THE ROLE OF PELAGIC CRABS IN THE GRAZING OF PHYTOPLANKTON OFF BAJA CALIFORNIA[1]

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Abstract. The galatheid crab *Pleuroncodes planipes,* which occurs in very dense and extensive pelagic concentrations to the west of Baja California, is capable of filter-feeding on natural diatom blooms. Its filtering mechanism is similar to that previously known in *Porcellana.* It is only in regions of coastal diatom blooms that *Pleuroncodes* feeds exclusively on phytoplankton; elsewhere, it feeds on protista and zooplankters. A study of production and grazing in a coastal upwelling situation suggested that the observed zooplankton community would have been incapable of sustaining more than about 10% of the apparent grazing rate, and calculations based on estimated grazing rates for *Pleuroncodes* suggested that the observed standing stock of this species could go far towards supplying the remainder of the apparent grazing pressure. Pelagic crabs may thus, at least in certain situations, play a dominant role in grazing down diatom blooms in the southern part of the California Current.

Introduction

The galatheid crab *Pleuroncodes planipes* Stimpson occurs as adults in both benthic and pelagic phases to the west of Baja California in the California Current and to the east in the Gulf of California; its distribution and general biology have recently been reviewed by Boyd (1963) and by Longhurst (1966).

Laboratory observations indicate that in its benthic phase this crab is able to feed on detrital matter and on large organisms or parts of organisms from the benthic community, and that in both benthic and pelagic phases it can visually capture small and actively moving prey. Recent observations at sea off Baja California have shown that pelagic *Pleuroncodes* can capture single copepods (*Labidocera acutifrons*) by purposeful and directed snatching movements of its chelipeds.

Other genera of anomuran crabs have been shown to be capable of filter-feeding on suspended small particulate matter using the third maxilliped as the organ of filtration (Nichol 1932). Boyd (1963) demonstrated in the laboratory the ability of *Pleuroncodes planipes* to feed on suspended cells in unialgal cultures when the cells were large (30–80 μ) or in dense concentrations (10-μ cells at $> 10^5$ cells/ml). The observations of Beklemishev (1960) at sea indicated that small organisms such as radiolarians may at times form a significant part of the diet.

The purpose of the investigations reported in this paper was to establish the relative importance of phytoplankton in the diet of pelagic *Pleuroncodes.* It was realized that if phytoplankton did contribute a significant part of the diet then the great concentrations of these crabs, preyed upon very heavily by large predators including tropical tuna, might play a dominant role in the economy of the area, particularly in making available to such predators the energy derived from coastal upwellings, along a food chain with only one intermediate stage.

The Filtration Apparatus

The filtration mechanism, described briefly by Boyd (1963), proves upon reexamination to be essentially similar to that of *Porcellana longicornis* (Nicol 1932, Fig. 7a-d); filtration is achieved by a casting action of the fan-shaped endopodites of the third maxilliped, which beat in a manner recalling the feeding of barnacles in still water. Unlike *Porcellana,* in which the two appendages beat alternately, the casting action of the pair of appendages occurs simultaneously in *Pleuroncodes.*

In both genera the posteriad filtering stroke is made against an anteriad efferent current which emerges from the branchial chamber, thus increasing the effective length of the stroke and hence of the volume filtered during each stroke. This current is maintained by the scaphognathites of the second maxillae and of the third maxillipeds, and is augmented by the flagella of the second and third maxillipeds; during periods of quiescence the flagella beat during short (4- to 5-sec) bursts of activity every 15–30 sec, but when the crab is grazing very actively the beat of these flagella is continuous for periods of several minutes and the efferent current is much strengthened.

During the recovery stroke the filtering appendage is combed by the brushlike endopodite of the second maxilliped, again in a manner similar

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to that described by Nicol for *Porcellana*. Between each stroke this brush is itself combed clean by the endopodites of the first and second maxillae which are themselves in close conjunction during part of their stroke with the mandibular palps; food is apparently thrust into the mouth by these palps along two grooves in the anterior lip when the heavily chitinized mandibles are withdrawn.

The apertures of the filter itself are not very regular in a preserved specimen since they are formed by the apposition of two series of setules along each of the setae, but Nicol was struck by the manner in which the muscular control of homologous setae in *Porcellana* maintained the regularity and integrity of the filter. It is likely that the same is true of *Pleuroncodes* and that the effective filter aperture may be close to the distance between the units within a series of setules.

Examination of the filtration setules on the second maxillipeds of a specimen of *Pleuroncodes* having a standard carapace length of 2 cm shows that the apertures between them are about 30 μ wide. The normal filtration setules are replaced near the tip of each seta by a series of short, stout, thornlike setules having their tips only 3–4 μ apart, and it is difficult to see how these—which clearly cannot be opposed—can have a filtration function; they may be of service when the filtration fan is used to sweep large particulate matter from the deposits during benthic feeding.

It has been possible to confirm at sea the major features of the grazing behavior of pelagic individuals and to confirm the reality of the above description, which was based upon laboratory observations. In an aggregation of actively grazing pelagic crabs in an upwelling area off Baja California the individual crabs swam upwards to near the surface by abdominal flexion and then descended with outspread thoracic limbs, the fringing setae of which presumably slow the sinking rate; during the descent the crabs made grazing movements with their mouthparts which appeared to correspond with those observed in the laboratory. Virtually all the animals in such surface concentrations at night were behaving in this manner, so it is probable that individuals maintain themselves in the zone of most dense phytoplankton by this alternation of sinking and swimming back up again.

Grazing Experiments with Natural Phytoplankton

During two cruises to the west coast of Baja California in 1964 (Scripps Institution Cruises TO–64–1 and TO–64–2) some simple experiments were set up at sea to determine whether or not pelagic crabs were able to graze effectively on natural mixed-species phytoplankton populations. The only previous evidence of ability to graze was derived from Boyd's laboratory experiments with dense unialgal cultures

The principle of the experiments was to label natural phytoplankton with C–14 and to observe the reduction in particulate radioactivity in an experimental vessel in which one or more pelagic crabs had been allowed to graze during a 12-hr period overnight. The reduction in activity was assumed to be due to a reduction in cell number by grazing, an assumption checked in one experiment by an actual cell count.

