

Aggregation of pelagic *Munida gregaria* (Fabricius) (Decapoda, Anomura) by coastal fronts and internal waves

John R. Zeldis and John B. Jillett

Portobello Marine Laboratory, University of Otago, Dunedin, New Zealand

(Received November 1981; accepted April 1982)

Abstract. Aerial photographic surveys were used to study the distribution and abundance of the near-surface shoaling juvenile phase of the galatheid crab *Munida gregaria* in southeastern N.Z. continental shelf waters. On numerous occasions shoals were concentrated into aggregations many metres to a few kilometres long at river plume and headland fronts, and in mid-shelf internal waves. Laboratory experiments established that *M. gregaria* juveniles showed strong positive phototaxis and that they could sustain swimming speeds of $\approx 16 \text{ cm s}^{-1}$. Field experiments showed that when *M. gregaria* were displaced to deeper waters, their response was to swim back towards the surface. These results suggest that juveniles swept into convergent zones would resist downward displacement. Since convergent zones occur at coastal front and internal wave sites this mechanism could explain the aggregations of shoals observed and photographed from the air. This mechanism is discussed in relation to literature on physical processes at such sites and to studies of plankton distribution and behaviour.

Introduction

Massive shoals of the post-metamorphic phase (juveniles) of the galatheid crab *Munida gregaria* (Fabricius, 1793) are present in continental shelf surface waters of southeastern New Zealand nearly every summer prior to settling to the bottom (Williams, 1980). Since these animals are bright red and occur in dense shoals at the surface during daylight, aerial surveys were used to study their distribution and abundance as part of a wider study of the population dynamics of *M. gregaria*. Our observations from the air indicated that in many instances the shape, size and orientation of *M. gregaria* patches reflected the effects of recognisable coastal fronts and internal waves. Here, we present results from these surveys and discuss them in the light of laboratory and field experiments on the tactic responses of *M. gregaria*.

In this paper, the term "shoal" is used to describe clusters less than a few square metres in area and the term "aggregation" is used to describe a group of shoals arranged in a formation many metres to a few kilometres in longest dimension. The term "patch" is used in a general sense.

Methods

Aerial surveys

Nine flights were made during this study (1978–1981) along various sections of the east coast of the South Island of New Zealand between Nugget Point and Banks Peninsula (the study area, Figure 1). Aerial observations were undertaken in the months December through April when pelagic juveniles were known to be present. Flights were made on clear mornings with little wind. These surveys provided information on:

- (1) the general geographic position of aggregations of *M. gregaria* in the study area in longshore and offshore directions,
- (2) the precise shape and orientation of the aggregations in relation to coastal and near surface features and
- (3) the sea area occupied by shoals for use in biomass estimates of pelagic *M. gregaria*.

Biomass estimates are not considered here. Flights were made in highwing aircraft (Cessna 172 or 182) with either a photographic floor hatch or an opening window. Searching flight paths 5–8 km offshore were selected because plankton tow data consistently indicated that by mid-summer pelagic juveniles were restricted to these nearshore waters (unpublished results). Several seaward excursions failed to locate shoals beyond 12 km from the coastline. Searching altitude was usually between 900 m and 1500 m, from which height shoals could be sighted 3–4 km on either side of the aircraft, depending on shoal depth, sea surface state and sun direction and angle. Once shoals were encountered, the altitude was adjusted to allow synoptic photography of large portions of shoal zones (from around 2100 m) or detailed study (600–900 m).

Cameras used were hand-held, 35 mm format (Ashahi Pentax, models Spotmatic F and K 1000) fitted with 50 mm, 35 mm or 28 mm lenses and a polarising filter to improve sea surface penetration. High speed film (Ektachrome 200 or 400 ASA) was used because of low reflected light levels from the sea even on cloudless days.

Subsequent analysis of the photographs used the following information:

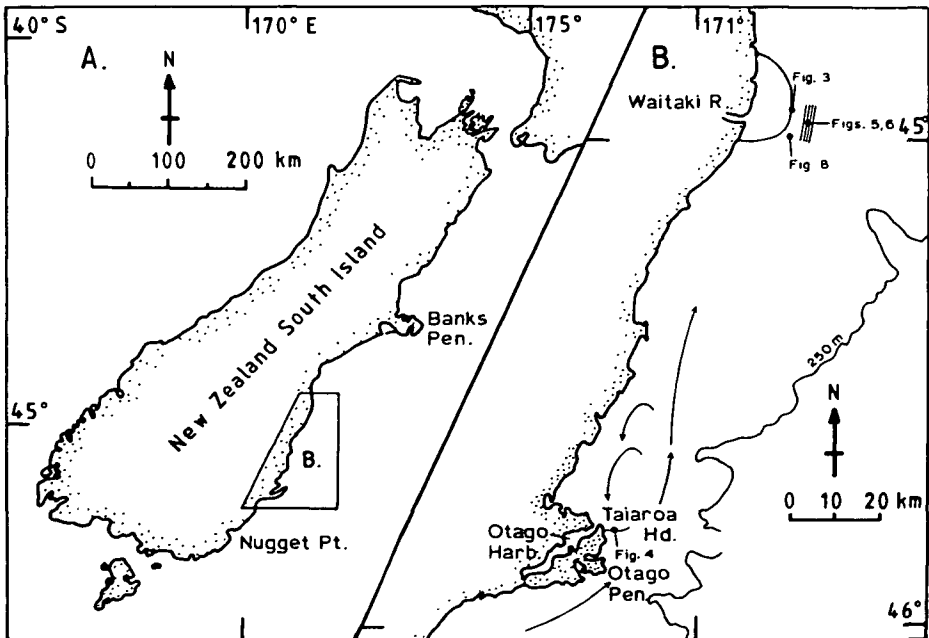


Fig. 1. A. Location of study area in New Zealand (Banks Peninsula to Nugget Point). B. Place, figure locations and hydrographic features referred to in this study.

altitude, time, compass bearing and approximate position of the aircraft. Observed aggregations and relevant sea surface features were mapped.

Laboratory and field experiments

A series of experiments was designed to study:

1. the relative importance of current and light direction in determining the swimming orientation of individuals,
2. the swimming ability of individuals and
3. the response of groups of animals when displaced from surface to deeper water.

