PHYSICAL OCEANOGRAPHY, LARVAL DISPERSAL, AND SETTLEMENT ACROSS NEARSHORE FRONTS

by

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A DISSERTATION

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DISSERTATION ABSTRACT

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The larvae of coastal species interact with nearshore currents that are complex and can alter dispersal. I investigated two sites in southern Oregon with different nearshore hydrodynamics: the first site, Sunset Bay, is a small cove with a topographic front that extends across the mouth during upwelling-favorable winds. Using holey sock drogues at 1.5 m and 5.5 m depths and surface drifters at 10 cm depth, I found that, when the front was present, water at 1.5 m was retained within the bay whereas water was exchanged across the front at a depth of 5.5 m. Surface drifters indicated a surface convergence. Surface plankton tows on either side and within the frontal convergence (a shore-parallel foam line) found significantly higher concentrations of barnacle cyprids, crab megalopae and zoea, polychaete larvae, platyhelminthes juveniles, isopods, amphipods, harpacticoid copepods, and fish eggs. Crustacean nauplii (barnacle, euphausiid, and copepod) and calanoid copepods were not concentrated in the convergence, and when the front and foam line were absent, no taxa were concentrated. Plankton tows taken within the foam line as it dissipated shoreward during a wind-reversal event found that concentrations of cyprids, megalopae, and gastropod veligers remained high as the foam line moved, suggesting that it acts as a moving convergence propagating competent larvae shoreward.

I measured settlement of two taxa at Sunset Bay and Shore Acres, an open-coast site <2 km away. Barnacle settlement measured every other day from June-September 2013 was significantly cross-correlated with the maximum daily tidal height at lags of −2 days at Sunset Bay and +2 and +4 days at Shore Acres. Settlement was also significantly negatively cross-correlated with wave height at a lag of −4 days at Sunset Bay. Coralline algae settlement measured during eight 48-hr periods in July-August 2013 was significantly negatively correlated with wave height ($n=8$, $R^2=0.76$, $P=0.0049$) at Shore Acres but not at Sunset Bay. Despite the close proximity of the Sunset Bay and Shore Acres sites, settlement patterns differed between taxa, suggesting that differences in nearshore hydrodynamics might affect the supply of water and larvae to shore.

This dissertation includes unpublished co-authored material.

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TABLE OF CONTENTS

LIST OF FIGURES

Figure Page

Figure Page

LIST OF TABLES

Table Page

CHAPTER I

GENERAL INTRODUCTION

A defining goal of species management techniques such as marine reserves or fisheries quotas is population persistence. A population will persist if the number of births + immigrates are equal or greater than the number of deaths + emigrants (e.g., Tomas & Kunin 1999). Immigration and emigration occur in a population by individuals entering the population that were born elsewhere and when individuals born locally leave to join another population, respectively. In terrestrial ecosystems, the dominant form of immigration and emigration in animals is through juvenile and adult migrations (i.e., seeking new food or habitat resources, or for mating), which can be relatively easy to track and study (e.g., Paradis et al. 1998, Riley et al. 2006, Pauli et al. 2012). In the ocean, however, many animals are sessile and do not disperse as juveniles or adults (but see Highsmith 1985, Johannesson 1988, Garrison & Morgan 1999). The large difference in density between air and propagules such as eggs, larvae, or young has made long-distance wind dispersal on land costly and relatively rare in terrestrial animals (see Strathmann 1990 for discussion). In contrast, the vast majority of marine organisms, including fish, invertebrates, and seaweeds, have evolved a multi-part, complex life cycle that alternates between benthic (attached to or living near bottom) and pelagic (free-living in the water column, swimming or floating) phases. Marine larvae are thought to have evolved a planktonic development period to escape benthic predation, to feed, and to enhance dispersal by ocean currents, among many other hypotheses (Strathmann 1978, Strathmann 1980, Palmer & Strathmann 1981, Strathmann 1985, 1993, Rieger 1994, Nielsen 1998). For most coastal marine invertebrates and fishes, the exchange of individuals between populations occurs at the planktonic larval stage, which are difficult to track. Although a long time in the plankton does not necessarily mean a larva will settle far from its parents (Shanks 2009c), the planktonic stage does allow for larval dispersal and transport on ocean currents, thus playing an important role in structuring marine populations with complex, biphasic lifecycles (Morgan 2001, Underwood & Keough 2001).

Many factors can affect larval dispersal and supply, including adult behaviors such as spawning location and timing, larval behavior and sensory capabilities, and the masses of water encountered by the larvae during their time in the plankton (Chia et al. 1984, Morgan 1995b, a, Shanks 1995, Young 1995, Levin 2006). Despite a long history of research in larval biology (see Young 1990 for a review), larvae are still sometimes assumed to be passive particles (e.g., Siegel et al 2003, Edwards et al. 2007). Larval distributions are often viewed as the result of stochastic physical oceanographic processes that affect mortality and transport of larvae in a chaotic way (Okubo 1994, Mitarai et al. 2008, Siegel et al. 2008). However, many of these processes are common and predictable features in time and/or space (i.e., tidally-driven internal waves, headland eddies, coastal upwelling, the surf zone, etc.). There is a large body of evidence that suggests that larvae are not hapless drifters on ocean currents, but instead, have evolved complex behaviors to be able to perceive and control their position with respect to the ocean around them, undergoing often very specific, remarkable migrations despite their small size (Peterson et al. 1979, Forward & Tankersley 2001, Shanks & Eckert 2005, Queiroga et al. 2007, Morgan et al. 2009, Shanks & Shearman 2009, Leis et al. 2011, Morgan 2014). In short, larvae are well adapted to their planktonic existence and are largely the masters of their fate.

Estimates of dispersal distances of marine species vary from only a meter to 1000s of kms. Dispersal distances in marine animals appear to be bimodal with two main life history strategies: larvae seem to either limit dispersal to less than 1 km, or disperse greater than 20 km (Shanks 2009c). Intertidal and shallow subtidal species represent both life history strategies. The larvae of coastal species are spawned in the nearshore and thus regardless of dispersal distance, must interact with nearshore hydrodynamics at least in the beginning and end of their larval development. Additionally, the larvae of many coastal taxa, including bivalves, gastropods, fish, and many types of crustaceans, have been found in highest concentrations within 3 km of shore (Shanks & Brink 2005, Morgan et al. 2009, Shanks & Shearman 2009, Nickols et al. 2013, Fisher et al. 2014). Thus the larvae of intertidal and shallow subtidal organisms all encounter nearshore flows for part, if not all, of their planktonic existence. As a result, connectivity between populations of coastal species is likely to be controlled by larval interactions with currents in the nearshore.

Unfortunately for the intertidal ecologist wishing to study larval supply, nearshore hydrodynamics are complicated and poorly understood because of the difficulty of gathering data in such a dynamic environment. In shallow water, flow is strongly affected by the benthic and surface boundary layers, the shoaling bottom, tides, surf zone dynamics, and coastal topography. With the slowly-building acceptance that the cross-shelf distributions of coastal larval are typically much more limited than previously thought, the attention of biological and physical oceanographers is beginning to shift to the nearshore (Shanks & McCulloch 2003, Shanks et al. 2003b, Tapia & Pineda 2007, Shanks et al. 2010, Nickols et al. 2012, Nickols et al. 2013, Fisher et al. 2014, Fujimura et al. 2014, Shanks et al. 2014, Weidberg et al. 2014). Despite recent attention, flows in the nearshore are without question complex and the nearshore zone remains a relatively understudied region of the ocean. Man questions related to larval dispersal remain unanswered.

Currents in the nearshore interact with coastal topography including islands, sea stacks, headlands, and coves. As nearshore currents flow into and around shoreline irregularities, secondary circulation features that can affect larval distributions, and therefore recruitment, are formed, including eddies and fronts (Okubo 1973, Pingree & Maddock 1979, Wolanksi & Hamner 1988, Signell & Geyer 1991, Shanks et al. 2003b). A front is a boundary between two water masses that differ in one or more physical properties such as turbidity, temperature, density, or salinity. Fronts have been studied for over 100 years as ecologically important zones of intense biological activity (e.g., Le Fevre 1986 and the references therein). Detritus, foam, flotsam, jetsam, and organisms of many trophic levels aggregate at fronts as a result of both passive and active transport, including bacteria, zooplankton, fish, whales, and even fisherpeople (Murray et al. 1912, Uda 1938, Bowman & Esaias 1977, Owen 1981, Olson & Backus 1985, Le Fevre 1986, Franks 1992, Govoni & Grimes 1992, Podesta et al. 1993). Research has typically focused on large-scale fronts such as those occurring at the shelf break or along western boundary currents such as the Gulf Stream (Bowman & Esaias 1977, Owen 1981, Le Fevre 1986). Relatively few researchers have focused on circulation, zooplankton distributions, and settlement around small-scale topographical features of several 100 m to a few km from shore (Pingree et al. 1974, Pingree & Maddock 1979, Archambault et al. 1998, Archambault & Bourget 1999, McCulloch & Shanks 2003, Shanks & McCulloch 2003, Shanks et al. 2003b, Weidberg et al. 2014). Such nearshore features are often accompanied by slicks and foam lines on the ocean surface.

Foam lines oriented parallel to shore are sights familiar to many beachgoers and have been observed on rocky coastlines world-wide including Oregon, California, the Gulf of Mexico, Hawaii, Barbados, Ireland, Chile, New Zealand, Australia, and Spain (Shanks and Jarvis, personal observations). Shore-parallel foam lines can mark the surface of a front, and can be generated by at least three different forces on the Oregon coast: boundary mixing, wind, and differential solar heating (Shanks et al. 2003c). Many studies have shown that fronts resulting from tidal currents interacting with shoreline topography can affect the distribution of buoyant coral eggs, larvae, and other zooplankton (Alldredge & Hamner 1980, Hamner & Hauri 1981, Wolanksi & Hamner 1988, Wolanski et al. 1989, Willis & Oliver 1990). Data on other kinds of nearshore fronts, however, is very limited, and is the focus of the research presented here. In this dissertation, I investigate flow across different kinds of nearshore, small-scale (several 100 m to a few km from shore) fronts and their effects on the dispersal and settlement of several marine taxa. I addressed three main questions: 1. How do hydrodynamics and larval distributions vary between different front types? 2. Do fronts limit the seaward transport of larvae or spores with short pelagic larval durations? 3. Do fronts affect the alongshore variations in settlement?

In Chapter II, I give an overview of the physical oceanography of the nearshore topographic front at Sunset Bay where much of work for this dissertation occurs.

Previous research found that a front forms across the mouth of Sunset Bay during upwelling-favorable winds and small waves. If conditions favorable for the front persist long enough, the waters landward of the front become warmer relative to waters seaward of the front. The data presented in Chapter II suggest that the front limits the exchange of surface water between the cove and offshore, likely explaining the presence of warmer waters inshore of the front when present. Additional data on flow across the front at depth are summarized to provide an overall schematic representation of circulation around the front at Sunset Bay. The remaining chapters address how nearshore hydrodynamics affect zooplankton distributions and the settlement of barnacles and crustose coralline algae measured on shore.

In chapter III I provide evidence that the foam line at the surface of the front at Sunset Bay is a convergence that concentrates some taxa and developmental stages of zooplankton, including larvae, orders of magnitude greater than adjacent waters. In addition, I present data suggesting that when the front at Sunset Bay dissipates during periods when upwelling-favorable winds relax or reverse, it travels shoreward as a distinct foam line and can transport high concentrations of some zooplankton, including the competent larval stage of barnacles, toward shore. Chapter III will be submitted for publication with Alan Shanks as co-author.

As it was found in Chapter III that the front at Sunset Bay can concentrate and transport the competent larval stage of barnacles (cyprids) shoreward, I hypothesized in Chapter IV that I would see a spike in barnacle settlement on shore when upwelling-favorable winds either relaxed or switched to downwelling favorable and the foam line propagates shoreward. A time series of barnacle settlement measured every other day from land inshore of this front tests this hypothesis. I also present a simultaneous time series of barnacles measured at a nearby open-coast site (Shore Acres) to test the hypothesis that a different pattern in settlement would be seen at a site without a topographic front.

In Chapter V, I investigated the settlement patterns of a taxon with dispersive propagules that are have a much shorter pelagic duration: the spores of crustose coralline algae, which are thought to settle within hours of release. If spores are released within Sunset Bay during conditions favorable for a front, I hypothesized that the hydrodynamics detailed in Chapter II would retain water and spores nearshore, potentially enhancing settlement of coralline algae at Sunset Bay when the front is present. In chapter V I investigate this hypothesis and present settlement data of coralline algae taken during eight 48-hour settlement experiments. I also present data from simultaneous measurements of settlement of coralline algae at Shore Acres to test the hypothesis that a different pattern in settlement would be seen at a site without a topographic front.

CHAPTER II

ASPECTS OF THE PHYSICAL OCEANOGRAPHY OF SUNSET BAY

INTRODUCTION

The nearshore is a dynamic and complex part of the ocean: here, currents interact with coastal headlands, islands, and reefs to generate complex flow features such as upwelling shadows, eddies, and fronts. These features can affect the exchange of planktonic organisms as well as water, nutrients, sediment, pollutants and other matter between the shore and the open ocean (Caffey 1985, Oliver & Willis 1987, Wolanksi & Hamner 1988, Kingsford 1990, Graham & Largier 1997, Wing et al. 1998, Roughan et al. 2005, Morgan et al. 2011). There is currently a knowledge gap in the understanding of the biological and physical processes of this region of the ocean. The nearshore is a transition zone between estuaries and beaches that are well studied by coastal engineers and the offshore waters accessible by oceanographers in large ships, and thus is often ignored. However, a growing appreciation for the important role this region plays in biological processes such as population connectivity and larval dispersal has lead to an increase in studies focused on nearshore hydrodynamics of the inner shelf (Shanks et al. 2003b, Kirincich et al. 2005, Tapia & Pineda 2007, Rilov et al. 2008, Lentz & Fewings 2012, Nickols et al. 2012, Fujimura et al. 2014, Shanks et al. 2014, Weidberg et al. 2014).

Presently there is no generally agreed upon definition for what constitutes the “nearshore”. Regions of the continental shelf are often sub-divided into the outer, mid, and inner shelf. The shoreward boundary of the inner shelf is typically defined as the outer edge of the surf zone; the term “nearshore” can also include the surf zone. The seaward boundary of the inner shelf, however, changes in the literature depending on the particular dynamics being studied, and no general consensus appears to have formed (Garvine 2004, Lentz & Fewings 2012). In this dissertation I use the terms “inner shelf” and “nearshore” interchangeably to refer to the region of the ocean from the outer edge of the surf zone out to water depths of approximately 30 m, which on the Oregon coast is about 2-3 km from shore. Occasionally, however, I will use “nearshore” to refer to the coastal band of ocean that includes both the inner shelf and the surf zone. On the inner shelf the wind-mixed surface layer and the tidally-mixed bottom boundary layer begin to interact, and the rotation of the earth (Coriolis force) plays a much less important role in determining flow patterns than in mid and outer continental shelf waters. Instead, wind, waves, tides, and buoyant plumes are the dominant processes that drive circulation in the nearshore (Lentz & Fewings 2012).

Perhaps the most prevalent oceanographic features of the nearshore ocean visible from land are foam lines. Although beachgoers often assume sea foam to be of anthropogenic origin, the creation of foam by turbulent mixing in the ocean is a natural phenomenon (see Schilling & Zessner 2011 for a review). Sea foam is the product of air bubbles dispersed into water and stabilized by a surfactant or surface-active compound (has both a hydrophobic and hydrophilic component) that usually includes lipids, proteins, and carbohydrates. A common source of these compounds in seawater is the breakdown of phytoplankton, especially in areas where coastal upwelling is prevalent. Surface-active compounds are also produced from aquatic and terrestrial plants, macroalgae, soils and sediments, and anthropogenic pollutants (Schilling & Zessner 2011) as well as blooms of the dinoflagellates *Akashiwo sanguinea* (Du et al. 2011).

Waves in the surf zone, strong currents, or mixing between fresh and salt water provide the mechanical impact to disperse air bubbles into water (Craig et al. 1989, Ettema et al. 1989, Fisenko 2004). Due entrained air bubbles and lipid-rich hydrophobic components, foam is positively buoyant and floats on the surface of water, thus serving as a marker for convergent surface currents. Foam can accumulate in large patches in retentive calm-water areas like eddies behind rocks or sea stacks. In addition to foam patches, lines of foam are very common and typically occur where currents meet (converge) and dive below the surface (downwell), pushing foam together into a line. These surface convergences often form as the surface manifestation of a very common hydrographic feature called a front.

A front is a boundary between two different masses of a fluid that differ in temperature, density, or another physical variable. They can produce intense gradients in the ocean, and are often areas of biological significance (Owen 1981, Le Fevre 1986, Olson et al. 1994). The ocean is not well mixed: fronts are quite common and have been written about for over two centuries, long before a cohesive definition and name were given to the phenomenon (e.g., Franklin 1786, Murray et al. 1912, Uda 1938). Fronts have been found to aggregate organisms either through passive or active (behavioral) transport across a wide range of trophic levels including bacteria, phytoplankton, the larvae of many invertebrates and fish and other zooplankton, tuna, whales and even humans (Uda 1938, Bainbridge 1957, Bowman & Esaias 1977, Olson & Backus 1985, Franks 1992, Govoni & Grimes 1992, Podesta et al. 1993, Olson et al. 1994).

Many coastal marine species reproduce by releasing thousands to millions of tiny embryos, larvae, or spores into the surrounding seawater that develop within 3 km of shore before returning to the shore to settle as juveniles. Thus, despite developing in the plankton, most of these larvae do not drift out to sea far enough to interact with the shelf-break front or other large-scale features 10s of km from shore that have been the historical focus of research on fronts. Nearshore hydrodynamics are therefore important to study if one wishes to understand the larval dispersal and migration patterns of numerous species that take place on the inner shelf. Despite the frequent occurrence of nearshore fronts, very little is understood about hydrodynamics of different front types and how they affect larval dispersal. Fronts may play an important role in structuring intertidal and shallow subtidal communities by affecting the exchange of water, and thus the supply of larvae, phytoplankton, and nutrients, to the nearshore (Wolanksi & Hamner 1988, McCulloch & Shanks 2003, Shanks & McCulloch 2003, Shanks et al. 2003b, Weidberg et al. 2014).

In this study I focus on a nearshore front that occurs at the mouth of Sunset Bay, a small cove on the southern Oregon coast (McCulloch & Shanks 2003, Shanks & McCulloch 2003, Shanks et al. 2003b). Sunset Bay is located along Cape Arago, which is made up of a series of headlands, coves, islands, and intertidal rocky reefs that is the first significant rocky intertidal habitat on the southern Oregon coast following roughly 100 km of sandy beach habitat to the north. Shore-parallel foam lines are common along Cape Arago (Fig. 2.1B), and are likely caused by at least three different physical mechanisms: boundary mixing, wind, and differential solar heating (Shanks et al. 2003, and see Appendix A for description of boundary mixing fronts). In this chapter I focus on the second of these mechanisms: a wind-driven topographic front that commonly occurs at the mouth of Sunset Bay.

A rocky outcropping that extends about 1 km seaward forms the northern end of Sunset Bay (Fig. 2.1). Upwelling favorable winds (from the N or NW) produce an alongshore, SW-flowing current that encounters this outcropping, creating a foam line and front in the lee of the headland. Shanks et al. (2003) found that this foam line delineates the surface of a front that separates coastal ocean waters from the waters of the bay. The foam line can be disrupted by waves larger than about 2 m, but does not appear to change position with the ebb and flood of tides. The foam line is a persistent feature during much of the summer, with an average duration of 6 days (range 1-21 days) (Shanks et al. 2003b). The cove can be isolated from the ocean long enough that a warm surface lens of water (Fig. 2.2A), often low in chlorophyll a (Chl a) (Fig. 2.2C), develops inshore of the front and foam line and plankton communities differ across the front.

When upwelling favorable winds relax or reverse (to southwesterly), no foam line is present, and the warm lens typically seen inshore of the front and foam line is either absent or the temperature difference between the waters in the bay and offshore is much reduced as offshore waters warm due to wind-driven onshore transport (Fig. 2.2B). On multiple occasions, we have witnessed the foam line moving shoreward when upwelling winds relax (Jarvis & Shanks, unpublished data).

Previous work at Sunset Bay has characterized the conditions necessary for a front to form at Sunset Bay, as well as describing the physical properties of the water column during conditions with and without a front (McCulloch 2001, Shanks et al. 2003b). Additionally, Shanks and colleagues (2003c) provided preliminary evidence for flow around the front. Fluorescent dye deployed on either side of the front was advected towards the front, and then downwelled at the foam line, indicating the foam line

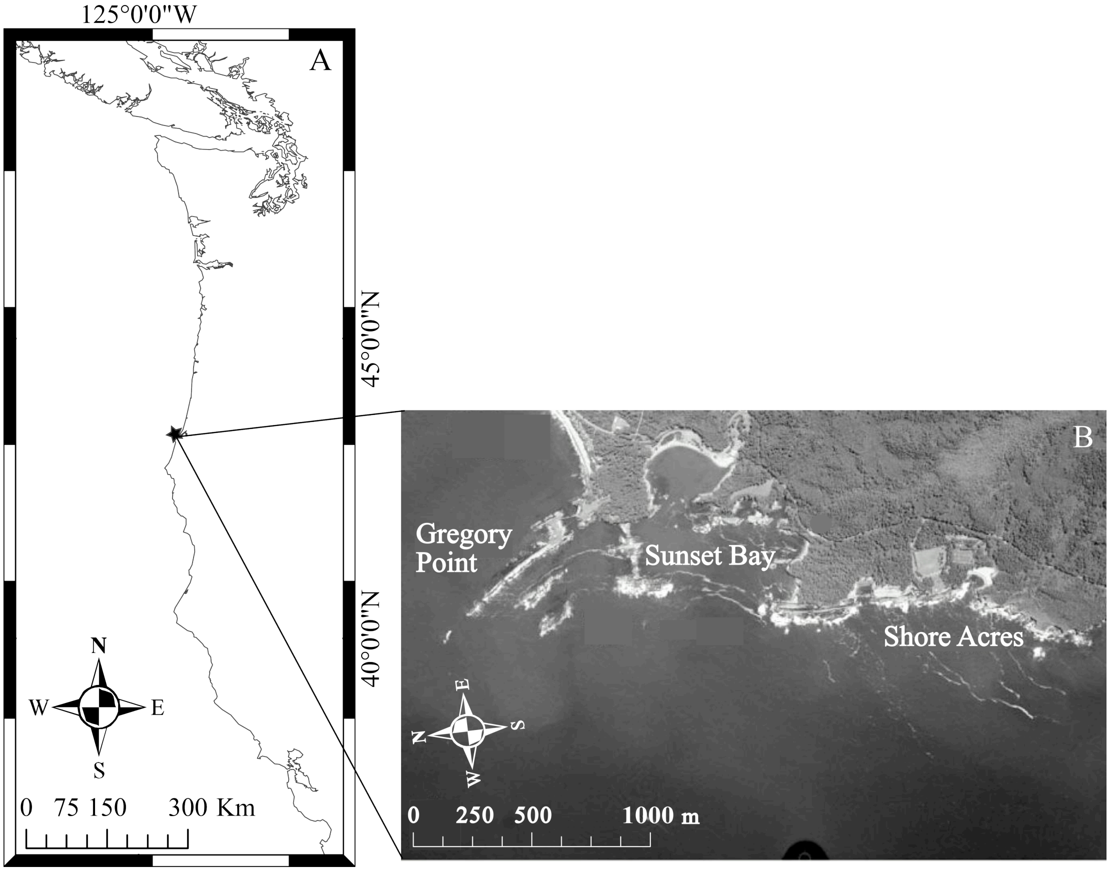

Fig. 2.1. Map of study site (A) and areal photograph of foam lines delineating the fronts at Sunset Bay and Shore Acres (B). Foam lines (or slicks) can mark the surface of very nearshore fronts caused by at least three mechanisms (Shanks et al. 2003). The foam line at Sunset Bay marks the surface convergence of a topographical, wind-driven front present during upwelling favorable winds and small waves; often a large percentage of the spring and summer. Figure adapted from Shanks et al. 2003.

delineated the surface convergence of the front between the two water masses (McCulloch & Shanks 2003; Shanks et al. 2003c). Other than these preliminary dye studies, however, very little is known about flow around the front at Sunset Bay or any other similar nearshore front. The first aim of this study was to confirm that the foam line at the mouth of Sunset Bay is a convergence using surface drifters, and, by tracking the movement of the drifters, to describe flow within the foam line.

The second aim of this study was to attempt to characterize flow across the front at depth. Waters landward of the wind-generated front at Sunset Bay are characterized by a warm, shallow (typically < 5m depth) lens of water (McCulloch 2001). Temperature contours (isotherms), however, are typically relatively flat across the front below 5 m (e.g., Shanks et al. 2003c). I hypothesized that the warm lens of water inshore of the front is due to the front limiting the exchange of water at depths < 5m (when the front is present). Additionally, I hypothesized that the colder waters below the surface warm lens indicated that water is able to exchange across the front only at depths greater than 5 m.

MATERIALS AND METHODS

During the summer of 2012 I characterized physical water column characteristics and flow along a transect at Sunset Bay (43.3334º N, 124.3718º W) (Figure 2.1). I measured temperature, salinity, density, and relative Chl a levels with a Seabird model 19 Conductivity-Temperature-Depth (CTD) profiler. CTD casts (surface to bottom) were taken on each sampling day along a transect perpendicular to shore across the front. The number and exact location of CTD stations varied, but ranged from 8–11 stations from 0.2 to 1.5 km from shore, with individual stations 100–400 m apart. Contour plots were created using Matlab (Mathworks, R2011a).

To test the hypothesis that the foam line at the mouth of Sunset Bay is a convergence, I deployed surface drifters on four days during July 2012. Four to five drifters were released approximately 30 m both seaward and shoreward of the foam line and retrieved when they drifted near the rocky shore. On July 10, 25, and 26, drifters consisted of 30 cm long, 1.5 cm diameter dowels fitted with a small float and weight at opposing ends of the dowels (Fig. 2.3). In the water, the top 20 cm of the dowel was visible, and the weight and part of the float were submerged so that the drifters tracked

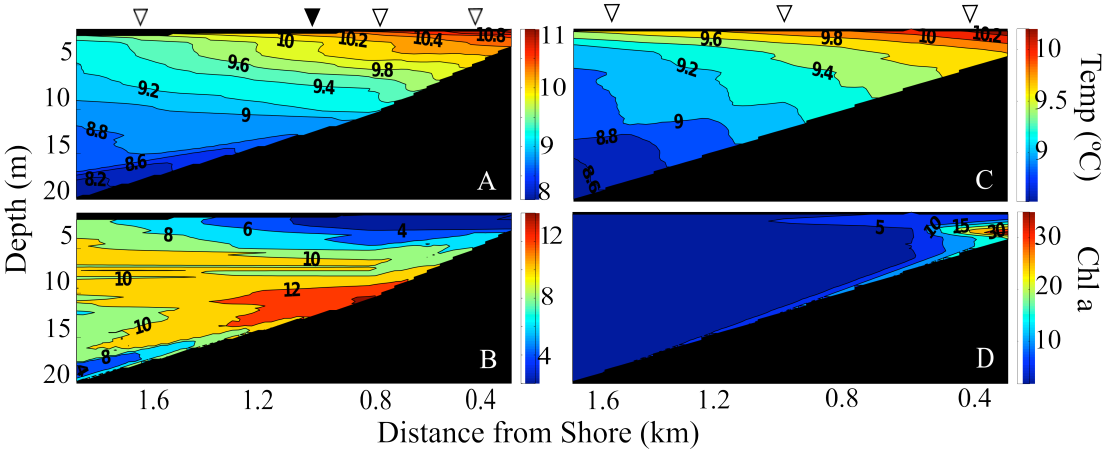

Fig. 2.2. Characteristic temperature (A, C) and chlorophyll (Chl a) (B, D) profiles at Sunset Bay when the front is present (left boxes) and when the front is absent (right boxes). When winds are from the north or northwest (upwelling-favorable) and waves are less than about 2 m, a foam line and front typically form across the mouth of Sunset Bay. When the front is present long enough, the waters inshore of the front heat up due to solar insolation forming a surface lens (< 5 m) of warm water (A) that is often low in Chl a (B). Isotherms tend to slope upwards towards the surface near the foam line. When upwelling-favorable winds relax or reverse, the foam line and front are typically absent, and the difference in surface water temperature across the usual location of the front is absent or much reduced (C). Often when the front is absent, highest Chl a concentrations are found inshore (D), in contrast to the Chl a-poor waters commonly found inshore of the front when it is present. White triangles mark the location of CTD casts, and the filled triangle marks the foam line location, if present.

approximately the top 10 cm of water. The time and location of the drifters were recorded using a hand-held GPS (Garmen Etrex H™) upon release and retrieval, and on July 26, at several time points while in the foam line to test if drifter velocities slow as the foam line approaches the rocky boundary at the south end of the cove.

On July 24, two parallel foam lines were present: one at the usual location at the mouth of Sunset Bay and one just inshore. A change in water color was observed at the outer foam line. GPS-tracked drifters, 6 x 8 x 15 cm waterproof plastic cases (OtterBox™) containing a GPS that recorded position every second (surface float depicted in Fig. 2.4), were deployed both landward and seaward of the outer foam line allowing me to calculate the time it took the drifters to converge at the foam line from either side. Tracks and waypoints were downloaded and processed using MacGPS Pro (James Associates Inc.) and were visualized using ArcGIS (ESRI).

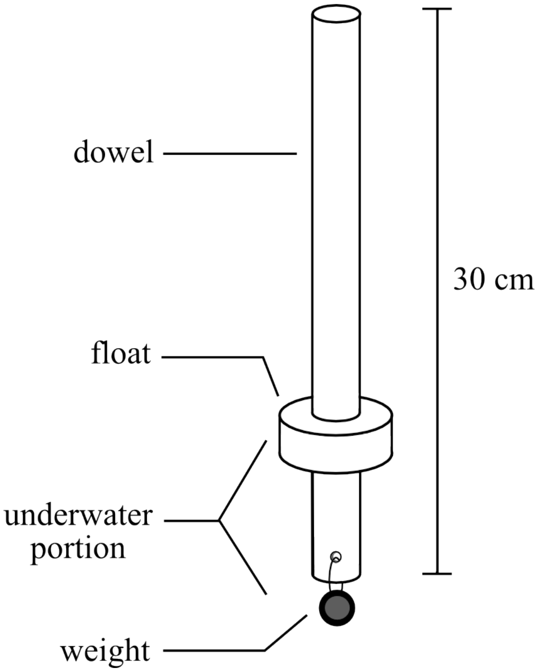

Fig. 2.3. Surface drifters used on July 10, 25, and 26, 2012 consisted of 30 cm long, 1.5 cm diameter dowels fitted with a small float and weight at opposing ends. In the water, the top 20 cm of the dowel was visible, and the weight and the float were submerged so that the drifters tracked the top 10 cm of water.

To investigate flow at depth across the front at Sunset Bay, I used a holey sock-type drogue design modified (shortened) for use in the nearshore environment. The drogue consisted of a 0.8 m x 1 m hollow “holey sock” tube of nylon fabric with holes cut haphazardly in the tube to allow the sock to trap and follow a parcel of water at the drogued depth (modified from Niiler et al. 1987, Fig. 2.4). The sock portion of the drogue was attached by a tether to a waterproof case (GPS unit inside) that was positively buoyant and served as the surface float. The sock was submerged and weighted to maintain a desired, pre-determined depth as set by the length of the adjustable tether. The sock has a much larger drag-to-area ratio than the tether and float components, which minimizes the effects that wind on the surface float or drag on the tether have on the drogue's trajectory. The difference between currents at the depth of the drogue and any directional interference caused by wind on the surface float, drag on the line, and surface waves, is called "slip" (Niiler et al. 1987). To minimize slip, the line was made out of tuna leader line, which is a strong but fine material with a diameter of about 1 mm, and the float was as spherical and as low-profile as possible (Niiler et al. 1987; Niiler et al. 1995). Downwind slip for similar, though much larger, drogues is estimated at 0.7 cm/s per 10 m/s of wind speed (Poulain and Niiler 1989). Due to proximity to shore, the drogue deployments in this study were very short (less than 2 hours) due to proximity to the shore. Therefore, an estimate of the maximum slippage of a drogue during a two-hour deployment would be only about 25 m in the down-wind direction. Our drogue deployments were often less than two hours and during winds <10 m/s so this is likely a conservative estimate; therefore, slip was not assumed to play an important role in drogue trajectories in this study.

GPS units were set to record position every two seconds, and deployments typically ranged from 45 min to 2 hrs depending on trajectory (i.e., if drogues traveled towards land or out to sea, respectively) and wind or wave conditions. Drogues were released in pairs whenever possible, and were removed from the water when they drifted near the rocky shore or too far out to sea. Tracks and waypoints were downloaded and processed using MacGPS Pro (James Associates Inc.) and were visualized using ArcGIS (ESRI).

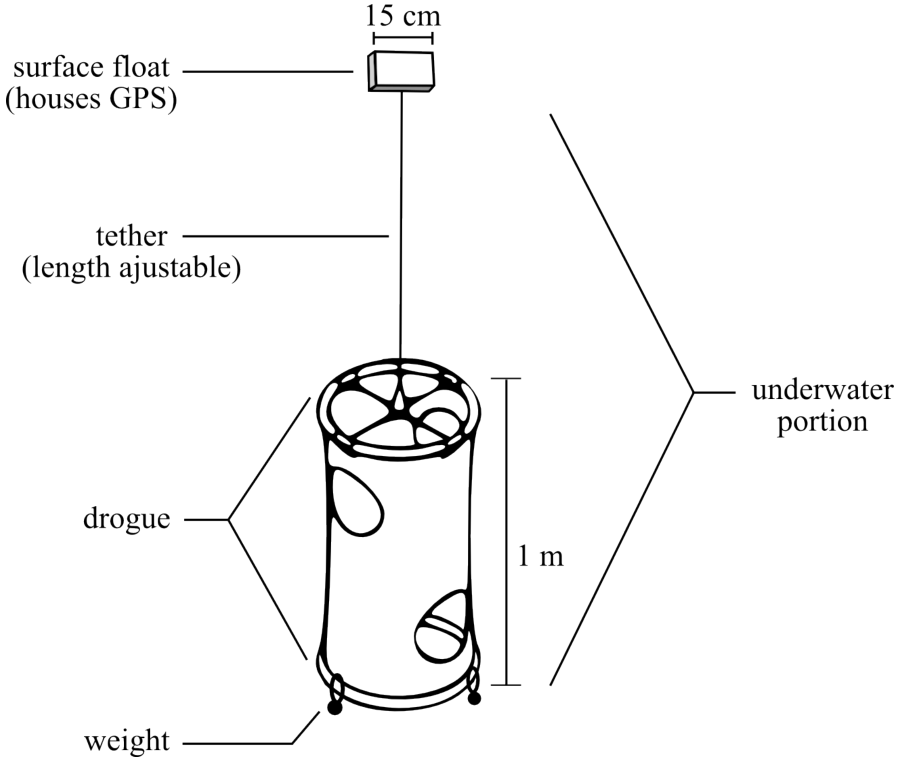

Fig. 2.4. Holey sock-type drogue modified for nearshore use. The drogue is submerged and weighted to maintain a desired, pre-determined depth set by the tether length. The holey sock portion of the drogue has a much larger drag-to-area ratio than the tether and float components so that the drogue tracks a parcel of water at depth with minimal effects of wind on the surface float or drag on the tether. Surface float and drogue are not drawn to scale.

RESULTS

Physical characteristics of the nearshore water column

During the study, winds were typical of the spring/summer seasonal wind cycle on the Oregon coast, alternating between strong winds from the north or northwest (upwelling-favorable) persisting from several days to weeks and intermittent periods of several days of weaker winds from the south or southeast (relaxation or downwelling-favorable). When waves were small (less than about 2 m) and winds were upwelling-favorable, the foam line (or a pair of foam lines) was typically seen across the mouth of Sunset Bay approximately 1 km from shore (Fig. 2.1 and Fig. 2.5). When the foam line was present under these conditions, it marked a front. The waters landward of the front and foam line on days with upwelling winds were 0.2-0.6ºC warmer than waters seaward of the front. Waters seaward of the front, in addition to being colder, were sometimes more saline and more dense (Fig. 2.5). I was not able to obtain CTD casts on one drogue-sampling day with a front present (June 21) and one drogue-sampling day without a front (June 25) due to CTD malfunction.

On July 10, north winds were light (2-4 m/s) at the start of sampling (8:00AM), and a single foam line was present at the mouth of Sunset Bay. The foam line was "light", i.e., had comparatively little foam in it compared with days with stronger winds, until around 10:30AM when winds picked up to about 4-5 m/s and we conducted the drifter study. The lens of warm water inshore of the front extended down to about 5 m, and surface isotherms (contour lines of equal temperature) bent upwards and contacted the surface about 100 m seaward of the foam line. Waters inshore of this point were about 0.2ºC warmer than waters seaward (Fig. 2.5A). This warmer mass of water was slightly less saline than surface waters offshore of the front (33.3 inshore vs. 33.4 offshore), and surface isohalines (contour lines of equal salinity) bent upward and contacted the surface near the foam line (Fig. 2.5B). The surface isopycnals (contour lines of equal density) were less pronounced, and density contours appeared to follow the 9.4ºC isotherm (Fig 2.5C).

On July 24, winds were from the north and 4-5 m/s at the start of sampling and a strong foam line was present at the mouth of Sunset Bay (1.1 km from shore). An inner, less prominent foam line was present at about 0.8 km from shore, and was attached to the rocky shore at the north and south ends of Sunset Bay. A change in water color was present at the outer foam line, and the warmest waters were present between these two foam lines. Surface isotherms bent up and contacted the surface at both of the foam lines. The surface lens of warm water was shallower on this date, only extending several meters down. Surface waters offshore of the outermost foam line were about 0.2ºC cooler than waters within the warm surface lens (Fig. 2.5D). This surface water mass did not appear to be lower in salinity or density (Fig. 2.5E, F).

On July 25, winds were from the north at 3-5 m/s and a single foam line was present. The difference in temperature between waters inshore and offshore of the front was about 0.6ºC, with warmest waters again inshore of the front. Isotherms, isopycnals, and isohalines all bent upward and contacted the surface at the foam line. The warmest waters extended to a depth of about 2 m (Fig. 2.5G). Waters inshore of the front were slightly less saline throughout the water column (Fig. 2.5H), and the warm surface lens was slightly lower in density than offshore waters (Fig. 2.5I).

On July 26, winds were from the north at 2-4 m/s and a single foam line was present. The warm surface lens inshore of the foam line was very shallow, only extending about a meter in depth. