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## **Zooplankton abundance in relation to state and type of intrusions onto the southeastern United States shelf during summer**

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### **ABSTRACT**

The vertical distribution of zooplankton on the continental shelf of northeastern Florida was determined in and around upwelling events and related to concentrations of particulate matter. Doliolida and the cladoceran *Penilia avirostris* were significantly more abundant in upwelled water <22°C and the cyclopoid genus *Oncaea* more abundant at warmer temperatures. The abundance of doliolida, *Oithona* and *Oncaea* in intrusions and the thermocline was significantly higher in older than in recently upwelled waters. The vertical sequences of the abundance of zooplankton and particulate matter (2-114  $\mu\text{m}$  ESD) were identical. Zooplankton maxima co-occurred primarily with maxima in phytoplankton biomass (chlorophyll *a*) and only partly with primary productivity.

### **1. Introduction**

During the summer the combined effect of diverging isobaths north of Capes Canaveral, Fear and Lookout (Blanton *et al.*, 1981) and upwelling favorable winds (Green, 1944; Taylor and Stewart, 1959) cause enhanced upwelling and cross-shelf intrusions. These intrusions are cold upwelled waters from greater depths of the Gulf Stream that contain high amounts of nutrients (Atkinson *et al.*, 1978) and cause increased primary production (Yoder *et al.*, 1983). The intensity of frontal disturbances of the Gulf Stream controls the depth from which water is upwelled, and therefore, its temperature. Because nitrate concentrations and temperatures <22°C are inversely related (Atkinson *et al.*, 1978) the effect of upwellings on primary production is variable within each upwelled water mass. Once the upwelled water is stranded on the shelf it remains there for a month or more (Atkinson *et al.*, 1984).

Our goal was to determine zooplankton concentrations in and above newly intruded waters and in intrusions which had separated from the cold source water (stranded intrusions). Zooplankton concentrations were related to hydrographic variables and to time. The study was carried out over 5 consecutive weeks during July and August 1979 when the probability of intrusion stranding is high. We tested several hypotheses: (1) Zooplankton abundances are higher in particle-rich, low temperature (<22°C) upwell-

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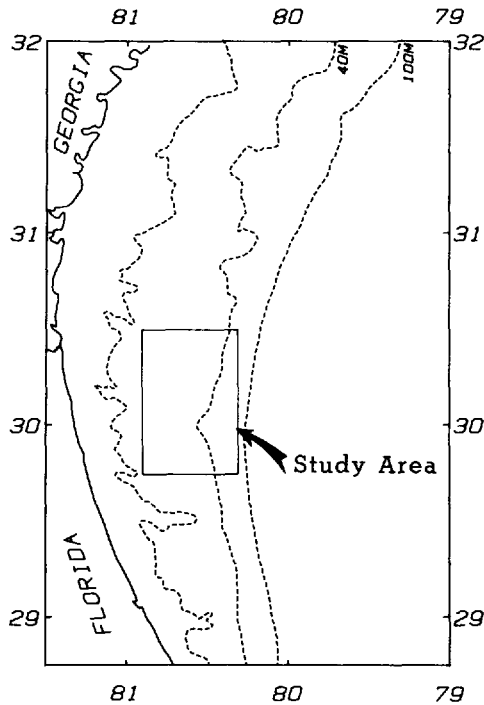


Figure 1. Study area from 17 July to 16 August 1979.

ings than in particle poor, high-temperature ( $>22^{\circ}\text{C}$ ) upwellings. (2) Zooplankton concentrations are higher in and near upwelled water which moved onto the shelf earlier, than in water which was upwelled more recently. (3) In a vertically stratified water column zooplankton are most abundant at depths where particle (food) concentrations are highest.

## 2. Methods

We observed a succession of upwelling events between 17 July and 17 August 1979 on the southeastern shelf of the U.S.A. (Fig. 1 shows study area). Areas of upwelling were located by towing a temperature-depth (T/D) sensor approximately 4 m above the seafloor on the mid ( $\sim 30$  m isobath) and outer shelf ( $\sim 50$  m isobath). Temperatures were recorded every 20 min., or at distances of 5.6 km. To obtain the dimensions of an upwelling event up to 5 onshore-offshore transects were run (determining the temperature structure of the water column) using expendable bathythermographs (XBT). This usually required less than 25 h. The distance between transects was 18.5 and 9.3 km between stations. To obtain a time-series a station near the center (lowest bottom temperature) of an upwelling event was occupied three times between 7 and 9 August and 14 to 16 August, 1979.

Table 1. Dates and station location of zooplankton sampling.

Date	Station	Latitude	Longitude	Bottom temperature (°C)
17 July 1979	168	30°25.0'N	80°41.5'W	25.8
18 July	176	29°50.0'N	80°41.5'W	25.1
26 July	292	30°05.0'N	80°18.5'W	25.2
26 July	295	30°05.0'N	80°36.0'W	24.4
26 July	298	30°05.0'N	80°54.0'W	24.2
1 August	370	30°00.0'N	80°18.5'W	17.0
2 August	372	29°58.2'N	80°35.5'W	19.0
2 August	374	30°00.0'N	80°53.7'W	24.4
9 August	457	30°00.0'N	80°27.1'W	17.1
9 August	458	30°00.0'N	80°27.1'W	17.2
14 August	530	30°09.9'N	80°35.6'W	17.6
16 August	540	30°15.1'N	80°36.1'W	19.1
16 August	541	30°15.2'N	80°36.1'W	19.4

Once the dimensions of the area occupied by upwelled water were determined by temperature another transect was run immediately afterwards across the center of the intrusion to obtain biological and other hydrographic data using a General Oceanics Models 1015 Rosette Sampler and a Plessey 9400 CTD (conductivity/temperature/depth) system or XBTs followed by a hydrowire cast with 5-1-Niskin bottles. The horizontal dimensions of the intrusions from 31 July, 7 August and 14 August are presented in Atkinson *et al.* (1984, their Figure 8). Concentrations of particulate matter in any size range from 2 to 114  $\mu\text{m}$  equivalent spherical diameter (ESD) were determined using a Coulter Counter Model TAI equipped with orifices of 100  $\mu\text{m}$  and 400  $\mu\text{m}$  diameter. Depths from which water samples were obtained and zooplankton sampling depth ranges were selected after temperature profiles had been obtained. We then consecutively sampled the upper mixed layer (UML), the thermocline and the bottom layer (Table 1). Zooplankton sampling was carried out with a diaphragm pump drawing water through a hose of 7.5 cm diameter into containers of 200 l volume. Sampling was started at a depth of 2 m and continued at intervals of 1 min per meter to 28 to 38 m, usually about 2 to 4 m above the seafloor. The depths from which samples were obtained were determined with a depth sensor fastened to the hose intake providing immediate deck readout through conducting wire. The pump flow rate, averaging  $140 \text{ l} \cdot \text{min}^{-1}$ , was determined at 3 depths during each vertical profile. At each depth interval samples were taken in duplicate while lowering and retrieving the hose. Water from the 200-l-containers was passed first through 103  $\mu\text{m}$  mesh and then through 30  $\mu\text{m}$  mesh. The latter collected most naupliar stages of copepods.