A current flume was used to investigate points 1 and 2. This apparatus (Figure 2) was similar to that described by Arnold (1969) but was smaller and simpler. It was installed in a light-tight room supplied with running seawater. The construction and circulation system of the flume was as follows: from a sump tank (125 cm x 110 cm x 35 cm) a submersible pump (output 383 l min⁻¹) supplied seawater to the bottom of the stilling tank through a 4 cm i.d. rubber hose ending with a T-piece. The stilling tank (95 cm x 57 cm x 45 cm) was divided by 3 screens to still turbulence. The first screen was of marine plywood drilled with 2.3 cm holes at 3.0 cm centres, the second of woven 3 mm mesh and the third of 800 μm nylon mesh. After passing the third screen the water either returned to the sump tank through an adjustable ball-valve (6 cm i.d.) and a 5.5 cm i.d. pipe, or entered a flat sided horn and flowed into the flume. Water flowed along the flume (6 mm clear perspex, 90 cm x 15.5 cm x 17.5 cm), spilled over a 9 cm high wooden weir into a drain tank and then back into the sump *via* a 5 cm i.d. pipe. Fresh seawater was slowly circulated through the system *via* the sump inlet. The flume was marked along its length into 5 cm divisions to track the positions of experimental animals and the drain tank was covered by a net to catch animals swept from the flume. By opening or closing the stilling tank valve current speed in the flume could be varied between 7.3 and 21.1 cm s⁻¹. Current speeds at various valve settings were determined by timing the passage of fine bubbles as they traversed a 50 cm long segment of the flume.

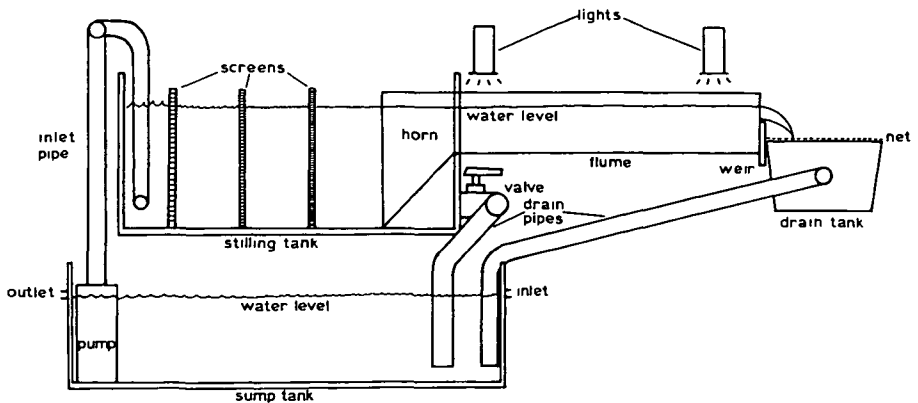


Fig. 2. Diagram of current flume apparatus (side view, see text for description).

Lighting was provided by 2 microscope spotlights (tungsten, Olympus Tokyo) shining vertically downward, one near either end of the flume, 22 cm above the surface of the water. The lights were fitted with filters (70 cyan) to approximate the spectral distribution of midday sunlight at 1 m depth in seawater as measured using a Melico PM2A colour analyzer beneath a perspex aquarium with shrouded sides.

Measurements of filtered light intensity within the flume at half its depth were made with an underwater light meter (Li-Cor 185A) with the quantum millivolt cosinus sensor pointed at the light source. When only one light was on the intensity was $21.6 \mu\text{E m}^{-2} \text{s}^{-1}$ immediately beneath and fell to 5.0 and $0.03 \mu\text{E m}^{-2} \text{s}^{-1}$ at 5 and 80 cm distances along the flume. Although a strong light gradient was established in the flume the absolute intensity was low compared with that at 1 m depth in sunlight sea around midday (Table I).

Batches of pelagic juveniles were brought into the laboratory from Otago Harbour. Individual animals were successively introduced into the flume where their responses to current and light direction were tested, and their maximum swimming speed was determined. Each animal was introduced to the centre of the flume with both lights on and with the current speed set at minimum. After the animal had swum to one end of the flume or the other, its position was noted and the right hand light (downstream) was switched off. Thirty seconds later the lighting was reversed, and after a further 30 s reversed again, with the animal's position noted at the end of each 30 s interval.

After each animal was tested for its tactic responses its swimming speed was estimated. The animal was attracted to the lefthand (upstream) light and the current velocity increased stepwise every 30 s. When the animal was no longer able to maintain its position under the light the corresponding current velocity was taken as the maximum sustainable swimming speed. The carapace length of each animal tested was then measured.

Responses of groups of juveniles to vertical displacement were investigated in the field by diving with SCUBA in the main shipping channel of Otago Harbour (depth 10–40 m). Dives were made at 1400 h on 22.1.81 and 1130 h on 24.1.81. Groups of 100–1000 juveniles were hand netted by a diver who took them down

Table I. Downward and upward irradiances and their percentage with depth.

Depth (m)	Irradiance ($\mu\text{E m}^{-2} \text{s}^{-1}$)		% up/down
	Downward	Upward	
1	450	16	3.5
2	330	14	4.1
3	200	13	6.5
4	150	11	7.3
6	84	18	21.4
7	75	12	16.0
8	75	7	9.3
9	42	8	19.0
10	30	3	10.0

to a predetermined depth where they were released after which the responses of the animals were noted. Light intensity profiles over the depth range studied were made on 24.1.81 with the light meter and sensor described previously. Both downward and upward horizontal irradiance profiles were made, to compare the relative amounts of light coming from above and reflected from below. On 22.1.81 skies were partly cloudy, on 24.1.81 skies were clear except for occasional cloud.

Results

Aerial surveys

Aerial surveys proved to be very effective for studying the precise arrangement and distribution of shoals. The photomosaic in Figure 3 shows most of an aggregation of pelagic *M. gregaria* directly seaward (East) of the Waitaki River mouth (Figure 1B) on 25.1.79 from 670 m altitude. This aggregation was associated with the sharp front formed between riverine plume water and receiving ambient coastal water at the most seaward extent of the plume, ~ 10 km from shore. The plume of riverine water appeared light blue and was approximately semi-circular in shape, intercepting the coast ~ 10 km north (down current) of the river mouth. The southern coastal intercept could not be seen clearly but from other flights the plume typically extends no further than 1 or 2 km south of the river mouth, depending on the state of tide.

The linear aggregation in Figure 3 was composed of a continuous 5 km long series of shoals orientated in a north-south direction. In the south, the aggregation appeared as a broad arc dissociated from the river plume front. Further north these two features became congruent and tightly associated with one another over a distance of some 2 km. In the north the shoals were dissociated from the front and more dispersed than elsewhere in the aggregation. The precise dynamics of the relative motions between the front and the shoals were unclear. It was evident though that the front was exerting an "organising" influence (see **Discussion**) on the shoals and it appeared that the shoals near the south end had recently encountered this influence judging by their extreme linearity and continuity with the segment of the aggregation directly at the front. It also appeared that the shoals at the northern end had not been influenced by the front except at their extreme westward edge. Generally, in the northern and middle segments, *M. gregaria* shoals were aggregated at the front itself but some were also visible within or beneath the plume water and in ambient coastal water. This suggests that the retention of *M. gregaria* at the front was only temporary.

