NEARSHORE TOPOGRAPHIC FRONTS: THEIR EFFECT ON LARVAL SETTLEMENT AND DISPERSAL AT SUNSET BAY, OREGON

by

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This study investigated the nearshore small-scale circulation patterns and the effects on larval dispersal and settlement at Sunset Bay, Oregon. From January through September 2000, observations were made of the shore-parallel foam line at the mouth of the bay. The foam line was present during upwelling favorable winds and a small swell (<2m). This study investigated whether the front isolated bay waters from the coastal waters offshore. During upwelling favorable winds, the waters seaward of the front were colder, denser, and more saline than bay waters. Plankton tows and subtidal moorings containing settlement plates and Tuffys were sampled every other day. Significantly more *Balanus glandula* cyprids were found landward of the front. Settlement offshore was highest during upwelling conditions and several days after neap tide; however, inshore of the front, peaks in settlement tended to occur during downwelling winds. Significantly more *Mytilus* sp. settlement tended to occur seaward of the front.

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CHAPTER I

INTRODUCTION

The majority of coastal invertebrates have complex life cycles that include planktonic larval stages that return to the benthos for settlement. Transport by coastal currents has been shown to affect larval supply, recruitment, and the population dynamics of sessile adults (Gaines et al., 1985; Shanks, 1986a; Shanks and Wright, 1987; Roughgarden et al., 1988, Jacobsen et al., 1990; Farrell et al., 1991; Pineda, 1991; Roughgarden et al., 1991; Miller, 1992; Alexander and Roughgarden, 1996). Nearshore circulation patterns affected by shoreline irregularities, such as headlands and embayments, can modify current patterns to create eddies and fronts (Okubo, 1973; Pingree and Maddock, 1979; Wolanski and Hamner, 1988; Black et. al., 1990; Geyer and Signell, 1990; Signell and Geyer, 1991; Laval, 1995; Van der Baaren et al., 1995) that may impact larval recruitment. Several studies have investigated circulation within larger bays and behind headlands (Grundlingh and Largier, 1991; Rosenfeld et al., 1994; Graham and Largier, 1997), but few have focused on small-scale circulation of several 100 m to a few km from shore (Archambault, et al., 1998; Archambault and Bourget, 1999). This study investigates nearshore, small-scale circulation patterns and their effects on larval dispersal and settlement.

One of the physical features likely to be found in coastal waters that may affect larval availability is a front. A front is a boundary between two different water masses and is typically characterized by a surface convergence that frequently produces a large horizontal gradient in temperature, salinity, or density (Owen, 1981). A foam line often delineates the surface convergence and may be indicative of a front. There are several types of small-scale circulation patterns that occur adjacent to shore (Bakun, 1986; Wolanski and Hamner, 1988) that may produce fronts. 1) Circulation due to buoyancy input can be driven by freshwater input and surface heating. For example, a front is often found at the mouth of estuaries where the less saline estuarine water meets the more saline ocean water (Dyer, 1997; Largier, 1993). Also, a front may form where there is local surface heating of waters retained in bays (Boden, 1952), which can commonly occur in bays in upwelling systems (Graham and Largier, 1997; Largier et al., 1997; Monteiro and Largier, 1999; Wolanski and Hamner, 1988). 2) Another type of small-scale circulation that may form nearshore is due to boundary mixing. In shallow waters, strong currents coupled with rough bottom topography can lead to vertical mixing. A surface front can form where the warm offshore surface layer meets the cooler mixed nearshore waters (Wolanski and Hamner, 1988). 3) Waves breaking against a shore drive water shoreward. Rip currents and associated surf-zone recirculation form as a release of the buildup of waters (Talbot and Bate, 1987). A front is often found at the seaward edge of strong offshore rip currents (Smith and Largier, 1995). 4) During upwelling favorable winds, surface waters are pushed alongshore and offshore where cold dense waters are upwelled. An upwelling front can form between the cold upwelled waters and the warmer waters pushed offshore (Wolanski and Hamner, 1988). 5) Lastly, alongshore flow can generate nearshore fronts. Alongshore flow separates from the shore at abrupt changes in the orientation of the coast, such as at headlands and the upstream edges of bays. In the lee of a headland or within a bay, an eddy will develop if the water is deep enough and the bay long enough. Along the separation line (between mean flow and the eddy), a front may be observed. These have been studied in the case of islands (Wolanski, 1988), but also in larger bays (Graham and Largier, 1997; Wolanski and Hamner, 1988).

Many studies have shown that topographically generated fronts can affect the distribution of buoyant eggs, larvae, and plankton (Alldredge and Hamner, 1980; Wolanski and Hamner, 1988; Kingsford et al., 1991; Signell and Geyer, 1991; Wolanski, 1993). High concentrations of plankton, including meroplankton, are often associated with eddy generated surface convergences (Alldredge and Hamner, 1980; Hamner and Hauri, 1981; Willis and Oliver, 1990; Wolanski et al., 1989; Wolanski and Hamner, 1988). These studies have focused on tidally generated fronts. The front and associated concentrations of plankton are dispersed by each change in the tides. If, however, a persistent flow field generates the front, then the front may exist for long enough to have an important ecological effect.

Along rocky coastlines, foam lines that are oriented parallel to shore (hereafter shore-parallel foam lines) have been observed at the mouths of small bays and coves at a number of locations including Chile, New Zealand, Australia, California, and Oregon (Shanks, personal communication). An accumulation of foam suggests that the foam lines delineate a convergence or front. At Sunset Bay, Oregon, a shore-parallel foam line was observed only during the summer months. During this time, winds are predominantly from the Northwest, producing upwelling conditions; occasionally winds from the Southwest, produce relaxation events (Huyer, 1983). Because alongshore wind driven currents can persist for up to several weeks, the secondary circulation patterns generated where this alongshore flow separates from the shoreline may persist for weeks.

A difference in watercolor across the foam line at Sunset Bay suggests that the front may inhibit the exchange of water, and create a barrier to cross-front movement of planktonic larvae. Larvae may exploit these flow regimes to limit their dispersal. This front may also act as a barrier preventing larvae that have gone through their development in offshore waters from migrating to coastal settlement sites.

Past studies have provided evidence that nearshore larval transport processes can impact recruitment to benthic and subtidal populations (Ebert and Russell, 1988; Gaines and Roughgarden, 1985; Shanks, 1995). To better understand the effects of nearshore circulation on the dispersal and settlement of larvae, I focused on the larval distribution and settlement of two important organisms of the rocky intertidal community: barnacles (*Balanus glandula*) and mussels (*Mytilus* sp.). *B. glandula* is found in the high and mid intertidal zone from Baja California to Alaska (Morris et al., 1980). Larvae are released beginning in the early spring and continuing throughout the summer (Barnes and Barnes, 1958; Connell, 1970; Hines, 1978). Lab studies have found barnacle larvae to develop from 12 days (Emlet, personal observation) to four weeks (Brown and Roughgarden, 1985) as nauplii (six stages) followed by a non-feeding cyprid stage in which settlement occurs. Adult *Mytilus* sp. are found in the mid-intertidal zone from southern Baja California to the Aleutian Islands. Spawning occurs throughout the year (Suchanek, 1981), with peaks in July through November (Edwards, 1984). The larvae are in the plankton approximately 17 to 24 days. Mussel eggs and sperm are released into the plankton. They start as trochophore larvae, develop into veliger larvae, and then settle as pediveligers.

The goal of this study was to evaluate the persistence and importance of nearshore topographically generated currents on the dispersal and settlement of larvae. I addressed several questions: 1) How long do conditions maintain a shore-parallel foam line? 2) Is there a front associated with the foam line? 3) What are the physical characteristics of the waters across the foam line or front location? 4) Is there a difference in the distribution of meroplankton associated with the foam line? 5) Is there a difference in settlement of barnacles and mussels across the front? 6) Is this difference in settlement correlated with larval distributions?

CHAPTER II

METHODS

Description of the Sunset Bay Study Site

This study was carried out within Sunset Bay, Oregon, USA (43° 20' 100 N; 124° 22' 750 W) (Fig. 1). Sunset Bay is located 4 km north of Cape Arago and 3 km south of the Coos Estuary. The surrounding area (Miller's Cove & Gregory Point) is a complex of bays, small islands, and intertidal reef rocks. Gregory Point is a series of small islands 0.5 km north of Sunset Bay that extends 1 km from shore. Gregory Point is the first significant headland along the southern coast of Oregon. Miller's Cove is located just south of Gregory Point and just north of Sunset Bay and separated from Sunset Bay by Squaw Island and intertidal rock reefs. Sunset Bay consists of a small inner bay connected to an outer larger bay. For this study the Sunset Bay region and adjacent shelf was divided into three zones: 1) inner bay, 2) mid bay, and 3) seaward of the front (Fig. 2). The seaward edge of Sunset Bay was defined as the outer edge of the rock reefs north and south of the study area (Fig. 2).

Tides along the Oregon coast are mixed and semidiurnal with a mean annual range of 1.7 m (Oregon Dept. of Transportation, 1983). During the winter (October - March), southwest winds produce downwelling conditions and frequent large swells. Starting in April or May, winds are predominantly from the northwest producing upwelling conditions with unpredictable and short relaxation events due to reversals in the wind direction or weakening of the winds for one to several days (Halpern, 1976). Swells tend to be smaller during the summer months.

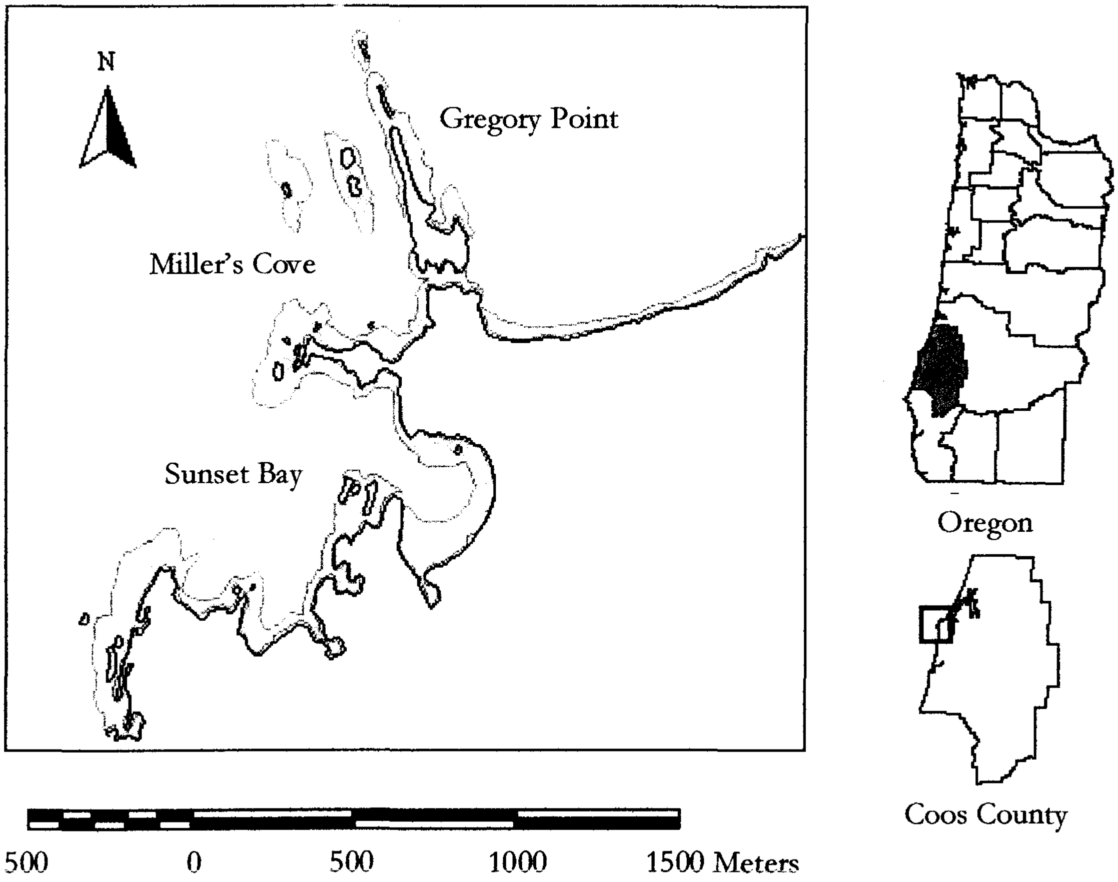


Figure 1. Location of the study site, Sunset Bay, Oregon, and surrounding area, including Miller's Cove and Gregory point (43° 20' 100 N; 124° 22' 750 W). The grey shaded area is the intertidal zone and land is to the East. The time-series of settlement and abundance of barnacles and mussels were measured inshore and offshore of Sunset Bay. Temperature, salinity, density, and chlorophyll were also measured inshore and offshore of Sunset Bay. Wind speed and direction were measured by the NOAA Cape Arago Weather Station (CARO3), located at Gregory point.

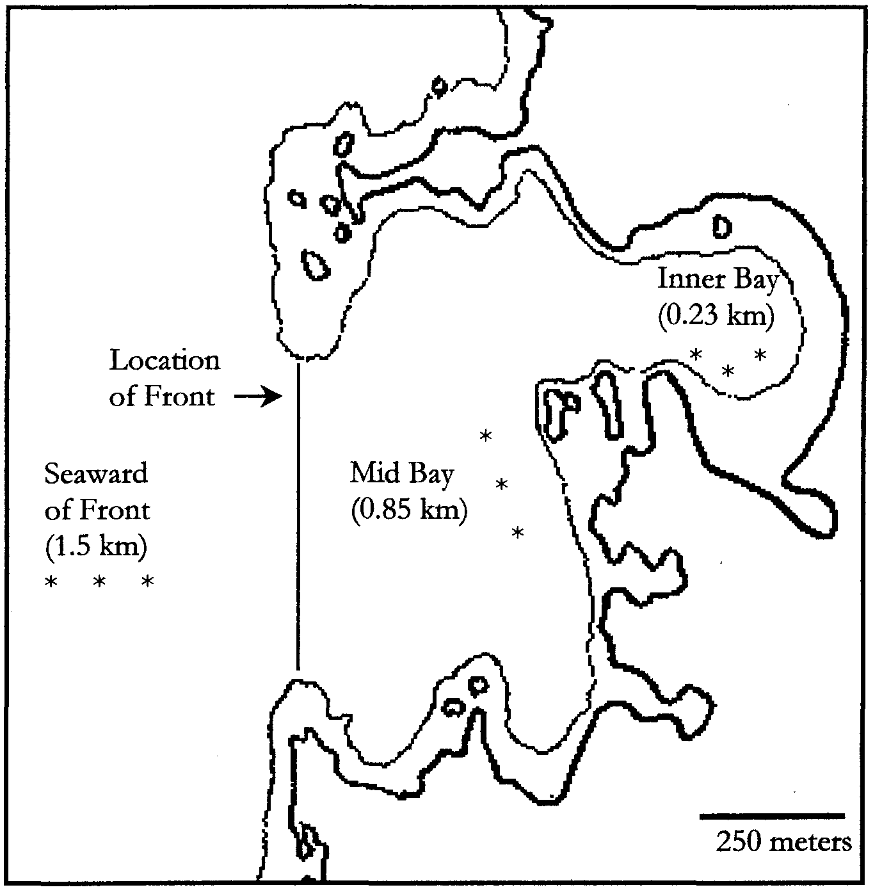


Figure 2. The study site, Sunset Bay, Oregon, was divided into three zones (Inner bay, Mid bay, and Seaward of the front). The grey shaded area represents the land and the area just offshore of land represents the intertidal zone. The front was located at the seaward edge of Sunset Bay, or the outer edge of the rock reefs. Moorings (*) were established approximately 3 m apart at 0.23 km (Inner bay), 0.85 km (Mid bay), and 1.5 km (Seaward of front) from shore.