Zooplankton were carefully removed from the two meshes and preserved in 2%

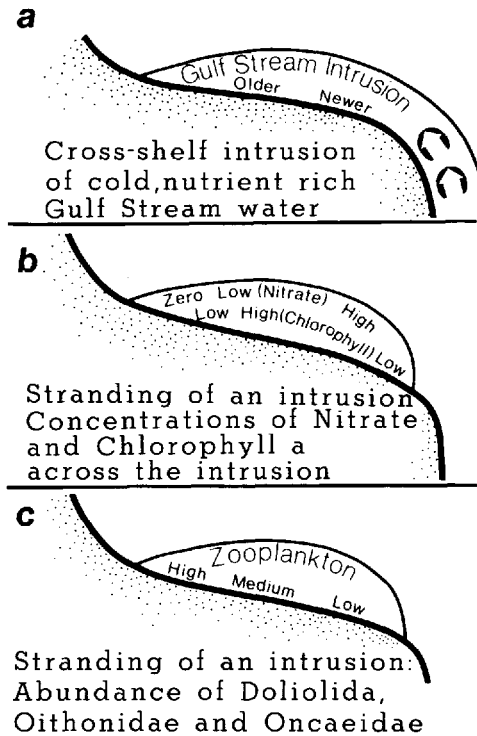


Figure 2. Schematic onshore-offshore distributions of temperature, chlorophylls, nitrate and zooplankton in an intrusion.

formaldehyde. The 103  $\mu\text{m}$  plankton were transferred to propylene glycol/propylene phenoxetol  $\sim 4$  weeks later (Steedman, 1974). For further details on sample processing see Paffenhöfer (1983).

### 3. Results

We present information from 5 consecutive weeks studying, together with O'Malley (1981), upwelling events with different minimum temperatures on the outer and mid continental shelf off St. Augustine, Florida. Atkinson *et al.* (1984) describe the hydrography, nutrient and chlorophyll regime. First, we discuss temperature distribution and particle concentrations from representative offshore-onshore transects. Secondly, we show particle size distribution and thirdly, zooplankton abundances.

The general schematic picture of a summer intrusion is as follows (Fig. 2): The older part of an intrusion is the one which upwelled earlier and the newer part upwelled lately; chlorophyll *a* concentrations near the leading edge are lower—because of grazing/sinking—, in the middle higher, and in lately upwelled water lower as that water moved only recently into the euphotic zone; nutrient concentrations decrease

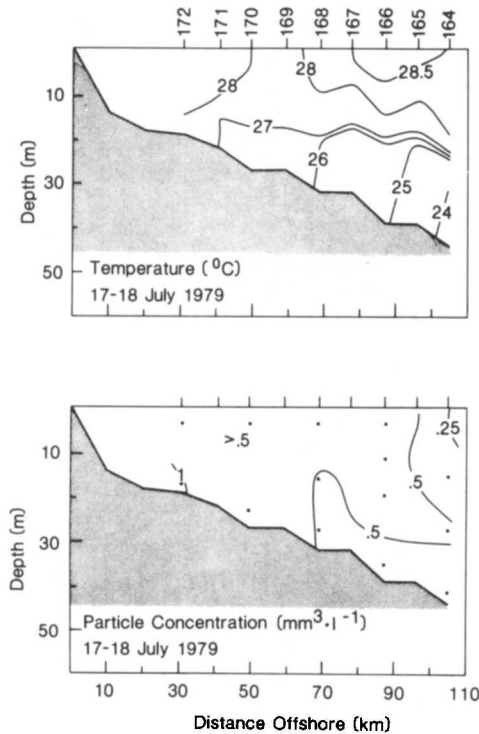


Figure 3. Vertical distribution of temperature and particulate matter on 17–18 July 1979 at 30°25.0'N.

from offshore to nearshore; the concentration of certain abundant zooplankton taxa in onshore-offshore transects—as also shown here—will be presented later.

*a. Temperature and particulate matter.* On 17–18 July, 1979 we observed a weak upwelling at 30°25'N which had lower particle concentrations than that of the warmer water closer to shore (Fig. 3). No particle peaks were evident (Fig. 8). One week later (25 July) when water of 23 to 24°C was upwelled onto the shelf at 30°05'N (Fig. 4) particle peaks at 37  $\mu\text{m}$  ESD were observed in the UML and thermocline at midshelf (Fig. 8). During the following weeks stronger upwellings were located (Atkinson *et al.*, 1984, their Fig. 8): On 1–2, 8 and 15 August cold, nitrate-rich water (Atkinson *et al.*, 1984) intruded onto the shelf, resulting in the establishment of sharp thermoclines (Figs. 5 to 7). Maximum particle concentrations of 5.4, 1.9 and 3.0  $\text{mm}^3 \cdot \text{l}^{-1}$  were observed in each of the three upwelling events at different depths (40 m, 18 m, and 26 m). On 1–2 August high particle concentrations were observed only below the thermocline, on 8 August in and below the thermocline, with the maximum at 24°C, and on 15 August at the thermocline.

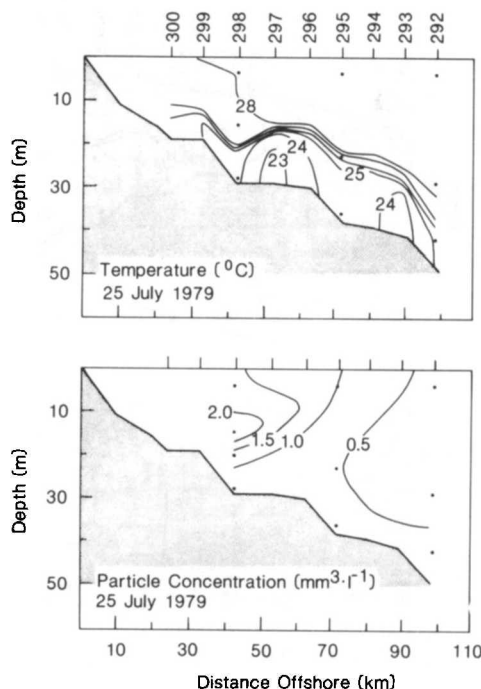


Figure 4. Vertical distribution of temperature and particulate matter on 25 July 1979 at 30°05.0'N.

Particle size frequency distributions reveal ungrazed maxima between 9 and 72  $\mu\text{m}$  ESD from 25 July to 15 August (Figs. 8 and 9). There were considerable similarities in particle spectra between stations within a given upwelling event (e.g., 36 m depth spectra at Stations 371 vs. 372) but not between upwelling events. One finds strong similarities between spectra within an intrusion (Station 370: 40 vs. 47 m; Station 533: 30 vs. 35 m; Station 534: 26 vs. 31 m) and also dissimilarities (Station 371: 36 vs. 40 m; Station 439: 29 vs. 44 m). The recent upwelling on 15 August (Station 531) has not yet developed a phytoplankton bloom (Fig. 9). A general observation of the particle size distributions from 1–2, 8 and 15 August indicates limited impact from grazing zooplankton and abundant food for zooplankton which graze on small (<10  $\mu\text{m}$ ) and large (>20  $\mu\text{m}$ ) particles.

*b. Zooplankton.* Zooplankton samples were obtained for 5 consecutive weeks to compare abundances in upwellings of different temperatures and particle abundances and also to compare abundances in earlier and later upwelled water of the same intrusion (Fig. 2). On 17–18 July, when upwelling was weak, we sampled only at midshelf (Fig. 11). During the 2 following weeks we sampled across the upwelling events (Figs. 12 and 13) and during the weeks of 8–15 August, assuming that the 8

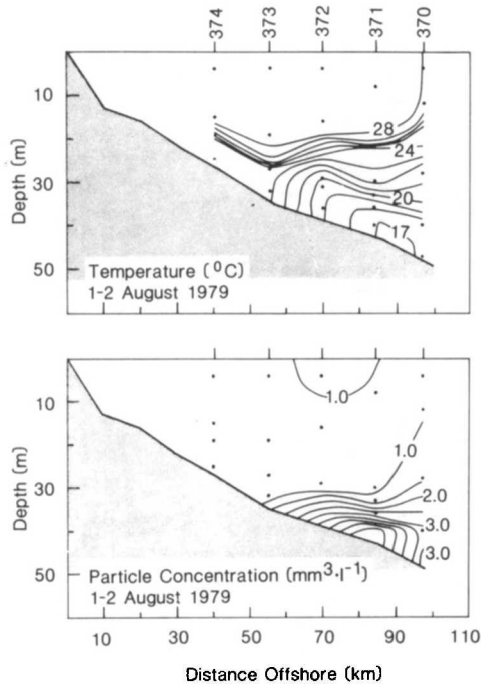


Figure 5. Vertical distribution of temperature and particulate matter on 1–2 August 1979 at 29°58.2'N.