Each experiment consisted of a series of 20-liter plastic containers set up at dusk, each with 7.5 liters of seawater from an area of a diatom bloom, in which the phytoplankton had been previously labelled by allowing 6 hr photosynthesis after the addition of 30 μc of C–14 per liter. The series of containers was arranged to contain from zero to eight crabs each, taken from individuals dip-netted at the ship's side out of a grazing population. The failure of the crabs to graze in some experiments could be traced to their having been held too long under crowded conditions before the start of the experiment, or to disturbance during the experimental period.

At dawn on the next day triplicate 250-ml samples were taken from each container, of which two were filtered on *Millipore* filters in the manner normal in productivity studies for subsequent counting of activity, while the third was preserved in Lugol's iodine for subsequent cell counts. In one of the experiments the above series was duplicated, the first being taken as described, the

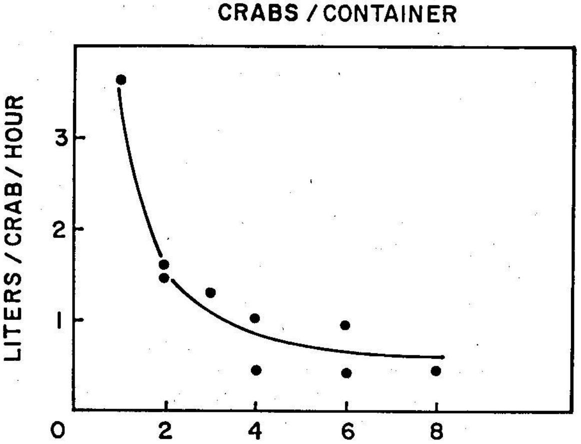

Fig. 1. Individual grazing rates of crabs at the indicated densities in each experimental container, expressed as liters cleared per hour; the rate is derived from the percentage decrease in particulate radioactivity at the end of the experiment compared with a blank container with no crabs.

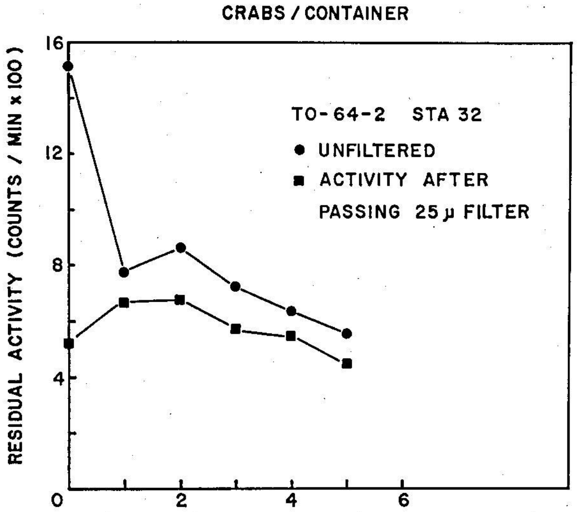

FIG. 2. Experimental data to show differential grazing on total phytoplankton and on cells smaller than 25 µ major diameter, determined by residual particulate radioactivity after a period of grazing, for a series of densities of crabs per container.

TABLE 1. Numbers of phytoplankton cells per ml in various experimental containers at station 32, TO–64–2, after 12 hr grazing by the indicated number of crabs per container, to show individual grazing rate as a function of the density of crabs in each container

Crabs per container	*Coscinodiscus*		*Ceratium*	
	Cells per ml	Percentage of cells removed per crab	Cells per ml	Percentage of cells removed per crab
0	101.4	—	8.52	—
1	39.1	61.4	3.48	59.1
2	44.8	27.9	2.45	35.5
3	55.3	15.2	1.05	29.2
4	45.1	13.9	1.31	21.1
5	63.5	7.5	2.30	14.5
6	62.5	6.4	3.75	9.3

second being taken from grazed water after it had been passed through a 25-µ *Nitex* filter.

The results of these experiments are shown in Figures 1 and 2. Grazing did occur under these conditions, and the ability to graze on natural phytoplankton was thus confirmed. It was hoped that useful data on the rate of grazing would be obtained from the experiments, but this hope was not realized and the apparent grazing rates are certainly too low for two reasons. Firstly, there is a very clear effect of crowding on the rate and it is very probable that there would have been an effect of container size in depressing the rate even in the case of a single crab per container. Secondly, later laboratory experiments on grazing rates on *Chaetoceros* cultures indicated that single crabs were able to clear all the cells available to them from 4 liters in 3–4 hr, so that, in the experiments described above, it is very probable that grazing ceased long before the end of the experimental period, for lack of any cells of suitable size left to graze.

The fractionation of the grazed water by means of a 25-µ filter indicated that virtually all the reduction in radioactivity by grazing was confined to the removal of cells large enough to be retained by such a filter: there was no grazing effect on organisms smaller than 25 µ (Fig. 2). This finding was consistent with the above-mentioned observations of Boyd (1963) and with those on the size of the filtration apertures.

From the composition of phytoplankton at the stations at which these experiments were made, it appears that the majority of the phytoplankton cells available for grazing by pelagic crabs were of the genera *Coscinodiscus* and *Ceratium*. The results of the cell counts from one of the grazing experiments (Table 1) show that these genera were, in fact, grazed down in the course of the experiment and that their reduction followed a pattern similar to that given by the radioactivity data. About 60% reduction in numbers was achieved by single crabs, representing a total of about 467.2×10^3 *Coscinodiscus* and 37.8×10^3 *Ceratium* cells consumed per crab per night.