Shoals of *M. gregaria* were observed in association with visible fronts on numerous occasions, their aggregation usually being more intense at the immediate frontal boundary than on either side. A further example of frontal aggregation (Figure 4) was photographed on 24.4.79 from 1130 m altitude approximately 1.5 km S.E. of Taiaroa Head, an area where fronts were frequently observed during the study. In this area it is thought that headland fronts form where an inshore, southward moving counter-current in the lee of the Otago Peninsula converges with the inner edge of the northward mainstream of the

Southland Current. Drift card and fish egg distribution studies (Robertson, 1980) and hydrographic and satellite imagery studies (Murdoch, Jillett and Zeldis, unpublished observations) all confirm this interpretation of circulation patterns in this area. Again the *M. gregaria* shoals were highly concentrated at the front and also in its immediate vicinity.

Extensive plumes of river water were commonly seen within the study area on all flights and internal wave activity was often visibly associated with them. Internal waves were usually arranged in multiple light and dark blue alternating bands, the light bands often manifested at the surface by slicks. Since the orientation of the band bore no consistent relationship to surface swell or wind direction it is unlikely that they were caused by Langmuir cell circulation (Langmuir, 1938). The bands were usually curved into meanders or severely perturbed, often by interactions with other internal waves differing in direction and wavelength. Internal waves were usually grouped into packets of 5–30 visible bands and typically their wavelength decreased across the packet. This decrease in wavelength indicates the direction of propagation of the waves (Apel *et al.*, 1975) with the longest wavelength at the leading edge of the packet.

Nine sites of internal wave activity were photographed in this study, all associated with plumes from major rivers. Seven sites were near the Waitaki River mouth and, of these, four had associated shoals orientated in long lines parallel with light-dark banding and conforming to meanders in the internal wave pattern. One particularly striking aggregation (Figures 5 and 6) was photographed on 9.1.81 at the leading edge of a 27 wave packet heading shoreward ~ 12 km from the Waitaki River mouth. The shoals were aggregated at the leading edge of the light blue bands which were seen as the slick-lines in more oblique photographs. This association with slick-lines is consistent with our other observations of *M. gregaria* – internal wave interactions. *M. gregaria* were seen clearly in only the first 6 waves of the packet suggesting a “sweeping up” effect of disorganised shoals by the passage of the first few waves. Other photographs of this event showed irregular patches in front of the leading two waves and none behind them. It is significant that this wave packet was photographed ~ 1.5 h earlier than the photographs in Figure 5. At that time no shoals were associated with the waves suggesting a rapid formation time for the aggregations.

During this study shoals were frequently associated with sea surface slicks but in most cases the cause of the slicks was not obvious. On a few occasions multiple *M. gregaria* aggregations were seen orientated approximately parallel to surface wind direction, as judged by wind swell direction. In no case, however, were the aggregations and associated slicks sufficiently concordant with wind direction to have been definitely caused by Langmuir circulations, even taking into account deflection influences due to the Coriolis effect (Faller, 1964). Bottom friction may have caused the slicks to deviate from the wind direction in these shallow (15–30 m depth) shelf areas (Ewing, 1950). Generally, though, no immediate hydrological explanation was evident for the majority of aggregations seen during the flights, at least on scales fine enough to explain their precise shapes. This was probably the result, in large part, of the apparently ephemeral and mobile nature of these hydrological processes. Another problem was the variable condi-

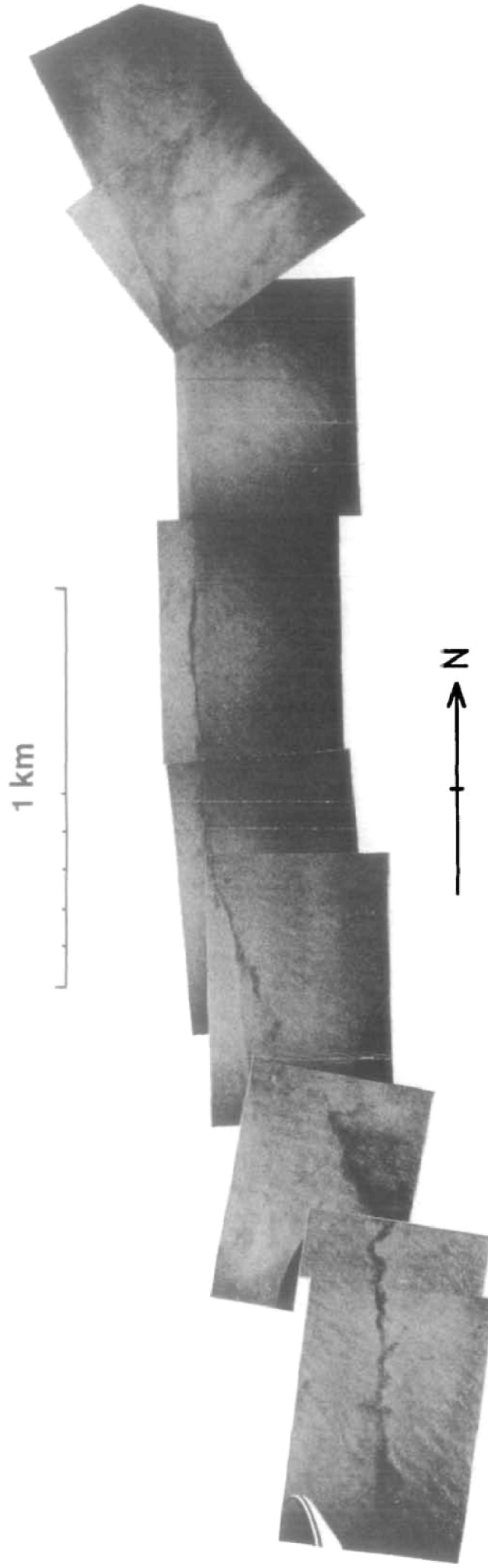


Fig. 3. Photomosaic of section of front at eastern edge of Waitaki River plume showing *M. gregaria* aggregation (dark) in relation to river plume water (west) and coastal water (east). Vertical view, 670 m altitude. Date 25.1.79.