August upwelling event would become stranded, we sampled at the upwelling center (lowest temperature) to observe the development of zooplankton assemblages with time (Figs. 14 and 15).

Non-parametric statistics tests were used to test the three above mentioned hypotheses. For the first hypothesis (zooplankton abundances in cold vs. warm upwellings) concentrations of abundant and dominant zooplankton taxa from 5 stations each (Table 2) were compared. Doliolida and the cladoceran *Penilia avirostris*, both strong asexual reproducers, were significantly more abundant in cold than in warm intrusions; for *Oncaea* sp. the opposite was observed.

To test hypothesis 2 (zooplankton abundance vs. age of upwelling) and 3, Kendall's coefficient of concordance was determined (Tate and Clelland, 1957). Only the data set from 1–2 August could be used for hypothesis 2 as the set from 25 July did not have an intrusion sample at Station 292. From Figure 5 we conclude that Station 374 represented the oldest and Station 370 the most recently upwelled water. For the comparison we used zooplankton concentrations from the intrusion and the thermocline. The zooplankton concentrations of each taxon were presented with increasing station number, which was followed by ranking each taxon (within intrusion and thermocline separately) by abundance. If hypothesis 2 is true the sequence of



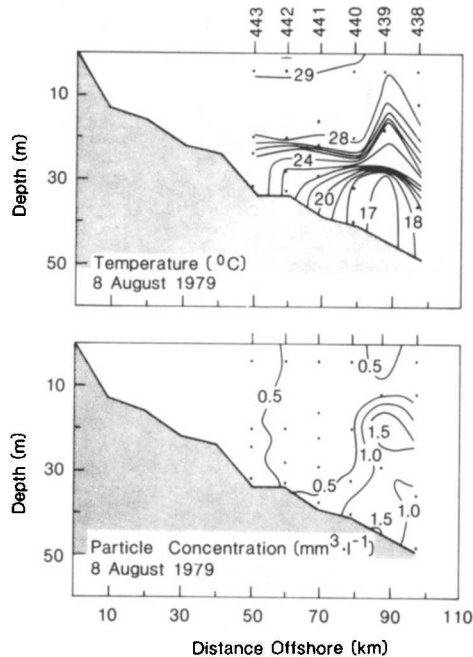


Figure 6. Vertical distribution of temperature and particulate matter on 8 August 1979 at 30°00.0'N.

abundance should be Station 374 > 372 > 370. This was significant for doliolida, *Oithona* and *Oncaea*, while *Paracalanus* was most abundant at 374 and least abundant at 372 (Table 3). All other abundant taxa showed no significant concordance.

To test the third hypothesis zooplankton abundance vs. particle concentrations of each taxon were presented for each station with increasing particle concentration ( $\text{mm}^3 \cdot \text{l}^{-1}$ ) and then each single taxon was ranked in sequence of its abundance (Paffenhöfer, 1983). If the hypothesis is true, each taxon should appear at each station in the same sequence and increase with increasing particle concentration. This was observed for 4 of 9 major taxa at Stations 457 and 458, which had particle maxima in the thermocline and minima in the UML (Fig. 10, Table 4). For *Oithona* and *Oncaea* the hypothesized sequence was found only among older copepodid stages retained by  $103 \mu\text{m}$  mesh (Stations 530, 540 and 541). When all specimens are considered the maxima occurred in the layer of medium particle concentration (thermocline) and minima were found in the UML. The vertical maxima of abundance of zooplankton co-occur not only with the particle but also the chlorophyll *a* and phaeopigment maxima and at the later date with the primary productivity maximum (Table 5); primary productivity maxima in both weeks were in the intruding layer, which had higher concentrations of nitrate than the thermocline ( $>1 \mu\text{M}$ , O'Malley, 1981; Atkinson *et al.*, 1984).

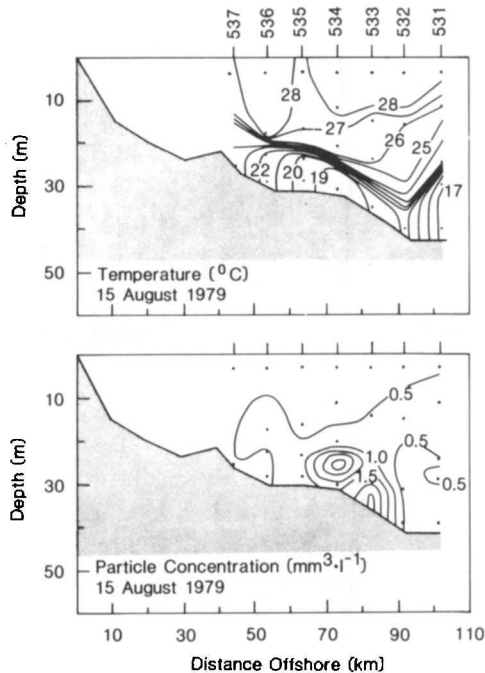


Figure 7. Vertical distribution of temperature and particulate matter on 15 August 1979 at 30°10.0'N.

We wanted to determine if differences in recent reproductive history (Stations 292 vs. 295 vs. 298; 370 vs. 372 vs. 374) and reproductive activity (time series Stations 530, 540 and 541) occurred (Fig. 16). A simple way was to present the abundance of young specimens (passing 103  $\mu\text{m}$  mesh) as a percentage of all specimens in a taxon. Each data point is the average of 2 measurements (Fig. 16). The percentage of early copepodid stages of *Paracalanus* and *Oncaea* increased in the UML from 13% and 27% at Station 292 (offshore) to 75% and 91% at Station 298 (mid-shelf). This was accompanied by a percentage increase of young *Oncaea* from Station 295 to 298 in the thermocline and the bottom layer. Strong similarities in the pattern of early juvenile percentages was observed at Stations 370, 372 and 374 for *Oncaea* at all 3 depth ranges and for *Oikopleura* and *Paracalanus* in the UML and bottom layer. Over a period of 2 days (Stations 530 to 541) early juvenile percentages of *Oncaea* changed little while those of *Paracalanus* slightly increased. Young *Oikopleura*, however, increased in each layer.