Since the data from these experiments cannot satisfactorily be used to estimate grazing rates in nature the only direct evidence on such rates comes from observations on the rates of production of fecal matter by pelagic crabs at station 32 of cruise TO–64–2, situated in an area of strong diatom bloom off Magdalena Bay. Pelagic crabs, seen actively grazing, were dip-netted and placed in small glass containers containing natural phytoplankton, and their fecal pellets were collected every hour during a 4-hr period. The results showed that the rate of defecation was at first heavy but fell significantly after the first 2 hr; the initial high rate is taken to be similar to that during active grazing in the sea.

Examination of these fecal pellets showed that they were composed almost entirely of plant remains in which a large number of cells, both whole and broken, could be identified (Table 2). A maximum of 21.55×10^3 cells was counted in the first hour's production of fecal material by one crab, though this number was presumably very much lower than the number ingested. Determinations of the dry weight of fecal material produced showed a mean hourly rate over the first 2 hours' production of 4.29 mg per crab; assuming that this rate is not higher than that immediately before capture (and there is no reason why it should be), and that grazing is continuous during the day and night, then one may estimate that each

TABLE 2. Numbers of recognizable cells ($\times 10^3$) in 1 hr production of fecal pellets by four crabs, immediately following their capture from a population of actively grazing crabs

Kind of cells	Crab 1	Crab 2	Crab 3	Crab 4
Coscinodiscus	12.90	4.44	6.70	2.95
Melosira	1.40	0.45	0.75	0.05
Other diatoms	0.75	0.70	0.50	0.30
Ceratium	0.35	0.15	0.10	0.05
Peridinium	2.05	2.25	2.45	1.10
Dinophysis	0.25	0.85	0.85	0.15
Coccolithophoridae	2.50	1.35	0.95	0.40
Tintinnidae	1.35	0.90	0.20	0.45
Total	21.55	11.09	12.50	5.45

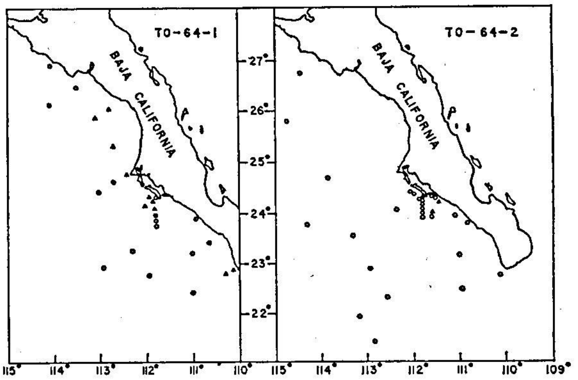

FIG. 3. The distribution of *Pleuroncodes* in the zooplankton samples within the survey area, June and August 1964, to show that those feeding predominantly on *Coscinodiscus* or other diatoms (triangles) were restricted to inshore areas.

crab produced approximately 102 mg of fecal material per day in nature while in an area of diatom bloom.

The dry weight of net-caught phytoplankton at this station was about 380 mg/m³, and thus the observed rate of defecation represents a filtration rate of approximately 270 liters per day, assuming no loss in weight of food material during digestion. In fact, of course, such loss occurs, and preliminary laboratory experiments indicate that it is about 50% on a dry weight basis during grazing on *Chaetoceros,* at rates of grazing comparable to those observed at sea. This figure is in agreement with what is known for other marine filter-feeding animals, in which it is commonly between 50% and 70% (e.g., Conover 1964). Thus, the real grazing rate to be deduced from these observations is probably nearer to 540 liters filtered per crab each day.

Such a volume seems to be very great, but a consideration of the filtration mechanism suggests that it is possible. At 20°C, near the environmental temperature, the rate of the beat of the filtration appendages is approximately 100 times per minute, and the effective volume of the space traversed during each beat is approximately 1 cm³ for a crab of 2 cm in standard carapace length. This implies that 100 ml per min or 6 liters per hr pass through the filter in still water; but since the filtration stroke is made against the efferent current of about 5 cm per sec, then the filtered volume is approximately trebled, giving a final estimate of 432 liters filtered per day, which is comparable with that given above.

GEOGRAPHICAL EXTENT OF GRAZING ON PHYTOPLANKTON

During the two 1964 cruises off Baja California, stomach contents were taken from a sample of pelagic crabs at each station at which they occurred in the standard zooplankton tows; the stomach contents were examined to determine the diet at each station and to identify the parts of the area surveyed in which phytoplankton was an important part of the diet. The survey areas (Fig. 3) comprised both oceanic and neritic, including upwelling-neritic, environments.

The stomach contents were sorted and each constituent ranked as absent, present, abundant, or dominant. The results indicate that the diet of the pelagic phase of *Pleuroncodes* is, in fact, very varied. Stomach contents were examined at 56 stations; they were entirely plant material at 9 stations and entirely zooplankton at 12 stations and a mixture of plant and animal remains at the remaining 35 stations.

The following list shows the number of stations at which each of the main components of the diet occurred:

Copepoda	41	Radiolaria	22
Diatomacea	36	Chaetognatha	17
Dinoflagellata	30	Silicoflagellata	15
Tintinnoidea	28	Coccolithophoridae	6
Euphausiidae	26	Pteropoda	2
Foraminifera	24	Ostracoda	1

In general, those organisms which occurred most often were also most often dominant in the stomach contents; thus, diatoms were dominant at 13 stations, and copepods at 11, followed by euphausiids, tintinnids and radiolarians on fewer occasions. Of the organisms which occasionally filled individual stomachs to the exclusion of other material, the large diatom *Coscinodiscus* sp., the copepods *Calanus helgolandicus, Pleuromamma* sp. and *Labidocera acutifrons,* and the euphausiid *Nyctiphanes simplex,* were the most common.

Figure 3 shows the distribution, during the two cruises, of pelagic crabs whose stomach contents were dominated by *Coscinodiscus* or other plant material. Such samples, it can be seen, were taken only near the coast in areas commonly occupied by local upwelling and diatom blooms, whereas farther offshore, or in non-upwelling coastal areas, the diet was more varied.