Aggregation of *Munida gregaria*

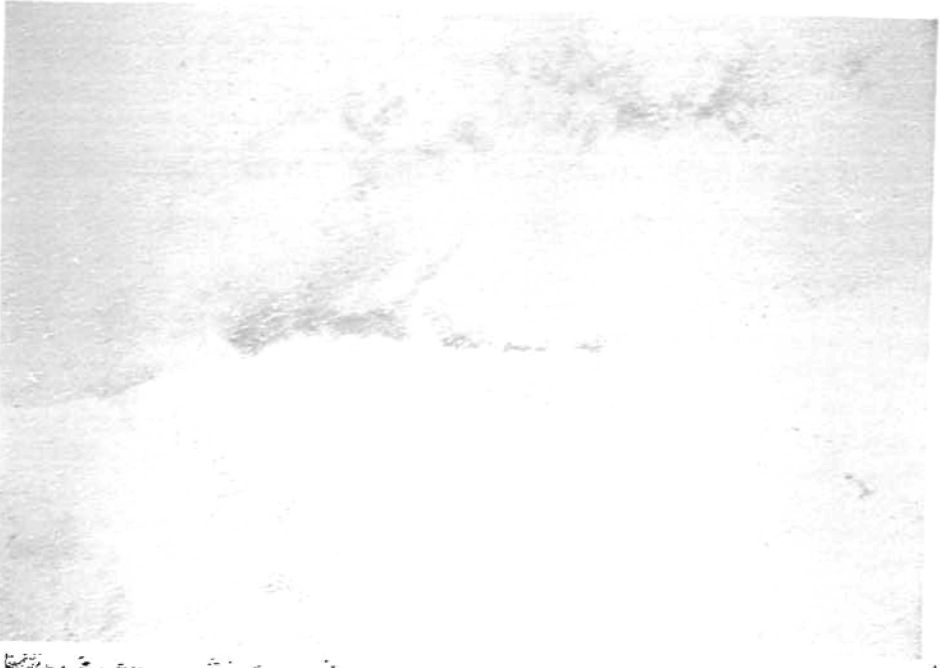


Fig. 4. *M. gregaria* aggregation at headland front south east of Taiaroa Head. Vertical view, 1100 m altitude, photograph width 1400 m. Date 24.4.79.

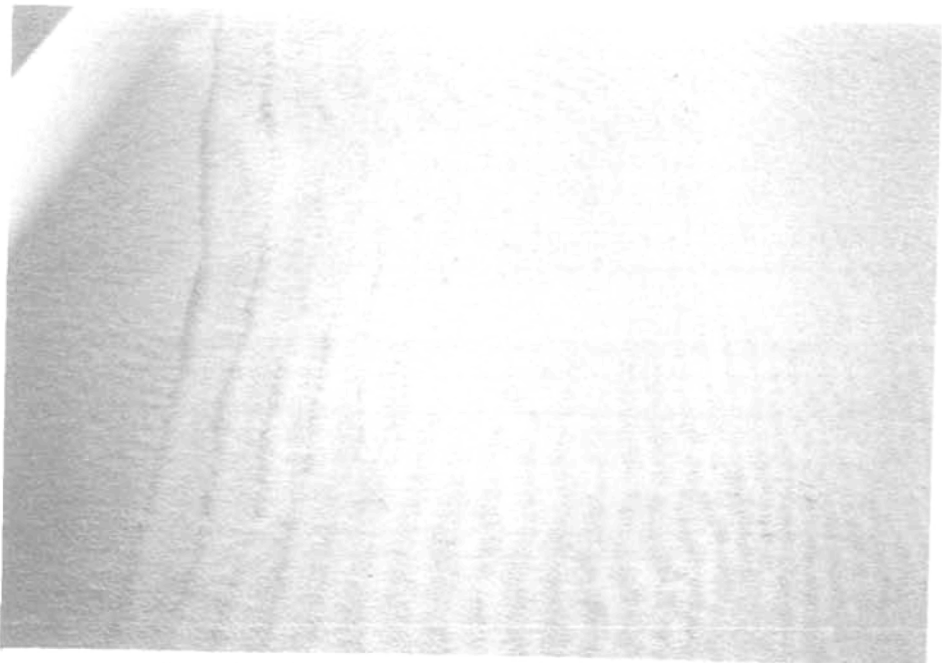


Fig. 5. *M. gregaria* aggregations associated with internal waves east of Waitaki River mouth. Oblique view, 1220 m altitude, approximate photograph width 760 m. Date 9.1.81.

tions for observation and photography, for example sun and camera angles, and film sensitivity which may have occluded subtle variations in sea colour or surface texture.

Laboratory and field experiments

The current flume proved an effective means for inducing sustained swimming by *M. gregaria* individuals, provided the animals were used within about 1 h of collection and were held in lighted aquaria. Otherwise, the animals tended to settle to the flume bottom or walls and would only swim if prodded. This behaviour is often seen in the field where *M. gregaria* settle on flotsam, wharf piles or sheltered beaches at high tide, a habit which often leads to massive strandings when the tide recedes.

All animals swam immediately to one or other light source but there was no consistent pattern in direction when lighting was similar at both ends of the flume. However, when only one end was lit, the response was always the same: each animal swam immediately to the brightest area of the flume regardless of whether this was downstream or upstream of its previous position (Table II). There was no evidence of orientation with respect to current direction. When animals were placed in the flume with both lights off and the current running, they were always swept out of the flume within a few seconds. It is therefore evident that phototaxis is a dominant factor in the determination of swimming direction.

Average maximum sustainable swimming speeds for the animals tested (Table

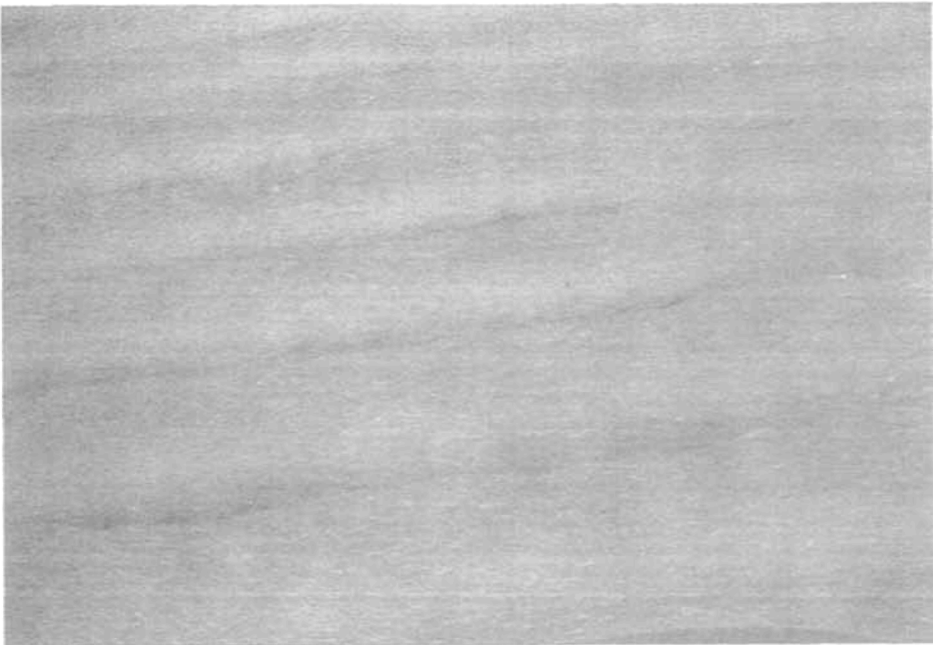


Fig. 6. *M. gregaria* aggregations associated with internal waves east of Waitaki River mouth. Vertical view, 610 m altitude, photograph width 380 m. Date 9.1.81.