Fish larvae were abundant throughout the study (Figs. 11 to 15) and occurred at highest concentrations in the thermocline (Table 6). To determine whether there was a significant vertical structure of fish larvae abundance Kendall's coefficient of concordance ( $W$ ) was determined in relation to depth. The coefficient was significant

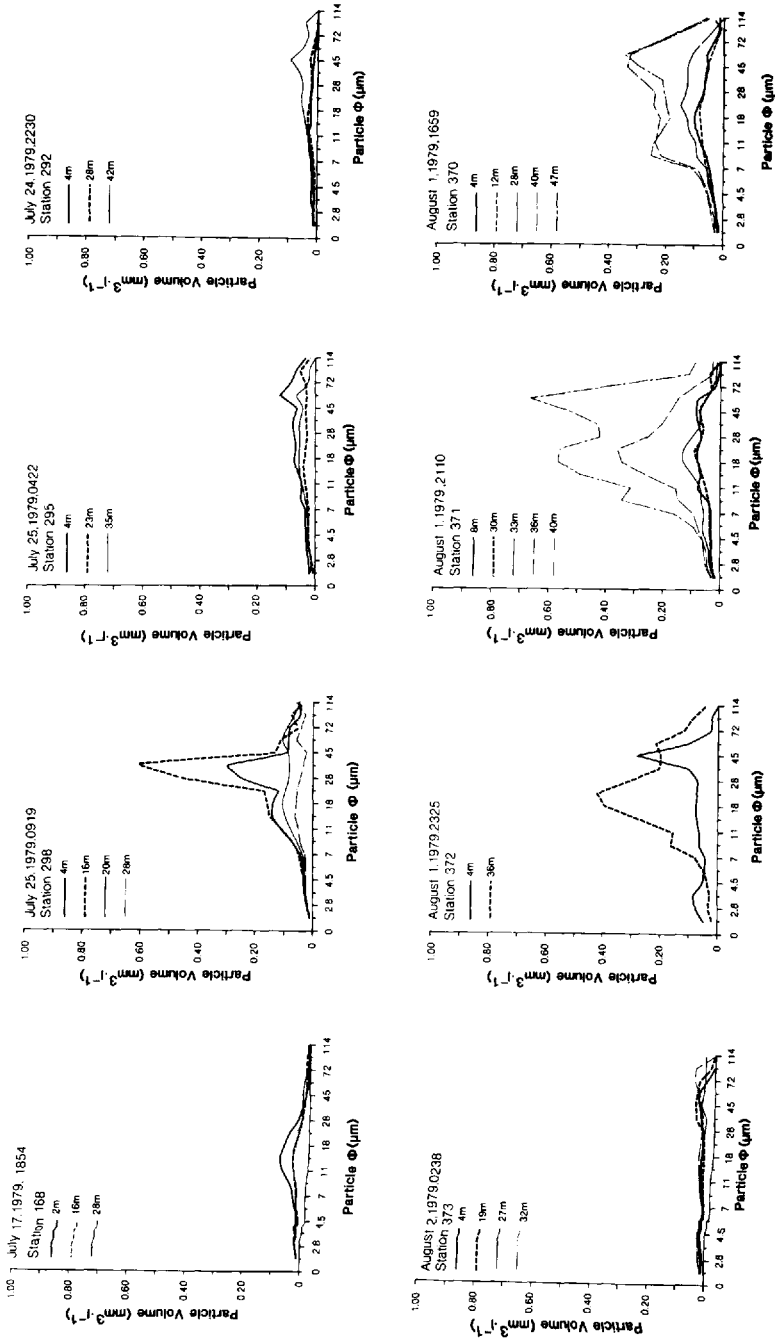


Figure 8. Particle size spectra at different depths from 17, 24-25 July and 1-2 August 1979.

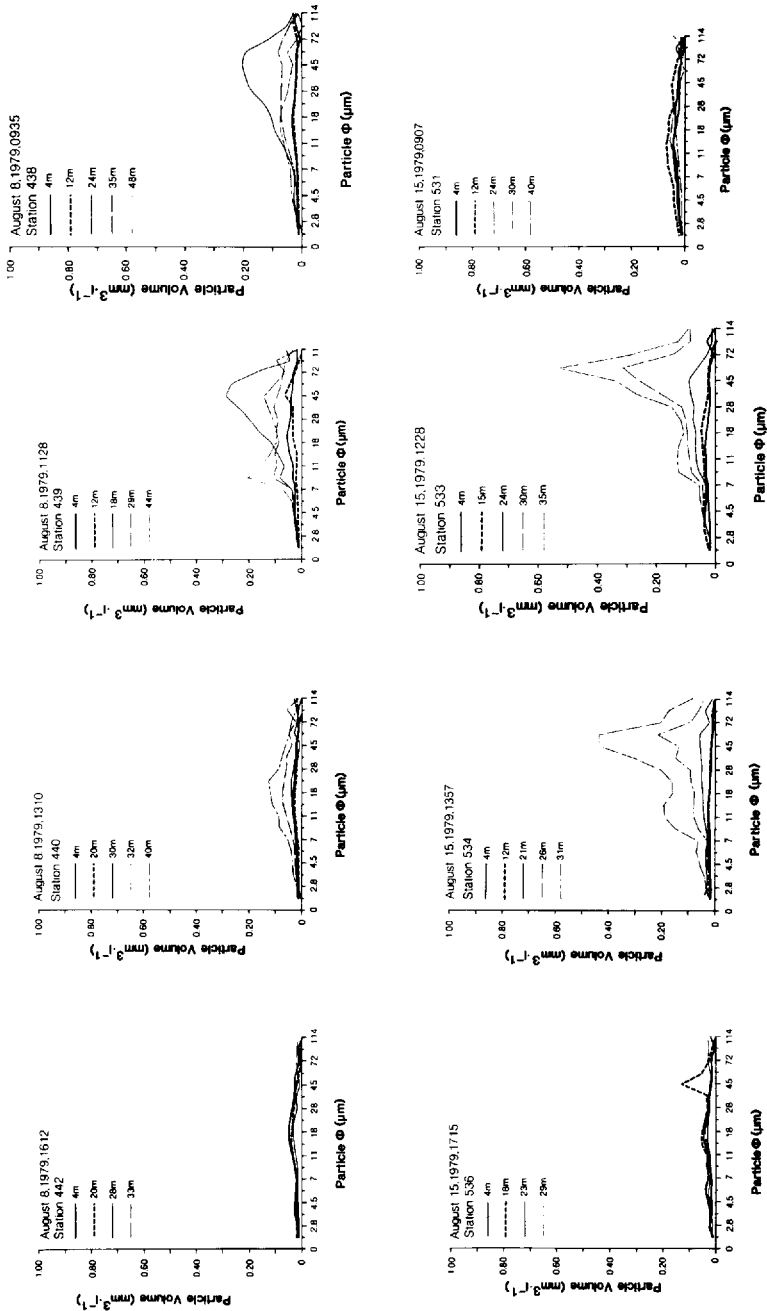


Figure 9. Particle size spectra at different depths from 8 to 15 August 1979.

Table 2. Comparison of zooplankton abundances in warm (>22°C)\* and cold (<22°C)\*\* upwellings (Mann-Whitney Test, Zar 1974).\*\*\*

Taxon	Probability	Sequence of abundance
Doliolida	<0.005	C > W
Oikopleura	>0.20	
P. avirostris	<0.01	C > W
Oithona	>0.20	
Oncaea	<0.001	W > C
T. turbinata	>0.20	
Paracalanus	>0.20	

C = cold, W = warm

\*Covers bottom layer of Stations 168, 176, 295, 298 and 374.

\*\*Covers bottom layer of Stations 372, 437, 457, 530 and 541.

\*\*\*Sample size  $n = 10$  for warm and cold upwellings, respectively.

( $p < 0.05$ ) suggesting that ranks of abundance agreed between the 16 stations in the sequence thermocline > UML > intrusion.

#### 4. Discussion

A study from summer 1978 presented concentrations of particulate matter and zooplankton in relation to depth (Paffenhöfer, 1983); this study presents the same variables in relation to depth and onshore-offshore direction.

*a. Temperature and particulate matter.* Because current meters were not deployed during the period of our study we cannot be sure if upwelling events that intruded onto the shelf on 1–2 and 8 August and became stranded on 15 August were the same. O'Malley (1981) and Atkinson *et al.* (1984) assume, from nitrate-deficits, that the shelf-break upwelling event on 15 August was recent and that those on 1–2 and 8 August were the same. Particle spectra near bottom at the intrusion centers at Stations 370, 439 and 534 reveal 2 peaks near 9 to 11 and 57  $\mu\text{m}$  ESD. Each peak is most likely

Table 3. Cross-shelf comparison (Stations 370, 372, 374) of zooplankton abundances including thermocline and intrusion (Kendall's coefficient of concordance  $W$ ).