Total seston estimates made with a 35-μ mesh phytoplankton net during cruise TO–64–2 showed that the seston off Magdalena Bay was composed almost entirely of *Coscinodiscus* and that the standing stock here was higher than elsewhere in the survey area by a factor of 10, reaching a maximum of 380 mg/m^3 dry weight. This was the only area in which stomach contents were dominated by *Coscinodiscus* during this cruise.

In the oceanic areas to the west of the 1964 surveys, pelagic *Pleuroncodes* occur in the southwest trending California Current as far as 1,000 miles from the coastline (Longhurst 1966). Individuals from these oceanic regions were examined by Beklemishev (1960) who identified the stomach contents as containing spicules of radiolarians (*Acantharia*) and skeletons of foraminiferans (*Globigerina*) embedded in a greenish mass composed of their cytoplasm and symbiotic algal cells. Examinations of the stomach contents of pelagic crabs in the Scripps Institution collections taken near the Revillagigedo Islands, about 500 miles from the coast, showed that these individuals had been feeding upon radiolaria and oceanic microzooplankton, mainly small copepods of the genera *Pleuromamma, Microsetella* and *Corycaeus.*

GRAZING IN AN AREA OF COASTAL UPWELLING

The results discussed above establish the ability of *Pleuroncodes* to graze on natural phytoplankton, and indicate that such a means of nutrition is important only in areas close to the coast, probably for reasons connected with the occurrence of coastal upwelling and diatom blooms.

Areas in which active upwelling was occurring were found during the 1964 cruises at a number of points along the western coast of Baja California. In one such place, a few miles off Point Tosco (24°15′ N) the role of *Pleuroncodes* in the ecosystem was investigated during a 5-day period in which serial observations were made close to a drifting parachute drogue designed to follow the surface water. The wind velocity during this period did not exceed 6 knots. It can be estimated from unpublished calibration experiments of Daniel M. Brown at the Scripps Institution that this wind would have had a negligible effect on the path of the parachute drogue.

The drogue was set adrift in what appeared to be an area of intense local upwelling and the following observations were made beside it each midday and midnight: a normal hydrocast to near the bottom; determination of inorganic nutrient concentrations through the water column; level of primary production by the C–14 method at local noon; standing stock of phytoplankton from water samples; standing stock of zooplankton from an oblique meter-net haul.

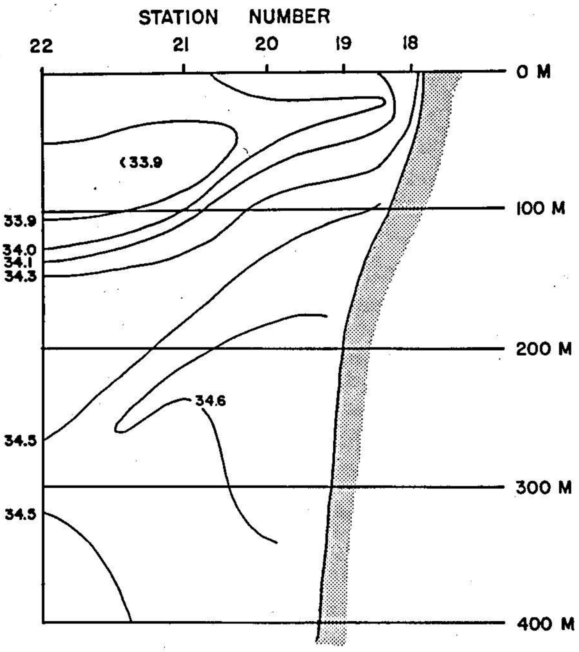

FIG. 4. Vertical salinity profile along a line of five stations running from Point Tosco to about 110 miles offshore, June 1964.

The hydrographic situation

Figures 4 and 5 show vertical profiles of salinity and temperature along a line of stations running seawards from Point Tosco. They show that coastal upwelling was occurring near the coast which was also evident from the horizontal distributions of surface properties. The isopleths show cold water of high salinity reaching the sea surface close to the coast; farther offshore, this water lies beneath warm water of low salinity which is characteristic of the California Current. After its arrival at the surface, the upwelled water appeared to move coastwise to the south and then into the bight behind Point Tosco, since this was the track of the drogue (Fig. 6). Property distributions on a larger scale showed that probably the upwelled water subsequently moved coastwise in a southerly direction, forming a tongue which was distinguishable in its biological and physical properties from the offshore surface water.

The hydrographic data from the drogue stations are consistent with their having been taken in a single parcel of upwelled water, with very few anomalies. During the 5 days of observations beside the drogue the changes in certain properties

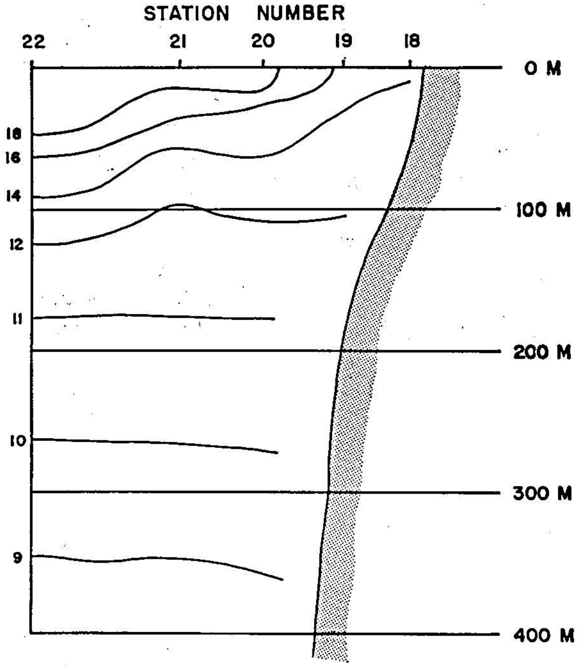

FIG. 5. Vertical temperature profile taken like salinity of Figure 4.