Persistence of the Sunset Bay Topographic Front

A foam line parallel to shore consistently occurs at the mouth of Sunset Bay during summer upwelling conditions. To measure the persistence of the front, observations were made approximately every other day from mid January through August 2000. An overlook on the Cape Arago highway located on the south side of Sunset Bay provided a clear view of the mouth of the bay. The presence or absence of the front, wave height, wind direction and speed were noted during each observation. The presence of the front was indicated and scored by an unbroken foam line extending across the mouth of the bay and, often, by an associated watercolor change.

Physical Characteristics of the Nearshore Water Column

To identify the front and describe the physical characteristics of the waters in Sunset Bay and the adjacent shelf, measurements of water temperature, salinity, density and chlorophyll *a* concentrations were recorded with a Seabird 19 Conductivity-Temperature-Depth (CTD) meter with an attached Wetstar Wetlabs fluorometer. One vertical cast (surface to bottom) was conducted on each sampling day along a nearshore transect with eight CTD sample stations located 0.2, 0.3, 0.5, 0.9, 1.0, 1.1, 1.2, 1.5 km offshore. The Noesys Transform program was used to generate contour plots of the water column conditions.

The time-series of physical oceanographic transects was coupled with coastal wind datasets (NOAA Cape Arago Weather Station CARO3; located 0.5 km north of Sunset Bay), and the upwelling index measured by the NOAA Yaquina Bay Buoy (located 160 km north of Sunset Bay). Cross-shelf and along-shelf wind stress were calculated from the wind speed and direction data (Pedlosky 1987) from the CARO3 Weather Station and reported as daily averages.

Larval Settlement Time Series

Three vertical plankton tows (one in each zone at the mooring site) were taken with a 53 μm mesh net with a mouth diameter of 0.25 m on each of the sampling days. The plankton net was lowered to the end of a 6.1 m line to a maximum depth of 6.1 m three times for a combined total tow length of 18.3 m for an individual sample. A total of 0.9144 m^3 of water was sampled at each plankton tow station (one in each zone). In the laboratory, the three samples were preserved in 10% $CaCO_3$ buffered Formalin. The samples were rinsed with water and transferred to a 250 ml beaker. Water was added to the sample until the electronic balance measured 200g (200ml). Three sub-samples were removed with a Stempel pipette (Omori and Ikeda, 1984; Peterson et al., 1979) after vigorous random stirring. The sub-sample size (10 ml) was determined by counting at least 100 individuals of the most common organisms. The sample standard deviation was approximately 10% for the most abundant organisms and between 10 and 20% for the less common species (Venrick, 1978). The sub-sampling method was tested for statistical differences by Shanks (in press) and was found to provide an accurate estimate of the concentration of animals in the entire sample. Organisms were identified and enumerated using a dissecting microscope equipped with polarizing filters (Shanks, in press). The polarizing filters allowed organisms containing $CaCO_3$ to be easily viewed.

The pattern of larval settlement was measured by providing artificial substratum attached to a set of moorings that were distributed across the front at Sunset Bay. Each mooring contained four plexiglass settlement plates (10 cm^2) coated with Safety-Walk tape (3M, Minneapolis, Minnesota, USA) and four artificial turf substrata units (Tuffy^{TM} scrub pads; 770 cm^3). Settlement plates and the artificial turf substrata units (hereafter ATSU) were affixed to moorings 0.5 m below the surface. Replicate moorings (n=3) were established approximately 3 m apart at 0.23 km (Inner bay), 0.85 km (Mid bay) and 1.5 km (Seaward of front) from the shoreline located in the Inner bay (Fig. 2).

From 3 July thru 15 September 2000, samples were collected from the moorings roughly every other day (n = 30 sample periods). Five sampling periods were longer due to high seas. For example, the sampling period was extended from two days to three days on Julian day 215 and four days on Julian day 194, 208, and 246. Moorings with attached settlement plates and artificial turf substrata units (ATSU) were exchanged in the field with new moorings. In the lab, settlement plates and ATSUs were removed, placed in separate bags, and frozen until processing (ATSUs) or analysis (plates).

The settlement plates were viewed with a dissecting microscope and cyprids and juvenile barnacles were counted and identified to species (Shanks, in press). The entire plate was typically counted; however, if the number of barnacles was greater than two hundred, then ten random squares (2 cm^2) were counted. The total number of barnacles on each plate was calculated from the mean/cm^2 of the random squares times the area of the plate. The ATSUs were rinsed with freshwater for one to two minutes into a 93 μm sieve to remove larvae. The ATSU samples were preserved in 10% $CaCO_3$ buffered Formalin. Organisms from the ATSU samples were identified and enumerated with a dissecting microscope with a polarizing filter. Organisms that were small or difficult to identify were identified with a compound microscope. All larvae were identified with standard identification guides (Shanks, in press; Martel et al., 2000).

Data Analysis

Along- and cross-shore wind stress was computed from the wind data using standard equations (Pedlosky, 1987). Data were averaged over each day. The maximum daily tidal range was defined as the maximum change in tidal elevation between a high and adjacent low tide during a 24 h period.

Time series analyses were used to investigate the relationships between the physical variables: alongshore wind stress, cross-shore wind stress, upwelling index, and maximum daily tidal range. To test the data for artificial inflation of the r values (Thorrold et al., 1994), the time-series was tested for significant auto-correlations ($p<0.05$). No significant autocorrelations were found. Cross-correlations were run between physical variables. Significant cross-correlations with positive and negative lags greater than 4 days were disregarded (Thorrold et al., 1994).

To test for differences in temperature, salinity, density, and chlorophyll *a* across the front location during upwelling and downwelling favorable winds, a two-way Analysis of Variance (ANOVA) was performed with condition (upwelling and downwelling favorable winds) and zone as the fixed factors. Input data included the average of the maximum and minimum values for all the vertical casts in each zone. For example, the maximum and minimum values from the CTD cast at 1.5, 1.2, and 1.1 km on Julian day 186 were averaged and used for the outer zone value for that day. The data were log transformed ($\log_{10}x+1$)

(Thorrold et al., 1994). The assumption of homogeneity of variances was tested by the Cochran's test (Underwood, 1981). All data met the assumptions of normality, and homogeneity of variances (Underwood, 1981). When significant ($p<0.05$) zone effects were found, then a post hoc pairwise comparison test (Tukey, $p<0.05$) was completed to determine the differences between zones.

Physical CTD data including temperature, salinity, density, and chlorophyll *a* were cross-correlated with alongshore wind stress. Input data for this analysis included all measurements collected at a depth of 1 m below the surface at each of the CTD stations. Because sampling occurred in the morning approximately every two days, alongshore wind stress was averaged for the days between sampling cruises. To test the data for artificial inflation of the r values (Thorrold et al., 1994), the time-series was tested for significant autocorrelations ($p<0.05$). No significant autocorrelations were found. Cross-correlations were run between alongshore wind stress and the physical CTD variables. Significant cross-correlations with all positive lags and negative lags greater than four days were disregarded (Thorrold et al., 1994). Significant positive lags were disregarded under the assumption that the CTD variables would not have an effect on the alongshore wind stress.

To determine if there was a significant ($p<0.05$) zone effect in concentrations ($\#/m^3$) of *Balanus glandula* cyprids and mussel larvae across the location of the front, a two-way ANOVA was completed with condition and zone as fixed factors. Concentrations of larvae were log transformed ($\log_{10} x+1$)(Thorrold et al., 1994). The assumption of homogeneity of variances was tested by the Cochran's test (Underwood, 1981). All data met the assumptions of normality, and homogeneity of variances (Underwood, 1981). When significant ($p<0.05$) zone effects were found, then a post hoc pairwise comparison test

(Tukey, $p<0.05$) was completed to determine the differences between zones.

To investigate the relationship between barnacle cyprid settlement and wind stress, a cross-correlation was performed. Daily cyprid settlement was log-transformed and detrended. To test the data for artificial inflation of the r values (Thorrold et al., 1994), the time-series was tested for significant auto-correlations ($p<0.05$). No significant autocorrelations were found. Cross-correlations were run between alongshore and cross-shore wind stress and cyprid settlement. An additional cross-correlation was run between the maximum daily tidal range and cyprid settlement. Significant cross-correlations with all positive lags and negative lags greater than four days were disregarded (Thorrold et al., 1994). Significant positive lags were disregarded under the assumption that the biological variable would not have an effect on the physical variables.

To determine if there was a significant ($p<0.05$) zone effect in mussel settlement across the location of the front, a one-way ANOVA was completed using zone as a fixed factor and ignoring condition. Concentrations of larvae were log transformed ($\log_{10} x+1$) (Thorrold et al., 1994). When significant ($p<0.05$) zone effects were found, then a post hoc pairwise comparison test (Tukey, $p<0.05$) was completed to determine the differences between zones.

CHAPTER III

RESULTS

Persistence of the Sunset Bay Topographic Foam Line

From January through September 2000, observations were made of the presence or absence of the front and an associated foam line parallel to shore at the mouth of Sunset Bay. During periods of large swells, foam lines were present, but oriented perpendicular to shore. They appeared to be associated with rip currents that extended out of the bay. During winds from the South (downwelling favorable), the foam line was either absent or extended only part way across the mouth of the bay. The foam line parallel to shore and, by inference, the associated front at the mouth of Sunset Bay was only present when there were upwelling favorable winds and a small swell. No foam line parallel to shore was observed on any day with large swells (>2m) (Table 1). When the winds were from the South (58 observations), or offshore (Northeast winds, 8 observations), a foam line parallel to shore was observed only once (Table 1). However, when the winds were upwelling favorable, from the Northwest (52 observations), foam lines parallel to shore and extending completely across the mouth of Sunset Bay were always present. Often, a water color change was associated with the front (Table 1).

Oceanographic Characteristics

During the study, the winds were typical of those observed during a summer on the Oregon coast with strong winds from the northwest and weaker winds from the southeast

Table 1. Wind direction, wave height, and observations of the presence or absence of the foam line parrallel to shore at the mouth of Sunset Bay, OR from mid-January through August 2000. Wind direction is that from which the wind was blowing. ND = no data.

Wave Size	Foam line parallel to shore is present	NE Winds	SE Winds	SW Winds	NW Winds
Large,	Yes	ND	0	0	0
> 2m	No	ND	2	13	6
Small,	Yes	0	0	1	46
< 2m	No	8	18	24	0

(Fig. 3). The peak in northwest winds (upwelling favorable winds) occurred on Julian day 240 with an alongshore and cross-shore wind stress of -1.05 dynes/cm^2 and -0.13 dynes/cm^2, respectively. The maximum alongshore and cross-shore wind stress due to southeast winds (downwelling favorable winds) was 1.12 dynes/cm^2 and 0.22 dynes/cm^2, respectively, and occurred on Julian day 246. There were five periods of downwelling favorable winds, about 21% of the study.

Significant cross-correlations were found between along and cross-shore wind stress, upwelling indices, and maximum daily tidal range. The alongshore wind stress was significantly positively cross-correlated with cross-shore wind stress at 0 and –1 d lag (Table 2). Therefore, when Northwest winds moved surface waters south, then surface waters moved offshore. A similar pattern to the wind stress was found with the upwelling index data from the Yaquina Bay NOAA Buoy (Fig. 3). The minimum and maximum upwelling indices were -31 and 346 and occurred on Julian days 245 and 213, respectively. The along- and cross-shore wind stress were both negatively and significantly cross-correlated with the upwelling indices at a 0 d lag (Table 2). Therefore, the upwelling index and wind stress data represented similar trends in upwelling and downwelling events. The maximum daily tidal range for spring and neap tides were 3.4 to 0.6 m, respectively (Fig. 3). Alongshore wind stress was significantly negatively cross-correlated with the maximum daily tidal range at lags of -2 and -3 days (Table 2). Cross-shore wind stress was significantly negatively cross-correlated with maximum daily tidal range at –2, -3, and -4 d lag (Table 2). Downwelling/relaxation events tended to occur two to three days after a neap tide. These correlations between the winds and tides are undoubtedly fortuitous.

Figure 3. Physical parameters during the period of the study from Julian day 182 through 248 (1 July through 5 September 2000). Alongshore and cross-shore wind stress data were collected from the NOAA Cape Arago Weather Station (CARO3), located 0.5 km north of Sunset Bay. Positive and negative values of alongshore wind stress represents winds to the north and south, respectively. Positive and negative values of cross-shore wind stress represent winds to the east and west, respectively. The shaded gray boxes highlight periods when, given the wind direction, downwelling/relaxation events probably occurred. Upwelling index data was collected from the NOAA Yaquina Bay Weather Buoy. More positive upwelling index values represent peaks in upwelling. Maximum daily tide data were collected from Harbor Master Tidal Software.

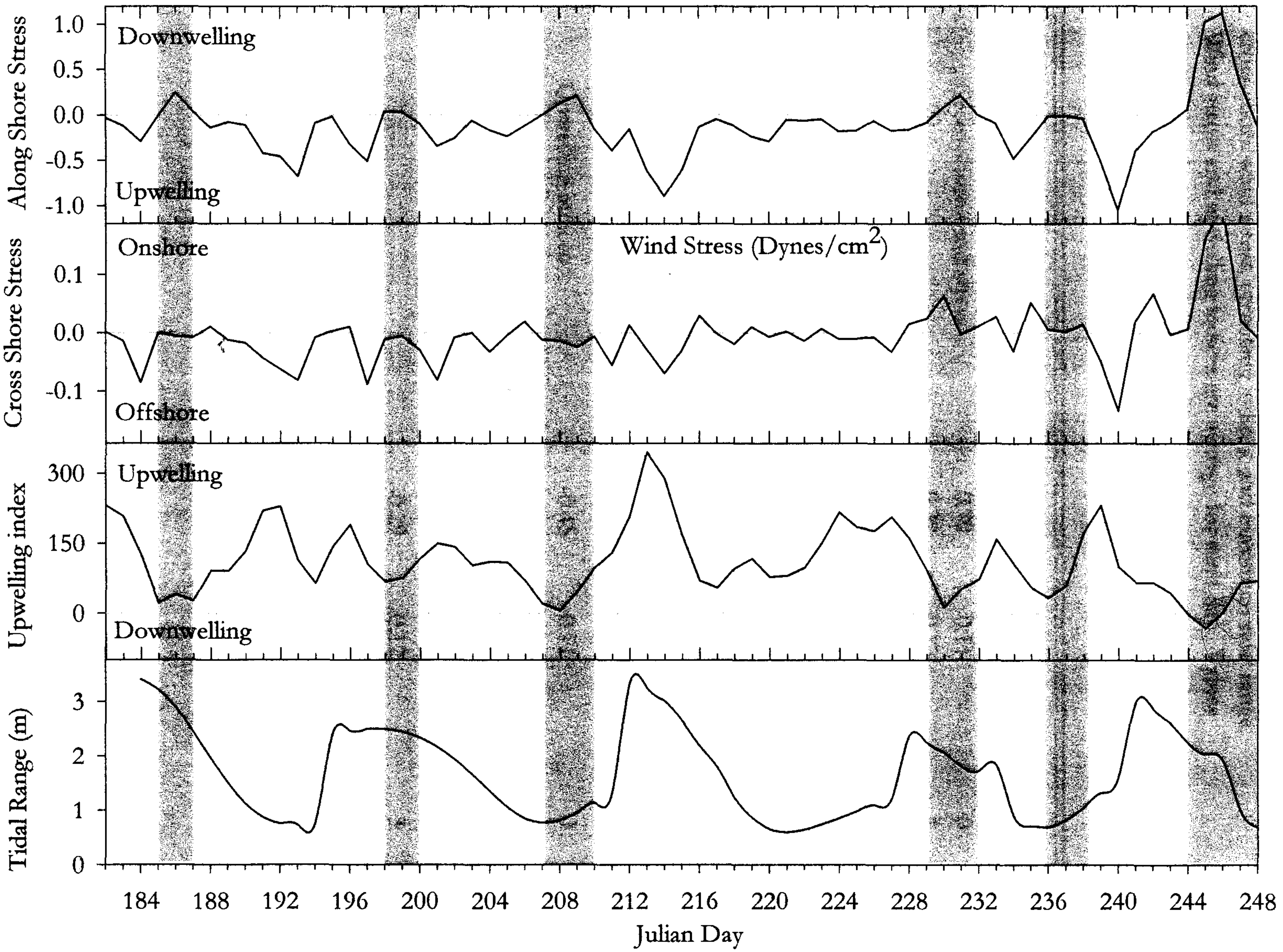

Along Shore Stress
1.0
0.5
0.0
-0.5
-1.0
Downwelling
Upwelling
Cross Shore Stress
0.1
0.0
-0.1
Onshore
Offshore
Wind Stress (Dynes/cm^2)
Upwelling index
300
150
0
Upwelling
Downwelling
Tidal Range (m)
3
2
1
0
184
188
192
196
200
204
208
212
216
220
224
228
232
236
240
244
248
Julian Day

Table 2. Results of cross-correlations between alongshore wind stress, cross-shore wind stress, upwelling indices, and maximum tidal range. Wind stress and upwelling indices are average for each day. Values are listed with cross-correlation coefficients, standard errors, and days lag. Only significant correlations are shown ($p<0.05$, $n = 76$ days of observations).

