576	7,219	7,810	5,015	1,651	972	888	1,115
Naupliar *Calanus*	950	810	424	2,180	1,833	837	456	391	193	128	196
Naupliar *Rhincalanus*	0	631	0	95	134	9	204	228	0	36	124
Other nauplii	2,740	14,601	15,091	18,210	14,232	8,216	5,327	3,990	3,414	2,570	1,927
Female *Acartia*	0	5,666	69	9,736	6,617	3,994	0	1,907	0	0	0
Male *Acartia*	0	5,645	27	14	6,617	7	0	0	0	0	0
Copepodite *Acartia*	36	643	1,758	1,756	1,807	288	0	1,905	1,903	0	0
Adult *Labidocera*	0	0	0	0	0	0	0	0	0	0	0
Copepodite *Labidocera*	153	79	7	0	0	0	0	0	0	0	0
Adult and copepodite *"Paracalanus"*[1]	5,646	6,200	1,726	1,796	2,279	4,808	6,434	3,090	1,371	660	435
Appendicularians	3,053	3,165	3,551	5,785	8,364	5,651	1,746	754	122	79	44
Adult and copepodite *Oithona*	21	696	391	983	814	1,617	1,953	1,044	730	567	516
Adult and copepodite *Euterpina*	5	229	1,196	2,358	962	190	80	23	0	25	0
Euphausiid nauplii	0	0	171	0	214	9	19	33	27	26	25
Euphausiid calyptopis	0	13	11	89	41	38	21	20	15	9	14
Euphausiid furcilia	0	0	12	15	23	36	27	28	19	16	20
Chaetognaths	8	164	511	251	190	60	42	24	12	6	12
Female *Calanus*	0	0	0	0	0	0	0	22	8	8	4
Male *Calanus*	0	0	0	0	0	0	0	20	4	0	4
C V *Calanus*	0	0	0	116	0	11	12	18	12	0	4
C IV *Calanus*	0	68	0	119	45	16	32	6	0	8	0
C III *Calanus*	0	0	0	119	90	43	14	8	0	0	0
C II *Calanus*	7	0	297	27	50	46	11	0	0	0.	0
C I *Calanus*	7	79	303	15	31	25	12	0	0	0	0
Adult *Corycaeus*	20	107	387	305	478	74	87	69	48	46	43
Adult and copepodite *Oncaea*	0	711	255	215	707	2,678	3,466	2,011	1,797	1,322	1,204
Microsetella	14	40	719	476	45	171	236	190	23	37	33
Adult *Metridia*	0	0	0	0	0	0	0	0	0	0	0
Adult *Pleuromamma*	0	0	0	0	0	0	0	1,047	0	0	0
Copepodite *Metridia* and *Pleuromamma*	0	0	0	0	0	0	81	153	176	135	115
Adult *Rhincalanus*	0	0	0	0	0	0	0	0	97	80	0
Copepodite *Rhincalanus*	0	0	0	0	30	31	57	8	99	80	6
Copepodite *Eucalanus*	0	0	0	0	23	16	0	7	97	80	0
Other copepods	0	0	0	15	0	17	6	8	10	0	6
Fish eggs	14	18	19	89	0	0	0	0	0	0	0
Fish larvae	0	11	15	95	19	0	0	0	0	0	0
Cladocerans (*Evadne*)	164	273	101	102	16	0	0	0	0	0	0
Polychaete larvae	0	100	294	193	375	256	181	101	52	33	19
Lamellibranch larvae	0	0	0	0	0	54	195	138	0	0	0
Cyphonautes larvae	0	193	20	36	15	58	0	8	0	0	0
CHLOROPHYLL					median micrograms per liter						
	0.74	1.08	2.30	2.91	2.05	0.86	0.62	0.52	0.36	0.31	0.21
PHYTOPLANKTON + CILIATES					median number per 100 ml						
Nitzschia spp. S	87	48	0	0	0	0	0	130	0		
Bacteriastrum spp. (chains)	0	20	24	8	4	4	4	12	0		
Chaetoceros spp.	7,957	3,186	265	1,416	1,099	696	87	565	174		
Rhizosolenia alata	28	24	8	16	8	0	0	0	0		
Rhizosolenia fragilissima	44	16	36	8	4	0	0	0	0		
Skeletonema costatum	0	0	0	0	0	0	0	0	24		
Ceratium spp.	64	80	72	104	56	0	0	4	0		
Gonyaulax polyedra/polygramma	16	56	88	32	16	0	0	0	0		
Prorocentrum sp. C	20	4	681	784	296	4	0	4	0		
Protoperidinium spp.	48	64	72	40	16	4	0	0	0		
Cochlodinium catenatum	52	368	1,837	1,672	1,720	680	56	52	4		
Gymnodinium splendens	0	0	672	583	320	4	0	0	0		
Torodinium robustum	24	24	26	28	8	0	0	0	0		
Umbilicosphaera sibogae	0	104	40	56	32	4	0	0	0		
Emiliania huxleyi	1,681	1,504	3,009	1,858	609	1,130	696	1,478	973		
Mesodinium rubrum	16	24	32	16	8	0	0	0	0		
Laboea spp.	52	464	326	184	204	116	32	20	4		
Lohmaniella spp.	148	520	580	568	616	152	36	16	6		