II) indicate the current velocity below which the animals could maintain position with respect to the light source over a 30 s observation period at each test velocity. Swimming capability is marginally higher in larger, late season animals.

The results of field observations of *M. gregaria* behaviour (Table III) when shoals were displaced to deeper water were consistent throughout the 10 trials: the animals returned to the water depth they had occupied when captured. As shown by the irradiance profiles (Table I) they swam towards the higher intensity light impinging on them from above.

Discussion

Although no plankton samples were taken exactly coincident in time and space with aerial observations, we are convinced that our identifications of *M. gregaria* from the air are valid. First, plankton surveys within a few days either side of flight dates indicated that pelagic juveniles were present in the study area. Incidental reports of *Munida* sightings from the research vessel crew, and survey returns from fishermen and lighthouse keepers were also important in planning flight times and paths. Second, patches we have assumed to be *M. gregaria* were quite different in appearance from the air to other organisms known to swarm in near surface waters of southern New Zealand coastal seas (Bary, 1953). On four occasions large red tide blooms were observed from the air. Samples taken next day from one of these blooms contained remnant chloroplasts of the cryptophycean ciliate *Mesodinium rubrum*, the commonest red tide organism around New

Table II. Phototactic responses and maximum sustainable swimming speeds of *M. gregaria* in the current flume. Values \pm 1 S.D.

Date	Number of animals	Positive response upstream (%)	Positive response downstream (%)	Average maximum sustainable swimming speed (cm s ⁻¹)	Average carapace length (mm)
19.1.81	22	100	100	15.8 \pm 1.5	11.6 \pm 0.9
3.3.81	15	100	100	17.5 \pm 2.9	13.0 \pm 1.4

Table III. Response of groups of *M. gregaria* when displaced from surface waters to deeper waters in the field.

Date	Number of trials	Collection depth (m)	Release depth (m)	Response
22.1.81	3	0.5 – 1.0	7	Animals swam upwards to within ~ 1 m of surface.
24.1.81	7	1.0 – 3.0	10	Animals showed random swimming (5 – 10 s) then swam upwards to within collection depths. Approximate ascent rate 10 cm s ⁻¹ (estimated from 1 trial).

Zealand (V. Cassie, personal communication). From the air these blooms appeared deep purple and diffuse in contour, distinctly different from presumed *M. gregaria* aggregations which were bright to deep red with sharp shoal edges. Other abundant organisms seen in the study area were cream coloured swarms which were probably the euphausiid *Nyctiphanes australis* and yellow aggregations, probably of the salp *Ihleia magalhanica*.

Ground truth for hydrographic phenomena observed was not possible within the scope of the overall study because appropriate instrumentation was not available. We believe, however, that the photographs themselves are sufficient to identify the phenomena and make some conclusions on their dynamics, especially in the context of other reported work based on direct observations, as discussed below.

Fronts form at the boundaries between water masses of differing density as in the case of shallow sea fronts (Pingree *et al.*, 1974; Simpson and Pingree, 1977) and estuarine and river plume fronts (Bowman and Iverson, 1977). They may also form between water masses of dissimilar gross tidal flow for example at headlands (Pingree *et al.*, 1977). Fronts are usually characterized by sharp horizontal gradients in colour and temperature (see remote sensing studies of Percy and Mueller, 1970; Simpson and Pingree, 1977) as well as in salinity and other chemical and biological parameters. In vertical section, fronts are characterized by descending isopleths, as less dense water is subducted by entrainment and interfacial friction between it and the more dense water descending beneath. Surface flows near fronts are usually convergent, causing them to be marked by lines of accumulated foam and flotsam or by slicks, the latter being the effect of concentrated organic surface film (Ewing, 1950).

The dynamics of coastal high frequency internal waves have been studied by previous workers using ships, aircraft and satellites (Ewing, 1950; Apel *et al.*, 1975; Curtin and Mooers, 1975; Cresswell and Boland, 1981; Orr, 1981). In vertical section, the presence of internal waves is characterized by regularly ascending and descending isopleths corresponding to a wave pattern in the water column. Characteristic features of the internal waves observed by these workers are summarized in Table IV, together with relevant observations from the present study. Our observations of internal waves are consistent with these authors' findings. Surface slicks associated with internal waves were considered by Ewing (1950) to result from "the periodic convergence and divergence of the horizontal component of orbital velocity associated with such waves [so as] to produce alternate bands of compaction and extension in the surface film sufficient to cause visible differences in the rippling of the water by a slight breeze". Ramsay (1962) showed how this orbital circulation caused submerged bubbles to destabilize as they rose over the wave crest, thereby releasing adsorbed organic material which became concentrated at the convergence behind the crest (Figure 7).

It appears then that coastal fronts and internal waves share the feature of convergent water flow accompanied by downwelling. If zooplankton which actively maintain themselves in particular water strata drift into such a convergence, they would tend to accumulate there by resisting vertical displacement in the associated downwelling. The degree of accumulation would be proportional to

their ability to swim against gradients in the micro-environment at the downwelling. These include local accelerations, turbulence, changing irradiance (involving both intensity and spectral shifts) and increased pressure. We believe that this combination of physical and biological events is the primary mechanism in the formation of the large (100 m–5 km length) aggregations of *M. gregaria* associated with river plume fronts, headland fronts and shallow internal waves seen in this study.

It is worthwhile to examine the physical conditions at fronts and internal waves in the light of our observations. Turbulence is probably a feature of convergent downwellings but *in situ* observations are rare. Pingree *et al.* (1974) in a dye marker study of a shallow sea front observed violent and dispersive turbulence which would be inconducive to orientation. Furthermore, our current flume experiments showed that rheotactic responses, if they existed at all, were subordinate to phototactic responses.

Hydrostatic pressure, as a trigger to stimulate swimming, perhaps under the directional cue of light source direction (Rice, 1964; Knight-Jones and Morgan, 1966) was not investigated here. The current flume experiments suggest that this mechanism is not necessary to stimulate a phototactic response. Our field observations that shoals displaced from surface waters to depth consistently returned to surface waters gave no clue whether the trigger was decreased light or increased pressure. The measured decreasing gradient of downward irradiance with depth and its much higher intensity than upward irradiance suggests that light *could* have operated as a trigger or cue, or both.