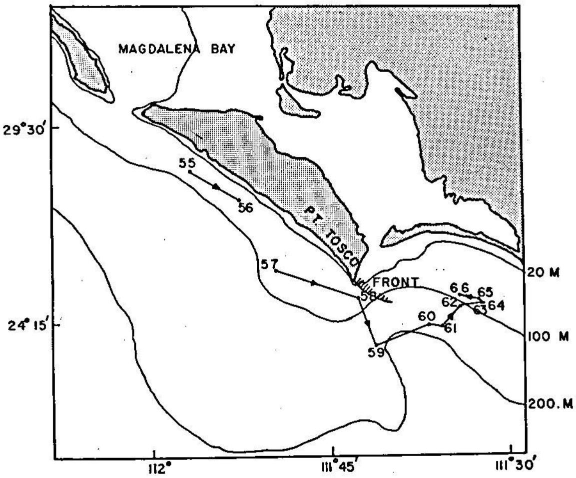

FIG. 6. The course of the parachute drogue at 10 m from 20–25 June 1964 off Point Tosco; between stations 56 and 57 the drogue was repositioned since it went into water too shallow for safety. A front between upwelled water and warm effluent from Magdalena Bay is indicated, but it was not crossed by the drogue.

of this upwelled water were similar to the spatial changes along the line of stations running seawards from Point Tosco; specifically, the surface water warmed from 14.84 to 16.75°C, and the nutrient concentrations decreased until values were reached which were similar to those found in the tongue of old upwelled water mentioned above. On the other hand, salinity changed very little at the drogue stations. It may reasonably be assumed that the observed changes represented the aging of upwelled water by biological and physical processes. The thermocline, when present, was weak; it occurred at depths (5–25 m) similar to those at which it was found in the offshore tongue of old upwelled water, and significantly shallower than the depths at which it occurred elsewhere. The level to which 1% of the illumination penetrated was approximately 13 m, so that the euphotic zone was extremely shallow.

Vertical stability, as measured by $E' = 10^{-3}\, d\sigma_t/dz$, of the upper 30 m of the water column increased throughout the period of observations due to the steady and continuous warming of the mixed layer by radiation. The implication of this

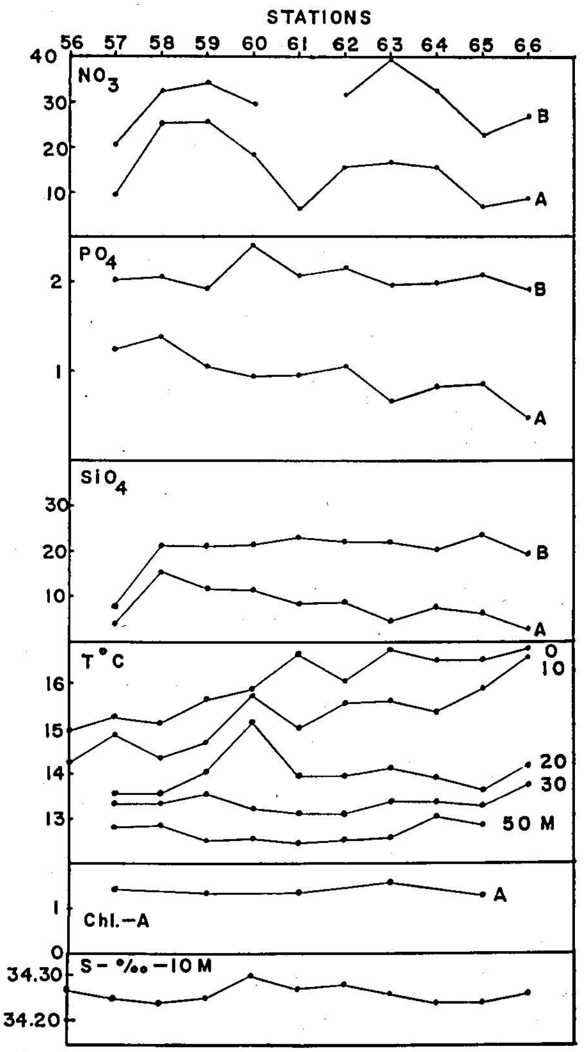

FIG. 7. Nutrient concentrations, mixed layer temperature and standing crop of chlorophyll-a at the drogue stations (2 stations per day); nutrient concentrations are expressed in μg at./liter and as mean values for 0–10 m (A) and for 20–50 m (B) depth ranges; chlorophyll-a expressed in mg/m³, and salinity in parts per thousand.

TABLE 3. Composition of the major components of the phytoplankton at drogue stations. (Cell volumes from original measurements)

Species	Stations 57	59	61	63	65	Avg
Cell volume as percentage of total						
Coscinodiscus excentricus	45.5	49.3	26.3	53.5	60.5	47.06
Nitzschia spp.	0.3	0.1	0.1	0.3	0.6	0.30
Tripodonesis spp.	35.0	37.1	57.2	37.0	22.1	37.68
	80.8	86.5	83.6	90.8	83.2	85.04
Number of cells/m³ × 10⁹						
Nitzschia pacifica + *pungens*	21.2	5.8	10.2	22.7	31.5	18.28
Nitzschia closterium	5.9	4.7	3.2	23.7	14.6	10.42
Leptocylindrica danica	6.7	8.7	7.2	1.2	1.4	5.04
Coscinodiscus excentricus	2.6	4.3	3.4	5.8	5.3	4.30
Coscinosira and *Actinopticus*	2.9	5.5	7.7	2.4	1.8	4.06
Total, all cells including nannoplankton	49.6	37.1	52.6	65.5	68.0	54.56

stability, and of the virtually unchanging salinity of the mixed layer (Fig. 7), is that the effects of vertical advection or diffusion must have been negligible.

Fig. 7 shows the changes that occurred in the concentrations of nitrate, phosphate and silicate during the study; values for nitrite and ammonia remained rather constant throughout. The selective depletion of these nutrients and the fact that depletion was restricted to the euphotic zone support the suggestion that such changes were the result of biological activity. The values at the start of the series of observations were within the ranges found as maxima at other upwelling sites during the same cruise, while those at the end were within the range of values found in the tongue of old upwelled water.

