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Macrozooplankton Assemblages in California Fronts

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Abstract

Coastal fronts are zones of intense biological activity, often defined by a narrow band of flotsam resulting from the convergence of two water masses. The accumulation of zooplankton at fronts has been reported many times in the literature, and is assumed to be the result of passive advection acting on organisms that lack the ability to swim effectively against currents. However, literature on zooplankton swimming behavior, specifically that pertaining to diel vertical migration, demonstrates that certain plankton groups are capable of swimming well over one hundred meters per hour. High rates of primary production are known to occur at fronts, and any behavior by zooplankton that would enhance the movement to and subsequent maintenance in these food sources should be conserved. However, it is unclear whether or not zooplankton aggregations at fronts are controlled exclusively by physical factors, or if behavior plays any role. The focus of this project is to quantify zooplankton abundance and behavior in the vicinity of a seasonally persistent front in Monterey Bay, California. This research is approached in two separate but related studies. The first uses a high-definition digital video camera mounted on a remotely operated vehicle to conduct transects along the Monterey front to visually sample the abundance and swimming orientation of the sea nettle, *Chrysaora fuscescens*. From initial observations, we hypothesize that sea nettles may be actively swimming towards the front, conceivably to take advantage of the rich feeding opportunity. The second study will address the distribution of smaller zooplankton in the vicinity of the front in an attempt to assess whether or not behavior plays any role in determining the observed distribution. This will be achieved by comparing different groups of zooplankton, for which swimming speeds are known, to that of non-swimming stages, namely fish and invertebrate eggs. Any difference between the distributions of swimming and non-swimming stages should provide a first-order estimate of behavior. These studies will offer further information on the biological dynamics at these important feeding zones.

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William M. Hamner (Professor, Advisor)

OVERVIEW

Oceanic fronts are physical manifestations marked by steep horizontal gradients at the sea surface. While fronts can be generated by many different physical processes and can exist over different scales of space and time, they all share the common feature of vertical flow around the convergence of water masses of different origins (Owen, 1981). The interplay of flow dynamics at fronts and the resulting distribution of zooplankton have been studied for over a century (Haeckel, 1893). The aggregation of biological and non-biological materials at fronts is well reported in the literature (e.g. Haeckel, 1893; Beebe, 1926; Knauss, 1957), yet in most aggregation studies of fronts, the behavior of the animals themselves has been neglected, and the concentration of animals at fronts is therefore assumed to be the result of flow characteristics acting solely in concert with buoyant forces (e.g. Kosobokova and Hirche, 2000; Labat *et al.*, 2002; and many others). Nonetheless, aggregations of animals can have profound ecological, evolutionary and behavioral consequences (Owen, 1981; Wolanski and Hamner, 1988; Haury and Pieper, 1988). Any behavior that promotes aggregation at fronts and which enhances feeding, survival, and/or reproductive success should be conserved over evolutionary time. Indeed, the life histories of many coastal marine and estuarine fish and invertebrates are tied to the formation and movement of fronts. For example, pulse recruitment events have been shown to coincide with the relaxation of coastal upwelling fronts that collide with shore as winds decline (Roughgarden *et al.*, 1991; Wing *et al.*, 1995a; Wing *et al.*, 1995b; Shanks *et al.*, 2000; Brubaker and Hooff, 2000).

Although researchers have begun to appreciate the extent to which animal behavior might contribute to patch formation (Omori and Hamner, 1982), few behavioral studies of plankton at fronts are reported in the literature (Shanks, 1986; Epifanio, 1987). This is likely due to the difficulty of conducting an *in situ* investigation of an oceanographic feature that is not fixed in space. Also, it is often exceptionally difficult to make direct behavioral observations of animals at sea. Yet, many observations of zooplankton behavior have been reported in the literature pertaining to swimming speed and diel vertical migration (e.g. Mileikovsky, 1973; Bryars and Havenhand, 2004). Devising a way to conduct similar detailed observations of behavior near fronts may offer insight into whether plankton are truly passive, or if behavior contributes to the distribution.