Changes in light and pressure to which animals are subjected in convergent fronts will be determined by the slope of the interface and rates of water movement. We know of no *in situ* measurements of slope, however, theoretical calculations by Bowman and Iverson (1977) place this value at or near infinity at the spreading edge of shallow fronts with rapid levelling off (slopes 2×10^{-2} to 8

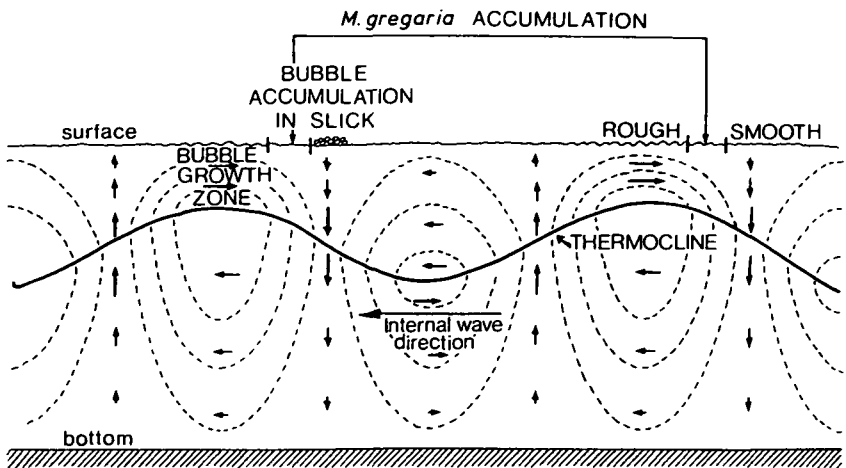


Fig. 7. Diagram of internal wave characteristics showing zones of *M. gregaria* accumulation (adapted from Ramsay, 1962).

$\times 10^{-3}$) at about 1 m depth of the overlying layer. Therefore, the steep interface slopes necessary for aggregation are likely to be adjacent to the surface boundaries of fronts. This suggests an interpretation of Figures 3 and 4 where dense aggregations of *M. gregaria* are to be seen at the surface front boundary as well as on either side. It appears that shoals became aggregated at the surface front boundary and subsequently drifted away remaining in dense aggregations. Values for downwelling rates at fronts are also rare in the literature but vary from the observations by Pingree *et al.* (1974) of a jelly fish being downwelled at 100 cm s^{-1} to theoretical calculations by Bowman and Iverson (1977) of 0.1 cm s^{-1} . Presumably these values vary considerably with the physical structure of the front and the distance of the observation from the initial downwelling site. Clearly more work is needed on this fine scale aspect of front behaviour, but from our observations it appears that *M. gregaria* swimming capability ($\sim 16 \text{ cm s}^{-1}$) is sufficient to maintain animals at or near downwelling sites for sufficient time to effect their aggregation.

In the case of internal waves vertical deformations of some metres amplitude cause downwellings of several cm s^{-1} behind the wave crests (Table IV). Internal waves propagate at rates proportional to the thickness of the over- and underlying layers, and the density difference between them (Ewing, 1950). Associated slicks propagate at the same velocity as the waves, since the zone of organic particle compaction is accreted at their leading edge and scattered at their trailing edge. It seems probable that tactic responses to light and/or pressure gradients in downwellings caused the aggregations observed in ordered bands on the trailing side of internal wave crests, immediately in advance of the associated slicks (Figures 5 and 6). Aggregation was most intense behind the leading wave, and successively less intense behind subsequent waves (Figure 5). An interpretation is that the wave packet had recently entered an area increasingly rich in disorganised *M. gregaria* shoals which became organised during the passage of the waves with the largest aggregation behind the leading wave crest.

Apparently, near surface hydrodynamic processes in coastal waters often cause *M. gregaria* shoals to form large, ordered aggregations. These aggregations persist for some time after they have lost contact with the original ordering processes. The reason for this persistence is the gregarious nature of *M. gregaria*. In calm water shoals from few centimetres to a few metres across are typically composed of individuals evenly spaced and swimming in concert, appearing much like a swarm of bees (see photograph in Williams, 1980). When a shoal is disturbed, as in the field experiments, the individuals regroup into a new cohesive shoal. Once aggregations are formed they probably persist until they are reorganized by new physical events. This type of reorganisation is apparent in Figure 8 where part of an elongate aggregation, several kilometres in overall length, is being re-ordered by the effects of internal waves. From its shape and location (10 km seaward of the Waitaki River mouth) we believe that this aggregation was originally formed at the Waitaki River plume front, though the front was no longer evident in the area.

Clearly, the tendency of *M. gregaria* to become organised into patches varying from metres to kilometres in extent presents sampling difficulties and also has im-

Table IV. Internal wave characteristics from the literature.

Reference	Wave length (m)	Propagation velocity (m s ⁻¹)	Vertical deformation of pycnocline (A)	Period (B) (s)	Average velocity of vertical deformation ^a (cm s ⁻¹)	Depth to pycnocline (m)
4(m)						
Ewing (1950)	365	0.19	2.0	1902	0.21 ^a	7.4
Apel <i>et al.</i> (1975)	4000 – 3000 800 – 450	0.25 0.35	– –	– –	– –	– –
Curtin and Mooers (1975)	143	0.27	11.0	480	4.6 ^a	≈ 20.0
Cresswell and Boland (1981)	450 – 360 –	0.50 –	– ≈ 20	900 960	– 4.2 ^a	100 35
Orr (1981)	–	–	≈ 30	420	10.0	–
This study	65 – 30	–	–	–	–	–

^aCalculated as $A + \frac{1}{2}B \times 100$.