Nature of the phytoplankton bloom

The presence of an active bloom of diatoms was very evident from the olive-green turbidity and the odor of the water as compared with the clarity and freshness of offshore water. This bloom was found to be dominated by the diatom *Coscinodiscus excentricus.*

The phytoplankters with a major diameter exceeding 5 μ (that is, with a cell volume exceeding about 125 μ^3) comprised 15 genera and 24 species of Diatomaceae, 6 genera of Dinoflagellata, and an undetermined number of taxa of Silicoflagellata. The data in Table 3 show that a high percentage of the total cell volume was contributed by a very few species, principally of diatoms.

Table 4 shows that the relationship between the daily level of carbon fixation and the standing stock at noon was approximately 1:3, indicating that the bloom was proceeding very rapidly, which is consistent with the data on the uptake of nutrients. There appears to have been some recycling of nutrients, for the apparent uptake was at the following ratio: C, 38.3; N, 19.1; P, 2.4. This gives an atomic ratio of C:N:P of approximately 15:8:1 which is rather different from published C:N:P ratios (e.g., Strickland 1960). However, there is nothing in the data to suggest that the simple thesis of uptake of nutrients to near depletion by the phytoplankton bloom is not correct.

An estimate of the amount of grazing that must have been occurring can be made from the daily difference between the potential standing stock of phytoplankton—that is, the amount of production added to the standing stock at the beginning of the day—and the actual stock at the end of each day; the mean value for this difference (Table 4) during the 5-day period was 23%, equivalent to 230 liters grazed clear per m³, or 184 mg dry weight per m³ per day assuming a dry weight: carbon ratio of 2 (e.g., Banse 1962).

TABLE 4. Data from chlorophyll-a observations at the drogue stations to show the relationship between standing stock, production and apparent grazing; all stations taken at local noon, 20–25 June 1964

Property	Stations 57	59	61	63	65	Avg
1. Chlorophyll standing stock, in mg/m³	1.21	1.17	1.17	1.28	1.15	1.19
2. Carbon standing stock, from cell counts and volumes, in mg/m³	190.0	282.0	436.0	343.0	292.0	308.0
3. Carbon fixation, by C–14 technique, in mg/m³ per day	115.0	91.0	98.0	86.0	70.0	92.0
4. Potential carbon standing stock, (2+3 above) in mg/m³	—	305.0	373.0	534.0	429.0	400.0
5. Carbon/chlorophyll–a ratio	157.0	241.0	362.0	268.0	254.0	258.0
6. Carbon, in cells, available for grazing (4−2 above)	—	—	—	—	—	92.0
7. Fraction grazed daily, in liters/m³ (6/4 above)	—	—	—	—	—	230.0

TABLE 5. Composition of the zooplankton community at the drogue stations as sampled by a standard 1-m net, expressed as individuals/m^3 and as a percentage; below, dry weight as mg/m^3 and as percentage

Taxa	Individuals /m^3	%
Herbivores (filter-feeders)		
Copepoda		
Calanus helgolandicus	114.8	76.68
Acartia tonsa	13.4	8.94
Clausocalanus spp.	6.4	4.26
Other species	2.5	1.64
Total copepods	137.1	91.52
Decapoda		
Nyctiphanes simplex	2.1	1.43
Mysidaceae	6.5	4.38
Total decapods	8.6	5.81
Mollusca		
Limacina spp.	0.2	0.11
Tunicata		
Oikopleura, Fritillaria	0.9	0.58
Total herbivores	146.8	98.02
Particulate feeders and carnivores		
Copepoda		
Euchaeta, Heterorhabdus, Labidocera spp.	1.3	0.88
Chaetognatha		
Sagitta euneritica and some *S. enflata*	0.9	0.65
Miscellaneous		
Coelenterata, Annelida, Amphipoda, etc.	0.5	0.26
Total particulate feeders	2.7	1.79
Biomass as dry weight	mg/m^3	%
Copepoda	15.98	76.68
Euphausiidae	2.86	13.72
Other Crustacea	1.72	7.86
Tunicata	0.04	0.40
Coelenterata	0.10	0.10
Chaetognatha	0.14	0.60
Total	20.84	99.36

The grazing organisms

The zooplankton community was of the unstable structure typical of areas of active primary production, having a very low specific and generic diversity and a negligibly small percentage of predatory organisms. The standing stock was high relative to that of the zooplankton of neighboring oligotrophic areas.

In the 10 hauls made with a meter net (0.3-mm mesh) at the drogue stations a total of only 39 species was taken, with never more than 20 species in a single haul; this was about one quarter of the numbers of species identified per haul in offshore and oceanic regions in the same survey cruise.

Table 5 shows that the filter-feeding copepod *Calanus helgolandicus* (*sens. lat.*) dominated the zooplankton, comprising 76.7% of all individuals, and that filter-feeding copepods formed 91.5% of all individuals, or about 75% of the total dry weight of the plankton. The euphausiid *Nyctiphanes simplex* and an unidentified mysid, both facultative filter-feeders, formed a further 8.6% of the individuals and 14% of the dry weight.

TABLE 6. *Calanus helgolandicus;* percentage composition of population by growth stages (III–VI) at the successive drogue stations

Stations	Stages						
				VI			
	III	IV	V	♀	♂	Total	N/m^3
55	1.2	6.7	37.4	8.0	46.6	54.6	43.5
56	—	2.5	12.5	55.0	30.0	85.0	6.0
57	4.0	15.4	36.2	17.4	26.8	44.2	65.9
58	4.0	12.1	42.2	12.1	28.3	40.4	98.4
59	0.5	3.3	37.5	34.2	24.1	58.3	75.4
60	—	1.1	52.7	23.0	23.0	46.0	37.3
61	1.0	13.7	48.6	13.7	22.9	36.6	55.6
62	1.3	6.9	48.1	18.9	24.6	43.5	43.9
63	—	2.6	31.9	25.0	40.4	65.4	603.1
64	0.5	2.1	25.3	41.9	30.1	72.0	250.3
65	1.0	12.5	30.8	21.1	34.6	55.7	11.3
66	1.3	12.6	32.4	23.2	31.8	55.0	87.0

The population of *Calanus helgolandicus* included a number of growth stages (Table 6) and the relative proportions of these remained essentially the same throughout the drogue experiment, though some day-to-day variation occurred; the between-haul variation in numbers of *Calanus* indicated that the population was highly aggregated and that swarms occurred which were denser than the background population by a factor of almost 100. The data do not show that such swarms were of a different composition of growth stages than the rest of the population.

The nekton was dominated by *Pleuroncodes* in its pelagic phase; this species was seen at night on the surface in dense concentrations and it occurred in the zooplankton hauls at every station. As with *Calanus,* the numbers of pelagic crabs varied considerably between hauls, by a factor of about 10, having a mean value of about one crab per 3 m^3; this density corresponds to a biomass of 192 mg/m^3 dry weight. Although the number of individuals was negligibly small compared with those of the zooplankton the contribution of *Pleuroncodes* to the total plankton-nekton dry weight was 89.4%, and at no station did its contribution to the total dry weight fall below 80%.

There were, presumably, other organisms present in the area which were capable of grazing on the phytoplankton bloom but which were not sampled by the procedure followed; in particular, clupeid fishes of the genus *Engraulis* may have been present, though no surface shoals were seen nor were any observed on the echo sounder. Fish-eating birds (e.g., *Pelecanus occidentalis*) were not present in sufficient numbers as to suggest important concentrations of small shoaling fish.

In fact, the majority of sea birds present were Tubinares, which presumably fed upon surface plankton.

The grazing process

The following examination of the grazing budget at the drogue stations necessarily ignores two elements of possible importance in the overall trophic web: the dissolved or small particulate nonliving organic matter in suspension which may, as Jorgensen (1962) suggests, heavily outweigh the living particulate matter; and the microzooplankton organisms which are capable of passing the meshes of the zooplankton net used, and which Banse (1962) suggests may outweigh the macrozooplankton by several times under certain conditions.

For the purpose of estimating their grazing capacity, all the herbivorous copepods present are assumed to have the same grazing characteristics as *Calanus helgolandicus;* this probably overestimates the overall copepod grazing intensity since the next most abundant species was the relatively small *Acartia tonsa.*

The potential grazing rate of *Calanus* of the size and form of the Pacific coast population of *C. helgolandicus* has been very variously estimated, from the early results (Fuller and Clark 1936) of less than 10 ml cleared per day to the calculated rates of more than 1 liter per day based upon the encounter theory of Cushing (1959). Obviously, the rate obtaining at any one time is a function of a set of factors as yet improperly understood—container size, concentration and type of available phytoplankton, past history, metabolic needs of the moment and so on—but it is reasonable to assume the rather high rate of 250 ml/day per copepod (e.g., Mullin 1963) when all conditions favor high grazing rates, and this assumption is made here.

The herbivorous copepods at the drogue stations, having an average population density of 137/m^3 (Table 5) should thus have been capable of clearing approximately 34.3 liters/m^3 per day. This clearing would have been restricted to the removal of organisms larger than about 3–4 μ in major diameter, assuming the filtration apparatus to have the same aperture size as in *Calanus finmarchicus* (Marshall and Orr 1955a).

Using the value for total dry weight of phytoplankton of 616 mg/m^3 (Table 4, using a conversion factor of 2 from carbon to dry weight) the grazing rate as estimated above implies a removal of 21.12 mg/m^3 per day or 0.154 mg per copepod, as dry weight of phytoplankton. From the cell numbers per m^3 shown in Table 3 it is evident that the same grazing rate implies a removal of 18.75×10^9 phytoplankton cells per m^3 or 1.47×10^9 *Coscinodiscus excentricus* per m^3 per day. This is equivalent to 1.07×10^7 *Coscinodiscus* cells per copepod per day, a rather high figure for such large cells (Marshall and Orr 1955b).

The average dry weight of a single copepod in the population was 0.116 mg, which is rather less than the apparent daily intake of 0.154 mg dry weight of phytoplankton per copepod calculated above. References in literature (e.g., Marshall and Orr 1955a, 1955b; Beklemishev 1960) suggest that, although the basic metabolic needs of a copepod may be met by an intake of 5% of the body dry weight daily, the fecal pellet production under certain conditions may rise to twice the volume of the organism daily; such observations show that the calculated rate of intake of 0.154 mg dry weight daily is not an unlikely figure.

Apart from the copepods the main group of grazing organisms in the plankton were the euphausiids and mysids, present at about eight individuals per m^3 (Table 5); filtration rates of these organisms are much less well known than for calanoids and an estimate of their grazing rate is perhaps best based on what is known of their metabolic requirements. Lasker (pers. comm.) has data for *Euphausia pacifica* which indicate that an intake of approximately 6% of the dry body weight will satisfy basic metabolic and growth needs, and that an individual scarcely exceeds this intake even under the most favorable conditions of food supply; the dry weight of euphausiids and mysids in the plankton was 2.86 mg/m^3 (Table 5) and Lasker's figure suggests that their intake would be limited to about 0.17 mg/m^3 per day which represents a filtration rate of less than 1 liter per m^3 per day at the observed level of standing crop of phytoplankton.

The inference to be drawn from the above discussion is that the zooplankton population had a potential grazing rate far below that required to explain the phytoplankton data of Table 4, and can hardly have cleared more than about 35 liters per m^3 per day.

The role of *Pleuroncodes* in the ecosystem may now be examined by reference to the grazing rate previously estimated from the rate of production of fecal material. This rate is 540 liters per day for each crab, which indicates a daily intake of dry weight phytoplankton of 332.6 mg per crab at the observed level of phytoplankton standing stock. This intake is credible, because later laboratory tests with a culture of the diatom *Chaetoceros* showed that single *Pleuroncodes* were able to ingest these diatoms at rates of from 23–33 mg dry weight per hr, or 552–790 mg per day.