Taxon	$W$	Probability of concordance	Sequence of abundance
Doliolida	1.00	<0.01	374 > 372 > 370
P. avirostris	0.75	>0.05	
Oithona	1.00	<0.01	374 > 372 > 370
Oncaea	0.81	=0.05	374 > 372 > 370
T. turbinata	0.75	>0.05	
Paracalanus	0.81	=0.05	374 > 370 > 372

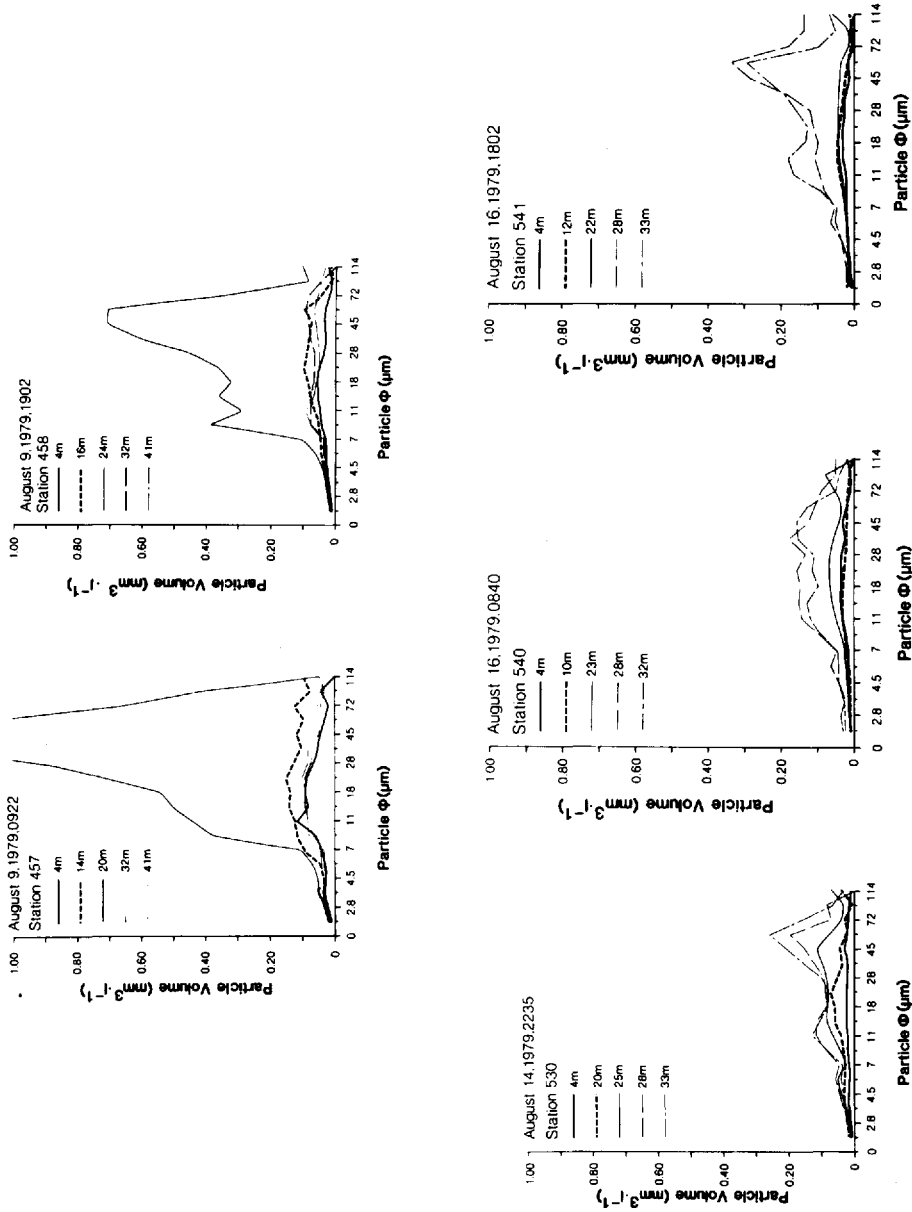


Figure 10. Particle size spectra at different depths from 9, 14 and 16 August 1979.

Table 4. Zooplankton abundance related to particle concentration employing Kendall's coefficient of concordance ( $W$ ).\*\*\*

Taxon	Stations	$W$	Probability of concordance	Sequence of abundance
Doliolida	457/458	0.44	>0.20	
Oikopleura		0.19	>0.20	
Penilia		0.81	=0.05	H > M > L
Oithona		0.19	>0.20	
Oncaea		0.81	=0.05	H > M > L
T. turbinata		0.81	=0.05	H > M > L
Paracalanus		0.06	>0.20	
Lucifer		0.75	>0.05	
Fish larvae		0.81	=0.05	H > M > L
Doliolida	530/540/541	0.86	<0.01	H > M > L
Oikopleura		0.76	<0.01	H > M > L
Penilia		0.86	<0.01	H > M > L
Oithona		0.78	<0.01	H > M > L > 103 $\mu\text{m}$
Oithona		0.72	<0.05	M > H > L ALL
Oncaea		0.78	<0.01	H > M > L > 103 $\mu\text{m}$
Oncaea		0.78	<0.01	M > H > L ALL
T. turbinata		1.00	<0.01	H > M > L
Paracalanus		0.53	>0.05	
Lucifer		0.78	<0.01	H > M > L
Fish larvae		0.19	>0.20	

L, M and H = low, medium and high particle concentration

> 103  $\mu\text{m}$  = all specimens of a taxon retained by 103  $\mu\text{m}$  mesh

ALL = all specimens of a taxon collected

\*Unless otherwise indicated this concordance test was applied to all specimens of each taxon collected.

\*\*Stations 457/458 = total of 4 vertical samplings; 530/540/541 = total of 6 vertical samplings.

Table 5. Phytoplankton uptake rates, chlorophyll  $a$  and chlorophyll  $a$  plus phaeopigment concentrations (J.A. Yoder, unpubl.).

Station	Depth (m)	Carbon uptake rate ( $\mu\text{gC} \cdot \ell^{-1} \cdot \text{h}^{-1}$ )	Chlorophyll $a$ ( $\mu\text{g} \cdot \ell^{-1}$ )	Chlorophyll $a$	Assimilation
				& phaeopigments ( $\mu\text{g} \cdot \ell^{-1}$ )	rate ( $\mu\text{gC} \cdot \mu\text{gChl}a^{-1} \cdot \text{h}^{-1}$ )
457	20	11.68	11.84	15.91	0.99
	41	12.39	1.41	1.65	8.79
540	23	3.34	0.25	0.38	13.37
	28	14.32	2.18	2.92	6.57