[1]Includes some *Clausocalanus*.

APPENDIX TABLE 3.—Nocturnal profiles before storm.

Depth (m):	0	5	10	15	20	25	30	35	40	45	50
ZOOPLANKTON	median number per cubic meter										
Naupliar *Acartia*	352	315	4,286	5,874	6,723	1,992	0	43	0	0	0
Naupliar *Labidocera*	1,636	870	75	0	0	0	0	0	0	0	0
Naupliar *"Paracalanus"*[1]	5,282	4,229	2,491	2,379	2,500	8,352	2,215	1,277	1,051	1,041	748
Naupliar *Calanus*	691	441	1,008	744	2,033	579	340	81	81	41	71
Naupliar *Rhincalanus*	0	72	0	8	8	97	23	0	0	0	0
Other nauplii	2,636	5,507	7,143	11,822	12,602	9,650	2,764	3,333	2,358	2,073	1,594
Female *Acartia*	14	8	25	59	52	16	0	0	0	0	0
Male *Acartia*	21	0	25	16	21	4	0	0	0	0	0
Copepodite *Acartia*	45	47	517	1,784	2,546	83	72	4	0	0	0
Adult *Labidocera*	0	0	0	0	0	0	0	0	0	0	0
Copepodite *Labidocera*	532	98	75	80	0	0	0	0	0	0	0
Adult and copepodite *"Paracalanus"*[1]	3,040	2,047	2,264	2,066	2,033	6,364	3,574	3,191	2,412	1,165	435
Appendicularians	2,535	2,907	3,218	4,164	6,134	1,736	488	255	45	37	7
Adult and copepodite *Oithona*	282	157	1,345	2,231	3,821	1,992	1,824	1,404	545	805	725
Adult and copepodite *Euterpina*	67	36	130	2,320	1,736	413	130	0	0	0	0
Euphausiid nauplii	0	0	4	33	4	17	0	8	4	0	0
Euphausiid calyptopis	14	13	4	40	46	21	0	4	0	4	7
Euphausiid furcilia	8	4	4	24	25	19	47	26	33	73	7
Chaetognaths	45	141	189	252	142	93	85	41	28	22	11
Female *Calanus*	0	0	0	4	16	4	0	0	0	0	0
Male *Calanus*	0	0	0	0	0	0	0	0	0	0	0
C V *Calanus*	0	11	17	15	21	4	0	4	0	0	0
C IV *Calanus*	14	14	17	19	10	4	4	0	4	0	4
C III *Calanus*	0	0	4	0	16	50	10	0	0	0	0
C II *Calanus*	0	0	0	12	21	161	20	0	0	0	0
C I *Calanus*	0	4	13	4	49	119	9	0	0	0	0
Adult *Corycaeus*	14	16	91	123	142	194	163	119	70	61	36
Adult and copepodite *Oncaea*	240	157	0	0	325	3,636	3,453	1,707	1,284	1,487	1,143
Microsetella	141	394	613	1,440	1,220	579	488	71	19	33	36
Adult *Metridia*	0	0	0	0	0	4	0	20	33	15	7
Adult *Pleuromamma*	0	0	0	4	0	11	23	45	28	26	18
Copepodite *Metridia* and *Pleuromamma*	4	0	4	45	29	153	293	203	167	134	112
Adult *Rhincalanus*	0	0	0	0	0	0	0	0	0	0	0
Copepodite *Rhincalanus*	0	0	8	7	10	23	51	33	4	0	0
Copepodite *Eucalanus*	0	0	0	0	0	12	8	8	0	0	0
Other copepods	4	4	0	0	0	0	0	8	12	23	24
Fish eggs	4	0	0	0	3	0	0	0	0	0	0
Fish larvae	21	7	67	59	28	11	8	0	0	0	0
Cladocerans (*Evadne*)	120	101	13	4	0	4	0	0	0	0	0
Polychaete larvae	14	22	50	96	366	257	169	80	12	31	32
Lamellibranch larvae	0	0	0	0	0	0	0	0	0	0	0
Cyphonautes larvae	0	0	0	20	8	4	0	0	0	0	0
CHLOROPHYLL	median micrograms per liter										
	0.24	0.29	0.49	0.68	0.85	1.82	1.42	0.97	0.51	0.32	0.26
PHYTOPLANKTON + CILIATES	median number per 100 ml										
Nitzschia spp. S	1,036	2,181	791	372	1,593	162	841	241	217		
Bacteriastrum spp. (chains)	36	90	44	78	14	168	108	50	18		
Chaetoceros spp.	5,974	1,855	3,628	2,008	1,814	3,585	2,035	1,428	435		
Rhizosolenia alata	88	122	96	72	34	28	6	2	4		
Rhizosolenia fragilissima	108	160	114	70	68	11	8	2	4		
Skeletonema costatum	56	74	70	8	10	18	96	52	116		
Ceratium spp.	18	24	38	32	18	28	4	2	0		
Gonyaulax polyedra/polygramma	10	2	54	26	18	2	0	0	0		
Prorocentrum sp. C	2	0	58	76	50	6	0	0	0		
Protoperidinium spp.	14	16	12	22	23	32	10	0	0		
Cochlodinium catenatum	46	96	456	1,092	1,869	2,064	522	68	0		
Gymnodinium splendens	0	0	2	12	241	21	0	0	0		
Torodinium robustum	28	30	12	12	7	0	0	0	2		
Umbilicosphaera sibogae	16	0	16	86	0	30	2	2	0		
Emiliania huxleyi	858	1,518	1,498	706	1,372	2,173	3,009	1,580	957		
Mesodinium rubrum	2	34	6	4	0	11	4	6	4		
Laboea spp.	102	74	134	122	217	125	44	24	14		
Lohmaniella spp.	210	84	152	174	118	123	30	20	12		

[1] Includes some *Clausocalanus*.

APPENDIX TABLE 4.—Nocturnal profiles after storm.

Depth (m):	0	5	10	15	20	25	30	35	40	45	50
ZOOPLANKTON	median number per cubic meter										
Naupliar *Acartia*	6,590	9,360	17,323	18,008	15,106	11,371	660	176	90	230	0
Naupliar *Labidocera*	1,172	1,181	394	336	0	0	0	0	0	0	0
Naupliar "*Paracalanus*"[1]	4,908	5,256	7,591	4,370	5,184	9,091	6,400	3,424	1,345	1,073	1,126
Naupliar *Calanus*	1,099	1,378	1,969	1,533	1,082	1,489	495	467	545	236	260
Naupliar *Rhincalanus*	0	0	0	0	0	167	7	4	0	0	0
Other nauplii	3,678	7,102	12,795	27,969	11,873	12,553	8,000	6,154	5,364	4,245	3,520
Female *Acartia*	11	23	66	138	13	0	0	0	0	0	0
Male *Acartia*	11	28	17	123	27	0	0	0	0	0	0
Copepodite *Acartia*	280	661	1,575	2,299	1,505	3,617	32	0	0	0	0
Adult *Labidocera*	11	0	0	0	0	0	0	0	0	0	0
Copepodite *Labidocera*	119	80	31	15	0	0	0	0	0	0	0
Adult and copepodite "*Paracalanus*"[1]	4,215	3,977	2,953	2,490	1,915	4,013	5,400	2,731	1,887	720	1,039
Appendicularians	2,835	4,400	4,921	5,556	2,814	4,255	4,200	881	377	307	80
Adult and copepodite *Oithona*	172	394	495	347	1,003	1,505	1,800	952	755	169	560
Adult and copepodite *Euterpina*	57	142	110	1,261	3,617	167	165	16	27	5	0
Euphausiid nauplii	0	0	0	0	0	0	14	9	14	20	13
Euphausiid calyptopis	57	40	37	83	17	4	13	7	9	8	0
Euphausiid furcilia	11	0	29	61	27	13	11	26	9	16	9
Chaetognaths	95	100	202	215	54	112	49	57	9	19	9
Female *Calanus*	0	0	0	15	17	0	0	0	0	0	0
Male *Calanus*	0	0	0	0	0	0	4	0	0	0	4
C V *Calanus*	4	11	0	15	9	13	0	0	4	0	0
C IV *Calanus*	4	23	26	0	43	27	7	0	0	4	0
C III *Calanus*	7	31	26	31	34	80	13	0	0	0	0
C II *Calanus*	0	16	26	42	43	85	0	0	0	0	0
C I *Calanus*	7	16	8	0	0	68	7	0	0	0	0
Adult *Corycaeus*	11	0	47	252	732	190	130	55	45	28	14
Adult and copepodite *Oncaea*	230	240	94	1,513	1,003	2,766	4,400	1,868	1,345	1,792	1,200
Microsetella	115	320	495	347	426	334	660	78	245	46	20
Adult *Metridia*	0	8	16	0	0	13	7	4	9	5	0
Adult *Pleuromamma*	8	16	16	0	0	0	32	44	31	5	9
Copepodite *Metridia* and *Pleuromamma*	8	8	16	17	0	202	366	229	188	88	44
Adult *Rhincalanus*	0	0	0	0	0	0	0	0	0	0	0
Copepodite *Rhincalanus*	0	0	12	0	17	67	18	4	9	0	4
Copepodite *Eucalanus*	0	0	0	0	0	0	0	0	5	0	0
Other copepods	4	0	0	15	27	51	16	18	54	15	26
Fish eggs	0	16	4	0	0	0	0	0	0	0	0
Fish larvae	0	0	26	42	0	0	0	0	0	0	0
Cladocerans (*Evadne*)	29	197	330	17	0	0	0	0	0	0	4
Polychaete larvae	18	20	106	276	272	334	165	311	47	27	20
Lamellibranch larvae	0	0	0	0	0	0	0	0	0	0	0
Cyphonautes larvae	0	0	4	56	121	67	25	0	0	0	0
CHLOROPHYLL	median micrograms per liter										
	1.17	1.34	2.87	3.87	4.15	3.11	1.01	0.61	0.46	0.38	0.35
PHYTOPLANKTON + CILIATES	median number per 100 ml										
Nitzschia spp. S	88	0	0	88	0	0	0	43	130		
Bacteriastrum spp. (chains)	194	9	8	0	0	0	12	12	0		
Chaetoceros spp.	5,221	9,469	3,363	442	4,071	4,690	783	174	217		
Rhizosolenia alata	56	19	32	19	8	0	0	4	0		
Rhizosolenia fragilissima	83	0	0	111	0	0	4	20	0		
Skeletonema costatum	0	0	0	0	0	0	40	0	8		
Ceratium spp.	111	46	80	167	32	24	4	0	2		
Gonyaulax polyedra/*polygramma*	0	28	40	37	41	0	0	0	0		
Prorocentrum sp. C	556	806	1,360	1,704	290	88	4	0	0		
Protoperidinium spp.	56	102	32	0	16	16	12	0	2		
Cochlodinium catenatum	1,833	1,519	1,488	3,259	3,343	3,424	516	56	10		
Gymnodinium splendens	306	352	464	370	4,102	1,016	32	0	0		
Torodinium robustum	56	37	64	74	16	40	4	0	0		
Umbilicosphaera sibogae	28	9	24	74	24	16	4	0	0		
Emiliania huxleyi	1,062	1,327	1,858	1,416	2,035	2,035	1,652	1,043	478		
Mesodinium rubrum	389	176	72	241	14	16	12	0	0		
Laboea spp.	472	222	344	389	97	400	72	36	8		
Lohmaniella spp.	528	435	512	1,185	207	552	180	24	4		

[1]Includes some *Clausocalanus*.