TABLE 7. Standing stock of various trophic levels and simplified grazing budget at the drogue stations

Organisms	Standing stock (mg dry weight /m^3)	Grazing rate (liters/m^3 per day)
Phytoplankton ($\leq 5\mu$)	616	−230[a]
Zooplankton:		
Herbivorous copepods	16	≤34
Euphausiids, mysids	3	1
Nekton:		
Pleuroncodes	192	178
Clupeid fish		
Total grazers	211	213

[a] The phytoplankton were growing at a rate which would have increased their standing stock by 23% per day. This growth can be expressed as a negative grazing rate, -0.23×1000 liters/m^3 which is equal to -230 liters/m^3 per day.

At the observed density of *Pleuroncodes* of 0.33 individuals/m^3 the grazing rate suggested above implies a clearance by grazing due to this species of 178.2 liters/m^3 day. This indicates that the population of *Pleuroncodes* was capable of grazing most of the difference between the grazing potential of the zooplankton and the total amount of phytoplankton removed by grazing (Table 7).

The microzooplankton capable of passing the meshes of the net used were not measured directly, but it is unlikely that such small organisms could have exerted a significant grazing pressure on a phytoplankton community so dominated by the very large diatom *Coscinodiscus excentricus,* as was that at the drogue stations.

DISCUSSION

These conclusions show that it is *Pleuroncodes* which is the most important grazing organism in the coastal upwellings at the southern end of the California Current, or at least that it is capable of so being; during normal years it is likely to be a dominant grazer southwards from Point San Eugenio, and during warm years (as 1958–1960) the grazing effect of the species may extend much farther to the north, perhaps as far as southern California.

The productivity of the California Current, as of other eastern boundary currents, depends on blooms of diatoms which occur in coastal upwelling situations. It is also characteristic of eastern boundary currents in low latitudes that they should support large populations of clupeid fishes which feed, at least for part of their diet, directly on the blooms of diatoms. It seems possible that the very large populations of *Pleuroncodes* present in the California Current are analogous to such clupeid populations and may play an important role in the utilization of the energy made available by primary production.

It is impossible with the presently available data to quantify the above statements; that the population of pelagic *Pleuroncodes* is extremely numerous is evident from many reports (e.g., Beklemishev 1960) of encounters with massive concentrations at sea, and as Shimada (quoted by Boyd 1963) wrote "a ship may sometimes appear to crunch through almost solid masses of crabs for miles on end." Blackburn (pers. comm.) found that *Pleuroncodes* form over 80% by volume of all micronekton taken off Baja California, and that here the standing crop of total micronekton is higher than anywhere else in the eastern tropical Pacific Ocean.

The importance of *Pleuroncodes* in the diet of many predatory animals in this area is well known: grey whales (Matthews 1932); albacore (McHugh 1952); yellowfin (Alverson 1963), reef fishes of various species (Quast MS quoted by Boyd 1963), yellowtail and dolphin (Longhurst unpublished); sea lions, gulls and pelicans (Boyd 1963); turtles (Fager, pers. comm.) and presumably others all feed readily on *Pleuroncodes.*

The numbers of crabs found by Alverson in the stomachs of yellowfin alone show that very great quantities of *Pleuroncodes* are taken by their predators; the mean volume of crabs contained in each yellowfin stomach examined was about 0.5 liters or (approximately 100 crabs). This figure must be less than the daily intake for each fish, in a population which yielded about 3.99×10^6 fish in 1960 to the American fishery off Baja California alone. Extrapolation from such figures to obtain an estimate of the weight or numbers of *Pleuroncodes* grazed down each year by the yellowfin stock would be possible, but would contain so many assumptions as to be of very doubtful value. It is certain that the figure is very high indeed and all the evidence suggests that *Pleuroncodes* play a dominant role in the biological economy of the area. Probably their extensive movements into oceanic regions enables them to transport far offshore the organic material accumulated while grazing in coastal upwellings, and to make available the energy so derived to pelagic fishes which are unable themselves to enter the cold and turbid upwelled water.

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ZONATION OF NEARSHORE MYSIDS[1]

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Abstract. Between the shore and 17 m depth, over sand bottom on the open coast of southern California, five species of hypopelagic mysids and four species of benthic mysids occurred in bathymetric zones roughly parallel with the shore. The possible causes and function of zonation of the numerically dominant pelagic species were examined. The information suggests that the zonation may have developed as observed mainly in response to the pattern of availability of food that was imposed by the nearshore circulation system, and that competitive exclusion of other pelagic species occurred. The zonation may provide a situation wherein population control can be effected by changes in reproduction rate.

INTRODUCTION

Major aspects of the ecology of mobile marine animals are concerned with spatial patterns. Studies of oceanic zoogeography (Johnson and Brinton 1963), community relations (Fager 1963) and productivity (Riley 1963) all deal with populations that are ordered in space rather than being randomly distributed (Hardy and Gunther 1935; Barnes and Marshall 1951; Bainbridge 1952; Cassie 1959). Little is known about the causes of nonrandom distributions in mobile marine invertebrates.

The mysids investigated here were ordered in space in three ways: usually they remained near the sea bottom; they were zoned with respect to depth of water; and the pelagic species formed schools within zones. This report describes bathymetric zonation, examines some environmental factors associated with the distribution of the numerically dominant pelagic species, and discusses the possible causes and function of the zonation.

STUDY AREA

Field collections and observations were made along three transect lines perpendicular to shore on the intercanyon shelf in the La Jolla bight (Fig. 1). Surf is higher and waves break farther from shore in the central area of the intercanyon shelf (*B*-range), because of convergence there, than near the canyon heads (*A* and *C* ranges), where the waves diverge (Munk and Traylor 1947).

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