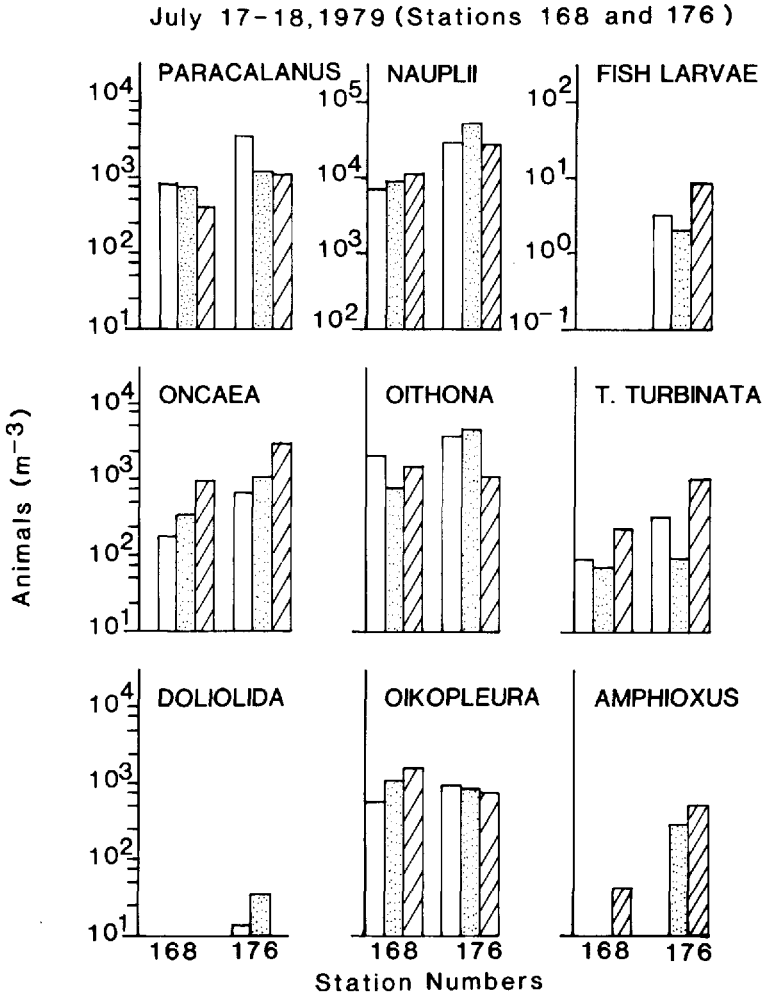


Figure 11. Zooplankton abundance at Stations 168 and 176; open = Upper Mixed Layer (UML); stippled = Thermocline; slanted = Intrusion (Bottom Layer).

indicative of a phytoplankton maximum (Paffenhöfer *et al.*, 1980). While peaks at nearly identical ESDs may indicate that the same algal taxon was encountered, considerable differences in peak heights could negate this assumption. Sinking and resuspension of phytoplankton, interactions at the thermocline and differential grazing due to temporary zooplankton invasions from the thermocline and UML could cause variations over time and within the same upwelling event, resulting in small-scale patchiness.

In general, the vertical profiles of temperature and particulate matter resembled



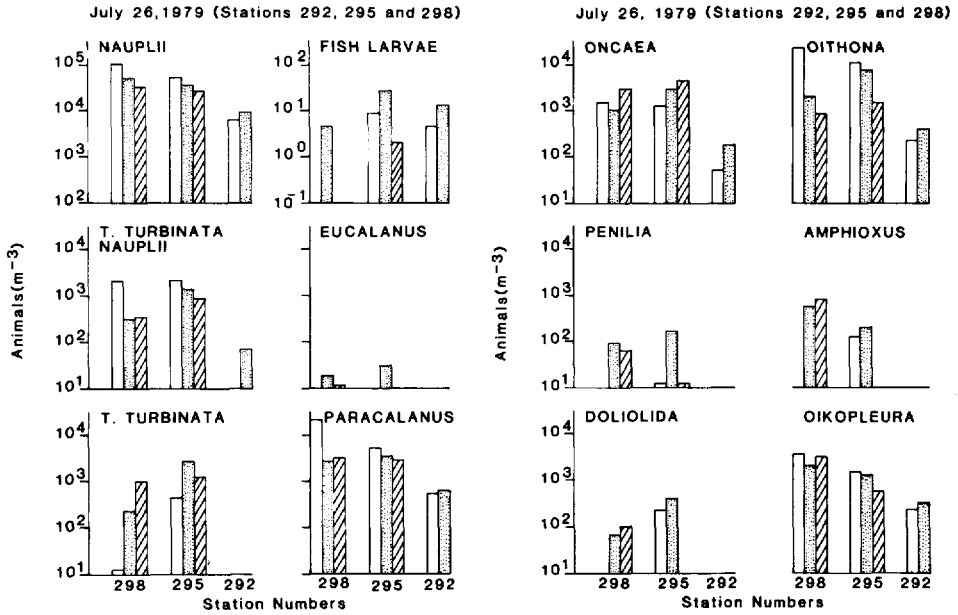


Figure 12. Zooplankton abundance at Stations 292, 295 and 298; no intrusion samples taken at 292; for explanations see Figure 11.

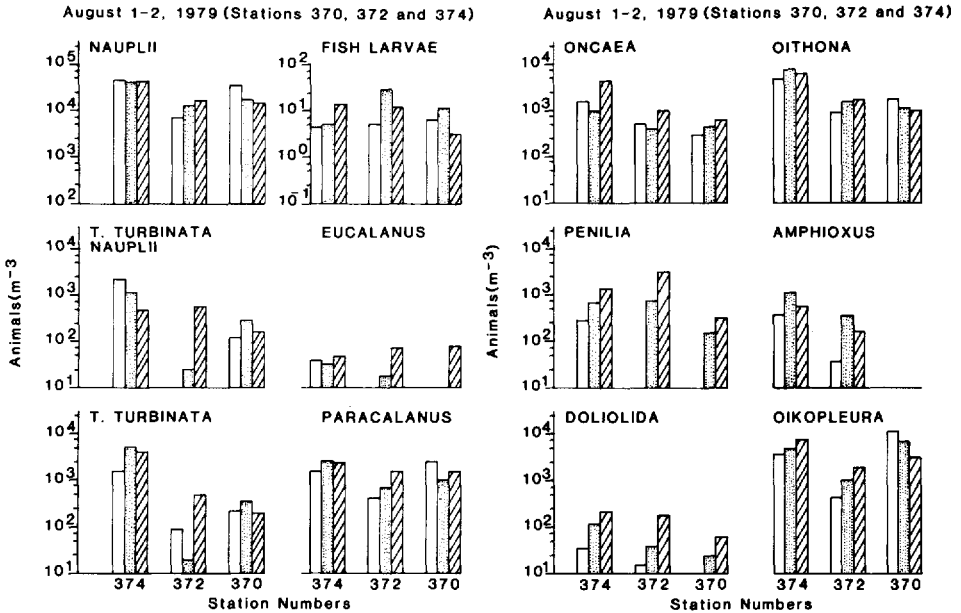


Figure 13. Zooplankton abundance at Stations 370, 372 and 374.

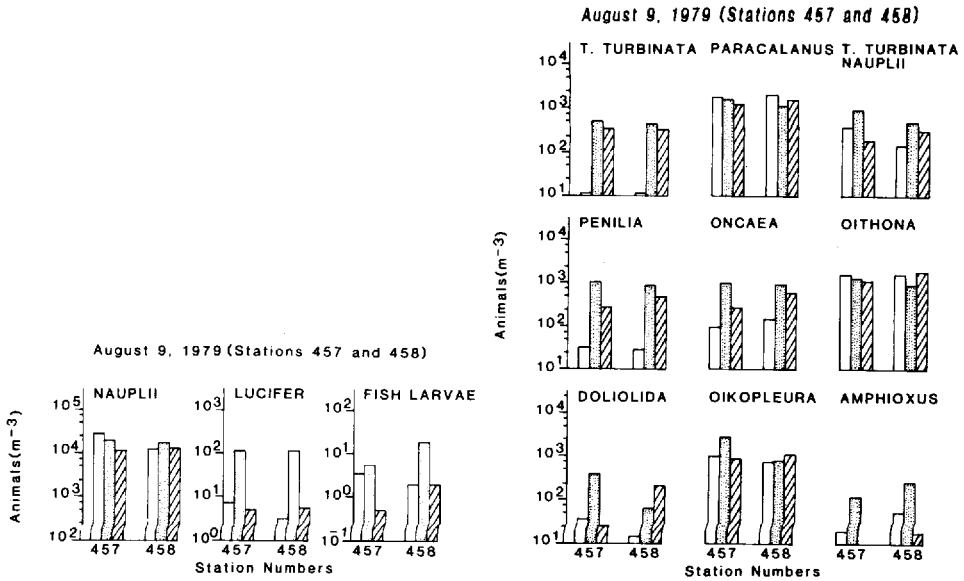


Figure 14. Zooplankton abundance at Stations 457 and 458.

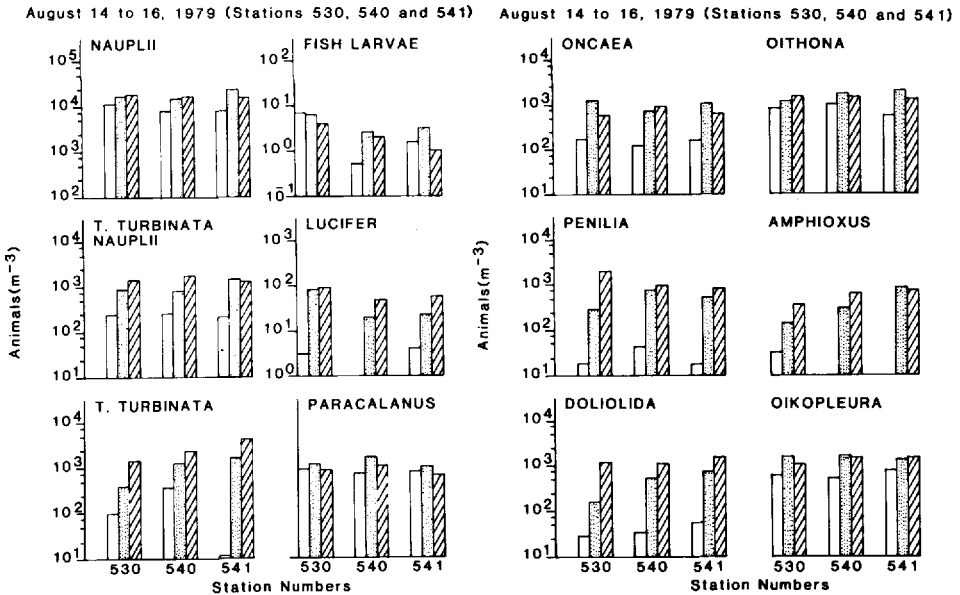


Figure 15. Zooplankton abundance at Stations 530, 540 and 541.

Table 6. Concentrations of fish larvae (larvae · m<sup>-3</sup>) in the water column.

	UML	Thermocline	Intrusion
$\bar{x}$	4.8	10.5	5.3
Range	0.5 to 17	1.5 to 29	0 to 22

patterns described earlier (Paffenhöfer *et al.*, 1980; Paffenhöfer, 1983). Particle abundance was highest in cold, nitrate-rich, near-bottom water except on 8 and 9 August when a pronounced maximum was at the thermocline, showing at Station 458 (Fig. 10) a spectrum which closely resembled those from Stations 371 (Fig. 8) and 534 (Fig. 9). Most spectra in particle-rich layers between 8 and 16 August (Figs. 9 and 10) indicate, compared to Stations 370 and 371 (Fig. 8), that particle volumes near 11  $\mu\text{m}$  were considerably lower than those near 57  $\mu\text{m}$ . Differential grazing by zooplankton, rather than phytoplankton sinking or growth, could account for the differences. No peaks below 7  $\mu\text{m}$  ESD were observed.

Of all particles encountered in the spectrum from 2 to 114  $\mu\text{m}$  those from 2 to about 30  $\mu\text{m}$  ESD should be preferentially removed as the majority of abundant zooplankton in early stages of upwelling events feed on smaller particles and hardly remove larger phytoplankton (Paffenhöfer, 1984).

*b. Zooplankton.* Two previous papers dealing with abundances of major zooplankton taxa on the southeastern continental shelf (Paffenhöfer, 1980, 1983) showed that ostracods, small calanoid and cyclopoid copepods, cladocerans and cephalochordates were dominant forms. Except for the ostracods the same species/genera which were abundant in upwelling events in 1976 and 1978 were dominant in July and August 1979, mostly in the bottom layer and thermocline. To these we add the doliolida (*Doliolletta gegenbauri*) which were at every station except 168 and 292. From its vertical distribution, and in relation to particle abundance, it appears that *D. gegenbauri* (along with *P. avirostris* and *T. turbinata*) is an indicator of particle-rich upwelling events. Doliolida and *P. avirostris* can respond quickly to favorable food conditions through asexual reproduction. The latter has an average generation time of 6 days at 20°C (Paffenhöfer, unpublished observations). As *P. avirostris* occurs in high concentrations only nearshore (Moore and Sander, 1979; Grahame 1976; Binet, 1975) and doliolida are abundant only in particle-rich environments (Atkinson *et al.*, 1978) seeding of the phytoplankton-rich upwelling waters is an important process. A small part of the large doliolid population in the eastward flowing Guinea Current is displaced into the westward flowing deeper cooler Counter Current, thus maintaining a supply of this taxon to the temporarily productive upwelling regions off the Ivory Coast (Binet, 1976). On the southeastern shelf of the U.S.A. the zooplankton species which occur dominantly in upwellings are either already in the upwelling water, thus originating from the Gulf of Mexico, or enter the upwelling waters from the UML. In

summer the UML is generally displaced offshore by winds from the south (Weber and Blanton, 1980).

Three hypotheses were tested: (1) that zooplankton concentrations are higher in cold, particle-rich than in warm, particle-poor upwellings because reproduction would be enhanced in the former and zooplankton would migrate from upper layers into the intrusions and remain there (Paffenhöfer, 1980). Of the abundant taxa only doliolida and *P. avirostris* follow this hypothesis significantly (Table 2). In establishing cause we suggest that doliolida and *P. avirostris* responded faster (through asexual reproduction) to sudden food abundances than most other multicellular zooplankton but that mortality levels are high when food levels become low because of the lack of energy reserves. Predation cannot be assessed. Copepods, with longer generation times, usually store energy (wax esters, Lee et al., 1970) which allows them to overcome times of food scarcity (or delay death). *Oikopleura* is different from other zooplankton as it can feed on particles as small as 0.1  $\mu\text{m}$  (Flood, 1978). *Oncaea*, however, showed a reverse trend in that it was significantly more abundant in warm than in cold upwelled water. As little is known of the biology of *Oncaea* we speculate that the copepodids do not rely so much on phytoplankton as food but feed on zooplankton like appendicularian houses (Alldredge, 1972), copepod carcasses, thaliacea or aggregates in general. Thus, they should reach highest concentrations later than abundant calanoid copepods which feed directly on phytoplankton (Paffenhöfer, 1983).

The second hypothesis was that zooplankton concentrations are higher in and near regions of an upwelling event which moved onto the shelf earlier (leading edge/frontal zone) than in those which upwelled later. This hypothesis could only be positive if initial concentrations and age composition throughout upwellings and thermoclines are similar. This could not be checked. Taxa which were in early upwelled water should have reproduced longer and thus be more abundant than those upwelled lately and therefore only recently encountering high food abundances. The differences in time between the leading edge moving onto the shelf and the part of the intrusion moving onto the shelf last could be up to 10 days or about equal to half the generation time of small copepods at 22° to 24°C. Our results show that doliolida, *Oithona* and *Oncaea* follow the hypothesized sequence of abundance (Table 3) but *T. turbinata*, *P. avirostris* and *Paracalanus* do not. *T. turbinata* follows the expected sequence in the intrusion but not in the thermocline. *P. avirostris* had its maximum at Station 372 and *Paracalanus*, with a different sequence, was most abundant at Station 374. In an incoming intrusion in Onslow Bay (Paffenhöfer, 1980) the concentration of *Paracalanus* decreased from the leading edge toward the most recently upwelled water, as found here for doliolida, *Oithona* and *Oncaea*. An interesting feature was observed on 1–2 August for doliolida, *Oncaea*, *Amphioxus* and, with reservations, *P. avirostris*: At each station, concentrations in the 3 water layers corresponded. For example, the concentration of doliolida in the intrusion increased from Station 370 to 372 as it did in the thermocline and in the UML. Due to mixing processes between the 3 water layers

zooplankton and their food could be displaced from the intrusion into the thermocline and the UML. If mixing forces are similar across the upwelled water, and no pronounced reverse migration occurs, then the gradient observed should be similar at all stations. Similar observations were made on 12 and 14 August 1978 when the concentration of large particles (diatoms) decreased from the intrusions to near the surface (Paffenhöfer, 1983).

Thirdly, we hypothesized that, in a water column, zooplankton are at highest concentrations at depths of highest particle concentrations. High particle or phytoplankton concentration does not imply that animals encounter the most favorable food quality in the same layer as: (a) sinking phytoplankton cells may accumulate but not divide (senescence), (b) dinoflagellates may aggregate but are then hardly eaten by copepods (Huntley, 1982; Fiedler, 1982), (c) most cells may be too large to be ingested by juvenile stages (Paffenhöfer *et al.*, 1980). Several authors observed co-occurrence of maxima of chlorophyll *a* with those of various zooplankton species (Ortner *et al.*, 1980; Bird, 1983). Another found co-occurrence of zooplankton maxima with temperature minima and maxima in particle volumes (Paffenhöfer, 1983). At 4 stations near upwelling near the Ivory Coast, maxima of copepod abundance were at the chlorophyll maximum at 2 stations and at the maximum of primary productivity at 2 other stations (Le Borgne, 1977). On the outer shelf off Nova Scotia Batfish profiles showed that highest concentrations of small and large copepods in the water column were consistently about 10 m above the chlorophyll maximum and coincided with the vertical maximum of estimated primary production (Herman *et al.*, 1981). Our data indicate that when there was significant concordance of the vertical distribution of zooplankton taxa at major upwellings the maximum concentration coincided with those of particles (9 and 14 to 16 August) and in one case (14 to 16 August) with primary production. Note that on 9 August primary productivity in the bottom layer was only slightly higher than in the thermocline. To arrive at a conclusive statement concerning the concentrations of mainly herbivorous zooplankton in the water column, detailed vertical profiles of primary productivity, chlorophyll *a*/particulate matter and zooplankton would be required. This study does not provide all of this information. Theoretically zooplankton should accumulate where they find food of the right size and quality. We hypothesize that when there are large differences in food abundance and small differences in primary production between adjacent layers (Table 5) some zooplankton taxa, like *T. turbinata* choose the layer with higher absolute concentrations. If food concentrations (chlorophyll, particles) are similar then food quality, (physiological state, size) and with it not the absolute but the relative primary productivity ( $\mu\text{g C assimilated} \cdot \mu\text{g chlorophyll } a^{-1} \cdot \text{h}^{-1}$ ), should become important. An additional factor is the phytoplankton cell volume and dimension as large cells cannot be ingested by small zooplankton and small cells are eaten only at low rates by large zooplankton (Paffenhöfer and Knowles, 1978; Paffenhöfer, 1984).

Maxima of the entire assemblages of *Oithona* and *Oncaea* (ALL) coincided with

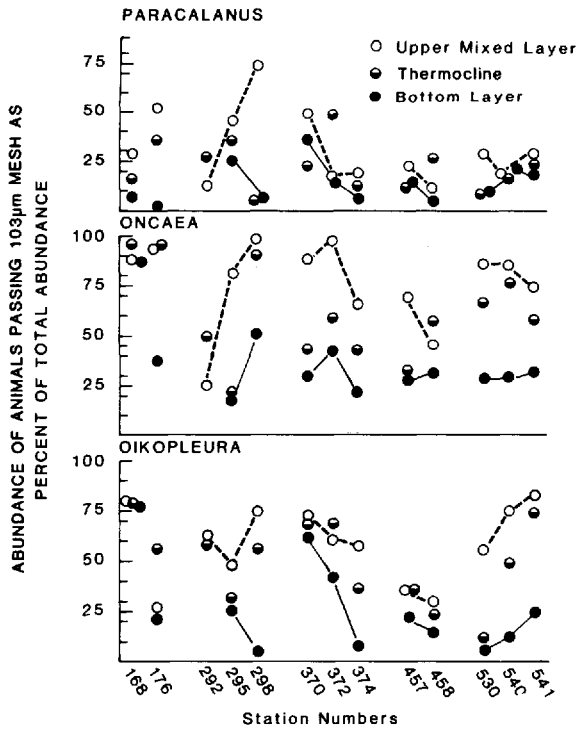


Figure 16. Abundance of 3 genera of zooplankton passing 103  $\mu\text{m}$ , ( $>30 \mu\text{m}$  mesh) as percentage of all specimens of each genus.

medium food concentrations at Stations 530 to 541. As early juveniles were in similar or greater concentrations than late copepodids/adults ( $>103 \mu\text{m}$ ) at these stations, compared to Stations 457/458, their vertical position dominated that of the entire assemblage. Maxima of early *Oncaea* copepodites ( $<103 \mu\text{m}$ ) at medium and low particle concentrations and of late copepodites and adults at higher particle abundances were also observed in summer 1978 (Paffenhöfer, 1983). Our observations that young *Oncaea* and *Oikopleura* are more abundant in the UML and thermocline and older forms are more abundant in the bottom layer confirms the results from a similar study in the same area during summer 1978 (Paffenhöfer, 1983). *Paracalanus* does not exhibit a general vertical pattern (Figures 11 to 16, Table 4) but early copepodid stages seem to have a slightly higher relative abundance in the UML (Fig. 16).

The abundances of fish larvae in the study were higher by a factor of five or more than in the Gulf of Mexico (Houde and Chitty, 1976). Avoidance of the pumping intake could have resulted in underestimation of abundances. Houde (pers. commun.) reported that mean densities of fish larvae were 8.5 times higher when a 35  $\mu\text{m}$  mesh bongo net was used, compared to a similar net with 333  $\mu\text{m}$ . Yolk-sac larvae were not

quantitatively retained by the larger mesh. Our 103  $\mu\text{m}$  mesh should have retained all larvae.

We observed high abundances of small, fast-reproducing zooplankton in and near upwelling water masses, confirming earlier findings. In the leading edge of upwelled water concentrations were higher than in water which moved onto the shelf more recently. Doliolida for the first time were consistently observed in high densities. Our findings also indicate that some zooplankton taxa are more abundant where phytoplankton concentrations are high rather than at the maxima of primary productivity.

*Acknowledgments.* This study was supported by U.S. Department of Energy Contracts number DE-AS09-76EV00936 and DE-AS09-76EV00889. Dr. J. A. Yoder provided data on chlorophyll concentration and primary productivity. Dr. M. M. Mullin provided plans to build the intake and vane for the pumping system. Dr. L. P. Atkinson provided the temperature data. The crew of the R/V *Blue Fin* contributed significantly to the success of our cruises. Ms. Suzanne McIntosh and Ms. Anna Boyette prepared the figures and Ms. Dannah McCauley typed the manuscript. We would like to thank all persons who were supportive, especially all those who participated in lowering and retrieving the 3-inch hose.

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