The aim of this study is two-fold. First, we will quantify the density and behavior of the sea nettle, *Chrysaora fuscescens*, near a front in Monterey Bay, California. This will be achieved by conducting transects using a high-definition digital video camera

mounted on a remotely operated vehicle (ROV) at night when the vertical migration of midwater micronekton occurs, accumulating most of the biomass in the water column above the thermocline. This creates intense vertical patchiness in addition to the horizontal patchiness generated at the surface convergence. Second, we will investigate the behavior of zooplankton in the vicinity of the Monterey Bay front, where large concentrations of zooplankton have been noted (Graham *et al.*, 1992; Graham and Largier, 1997). By analyzing net-gathered plankton samples, we will infer behavior by comparing the distribution of different species of motile zooplankton to that of passive planktonic eggs (of fish and invertebrates), which serve as slightly buoyant, non-swimming tracers whose spatial distribution is determined entirely by physical properties. We hypothesize that while the distribution of plankton will generally be greater at fronts, certain animals, particularly meroplankton whose development necessitates movement towards or away from shore, may not follow this pattern, and that even if such species are more abundant at the front, they will be skewed in their distribution differently than planktonic eggs.

SUMMARY OF FINDINGS

Study 1 – Sea nettle distribution and swimming orientation

We conducted fourteen transects, each averaging 370m distance, over the course of three days. In each transect, physical parameters such as temperature and chlorophyll concentration were recorded. By plotting temperature from the ROV, we determined that a thermal front was present during our study. Satellite observations made prior to the field effort suggest that this front was the result of the entrainment of upwelled water into the bay forming an upwelling shadow (*sensu* Graham and Largier, 1997). Three transects were recorded on the warmer northern side of the front, while eight transects were conducted on the colder southern side. Three transects passed directly through the front. We observed approximately 1,200 individual sea nettle medusae in all transects. Sea nettles showed a strong association with the northern warmer water mass, with the greatest overall abundance occurring immediately at the front. These distributions appear to be actively maintained by the swimming behavior and directional orientation as observed in the video data, where sea nettles north of the front were predominantly oriented in a southward swimming direction (mean compass angle = 137.2°) and sea nettles south of the front were oriented in a northward swimming direction (mean compass angle = 24.9°) (Watson-Williams, $N = 1197$, $F_{0.05,1,N} = 804.3$, $p < 0.00001$). This behavioral response generated a concentration of jellies along the front. Those jellies that occurred immediately next to the front were more randomly oriented. Presumably, once the jellies encountered increased concentrations of food at the front, the need for strongly oriented swimming would diminish, and shorter duration swimming pulses would maintain their position at the front.

The swimming behavior of the jellies we observed was recorded at night, thus sunlight cannot explain the swimming orientation. Information on ocean currents was not collected, although this may be somehow related to the directional swimming we observed. Nonetheless, it is not known if medusae can even sense differences in the

direction of water flow. Although clearly, sea nettles apparently can swim well enough to track the movement of these fronts. Despite the fact that the location of the front varied on each of the three sampling nights, the concentration of sea nettles was always located at the front. Few studies have examined swimming speeds of *Chrysaora* sp. *in situ*, but some laboratory experiments indicate these jellies can sustain average speeds of 2 cm s^{-1} (Matanoski *et al.*, 2001), with similar swimming speeds for *Aurelia* sp. (McHenry and Jed, 2003). These speeds are adequate to maintain aggregations near the front where horizontal flow velocities are generally slowest. Away from the front, the swimming orientation of jellyfish was strongly oriented to the north on the cold side and south on the warm side. In either case, this orientation is approximately perpendicular to the greatest flow, calculated previously at roughly 10 cm s^{-1} (Graham and Largier, 1997), further increasing the chance of encountering the highly productive front. This indicates how important behavior is in maintaining jellyfish aggregation (Omori and Hamner, 1982).