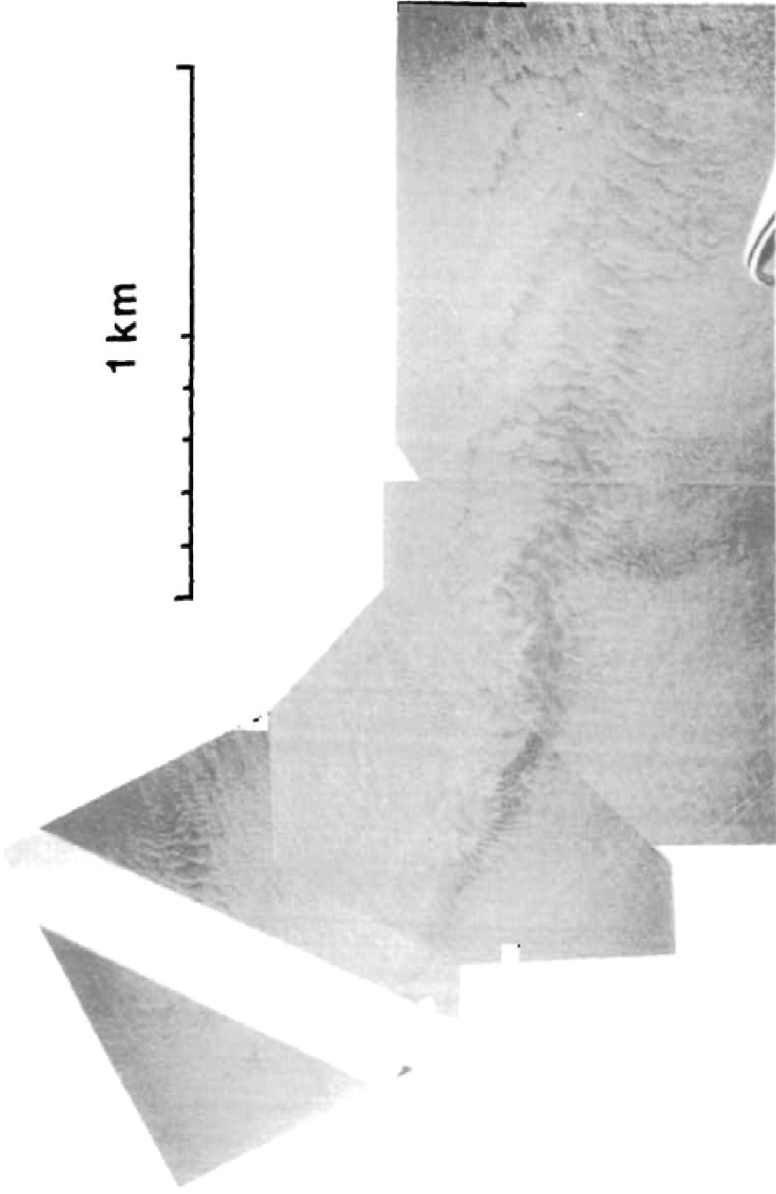


Fig. 8. Photomosaic of *M. gregaria* aggregation east of Waitaki River mouth undergoing re-organization by internal waves. Oblique view, 1070 m altitude. Date 25.1.79.

plications for the animal (see Haury *et al.*, 1977). Plankton samples specifically aimed at aggregations yielded 2705 *M. gregaria* m⁻³ (geometric mean, range 376–33 750), a value ~27 000 x greater than the background density of grid samples from the same general area (unpublished data). It is not surprising then, that shoals are the targets of heavy predation by most marine birds and mammals, pelagic feeding fish and even some normally demersal feeding fish.

Finally, we need to consider these results in relation to the general phenomenon of zooplankton patchiness. Zooplankton have been shown to be highly concentrated at tidal and shelf break fronts by Pingree *et al.* (1974) and Herman *et al.* (1981). A phototactic mechanism similar to that of the present paper was suggested by Tyler and Seliger (1981) to explain red tide dinoflagellate entrainment in frontal regions. Internal waves have been invoked by Haury (1976a) as the probable reason for variability in his zooplankton data obtained from replicate vertical Longhurst-Hardy plankton recorder tows. Haury *et al.* (1977) were also able to correlate chlorophyll fluorescence and zooplankton density with internal waves.

These studies implicate physical processes as dominant factors in controlling zooplankton variability over horizontal scales of hundreds of metres to a few kilometres. This is also suggested in numerous other studies of zooplankton distribution (e.g. Cassie, 1963; Wiebe, 1970; Fasham *et al.*, 1974; Smith *et al.*, 1976). An interesting aspect, pointed out by Fasham (1978) and Mackas and Boyd (1979), is that phytoplankton and zooplankton can have different spatial spectra over these medium space scales, zooplankton being more intensely aggregated. They considered that their observations were to be explained by the greater mobility of zooplankton and by social behaviour, such as swarming. Swarming in planktonic crustacea is a common phenomenon (e.g., copepods, Hamner and Carleton, 1979; mysids, Clutter, 1969; euphausiids, Marr, 1962 and Komaki, 1967; numerous orders, Bigelow, 1926). Furthermore, species of large copepods, euphausiids and brachyuran zoeae are capable of rapid directed swimming at speeds in the range 0.5–5 cm s⁻¹ often in response to light (Hardy and Gunther, 1936; Hardy and Bainbridge, 1954; Forward, 1977). Behavioural factors such as swarming and taxes probably accounted for much of the difference in appearance we noted from the air between red tides and *M. gregaria* aggregations.

It appears, then, that what we have observed with *M. gregaria* patches may be of significance to the study of zooplankton patchiness as a whole. The extent to which species become aggregated will depend in large part on their behaviour and the prevalence of turbulent phenomena in their environment. On continental shelves around the world, fronts and internal waves are regular features (see Bowman, 1977 and Apel *et al.*, 1975). Such heterogeneity of physical structure was concluded by Haury (1976b) to be the cause of the high variability he observed in zooplankton catches from the nearshore California Current compared to those from the relatively homogeneous North Pacific Central Gyre.

Acknowledgements

The authors would like to thank A. Padgett of Rexair Corporation and P. Meredith for their assistance

in flying these surveys and N. Johnstone for diving assistance. We are grateful too for the valued comments of Dr. P.J. Schembri and B.G. Williams who critically read the manuscript. This work was supported by a contract from Fisheries Research Division, N.Z. Ministry of Agriculture and Fisheries and grants from the University of Otago Research Committee.