Alongshore Wind Stress	r	S.E.	Days lag
Cross-shore wind stress	0.79	-0.11	0
	0.32	-0.12	-1
Upwelling indices	-0.58	-0.11	0
	-0.73	-0.12	1
	-0.41	-0.12	2
Maximum tidal range	-0.29	-0.12	-2
	-0.27	-0.12	-3
Cross-shore Wind Stress			
Upwelling indices	-0.45	-0.11	0
	-0.55	-0.12	1
	-0.27	-0.12	2
Maximum tidal range	-0.28	-0.12	-2
	-0.29	-0.12	-3
	-0.27	-0.12	-4

Physical Characteristics of the Nearshore Water Column

From July to mid September, transects of CTD stations were made across the shore-parallel front at Sunset Bay to investigate whether the bay waters were isolated from the coastal waters offshore. During upwelling favorable winds, the front (boundary zone between two water masses that differs in temperature, salinity, density, or chlorophyll *a* concentrations) was always found at the mouth of the bay approximately 1 km from shore (Figs. 2 & 4). The waters seaward of the front were colder (Fig. 4), denser, and more saline than the bay waters. Temperatures seaward of the front were 0.1 to 2.4° colder and salinity was usually higher (0.1 - 1.5 PSU) than in the bay. When the winds shifted to downwelling favorable winds, the shore-parallel foam line disappeared. During downwelling/relaxation events, warm, less dense, less saline offshore ocean waters were found in the bay, creating a mixed water column. There was almost no change in temperature (Fig. 5) and little change in salinity along the position where the foam line would otherwise occur. There were two strong downwelling events represented by a three-dimensional graph of water temperature throughout the entire sampling period (Fig. 6). Warm waters tended to occur onshore and offshore of the front location during downwelling events.

Differences in temperature, salinity, density, and chlorophyll were evaluated during upwelling and downwelling favorable winds with two-way ANOVA's. Input data included the average maximum and minimum value for all the vertical casts in each zone. For example, the maximum and minimum temperature values from the CTD cast at 1.5, 1.2, and 1.1 km on Julian day 186 were averaged and used for the outer zone value for that day. Significant zone effects were found. Temperature, salinity, and density, but not chlorophyll

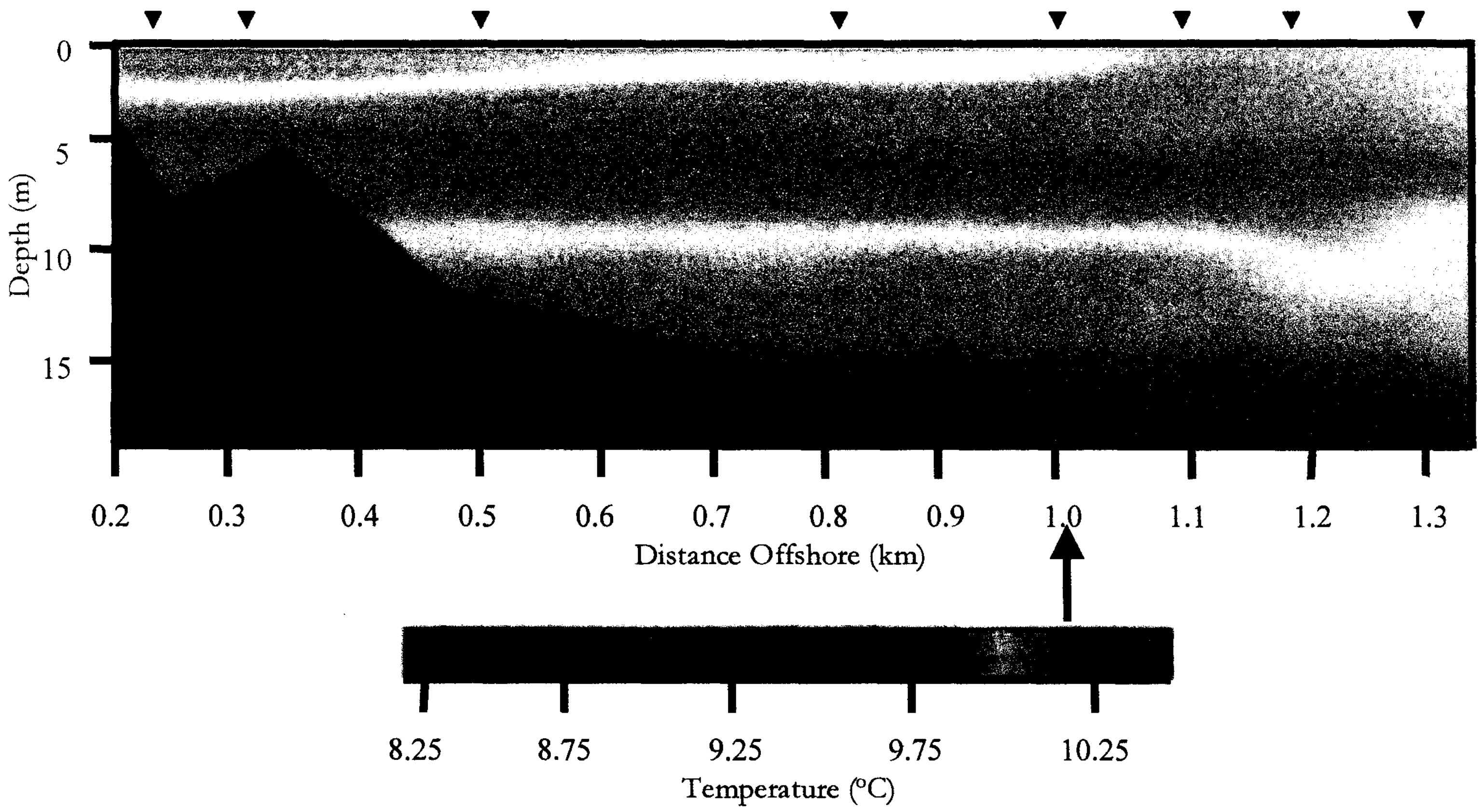


Figure 4. Distribution of the temperature during a period of upwelling favorable winds on Julian day 228. CTD profiles were obtained at eight sample stations within 1.5 km of the shore. The diamond symbols along the upper horizontal axis indicate the location of the stations sampled. The arrow indicates the location of the front.

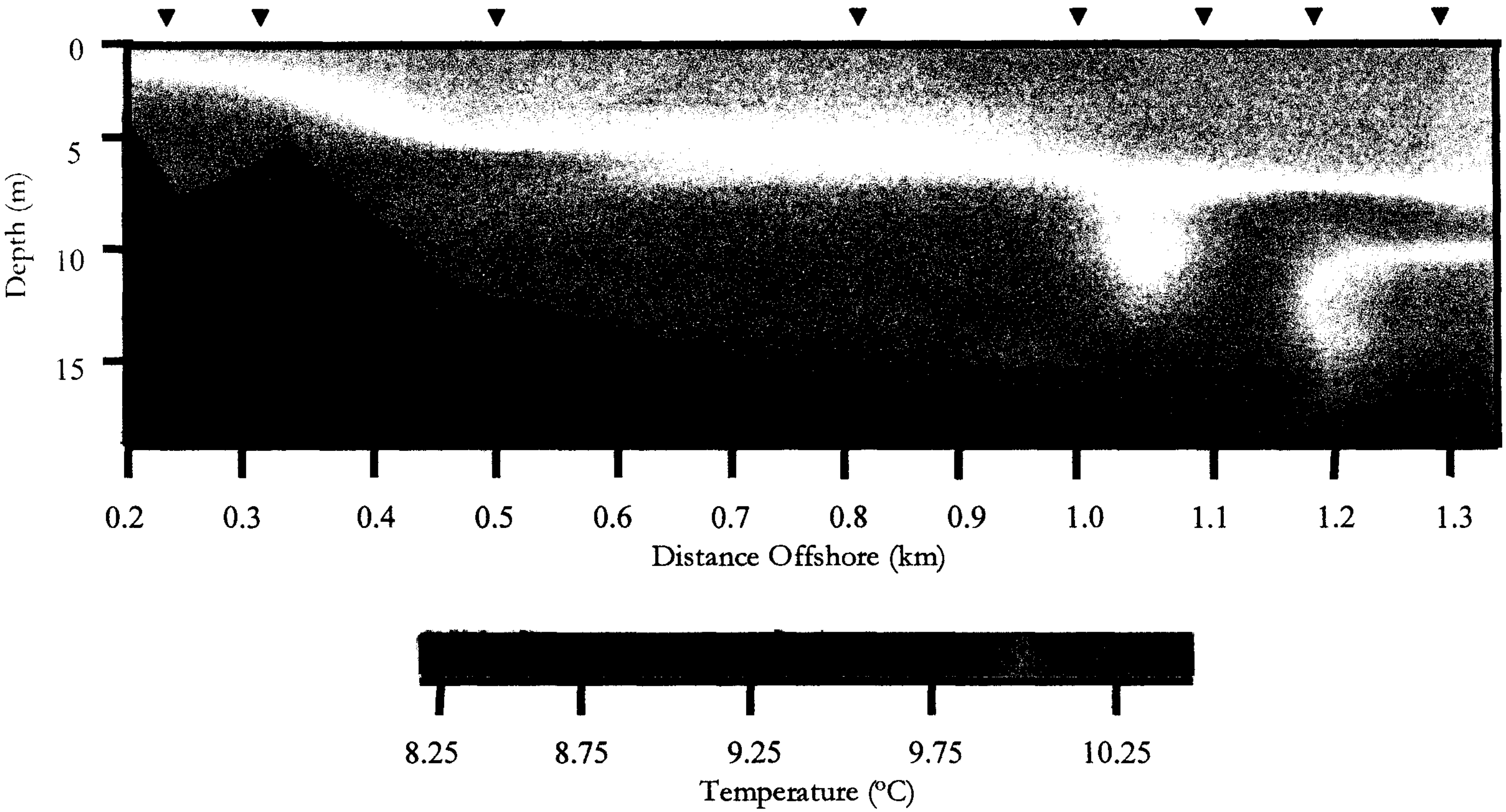


Figure 5. Distribution of the temperature during a period of downwelling favorable winds on Julian day 222. CTD profiles were obtained at eight sample stations within 1.5 km of the shore. The diamond symbols along the upper horizontal axis indicate the location of the stations sampled.

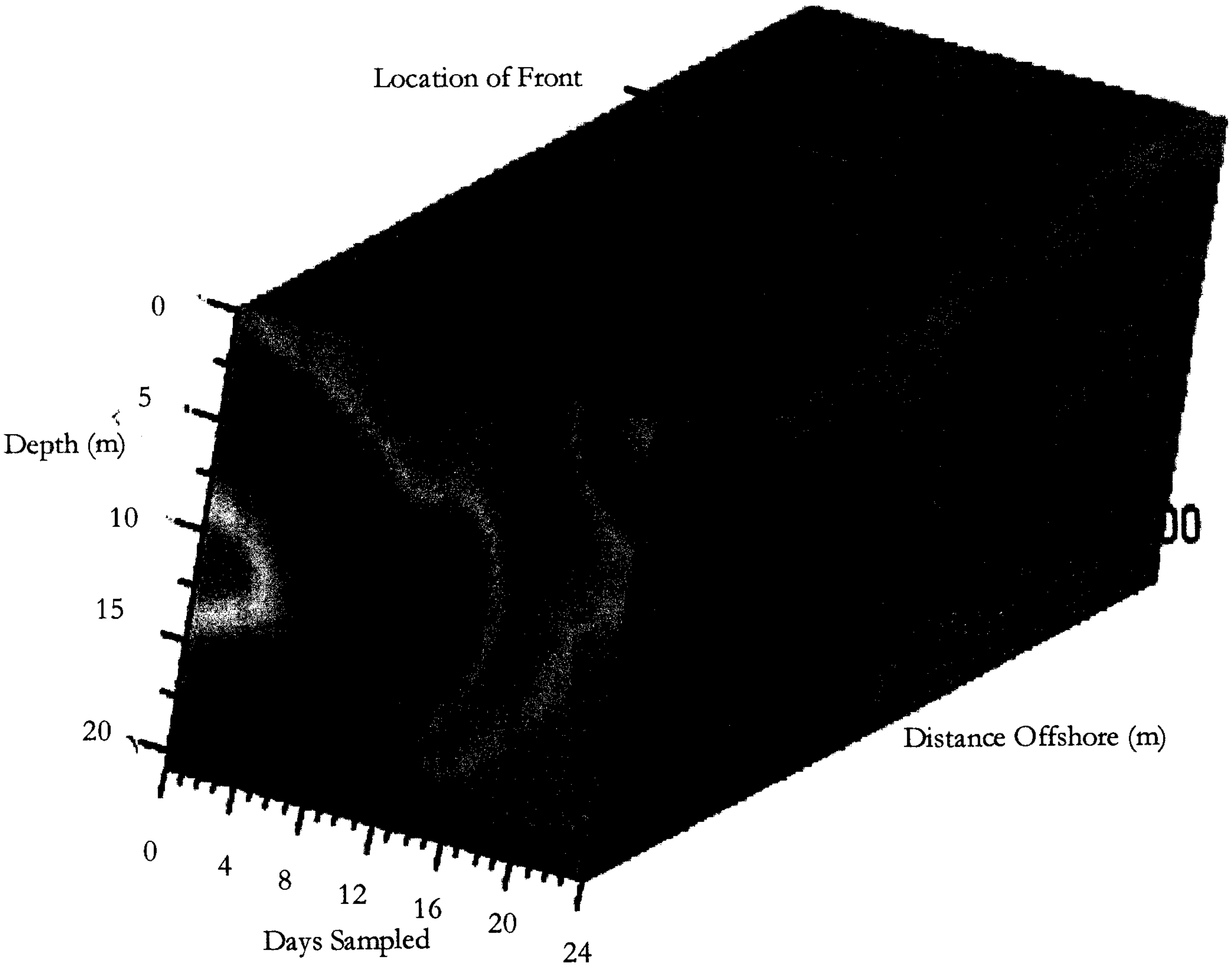


Figure 6. Three-dimensional view of water temperature at Sunset Bay, OR over the sampling period. Warmer temperatures are represented by red and colder temperatures by blue. The location of the front is approximately 1000 m offshore at the mouth of the bay.

varied significantly with zone during upwelling favorable winds (Table 3, Fig. 7). A post hoc pairwise comparison test (Tukey, $p<0.05$) was completed on significant zone effects to determine the differences between zones (Table 4). Significant temperature differences were found between waters seaward of the front and the bay waters (mid and inner zones). However, salinity and density comparisons revealed no significant differences between waters seaward of the front and the mid bay waters. Significant salinity and density differences were found between waters seaward of the front and inner bay waters, and between mid bay and inner bay waters (Table 4). During downwelling favorable winds, no significant differences were found across zones (Fig. 8). These results indicate that during upwelling favorable winds the temperature, salinity, and density of the waters seaward of the location of the front are different than bay waters.

Temperature, salinity, density and chlorophyll from CTD stations were cross-correlated with alongshore wind stress. Input data for this analysis included all measurements collected at a depth of 1 m below the surface at each of the CTD stations. Because sampling occurred in the morning approximately every two days, alongshore wind stress was averaged for the days between sampling cruises. For example, if CTD sampling occurred on Julian day 184 and 186, then alongshore wind stress for days 184 and 185 were averaged for analysis for Julian day 186. At all CTD stations, I found a significant and positive cross-correlation between temperature and alongshore wind stress at a lag of 0 days (Table 5). Temperature at 1 m depth tended to be lower during periods of upwelling favorable winds and warmer during downwelling favorable winds (Fig. 9). Salinity was significantly and negatively cross-correlated with alongshore wind stress at a 0 d lag at half of the stations (Table 5). During upwelling favorable winds, salinity tended to be higher, and

Table 3. Results of a two-way analysis of variance testing the effect of zone and condition (upwelling or downwelling) on temperature, salinity, density, and chlorophyll. The input data was the average of maximum and minimum values for all the vertical CTD casts in a zone.

Temperature	df	MS	F	Significance
Condition	1	4.87	9.84	p < 0.01**
Zone	2	5.39	10.35	p < 0.01**
Interaction	2	0.31	11.48	0.53 (NS)
Error	66	0.47		
Salinity				
Condition	1	0.32	0.42	0.52 (NS)
Zone	2	0.28	3.63	p < 0.05*
Interaction	2	0.01	0.16	0.85 (NS)
Error	66	0.08		
Density				
Condition	1	0.36	4.72	p < 0.05*
Zone	2	0.64	8.43	p < 0.01**
Interaction	2	0.02	0.16	0.86 (NS)
Error	66	0.76		
Chlorophyll				
Condition	1	0.28	0.12	0.91 (NS)
Zone	2	1.58	0.69	0.51 (NS)
Interaction	2	2.68	1.17	0.32 (NS)
Error	66	2.29		

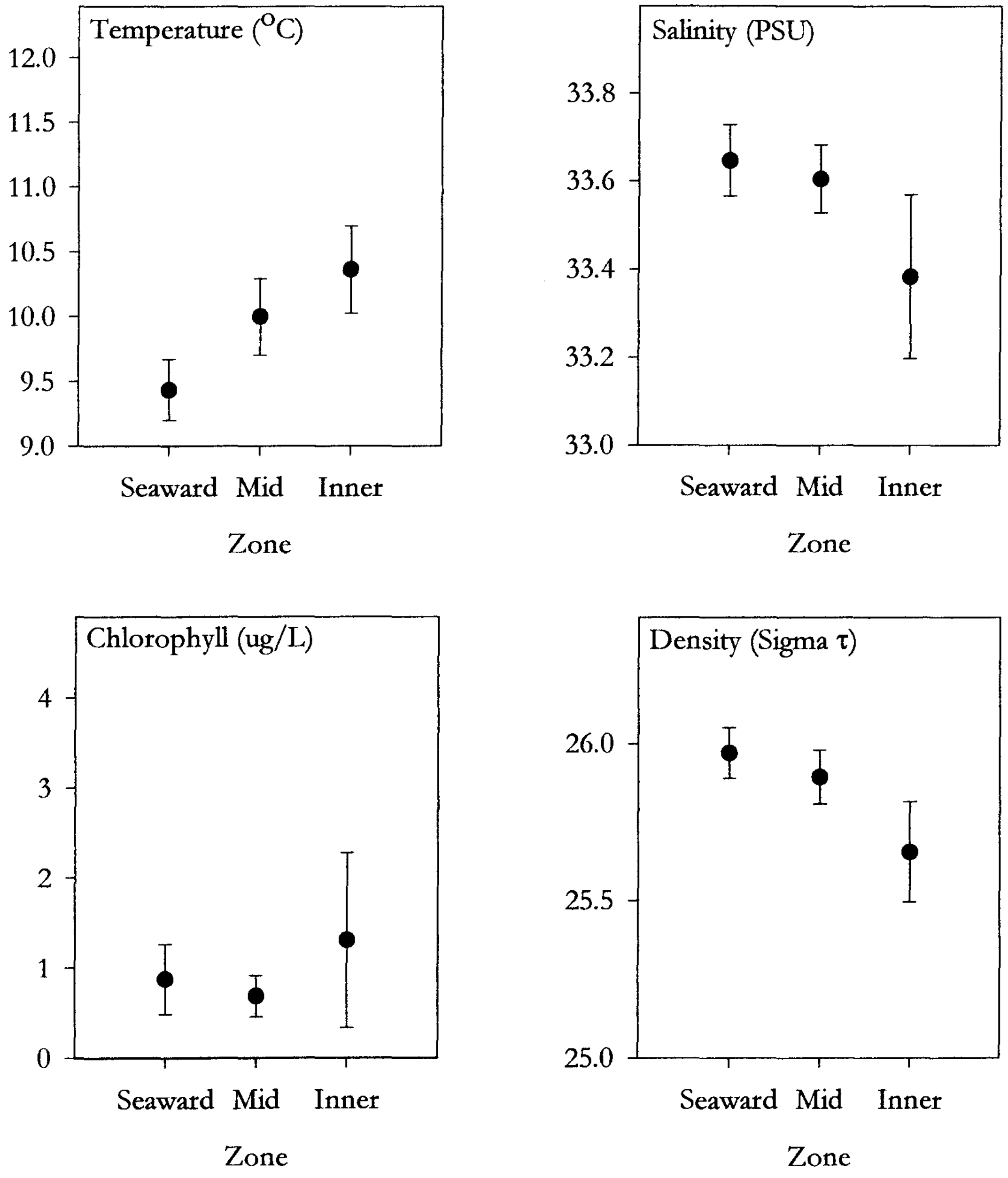


Figure 7. Average temperature, salinity, chlorophyll, and density during upwelling favorable winds from CTD casts across the front at the mouth of Sunset Bay, Oregon. Values are the average (+/– 95% CL) of the minimum and maximum values of CTD casts in each zone (n=24). Seaward zone represents the area seaward of the front and mid and inner bay represents the area inshore of the front.

Table 4. Results of post-hoc pairwise comparisons (Tukey, $p<0.05$) testing the effect between zones of temperature, salinity, density, and chlorophyll during upwelling favorable winds. Values were determined by averaging the maximum and minimum values for each CTD cast from each zone. (Degrees of freedom = 69)

Temperature		Significance
	Seaward vs. Mid Bay	$p < 0.05$*
	Seaward vs. Inner Bay	$p < 0.01$**
	Mid vs. Inner Bay	0.20 (NS)
Salinity		
	Seaward vs. Mid Bay	0.88 (NS)
	Seaward vs. Inner Bay	$p < 0.01$**
	Mid vs. Inner Bay	$p < 0.05$*
Density		
	Seaward vs. Mid Bay	0.63 (NS)
	Seaward vs. Inner Bay	$p < 0.01$**
	Mid vs. Inner Bay	$p < 0.05$*

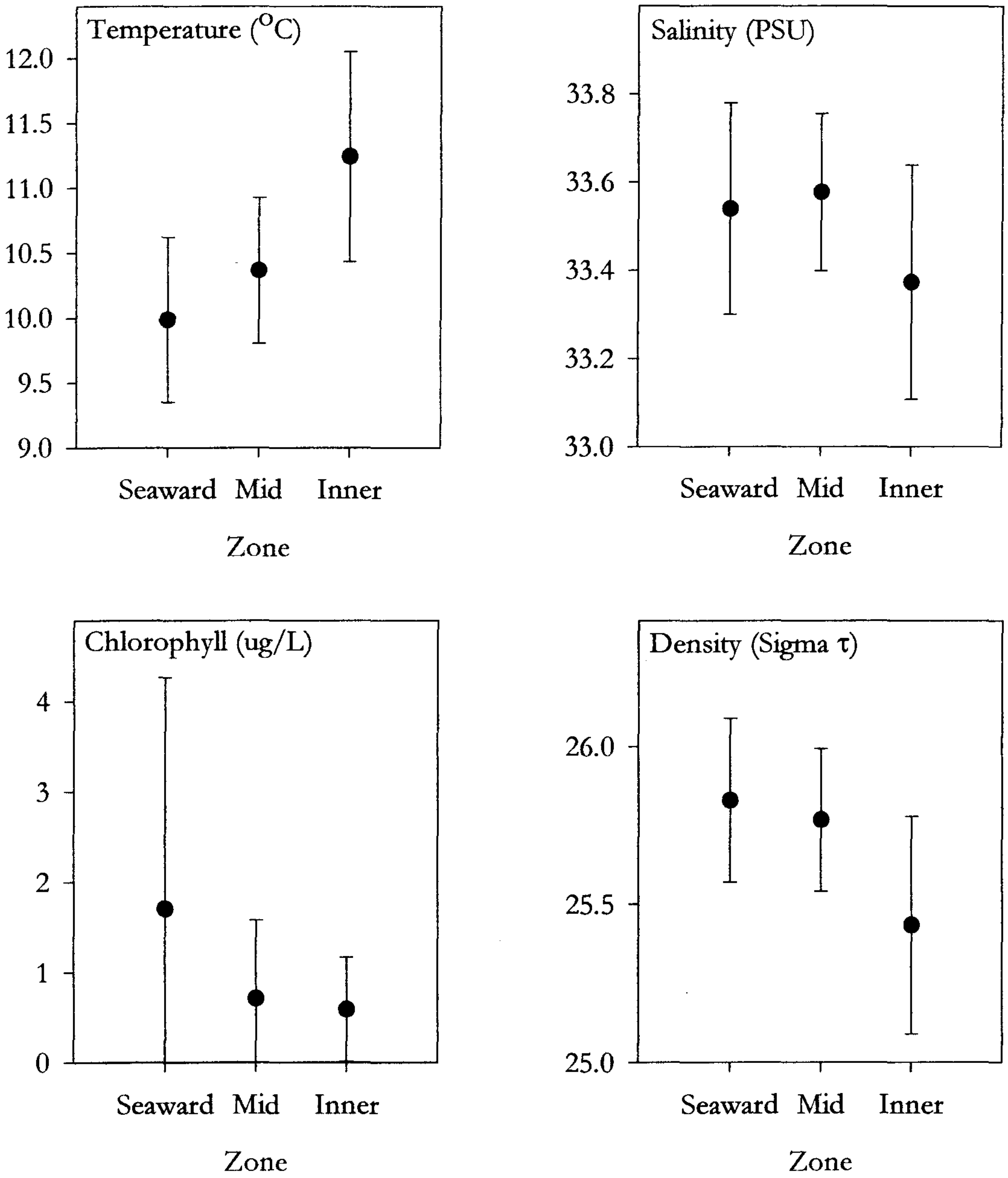


Figure 8. Average temperature, salinity, chlorophyll, and density during downwelling favorable winds from CTD casts across the front at the mouth of Sunset Bay, Oregon. Values are the average (+/– 95% CL) of the minimum and maximum values of CTD casts in each zone (n=24). Seaward zone represents the area seaward of the front and mid and inner bay represents the area inshore of the front.

Table 5. Results of cross-correlations between alongshore wind stress and parameters, such as temperature, salinity, and density. Alongshore wind stress CTD was averaged over two days prior to the sampling day. Values are listed with distances offshore from Inner bay shoreline, cross-correlation coefficients and days lag. The standard error for all coefficients is 0.2041. Chlorophyll is not shown because no correlations were significant. Only significant correlations are shown ($p<0.05$, $n = 24$).

Alongshore Wind Stress		r	Days lag
Temperature			
	1.5 km	0.55	0
	1.2 km	0.53	0
	1.1 km	0.50	0
	1.0 km	0.49	0
	0.85 km	0.50	0
	0.52 km	0.53	0
	0.33 km	0.49	0
	0.23 km	0.41	0
Salinity			
	1.5 km	NS	
	1.2 km	-0.41	0
	1.1 km	-0.45	0
	1.0 km	-0.56	0
	0.85 km	NS	
	0.52 km	-0.48	0
	0.33 km	NS	
	0.23 km	NS	
Density			
	1.5 km	-0.48	0
	1.2 km	-0.49	0
	1.1 km	-0.49	0
	1.0 km	-0.58	0
	0.85 km	-0.44	0
	0.52 km	-0.56	0
	0.33 km	-0.43	0
	0.23 km	-0.40	0

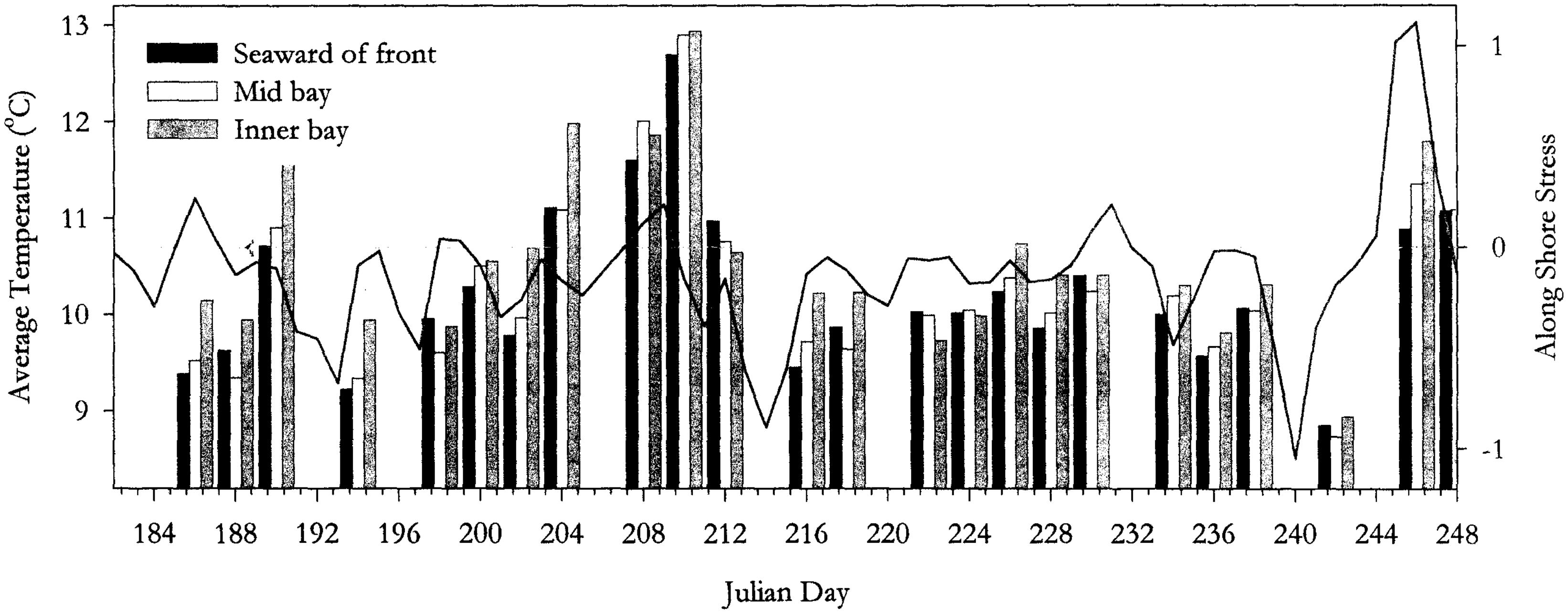


Figure 9. Temperature from CTD casts landward and seaward of the front at Sunset Bay from Julian day 186 through 248 (July 5th - September 5th) and alongshore wind stress. Values of temperature are the average temperature at 1 m depth from CTD cast made within each section. The black bars represent samples collected seaward of the front, while the white and grey bars are landward of the front at the mid and inner bay, respectively.

during downwelling/relaxation events, the waters seaward of the front and in the mid bay were less saline (Fig. 10). At all stations, density and alongshore wind stress were significantly and negatively cross-correlated at 0 d lag (Table 5). During downwelling/relaxation events, less dense waters tended to be found in all zones (Fig. 11). Chlorophyll, however, was not significantly cross-correlated with alongshore wind stress at any of the CTD stations (Fig. 12). In summary, warmer, less saline, and less dense offshore waters were found onshore across the location of the front during downwelling/relaxation events.

Distribution of Zooplankton Across the Nearshore Zones

Approximately every other day, plankton tows were made at mooring stations in each zone to determine the concentration of larvae seaward and landward of the front. Concentrations of *Balanus glandula* cyprids ranged from 0 to 140 (#/m^3) seaward of the front, 0 to 328 (#/m^3) in the mid bay, and 0 to 396 (#/m^3) in the inner bay. While the highest average daily concentrations tended to be landward of the front in the mid and inner zones (Fig. 13), the concentration of *B. glandula* cyprids was not significantly different across the front (2-way ANOVA, $p > 0.05$, Table 6).

On the other hand, concentrations of mussels varied across the front. Concentrations ranged from 0 to 817 (#/m^3) in the outer zone, 0 to 190 (#/m^3) in the mid zone, and 0 to 15 (#/m^3) in the inner zone. The average concentration of mussels was highest seaward of the front with extremely low numbers landward of the front (Fig. 13). Mussel concentration varied significantly with zone (2-way ANOVA, $p < 0.05$, Table 6). A significant difference was found with a post-hoc pairwise comparison test (Tukey, $p < 0.05$)

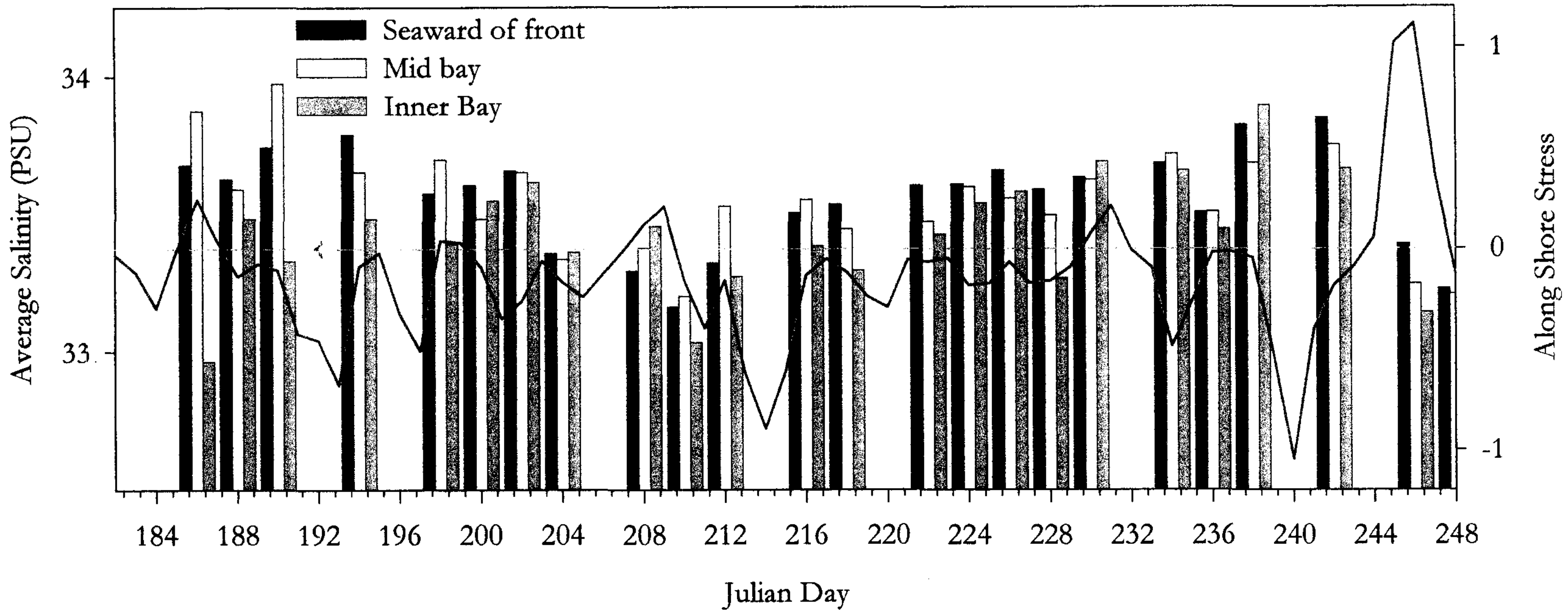


Figure 10. Salinity from CTD casts landward and seaward of the front at Sunset Bay from Julian day 186 through 248 (July 5th - September 5th) and alongshore wind stress. Values of salinity are the average salinity at 1 m depth from CTD cast made within each section. The black bars represent samples collected seaward of the front, while the white and grey bars are landward of the front at the mid and inner bay, respectively.

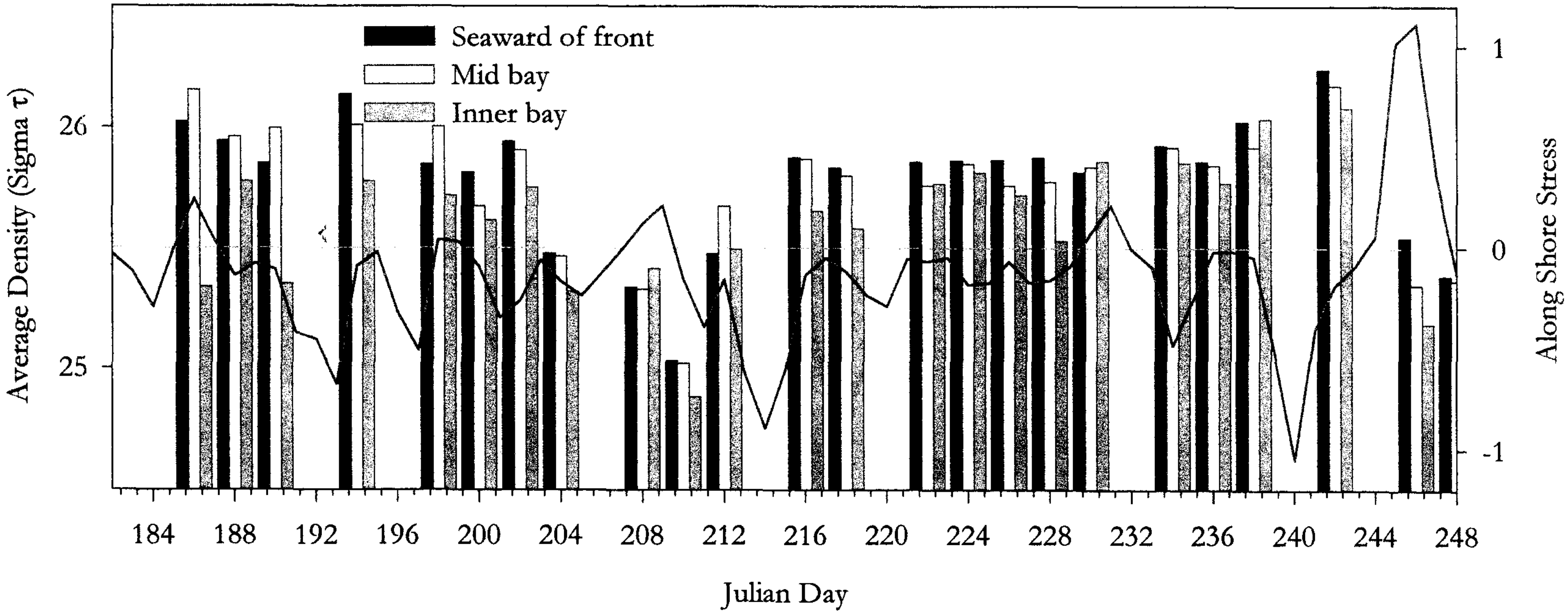


Figure 11. Density from CTD casts landward and seaward of the front at Sunset Bay from Julian day 186 through 248 (July 5th - September 5th) and alongshore wind stress. Values of density are the average density at 1 m depth from CTD cast made within each section. The black bars represent samples collected seaward of the front, while the white and gray bars are landward of the front at the mid and inner bay, respectively.

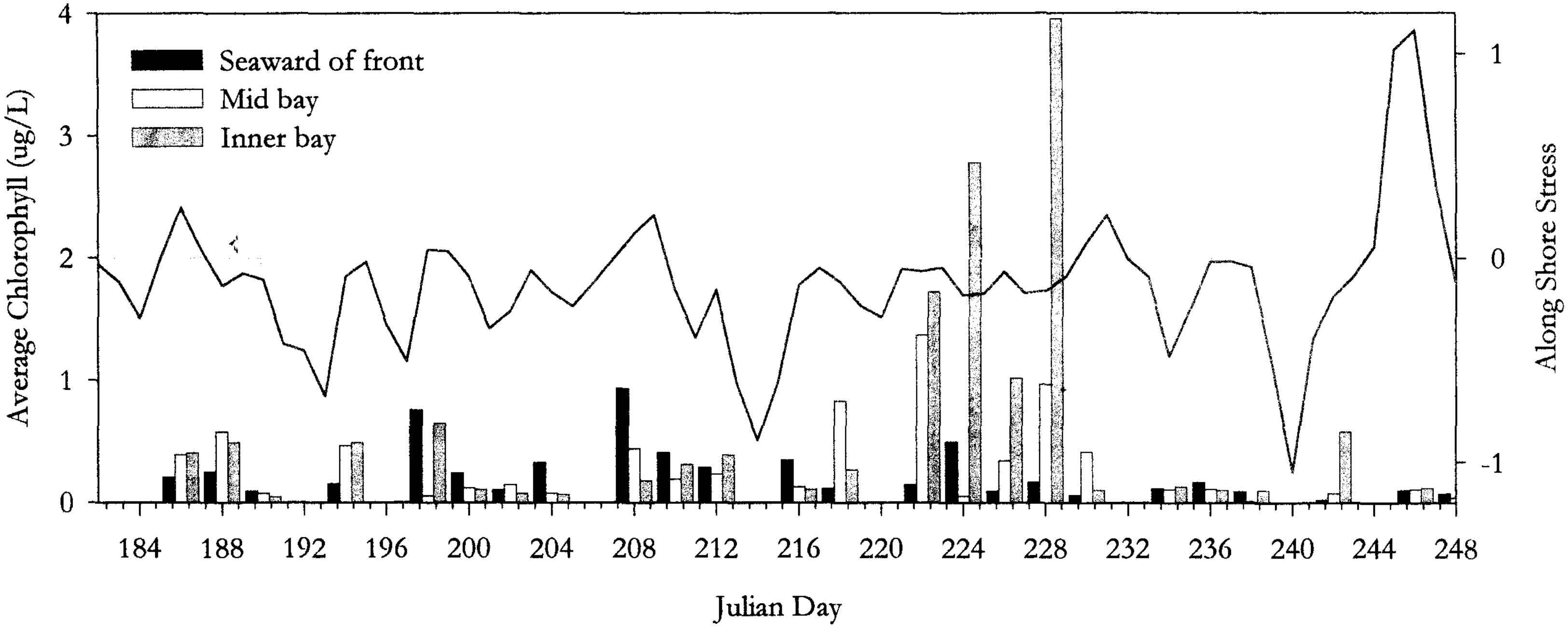


Figure 12. Chlorophyll from CTD casts landward and seaward of the front at Sunset Bay from Julian day 186 through 248 (July 5th - September 5th) and alongshore wind stress. Values of chlorophyll are the average chlorophyll at 1 m depth from CTD cast made within each section. The black bars represent samples collected seaward of the front, while the white and gray bars are landward of the front at the mid and inner bay, respectively.

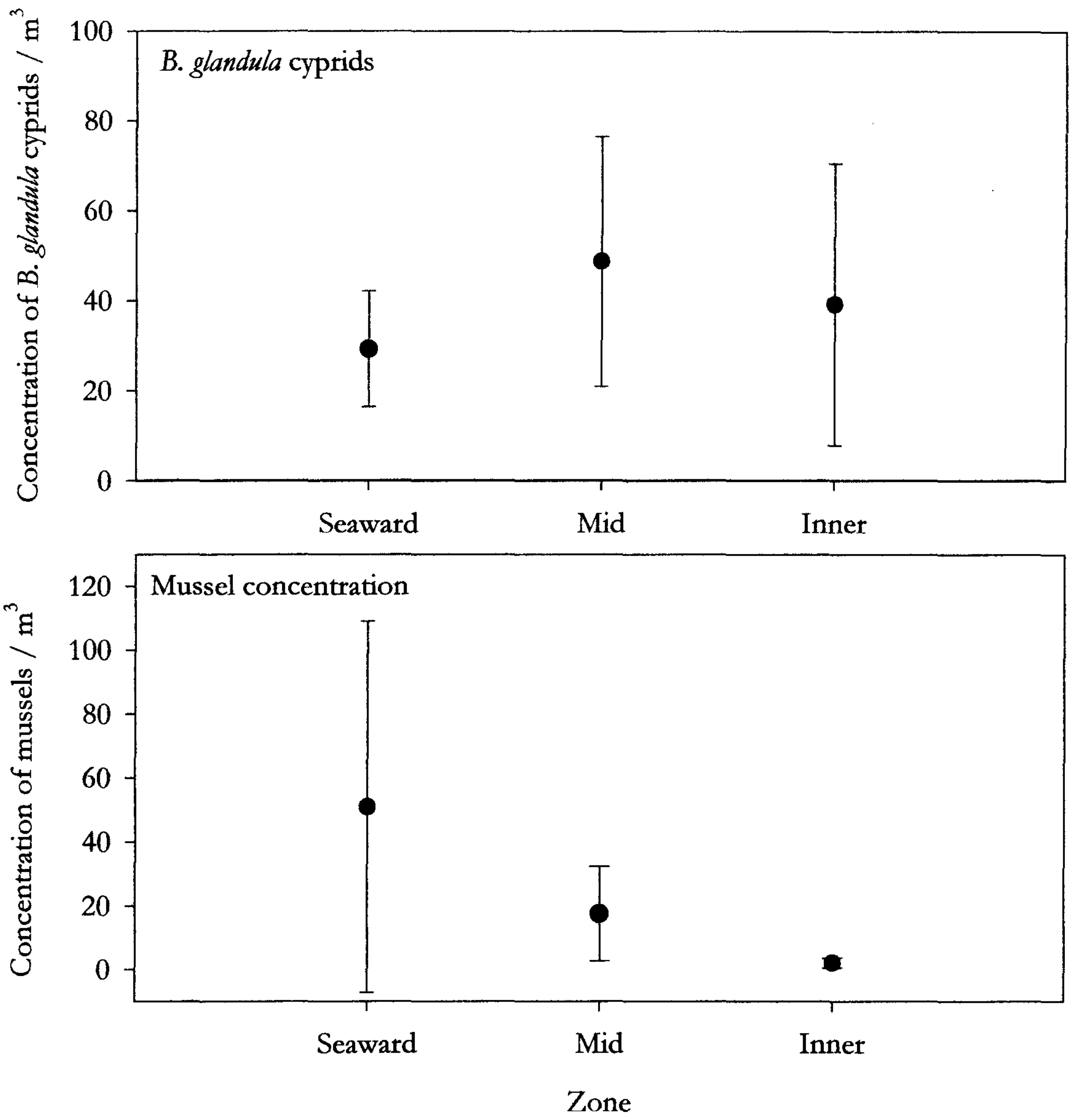


Figure 13. Distributions of *B. glandula* cyprids and mussels in plankton tow collected across the front at the mouth of Sunset Bay, Oregon. Values are the average (+/- 95% CL) larval concentrations of each zone from the sampling days over the study (n = 26 for Seaward and n = 28 for Mid and Inner). Concentrations are the number of organisms per m^3. Seaward zone represents the area seaward of the front and mid and inner bay represents the area inshore of the front.

Table 6. Results of a two-way analysis of variance showing the effect zone and condition on the concentration (organisms/m^3) of *B. glandula* cyprids and of mussels from plankton tows. Concentration of larvae were log transformed. Number of plankton tows were 26 for the Seaward zone and 28 for the Mid and Inner zones.

	df	MS	F	Significance
B. glandula				
Condition	1	0.96	1.80	0.18 (NS)
Zone	2	0.16	0.30	0.74 (NS)
Interaction	2	0.03	0.05	0.95 (NS)
Error	75	0.53		
Mussels				
Condition	1	1.62	4.27	$p < 0.05$*
Zone	2	2.87	7.54	$p < 0.01$**
Interaction	2	0.37	0.99	0.38 (NS)
Error	75	0.38		

between mussels seaward of the front and inner bay ($p < 0.001$, 81 df), as well as between mussels in the mid bay and inner bay ($p=0.026$, 81 df). No significant difference was found between the zone seaward of the front and the mid bay ($p>0.05$, 81 df).

Larval Settlement on Plates

Barnacle settlement was low (0-2 cyprids/plate) for the first two weeks of the study, but subsequently ranged over 3 orders of magnitude. Over the study, almost 54,000 barnacle cyprids settled on plates of which 99.8 % were *Balanus glandula.* Therefore, the following analysis will focus on *B. glandula.* Settlement ranged from 0 to 2690 *B. glandula* cyprids per plate per day, and was highly variable between sampling days. Much of the total settlement occurred during a few large peaks (Fig. 14). Settlement plates on each mooring were summed and the three moorings within each zone were averaged. Daily settlement was estimated by dividing the zone average by the number of days sampled. A total of 3905 individuals settled in the zone offshore of the front, 27,501 inshore of the front in the mid bay, and 22,392 in the inner bay (Fig. 14).

The similarity between the peaks in barnacle settlement and alongshore wind stress suggests that settlement was correlated with winds (Fig. 14). To investigate the correlation of the peak in barnacle settlement and wind stress, daily settlement was log-transformed and detrended. Cross-correlations were run between alongshore and cross-shore wind stress and *Balanus glandula* settlement. An additional cross-correlation was run between the maximum daily tidal range and *B. glandula* settlement. A significant negative correlation was found at 0 d lag between along- and cross-shore wind stress and barnacle settlement in the outer zone suggesting that settlement occurred during upwelling conditions (Table 7). Significant

Figure 14. Average daily settlement (± SE) of *B. glandula* cyprids on settlement plates in each of the three zones at Sunset Bay, Oregon plotted with the average daily alongshore wind stress. Seaward zone represents the area seaward of the front and mid and inner bay represents the area inshore of the front. Positive and negative values for alongshore wind stress indicate downwelling and upwelling, respectively. The grey boxes represent downwelling events. Sampling began on Julian day 184 (July 3rd, 2000) till Julian day 248 (September 5th, 2000).

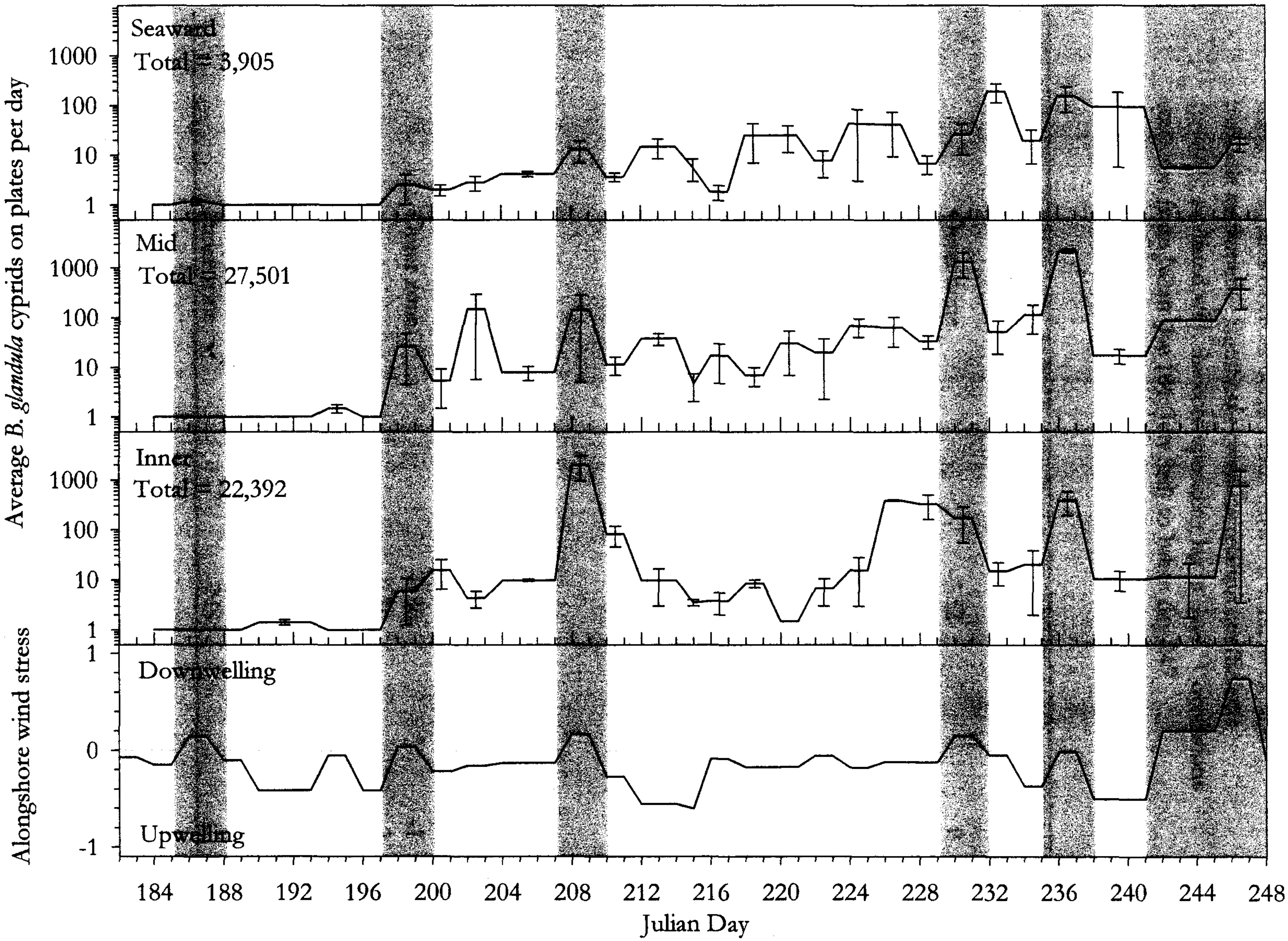

Seaward
Total = 3,905
Mid
Total = 27,501
Inner
Total = 22,392
Downwelling
Upwelling
Average B. glandula cyprids on plates per day
Alongshore wind stress
1000
100
10
1
-1
0
184
188
192
196
200
204
208
212
216
220
224
228
232
236
240
244
248
Julian Day

Table 7. Results of cross-correlations between wind stress and barnacle settlement. Significant cross-correlation coefficients ($p<0.05$) are listed with the corresponding lag in days. Correlations were run from Julian day 184 (July 3rd) to Julian day 247 (September 4th) (n=64 days).

Alongshore Wind Stress	r	lag
Outer zone	-0.32	0
Mid zone	0.34	0
Inner zone	0.33	0
Cross-shore Wind Stress		
Outer zone	-0.41	0
Mid zone	NS	
Inner zone	NS	
Maximum Tidal Range		
Outer zone	-0.36	-1
	-0.35	-2
	-0.29	-3
Mid zone	NS	
Inner zone	NS	

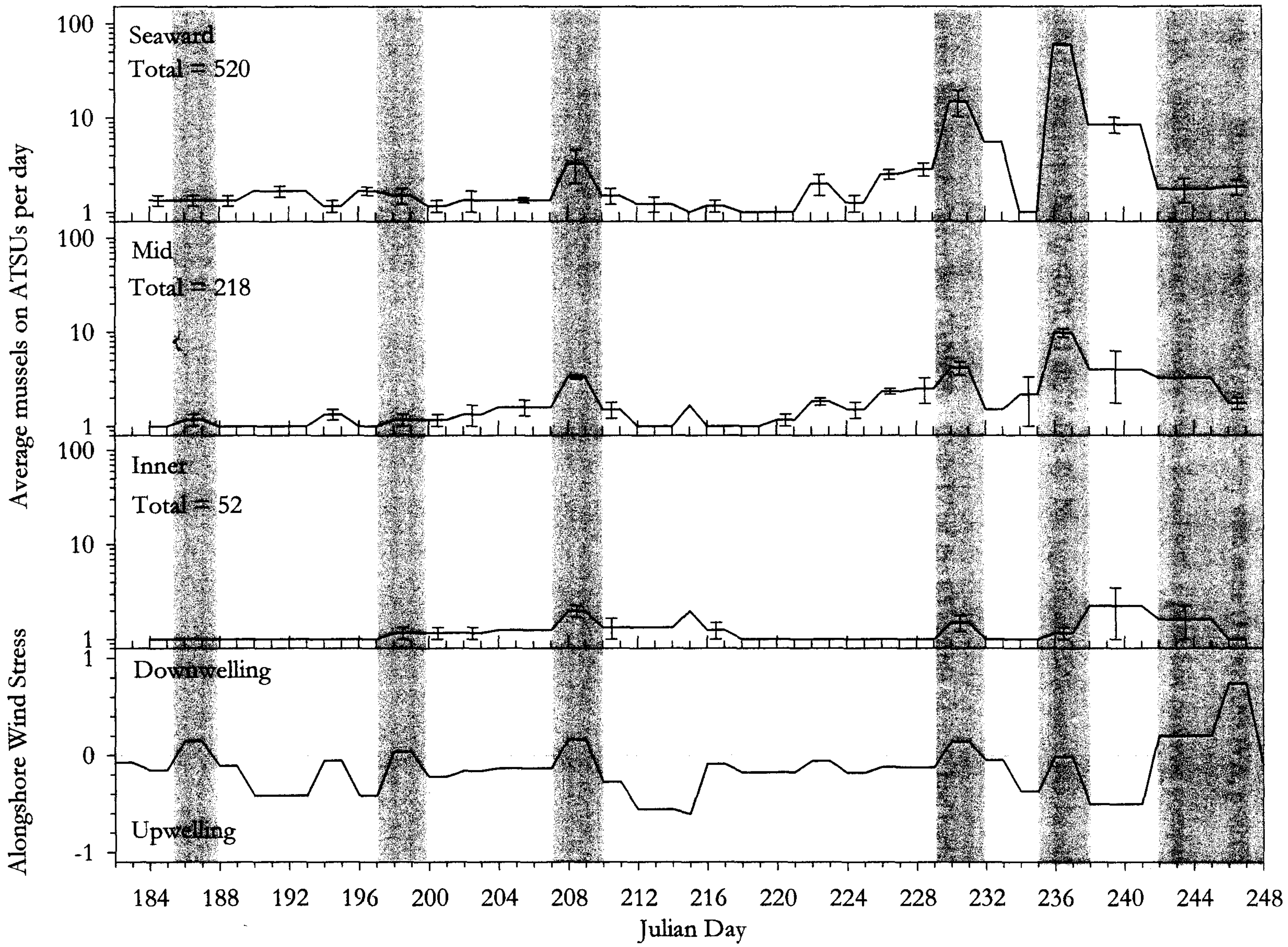
negative correlations were found at -1, -2, and -3 days lag between maximum daily tidal range and settlement seaward of the front (Table 7). At the mid and inner zones, there were significant positive correlations at 0 days lag between alongshore wind stress and barnacle settlement suggesting that peaks in barnacle settlement occurred during downwelling favorable winds (Table 7). No significant cross correlations were found between cross-shore wind stress or maximum daily tidal range and barnacle settlement in the mid and inner zones (Table 7). Offshore of the front, cyprids tended to settle highest during upwelling conditions and several days after neap tides; however, inshore of the front, peaks in settlement tended to occur during downwelling winds.

Larval Settlement on Artificial Turf Substrata

A variety of larvae were recovered from the artificial substrata including mussels and other bivalves, cyprids, nudibranchs, gastropods, and copepods. The following analysis will focus on mussel larvae.

Over the study, mussels generally settled in relatively low numbers with higher settlement during several peaks near the end of the study (Fig. 15). Mussel settlement ranged from 0 to 60 per artificial turf substrata unit (ATSU) per day with a total of 839 mussels that settled over the study. Settlement on the ATSUs was summed on each mooring and the three moorings were averaged for each zone. Daily settlement was determined by dividing the zone average by the number of days in a sampling period. Mussel settlement was low (0 to 5 mussels/ATSU) until Julian day 232 (Fig. 15). Two peaks in mussel settlement occurred on Julian day 232 and 238 (August 20th, and August 28th, respectively; Fig. 15). Sixty-eight % of the mussels were caught seaward of the front, 26% in the mid bay, and only 6% in the

Figure 15. Average daily settlement (± SE) of mussels on artificial turf substrata units (ATSU) in each of the three zones at Sunset Bay, Oregon plotted with the average daily alongshore wind stress. Seaward zone represents the area seaward of the front and mid and inner bay represents the area inshore of the front. Positive and negative values for alongshore wind stress indicate downwelling and upwelling, respectively. The grey boxes represent downwelling events. Sampling began on Julian day 184 (July 3rd, 2000) till Julian day 248 (September 5th, 2000).


Seaward
Total = 520
Mid
Total = 218
Inner
Total = 52
Downwelling
Upwelling
Average mussels on ATSUs per day
Alongshore Wind Stress
100
10
1
0
-1
184
188
192
196
200
204
208
212
216
220
224
228
232
236
240
244
248
Julian Day

inner bay. Mussel settlement varied significantly with zone (1-way ANOVA, $p<0.05$, Fig.16, Table 8). A significant difference was found with a post-hoc pairwise comparison test (Tukey, $p<0.05$) between mussels that settled seaward of the front and mussels that settled in the inner bay ($p<0.01$, 81 df, Table 8). No significant difference was found between mussels that settled seaward of the front and mid bay or with mussels that settled in the mid bay and the inner bay (Table 8). Only 17 of the 63 sample periods had high mussel settlement (> 2 per sampling period). Therefore, there was no significant cross-correlation found between alongshore and cross-shore wind stress.

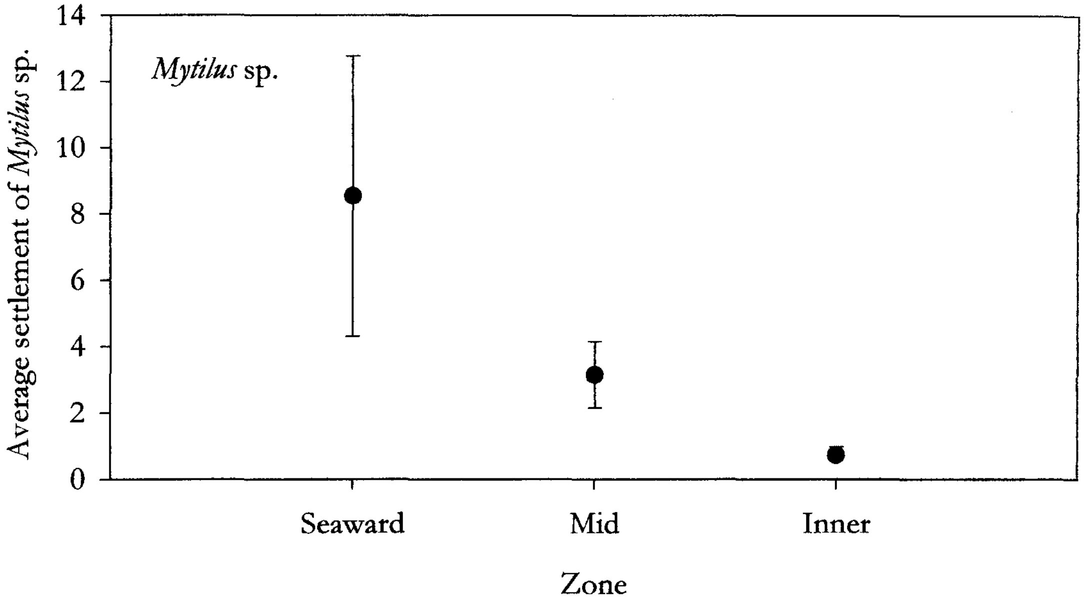


Figure 16. Average settlement of mussels from sampling period across the front at the mouth of Sunset Bay, Oregon. Values are the average (+/- 95% CL) settlement of larvae on artificial turf substrata units (ATSU) for each zone over the study (n = 29 for all zones). The seaward zone represents the area seaward of the front and the mid and inner bay represents the area inshore of the front.

Table 8. Results of a one-way analysis of variance and post-hoc pairwise comparison (Tukey, $p<0.05$, df = 81) showing the effect of zone on the settlement of mussels on artificial turf substrata units. Averages of larvae were log transformed. Number of sampling periods was 29 for all zones across the front.

	df	SS	MS	F	Significance
Mussels					
Between zones	2	1.79	0.89	5.41	$p < 0.01$**
Within zones	84	13.85	0.17		
Total	86	15.64			
Post-hoc pairwise comparison					
Seaward vs. Mid Bay					0.54 (NS)
Seaward vs. Inner Bay					$p < 0.01$**
Mid Bay vs. Inner Bay					0.08 (NS)

CHAPTER IV

DISCUSSION

Frontal systems have been known to have a major influence on the biology of organisms with planktonic larvae. Several studies suggested that larvae could be concentrated and transported by moving fronts (Kingsford, 1990; Kingsford et al., 1991; Roughgarden et al., 1988, 1991; Farrell et al., 1991; Pineda, 1991, 1994a,b, 1999; Shanks, 1983, 1986a,b, 1987, 1988, 1998; Shanks and Wright, 1987; Shanks et al., 2000; Wing et al., 1995a,b; Wolanski and Hamner, 1988). In coastal waters, the flow past topography can generate secondary circulation patterns that can trap and concentrate plankton. Bakun (1986) and Wolanski and Hamner (1988) reviewed types of small-scale circulation found nearshore that can potentially affect the distribution of larvae. In areas where the topography changes abruptly, such as headlands and bays, alongshore flow can separate from shore. In the lee of a headland or within the bay, an eddy can develop. High concentrations of plankton have been observed in association with eddy-generated convergences behind islands and reefs (Alldredge and Hamner, 1980; Hamner and Hauri, 1981; Willis and Oliver, 1990; Wolanski, et al., 1989; Wolanski and Hamner, 1988). These studies have focused on eddies generated by tidal currents. While these flow fields clearly altered the distribution of plankton, they may not be important to the dispersal of larvae because the circulation patterns are short-lived. If flow patterns persisted for extended periods, then they could be important to the biology of intertidal organisms. For example, some types of larvae have short planktonic stages and go through their entire development close to shore. Therefore, the front may act as a barrier to offshore dispersal of larvae with short planktonic stages or early stage larvae. On the other hand, the front may act as a barrier to the shoreward migration of settling larvae. Several studies suggested that fronts act as barriers to the offshore (Boden, 1952; Pedrotti and Fenaux, 1992) and shoreward (Graham et al., 1992) dispersal of larvae. The behavior and swimming ability of larvae at depth can determine the effect a front will have on the dispersal (Okubo, 1978; Olson and Backus, 1985; Franks, 1992). Our study focuses on a persistent type of circulation in the nearshore waters.

Gregory point (Fig. 1) is the first headland along the southern Oregon coast. Because of the extensive beaches north of Gregory Point, alongshore currents are less affected by shoreline topography. Previous studies have shown that headlands and embayments, like Gregory Point and Sunset Bay, can create topographically generated circulations (Bakun, 1986; Wolanski and Hamner, 1988).

At Sunset Bay, three types of foam lines were observed from January through September. During periods of large swells, perpendicular foam lines were observed apparently associated with rip currents. When the swells were small, but the winds were from the South, West, or East, foam lines were parallel to shore but extended only partially across the mouth of Sunset Bay. During upwelling favorable winds (Northwest winds) and small swells (<2 m), however, a foam line was always present and it extended completely across the mouth of the bay.

During the summer of 2000, winds were typical for the season and the Oregon coast. The dominant winds were upwelling favorable and from the Northwest with occasional periods of Southwest winds producing downwelling/relaxation events. During the summer sampling period (July through September), small waves and Northwest winds were observed on 63 days (about 84% of the time). The average duration of these conditions was eight days (range 2 to 20 days) and there were four periods that lasted a week or longer. The shore-parallel foam line was present at Sunset Bay at least 84% of the summer. The foam line was consistently found at the mouth of the bay throughout the tidal cycle and the position of the foam line did not obviously change over the tidal cycle (personal observation). If the foam line is an indicator of a frontal convergence, and if the front acts as a barrier to the shoreward migration of larvae that developed over the shelf, then for much of the summer, larvae may be prevented from settling in the intertidal zone in Sunset Bay.

Previous work (Shanks, unpublished data) indicates that the foam line is associated with a front that separates the coastal ocean waters from the bay waters. In this study, the foam line and front were present only during upwelling favorable winds, when winds pushed surface waters southward along the coast. During upwelling favorable winds, the temperature and salinity of the waters seaward of the front tended to be significantly colder and more saline than bay waters. The data suggest that the waters in the bay were isolated from offshore waters. I investigated the possibility that fresh water flow could be the potential cause of this difference in densities inside the bay from offshore. Appendix 2 demonstrates that there was no significant fresh water input into Sunset Bay from the Big Creek Basin during the sampling period. In fact, it was an unusually dry year.

During downwelling favorable winds, no significant differences were found between the physical characteristics of the waters seaward of the front location (~1 km from shore in Sunset Bay) and bay waters. During downwelling favorable winds, the waters seaward of the front location as well as in the bay tended to be warmer, less dense, less saline and the water column was mixed. These results suggest that during downwelling/relaxation events, the upwelling front and the warm low density surface waters seaward of the upwelling front moved onshore, the front at the mouth of Sunset Bay was not present during these periods, and the offshore waters were able to penetrate the bay. The observations combined with the CTD data suggest that the foam line represented a front and when the front was present, the offshore waters were separated from the bay waters.

The data suggest that the settlement of *Balanus glandula* cyprids and *Mytilus* sp. larvae were affected by the shore-parallel front at the mouth of Sunset Bay. Cyprid settlement was significantly lower seaward of the front than landward of the front. The small peaks in cyprid settlement observed seaward of the front tended to occur during upwelling events or a few days after neap tides. The results suggest that cyprid settlement seaward of the front could have been related to variations in wind driven or tidally driven shoreward transport. In the bay, however, large peaks in cyprid settlement were correlated with downwelling/relaxation events, periods when the front at the mouth of the bay broke down. The front apparently acted as a barrier to the shoreward movement of cyprids. When the front was present, settlement in the bay was about as low as was observed seaward of the front. When the front was absent, settlement was much higher (approximately 7x's) than was observed seaward of the front.

The cyprid data presents us with several puzzling questions: Why was there more cyprid settlement inside the bay than offshore? Why were the peaks in cyprid settlement offshore of the front correlated with upwelling, while settlement inside the bay was correlated with downwelling? How are the larvae being transported onshore? Ultimately, why was the pattern of cyprid settlement offshore so different from that observed in the bay, only a couple hundred meters apart?

There are several types of mechanisms that can transport larvae onshore: internal waves, internal tidal bores, upwelling fronts, winds, density driven currents, and the deep onshore flow during upwelling, and downwelling surface flows. In our study, the peak in cyprid settlement offshore of the front occurred during upwelling conditions and several days after the neap tide. Settlement patterns correlated with upwelling winds suggest onshore wind driven transport or transport shoreward by the upwelled waters. Settlement that varies with the spring-neap tidal cycle is typically generated by internal waves or internal tidal bores (Little, 1977; Shanks, 1986a; Doherty and Williams, 1988; van Montfrans et al., 1990; Boylan and Wenner, 1993; Olmi, 1995; Shanks, 1998). Tidally generated internal waves with associated convergences have been described by several studies (Zeldis and Jellett, 1982; Shanks, 1983; Kingsford and Choat, 1986; Shanks and Wright, 1987; Shanks, 1988). Inside the bay, peaks in cyprid settlement occurred during downwelling-relaxation events. Settlement that occurs immediately following upwelling events, during relaxation events, has been attributed to the upwelling front (Wing et al., 1995 a,b; Miller and Emlet, 1997). If cyprid settlement in all zones of Sunset Bay occurred during downwelling-relaxation events, then one would propose that transport was due to the upwelling front traveling back onshore. This was not the case. Therefore, we hypothesize a different transport mechanism for cyprid settlement inside the bay.

During upwelling conditions, when the front was present, cyprids may become concentrated in the convergence zone at the mouth of the bay. Several studies have demonstrated that cyprids can become concentrated in convergence zones (LeFevre, 1986;

Shanks and Wright, 1987). During downwelling/relaxation events, the front with aggregated cyprids may move onshore, transporting the cyprids concentrated in the convergence zone to settlement areas within the bay. Similar differences in blue crab settlement patterns in the bay versus along the open coast were found offshore of Duck, NC (Shanks et al., 2000). Roughgarden et al. (1991, 1994) and Farrell et al. (1991) hypothesized that the upwelling front along the central California coast can act as a convergence zone where barnacle larvae accumulate and were transported onshore during downwelling/relaxation events. Our data suggests that the transport mechanism was possibly a nearshore phenomenon.

Mussel larvae were affected differently by the front. Mussel settlement was significantly higher seaward of the front than inside the bay. The settlement of mussels closely followed the pattern of larval distribution, suggesting that the front acted as a barrier to the shoreward dispersal of mussel larvae. One possible explanation is that mussels were located in the surface waters where they were pushed by winds to settlement sites. This pattern of larval distribution is similar to other studies. This pattern is similar to that found by Gaines et al. (1985) for barnacle cyprids. Barnacle settlement differed by one to two orders of magnitude over a few tens of meters. The cyprid distribution was parallel to the cyprid settlement (Gaines et al., 1985).

In our study, the distribution of mussels was similar to their pattern of settlement, but the cyprid distribution was not correlated with settlement except for the inner zone. Since the barnacle cyprids are settling during downwelling/relaxation events and possibly aggregated in the front, it would be difficult to find correlations in the distribution of cyprids and settlement.

Many studies have looked at the effect of large-scale oceanographic patterns on the community structure of the rocky intertidal zone, but few studies have realized the importance of small-scale circulation patterns. Several studies suggest that the larvae of intertidal barnacles and other meroplankton accumulate in the upwelling front offshore of California (Roughgarden et al., 1988, 1994; Wing et al., 1995b; Grantham, 1998), and during relaxation events possibly move onshore (Roughgarden et al., 1988, 1991; Farrell et al., 1991; Wing et al., 1995b). Shanks et al. (2000) demonstrated the onshore transport of larvae in an upwelling front off the North Carolina coast. Roughgarden et al. (1988) predicted there was lower recruitment in central California than in the Pacific Northwest, because the upwelling season was longer, and relaxation events were less frequent (Parrish et al., 1981; Huyer, 1983). Consequently, the adult populations would be less abundant, freeing more space, which could explain weaker benthic interactions. It has been proposed that benthic interactions, rather than larval supply, structures the rocky intertidal populations in the Pacific Northwest (Roughgarden et al., 1988; Connolly and Roughgarden, 1998). Our observations suggest that patterns of larval supply affected by nearshore topography could, in fact, have a significant role in the community structure of the intertidal zone.

Menge et al. (1997a,b) hypothesized that large-scale variation in nearshore primary productivity affected the intertidal community dynamics at two sites along the central Oregon coast (Strawberry Hill and Boiler Bay). Later, research revealed differences in phytoplankton concentrations at adjacent sites, suggesting small-scale differences (10s to 100s of km). Sanford and Menge (2001) proposed later that differences in community dynamics between the two sites were due to zooplankton and water temperature differences. Strawberry Hill is a rocky bench located along a relatively straight stretch of coastline, while

Boiler Bay is a protected bay. Personal observations and aerial photographs (NOS Mapfinder Coastal Aerial Photography) indicate that a shore parallel foam line is often present at Boilers Bay, but not at Strawberry Hill. Greater concentrations of plankton were found at Strawberry Hill than Boilers Bay. Similar differences in plankton distributions have been observed at Cape Arago (rocky bench less than 1 km north of Sunset Bay) and Sunset Bay (Shanks, pers. observation). It is possible that studies that have attributed differences in community dynamics as being due to large-scale differences in coastal oceanography are, in fact, due to differences in the very small scale topographically generated flow field. This is an alternate hypothesis that has not been investigated by any study.

Previous studies have demonstrated larval transport mechanisms that vary on spatial and temporal scales. In this study we demonstrated that persistent nearshore topographic fronts influenced the settlement and dispersal of some planktonic larvae. The physics that generated the front at Sunset Bay is not unique to this site or coastline. The front was formed at the mouth of an embayment and embayments are common features along most coastal regions. The front was only present when the local winds were upwelling favorable and all coasts experience upwelling favorable winds. We predict that under oceanographic conditions similar to that observed at Sunset Bay that topographically generated secondary circulation have important affects on larval dispersal and settlement.

APPENDIX

WATER GUAGE DATA

Appendix 1. Water guage data (cubic ft./s) for the sampling period from the Big Creek Basin that flows into the Inner zone of Sunset Bay, OR. Data is from the Coos County Water Resources Department. "E" means the data was estimated.

Day	JUL	AUG	SEP	Day	JUL	AUG	SEP
1	1.3	0.37	0.67	16	0.63	.30E	.50E
2	1.2	.30E	0.82	17	0.68	.30E	.50E
3	1.1	.30E	1.3	18	0.69	.30E	.50E
4	1.3	.30E	1.5	19	0.64	0.41	0.55
5	1.5	.30E	1.3	20	0.64	.50E	0.66
6	1.2	.30E	1.1 E	21	0.9	.50E	0.74
7	1.1	.20E	.80E	22	0.76	0.66	0.72
8	0.95	.20E	.60E	23	.60E	0.68	0.54
9	0.91	.30E	.70E	24	.50E	.70E	0.48
10	0.8	0.37	.60E	25	0.44	.70E	.40E
11	0.73	.40E	.60E	26	.40E	.70E	.40E
12	0.71	.30E	0.7	27	.40E	.60E	.30E
13	0.66	.30E	0.6	28	.40E	.60E	.30E
14	0.66	.30E	0.61	29	.30E	.60E	.20E
15	0.66	.30E	0.52	30	.30E	.50E	.20E
				31	.40E	.60E	------

	JUL	AUG	SEP
TOTAL	23.46	13.19	19.41
MEAN	0.76	0.43	0.65
MAX	1.5	0.7	1.5
MIN	0.3	0.2	0.2
AC-FT	47	26	38

BIBLIOGRAPHY

Alexander, S. E., and J. Roughgarden (1996) Larval transport and population dynamics of intertidal barnacles: A coupled benthic/oceanic model. Ecological Monographs 66(3): 259-275.

Alldredge, A. L., and W. M. Hamner (1980) Recurring aggregation of zooplankton by a tidal current. Estuarine Coastal Marine Science 10(1): 31-37.

Archambault, P., and E. Bourget (1999) Influence of shoreline configuration on spatial variation of meroplanktonic larvae, recruitment and diversity of benthic subtidal communities. Journal of Experimental Marine Biology and Ecology 238(2): 161-184.

Archambault, P., J. C. Roff, E. Bourget, B. Bang, and G. R. Ingram (1998) Nearshore abundance of zooplankton in relation to shoreline configuration and mechanisms involved. Journal of Plankton Research 20(4): 671-690.

Bakun, A. (1986) Local retention of planktonic early life stages in tropical reef bank demersal systems: The role of vertically-structured hydrodynamic processes. IOC/FAO Workshop on Recruitment in Tropical Coastal Demersal Communities, Ciudad del Carmen, Campeche, Mexico, Unesco, Paris.

Barnes, H., and M. Barnes (1958) The rate of development of *Balanus balanoides* (L.) larvae. Limnology and Oceanography 3(1): 29-32.

Black, K. P., S. L. Gay, and J. C. Andrews (1990) Residence times of neutrally-buoyant matter such as larvae, sewage or nutrients on coral reefs. Coral Reefs 9: 105-114.

Boden, B. P. (1952) Natural conservation of insular plankton. Nature 169: 697-699.

Boylan, J. M., and E. L. Wenner (1993) Settlement of brachyuran megalopae in a South Carolina, USA estuary. Marine Ecology Progress Series 97(3): 237-246.

Brown, S. K., and J. Roughgarden (1985) Growth, morphology, and laboratory culture of larvae of *Balanus glandula* (Cirripedia: Thoracica). Journal of Crustacean Biology 5(4): 574-590.

Connell, J. H. (1970) A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. Ecological Monographs 40: 49-78.

Connolly, S. R., and J. Roughgarden (1998) A latitudinal gradient in northeast Pacific intertidal community structure: evidence for an oceanographically based synthesis of marine community theory. American Naturalist 151(4): 311-326.

Doherty, P. J., and D. Williams (1988) The replenishment of coral reef fish populations. Oceanography and Marine Biology Annual Review 26: 487-551.

Dyer, K. R. (1997) Estuaries: A Physical Introduction. John Wiley, Chichester.

Ebert, T. A., and M. P. Russell (1988) Latitudinal variation in size structure of the west coast purple sea urchin: A correlation with headlands. Limnology and Oceanography 33(2): 286-294.

Edwards, R. L. (1984) Remote sensing applications and interactive analyses in marine fisheries research. Oceans '84 Conference Record: Industry, Government, Education. Designs for the Future 1: 506-510.

Farrell, T. M., D. Bracher, and J. Roughgarden (1991) Cross-shelf transport causes recruitment to intertidal populations in central California. Limnology and Oceanography 36(2): 279-288.

Franks, P. J. S. (1992) Sink or swim: Accumulation of biomass at fronts. Marine Ecology Progress Series 82(1): 1-12.

Gaines, S., S. Brown, and J. Roughgarden (1985) Spatial variation in larval concentration as a cause of spatial variation in settlement for the barnacle, *Balanus glandula.* Oecologia 67(2): 267-272.

Gaines, S. D., and B. S. Roughgarden (1985) Larval settlement rate: A leading determinant of structure in an ecological community of the marine intertidal zone. Proceedings of the National Academy of Science 82: 3703-3711.

Geyer, W. R., and R. P. Signell (1990) Measurements of tidal flow around a headland with a shipboard acoustic doppler current profiler. Journal of Geophysical Research (C. Oceans) 95(3): 3189-3197.

Graham, W. M., J. G. Field, and D. C. Potts (1992) Persistent "upwelling shadows" and their influence on zooplankton distributions. Marine Biology 114(4): 561-570.

Graham, W. M., and J. L. Largier (1997) Upwelling shadows as nearshore retention sites: The example of Northern Monterey Bay. Continental Shelf Research 17(5): 509-532.

Grantham, B. (1998) Coastal upwelling, larval recruitment, and the dynamics of upper intertidal barnacle communities. Dissertation Abstracts International Part B: Science and Engineering 50(7): 3427.

Grundlingh, M. L., and J. L. Largier (1991) Physical oceanography of False Bay: A review. Transactions of the Royal Society of South Africa 47(4-5): 387-400.

Halpern, D. (1976) Structure of a coastal upwelling event observed off Oregon during July 1973. Deep Sea Research 23: 495-508.

Hamner, W. M., and I. R. Hauri (1981) Effects of island mass: water flow and plankton pattern around a reef in the Great Barrier Reef lagoon, Australia. Limnology and Oceanography 26(6): 1084-1102.

Hines, A. H. (1978) Reproduction in three species of intertidal barnacles from central California. Biological Bulletin 154: 262-281.

Huyer, A. (1983) Coastal upwelling in the California current system. Progress in Oceanography 12: 259-284.

Jacobsen, T. R., J. D. Milutinovic, and J. R. Miller (1990) Observational and model studies of physical processes affecting benthic larval recruitment in Delaware Bay. Journal of Geophysical Research (C. Oceans) 95(11): 331-345.

Kingsford, M. J. (1990) Linear oceanographic features: A focus for research on recruitment processes. Australian Journal of Ecology 15(4): 391-401.

Kingsford, M. J., and J. H. Choat (1986) Influence of surface slicks on the distribution and onshore movements of small fish. Marine Biology 91(2): 161-171.

Kingsford, M. J., E. Wolanski, and J. H. Choat (1991) Influence of tidally induced fronts and Langmuir circulations on distribution and movements of presettlement fishes around a coral reef. Marine Biology 109(1): 167-180.

Largier, J. L. (1993) Estuarine fronts: How important are they? Estuaries 16: 1-11.

Largier, J. L., J. T. Hollibaugh, and S. V. Smith (1997) Seasonally hypersaline estuaries in Mediterranean-climate regions. Estuarine, Coastal and Shelf Science 45(6): 789-797.

Laval, P. (1995) Hierarchical object-oriented design of a concurrent, individual-based, model of a pelagic tunicate bloom. Ecological Modelling 82(3): 265-276.

LeFevre, J. (1986) Aspects of the biology of frontal systems. Advancements in Marine Biology 23: 163-299.

Little, E. J. J. (1977) Observations on recruitment of postlarval spiny lobsters, *Panulirus argus*, to the south Florida coast. Florida Marine Research, Publication No. 29.

Martel, A. L., L. M. Auffrey, C. D. Robles, and B. M. Honda (2000) Identification of settling and early postlarval stages of mussels (*Mytilus* spp.) from the Pacific coast of North America, using prodissoconch morphology and genomic DNA. Marine Biology 137(5-6): 811-818.

Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub (1997a) Benthic-pelagic links and rocky intertidal communities: Bottom-up effects on top-down control? Proceedings of the National Academy of Sciences, USA 94(26): 14530-14535.

Menge, B. A., B. A. Daley, P. A. Wheeler, and P. T. Strub (1997b) Rocky intertidal oceanography: An association between community structure and nearshore phytoplankton concentration. Limnology and Oceanography 42(1): 57-66.

Miller, B. A., and R. B. Emlet (1997) Influence of nearshore hydrodynamics on larval abundance and settlement of sea urchins *Strongylocentrotus franciscanus* and *S. purpuratus* in the Oregon upwelling zone. Marine Ecological Progress Series 148: 83-94.

Miller, K. M. (1992) The biology of barnacles, Stanford University, Stanford, California, USA.

Monteiro, P. S., and J. L. Largier (1999) Thermal stratification in Saldanha Bay, South Africa, and subtidal density-driven exchange with coastal waters of the Benguela upwelling system. Estuarine Coastal and Shelf Science .

Morris, R. H., D. P. Abbott, and E. C. Haderlie (1980) Intertidal invertebrates of California. Published by Stanford University Press, Stanford, CA (USA).

Okubo, A. (1973) Effect of shoreline irregularities on streamwise dispersion in estuaries and other embayments. Netherlands Journal of Sea Research 6(1-2): 213-224.

Okubo, A. (1978) Horizontal dispersion and critical scales for phytoplankton patches. Pages 21-42 in J. H. Steele, ed. Spatial Pattern in Plankton Communities. Plenum Press, New York, NY.

Olmi, E. J. I. (1995) Ingress of blue crab megalopae in the York River, Virginia: 1987-1989. Bulletin of Marine Science 57: 753-780.

Olson, D. B., and R. H. Backus (1985) The concentrating of organisms at fronts: A cold-water fish and a warm-core Gulf Stream ring. Journal of Marine Research 43(1): 113-137.

Omori, and Ikeda (1984) Methods in marine zooplankton ecology. Wiley-Interscience, New York, NY (USA).

Owen, R. W. (1981) Fronts and eddies in the sea: Mechanisms, interactions, and biological effects. Pages 197-233 in A. R. L. (editor), ed. Analysis of marine ecosystems. Academic Press, New York, NY (USA).

Parrish, R. H., C. H. Nelson, and A. Bakun (1981) Transport mechanisms and reproductive success of fishes in the California Current. Biological Oceanography 1(2): 175-203.

Pedlosky (1987) Geophysical Fluid Dynamics. Springer-Verlag, New York.

Pedrotti, M. L., and L. Fenaux (1992) Dispersal of echinoderm larvae in a geographical area marked by upwelling (Ligurian Sea, NW Mediterranean). Marine Ecology Progress Series 86(3): 217-227.

Peterson, W. T., C. B. Miller, and A. Hutchinson (1979) Zonation and maintenance of copepod populations in the Oregon upwelling zone. Deep-Sea Research 26(5A): 467-494.

Pineda, J. (1991) Predictable upwelling and the shoreward transport of planktonic larvae by internal tidal bores. Science 253: 548-551.

Pineda, J. (1994a) Internal tidal bores in the nearshore: warm-water fronts, evidence of seaward gravity currents and the onshore transport of neustonic larvae. Journal of Marine Research 52: 427-458.

Pineda, J. (1994b) Spatial and temporal patterns in barnacle settlement rate along a Southern California rocky shore. Marine Ecology Progress Series 107: 125-138.

Pineda, J. (1999) Circulation and larval distribution in internal tidal bore warm fronts. Limnology and Oceanography 44: 1400-1414.

Pingree, R. D., and L. Maddock (1979) Tidal flow around an island with a regularly sloping bottom topography. Journal of Marine Biological Association U.K. 59(3): 699-710.

Rosenfeld, L. K., F. G. Schwing, N. Garfield, and D. E. Tracy (1994) Bifurcated flow from an upwelling center: a cold water source for Monterey Bay. Continental Shelf Research 14: 931-964.

Roughgarden, J., S. Gaines, and H. Possingham (1988) Recruitment dynamics in complex life cycles. Science 241(4872): 1460-1466.

Roughgarden, J., J. T. Pennington, D. Stoner, S. Alexander, and K. Miller (1991) Collisions of upwelling fronts with the intertidal zone: The cause of recruitment pulses in barnacle populations of central California. Acta Oecologica 12(1): 35-51.

Roughgarden, J., T. Pennington, and S. Alexander (1994) Dynamics of the rocky intertidal zone with remarks on generalization in ecology. Philos. Trans. R. Soc. Lond. 343: 79-85.

Sanford, E., and B. A. Menge (2001) Spatial and temporal variation in barnacle growth in a coastal upwelling system. Marine Ecology Progress Series 209: 143-157.

Shanks, A. L. (1983) Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Marine Ecology Progress Series 13(2-3): 311-315.

Shanks, A. L. (1986a) Tidal periodicity in the daily settlement of intertidal barnacle larvae and an hypothesized mechanism for the cross-shelf transport of cyprids. Biological Bulletin 170: 429-440.

Shanks, A. L. (1986b) Vertical migration and cross-shelf dispersal of larval *Cancer* spp. and *Randallia ornata* (Crustacea: Brachyura) off the coast of southern California. Marine Biology 92(2): 189-199.

Shanks, A. L. (1987) The onshore transport of an oil spill by internal waves. Science 235: 1198-1199.

Shanks, A. L. (1988) Further support for the hypothesis that internal waves can cause shoreward transport of larval invertebrates and fish. Fishery Bulletin 86(4): 703-714.

Shanks, A. L. (1995) Mechanisms of cross-shelf dispersal of larval invertebrates and fish. CRC Press, Boca Raton, Fl (USA).

Shanks, A. L. (1998) Apparent oceanographic triggers to the spawning of the limpet *Lottia digitalis* (Rathke). Journal of Experimental Marine Biology and Ecology 222(1-2): 31-41.

Shanks, A. L., J. Largier, and L. Brink (2000) Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. Limnology and Oceanography 45(1): 230-236.

Shanks, A. L., and W. G. Wright (1987) Internal-wave-mediated shoreward transport of cyprids, megalopae, and gammarids and correlated longshore differences in the settling rate of intertidal barnacles. Journal of Experimental Marine Biology and Ecology 114(1): 1-13.

Signell, R. P., and W. R. Geyer (1991) Transient eddy formation around headlands. Journal of Geophysical Research (C. Oceans) 96(2): 2561-2575.

Smith, J. A., and J. L. Largier (1995) Observations of nearshore circulation: Rip currents. Journal of Geophysical Research (C. Oceans) 100(C6): 10,967-10,975.

Suchanek, T. H. (1981) The Role of Disturbance in the Evolution of Life History Strategies in the Intertidal Mussels *Mytilus edulis* and *Mytilus californianus*. Oecologia 50(2): 143-151.

Talbot, M. M., and G. C. Bate (1987) Rip current characteristics and their role in the exchange of water and surf diatoms between the surf zone and nearshore. Estuarine, Coastal and Shelf Science 25(6): 707-720.

Thorrold, S. R., J. M. Shenker, R. J. Mojica, E. D. Maddox, and E. Wishinski (1994) Temporal patterns in the larval supply of summer recruitment reef fishes to Lee Stocking Island, Bahamas. Marine Ecology Progress Series 112: 1-2.

Underwood, A. J. (1981) Techniques of analysis of variance in experimental marine biology and ecology. Oceanography and Marine Biology: An Annual Review 19: 513-605.

Van der Baaren, A., R. G. Ingram, and J. Wang (1995) A report of numerical simulations on flow past a headland and within a small shallow bay: Anse du Petit Mitis. Bedford Institute of Oceanography. Internal Report, Darmouth, 48 pp.

van Montfrans, J., C. A. Peery, and R. J. Orth (1990) Daily, monthly and annual settlement patterns by *Callinectes sapidus* and *Neopanope sayi* megalopae on artificial collectors deployed in the York River, Virginia: 1985-1988. Bulletin of Marine Science 46(214-229).

Venrick, E. L. (1978) Systematic sampling in a planktonic ecosystem. Fisheries Bulletin 76(3): 617-627.

Willis, B. L., and J. K. Oliver (1990) Direct tracking of coral larvae: Implications for dispersal studies of planktonic larvae in topographically complex environments. Ophelia 32: 145-162.

Wing, S. R., L. W. Botsford, J. L. Largier, and L. E. Morgan (1995a) Spatial structure of relaxation events and crab settlement in the northern California upwelling system. Marine Ecology Progress Series 128(1-3): 199-211.

Wing, S. R., J. L. Largier, L. W. Botsford, and J. F. Quinn (1995b) Settlement and transport of benthic invertebrates in an intermittent upwelling region. Limnology and Oceanography 40(2): 316-329.

Wolanski, E. (1988) Island wakes shallow waters. Journal of Geophysical Research (C. Oceans) 93(2): 1335-1336.

Wolanski, E. (1993) Facts and numerical artifacts in modelling the dispersal of crown-of-thorns starfish larvae in the Great Barrier Reef. Australian Journal of Marine and Freshwater Research 44(3): 427-436.

Wolanski, E., and W. M. Hamner (1988) Topographically controlled fronts in the ocean and their biological influence. Science 241(4862): 177-181.

Wolanksi, E., D. Burrage, and B. King (1989) Trapping and dispersion of coral eggs around Bowden Reef, Great Barrier Reef, following mass coral spawning. Continental Shelf Research 9: 479-496.

Zeldis, J. R., and J. B. Jillett (1982) Aggregation of pelagic *Munida gregaria* (Fabricius) (Decapoda, Anomura) by coastal fronts and internal waves. Journal of Plankton Research 4(4): 839-858.