Study 2 – Zooplankton distribution and behavior

We conducted a spring and summer collection of zooplankton in the northern half of Monterey Bay, California. Four 10 km transects (one in spring and three in summer) were conducted perpendicular to the Monterey front. Along each transect, between 4 and 7 vertical plankton tows and physical water property data were gathered at evenly spaced distances.

The overall productivity in the Monterey bay was markedly different between the spring and summer surveys, although zooplankton densities were always highest along the front. An upwelling shadow was present during both sampling efforts, although the horizontal thermal gradient across the front was greater during spring when the average plankton biomass was more than two orders of magnitude greater and the species richness was 22% higher than in summer. Even with the far lower biomass, similar patterns were seen in a number of plankton groups in summer, suggesting that some may respond to general flow characteristics in similar ways, regardless of season. Planktonic eggs in spring were most highly abundant along the transect immediately at the front. However, in summer, this pattern was only seen in transects 1 and 3. In transect 2, planktonic eggs were skewed differently, with the greatest number of eggs taken in the offshore-most samples. High-frequency coastal radar (CODAR) data gathered on the summer sampling date reveal that convergent flow was present at the location of transects 1 and 3, but not near transect 2, where surface waters exhibited slower velocities, and water in the north and south portions of the transect flowed in parallel but opposite directions. The resulting flow field, with transects 1 and 3 crossing a buoyant front and transect 2 crossing a shear front, has been previously described (Graham and Largier, 1997), and is likely why eggs were not abundant along the shear front, where they could be effectively advected away.

Holoplankton generally followed a pattern of increased abundance on the fronts in both surveys. This was exemplified by the distribution of copepods, which were the most abundant group throughout the study site in both seasons and are among the most

competent swimming zooplankton (Mauchline, 1998). In spring, when the waters were highly productive, copepods were abundant everywhere, although they exhibited their highest density on the front. In summer, they were also highly abundant on the fronts and they appeared to decrease in density with distance from the front, although less rapidly in the offshore direction. When correlated with the distribution of eggs, the spring copepod spatial pattern was strongly similar to fish eggs (Pearson correlation, $N = 8$, $R = 0.897$, $p = 0.002$). A correlation was not revealed between planktonic eggs and copepods in summer. However, when the data from transect 2 were removed from the case-wise deletion, the copepod distribution was significantly correlated to planktonic eggs (Pearson correlation, $N = 12$, $R = 0.805$, $p = 0.0008$). Thus, even though planktonic eggs were advected away, as a result of the leaky nature of the shear front, copepods still remained in highest abundance along the front. Therefore, active swimming behavior is likely how copepod were able to maintain high densities on the shear front.

In both of our surveys, the juvenile euphausiid catch was dominated by calyptopis and early furcilia stages with proportionally very few late-stage furcilia and no adults. A comparison of offshore to nearshore euphausiid abundance in our surveys revealed that euphausiids were generally more abundant offshore of the front. Euphausiid distribution did not correlate to that of fish eggs in either survey. Intriguingly, euphausiid juveniles did not correlate significantly with euphausiid eggs. While the general distributions were similar in transects 1 and 3, which were likely both buoyant convergences, they were distinctly different in transect 2 where euphausiid eggs were strongly skewed offshore, due to the apparent adjacent flow along the front. Despite the higher offshore density of euphausiid eggs in transect 2, euphausiid juveniles were aggregated on the shear front.

A comparison of other holoplankters to planktonic egg distributions revealed intriguing patterns, some of which can be attributable in part to behavior. The appendicularian *Oikopleura* sp. was highly aggregated on the front during spring, but was only weakly associated with the front during the summer transects. This group was correlated very strongly with planktonic eggs in both seasons. Along transect 2 in summer, *Oikopleura* sp. were strongly skewed in the offshore direction, likely resulting from the comparatively slow swimming ability of this animal (Selander and Teselius, 2003). This offshore skew further suggests a shear front along transect 2, which starkly contrasts the denser aggregation of this group on the buoyant convergence seen in spring and summer. A similar scenario was found with the predatory chaetognath *Sagitta* sp., which is a competent swimmer (Saito and Kiørboe, 2001). *Sagitta* sp. was very abundant along the front in spring, showing a strong correlation with the distribution of planktonic eggs but in summer was not correlated with eggs. *Sagitta* sp. is known to prey heavily on copepods (Alvarez-Cadena, 1993; Saito and Kiørboe, 2001), and *Sagitta* sp. and copepods were strongly correlated in spring when copepod abundance was very high on the front (Pearson correlation, $N = 8$, $R = 0.796$, $p = 0.018$). However during summer, copepod numbers were an order of magnitude less abundant, and *Sagitta* sp. were not statistically associated with copepods (Pearson correlation, $N = 8$, $R = 0.254$, $p = 0.310$) and were distributed mostly offshore.

Hydromedusae and small scyphomedusae distributions followed a similar trend to that of the sea nettle *Chrysaora fuscescens*, with higher abundances always along fronts, with densities decreasing more rapidly in the colder waters to the south. The cydippid ctenophore *Pleurobrachia bachei* was very abundant during the spring survey, with 85% of the total occurring at the highly productive front, while numbers in summer were far reduced, likely due to the seasonality of this species in Monterey Bay. The distribution of *P. bachei* in spring was most strongly explained by the sharp temperature gradient at the front (forward step-wise multiple linear regression, $R^2 = 0.989$, $p < 0.0001$), while no variable measured in summer could explain the variance in distribution of this species. *P. bachei* is a very competent swimmer (Matsumoto, 1990) with the capacity to swim at or exceed the average flow speeds calculated in this region (Graham and Largier, 1997), and it is therefore feasible that it could aggregate on or away from a front by active swimming.

Brachyura zoea was the most abundant meroplanktonic group in spring, when it was in greatest abundance on the front. Horizontal temperature gradient was the only measured variable to significantly explain the spatial distribution of crab larvae in spring (forward step-wise multiple linear regression, $R^2 = 0.578$, $p = 0.017$), indicating that they were associated with the front. As with most other animals in the study, crab zoea were an order of magnitude less abundant during summer. A less abundant group, caridea zoea, mirrored the distribution of brachyura zoea in summer, although they appeared to have a different distribution in spring. Distributions were similar for crab and shrimp zoea, with high densities on the fronts, and higher abundance inshore compared to offshore. Larval crabs and shrimp are in general among the most competent swimming zooplankton. It is therefore likely that crab and shrimp zoeae may utilize the Monterey upwelling shadow front, not only as a rich food source but also as a transport mechanism to shore once they reach the age of settlement (Shanks *et al.*, 2000). Further study will be necessary to test this hypothesis.

Juveniles of the polychaete *Magelona* sp. were common in both surveys, with twice as many occurring on average in spring. Over 50% of the overall abundance occurred at the front in spring, while in summer, 67% were captured on the fronts. There was a slight offshore distribution in summer transects 1 and 2, however in transect 3, *Magelona* sp. was captured almost exclusively on the front with less than 5% of *Magelona* sp. along the transect occurring anywhere else. This distribution was much more highly aggregated than planktonic eggs. Although it is reported as a predator, the larval life history of this species is unknown (Johnson and Shanks, 2003), and its distribution has not been specifically considered in previous plankton studies in Monterey Bay.