References

- Apel, J.R., Byrne, H.M., Proni, J.R. and Charnell, R.L.: 1975, 'Observations of oceanic internal and surface waves from the Earth Resources Technology Satellite', *J. Geophys. Res.*, **80**, 865-881.
- Arnold, G.P.: 1969, 'A flume for behaviour studies of marine fish', *J. Exp. Biol.*, **51**, 671-679.
- Bary, B.M.: 1953, 'Sea-water discoloration by living organisms', *N.Z. J. Sci. Tech.*, Section B, **34**, 393-407.
- Bigelow, H.B.: 1926, 'Plankton of the offshore waters of the Gulf of Maine', *Bull. U.S. Bur. Fish.* **XL**, 1924, pt. II, Document no. 968:1-486.
- Bowman, M.J.: 1977, 'Introduction and historical perspective', in Bowman, M.J. and Esaias, W.E. (eds.), *Oceanic Fronts in Coastal Processes*, Springer-Verlag, Berlin-Heidelberg-New York.
- Bowman, M.J. and Iverson, R.L.: 1977, 'Estuarine and plume fronts', in Bowman, M.J. and Esaias, W.E. (eds.), *Oceanic Fronts in Coastal Processes*, Springer-Verlag, Berlin-Heidelberg-New York.
- Cassie, R.M.: 1963, 'Microdistribution of plankton', in Barnes, H. (ed.), *Oceanogr. Mar. Biol. Annu. Rev.*, **1**, 223-252.
- Clutter, R.I.: 1969, 'The microdistribution and social behaviour of some pelagic mysid shrimps', *J. Exp. Mar. Biol. Ecol.*, **3**, 125-155.
- Cresswell, G.R. and Boland, F.M.: 1981, 'Internal waves detected with a continental shelf current meter array', *Aust. J. Mar. Freshwater Res.*, **32**, 1-8.
- Curtin, T.B. and Mooers, C.N.K.: 1975, 'Observations and interpretation of a high frequency internal wave packet and surface slick pattern', *J. Geophys. Res.*, **80**, 882-894.
- Ewing, G.: 1950, 'Slicks, surface films and internal waves', *J. Mar. Res.*, **9**, 161-187.
- Faller, A.J.: 1964, 'The angle of windrows in the ocean', *Tellus*, **16**, 363-370.
- Fasham, M.J.R.: 1978, 'The statistical and mathematical analysis of plankton patchiness', *Oceanogr. Mar. Biol. Annu. Rev.*, **16**, 43-79.
- Fasham, M.J.R., Angel, M.V. and Roe, H.S.J.: 1974, 'An investigation of the spatial pattern of zooplankton using the Longhurst-Hardy plankton recorder', *J. Exp. Mar. Biol. Ecol.*, **16**, 93-112.
- Forward, R.B., Jr.: 1977, 'Occurrence of a shadow response among brachyuran larvae', *Mar. Biol.*, **39**, 331-341.
- Hamner, W.M. and Carleton, J.H.: 1979, 'Copepod swarms: attributes and role in coral reef ecosystems', *Limnol. Oceanogr.*, **24**, 1-14.
- Hardy, A.C. and Bainbridge, R.: 1954, 'Experimental observations on the vertical migrations of plankton animals', *J. Mar. Biol. Assoc. U.K.*, **33**, 409-448.
- Hardy, A.C. and Gunther, E.R.: 1935, 'The plankton of the South Georgia whaling grounds and adjacent water 1926-1927. Part IV. The zooplankton, section II', *Discovery Reports*, **11**, 194-272.
- Haury, L.R.: 1976a, 'Small scale pattern of a California Current zooplankton assemblage', *Mar. Biol.*, **37**, 137-157.
- Haury, L.R.: 1976b, 'A comparison of zooplankton patterns in the California Current and North Pacific Central Gyre', *Mar. Biol.*, **37**, 159-167.
- Haury, L.R., McGowan, J.A. and Wiebe, P.G.: 1977, 'Patterns and processes in the time-space scales of plankton distributions', in Steele, J.H. (ed.), *Spatial Pattern in Plankton Communities*, Plenum Press, New York and London.
- Herman, A.W., Sameoto, D.D. and Longhurst, A.R.: 1981, 'Vertical and horizontal distribution patterns of copepods near the shelf break front south of Nova Scotia', *Can. J. Fish. Aquat. Sci.*, **38**, 1065-1076.
- Knight-Jones, E.W. and Morgan, E.: 1966, 'Responses of marine animals to changes in hydrostatic pressure', *Oceanogr. Mar. Biol. Annu. Rev.*, **4**, 267-299.
- Komaki, Y.: 1967, 'On surface swarming of euphausiid crustaceans', *Pac. Sci.*, **21**, 433-448.
- Langmuir, I.: 1938, 'Surface motion of water induced by wind', *Science (Wash.)*, **87**, 119-123.
- Mackas, D.L. and Boyd, C.M.: 1979, 'Spectral analysis of zooplankton spatial heterogeneity', *Science (Wash.)*, **204**, 62-64.
- Marr, J.W.S.: 1962, 'The natural history and geography of the Antarctic krill (*Euphausia superba* Dana)', *Discovery Reports*, **32**, 33-464.
- Orr, M.H.: 1981, 'Remote acoustic detection of zooplankton response to fluid processes, oceanographic

Aggregation of *Munida gregaria*

- graphic instrumentation, and predators', *Can. J. Fish. Aquat. Sci.*, **38**, 1096-1105.
- Pearcy, W.G. and Mueller, J.L.: 1970, 'Upwelling, Columbia River plume and albacore Tuna', *Proceedings Sixth International Symposium on Remote Sensing of the Environment*. Univ. Mich. Ann Arbor, pp. 1101-1113.
- Pingree, R.D., Forster, G.R. and Morrison, G.K.: 1974, 'Turbulent convergent tidal fronts', *J. Mar. Biol. Assoc. U.K.*, **54**, 469-479.
- Pingree, R.D., Bowman, M.J. and Esaias, W.E.: 1977, 'Headland fronts', in Bowman, M.J. and Esaias, W.E. (eds.), *Oceanic Fronts in Coastal Processes*, Springer-Verlag, Berlin-Heidelberg-New York.
- Ramsay, W.L.: 1962, 'Dissolved oxygen in shallow near-shore water and its relation to possible bubble formation', *Limnol. Oceanogr.*, **7**, 453-461.
- Rice, A.L.: 1964, 'Observations on the effects of changes of hydrostatic pressures on the behaviour of some marine animals', *J. Mar. Biol. Assoc. U.K.*, **44**, 183-187.
- Robertson, D.A.: 1980, 'Hydrology and the quantitative distribution of planktonic eggs of some marine fishes of the Otago coast, southeastern New Zealand', *Fisheries Research Bulletin*, No. 21, N.Z. Ministry of Agriculture and Fisheries.
- Simpson, J.H. and Pingree, R.D.: 1977, 'Shallow sea fronts produced by tidal stirring', in Bowman, M.J. and Esaias, W.E. (eds.), *Oceanic Fronts in Coastal Processes*, Springer-Verlag, Berlin-Heidelberg-New York.
- Smith, L.R., Miller, C.B. and Holton, R.L.: 1976, 'Small-scale horizontal distribution of coastal copepods', *J. Exp. Mar. Biol. Ecol.*, **23**, 241-253.
- Tyler, M.A. and Seliger, H.H.: 1981, 'Selection for a red tide organism: physiological responses to the physical environment', *Limnol. Oceanogr.*, **26**, 310-324.
- Wiebe, P.H.: 1970, 'Small-scale spatial distribution in oceanic zooplankton', *Limnol. Oceanogr.*, **15**, 205-217.
- Williams, B.G.: 1980, 'The pelagic and benthic phases of post-metamorphic *Munida gregaria* (Fabricius) (Decapoda, Anomura)', *J. Exp. Mar. Biol. Ecol.*, **42**, 125-141.