In spring, gastropod veligers were most abundant on and inshore of the front. In summer, veligers were distributed offshore in transects 1 and 2, and highly aggregated on the front in transect 3. Although gastropod veliger swimming speeds are slow compared to other similarly sized zooplankton (Young, 1995), they are reported to actively regulate their depth by vertical swimming upwards and by sinking or swimming downward (Lough and Gonor, 1971). Gastropod veligers are known to aggregate near the bottom during the day (Poulin *et al.*, 2002), which may have occurred during the spring cruise when upwelling

was very strong. Their greater abundance inshore of the front may be related to inadequate sampling near the bottom in the deeper offshore waters when the vertical net tows only extended to 40m depth.

The distributions of all other meroplankton species were weighted either on or inshore of the fronts. In spring, this was the case for cirriped nauplii and brachyura megalopa. The cirriped nauplii captured were newly released based on their very small size (Arnsberg, 2001), and since they were mostly balanomorphan, their origin was likely rocky intertidal or subtidal. Unlike the cirripeds, the megalopa were at the end of their larval life and were probably concentrated inshore in preparation for settling. In summer, cirriped nauplii were marked different in their distributions along the transects. Transect 1, which was located west of the others near the seaward portion of the bay, had a mix of lepadomorphan and balanomorphan species (Arnsberg, 2001), which were distribution with greater abundance in the offshore direction. Distributions of cirriped nauplii in Transects 2 and 3, located within the bay, were weighted in the onshore portion of the transect. Far fewer lepadomorph nauplii were present in these transects. This pattern calls attention to the relatively effective role that such coastal fronts can have in hindering cross-shelf dispersal, causing some larvae to be retained or excluded inshore. Barnacles have been used as a model for study of dispersal in larvae of benthic sessile invertebrates (e.g. Roughgarden *et al.*, 1988), and recently, researchers have become more focused on the importance of oceanography in dispersal (Jenkins *et al.*, 2000; Botsford *et al.*, 2001). Seasonal wind-driven features such as the Monterey upwelling shadow may play an important role in enhancing or hindering dispersal in northern Monterey Bay, particularly during periods of frontal formation or relaxation when intense recruitment events have been observed (Roughgarden *et al.*, 1991).

The Monterey Bay upwelling shadow front clearly influences the distribution of zooplankton locally, although different taxonomic groups apparently react differently to its presence. This feature is highly productive during conditions of upwelling favorable winds, and it would be logical that animals in general would take advantage of the rich feeding opportunity. However, ontogenetic developmental concerns will also drive behavior (Mileikovsky, 1973; Sulkin, 1984, Young, 1995; Poulin *et al.*, 2002; Kingsford *et al.*, 2002), and swimming competence and the ability to take advantage of deeper favorable flow directions can lead to accumulation of animals away from a surface convergence. Also, the tracking of a food source by chemoreception or hydromechanic perception (Saito and Kiorboe, 2001) can result in the aggregation of predators to prey, even if the prey is not aggregated on a front.

Attributing behavior to the distribution of plankton along a buoyant convergence where the horizontal flow on either side of the front is opposing is subject to question, since swimming towards the front will produce a similar result as if no swimming were occurring. That is, whether or not active horizontal swimming is occurring, an aggregation will result on the front. However, through CODAR data and the pronounced skewing of planktonic eggs in the offshore direction along one of the transects, we established that at least one of the sampling efforts occurred across shear front, which was subject to considerable leakage. Despite the absence of eggs accumulating on this

shear front, many animals continued to aggregate there (e.g. euphausiid juveniles, medusae, *P. bachei*, *Magelona* sp., brachyura and caridea zoea, and cirriped nauplii). This would not have occurred if flow were the only mechanism determining the distribution of these species.

When examining the distributions of multiple different taxa over an area the size of northern Monterey Bay, our study suggest that it is important to consider behavior as a contributor to spatial distribution. In studies of vertical distributions, this has been understood for some time (e.g. Harder, 1968), however behavior has only recently gained appreciation as a determinant of horizontal distribution (Omori and Hamner, 1982; Kingsford *et al.*, 2002; Genin *et al.*, 2005). The present study calls attention to this point.

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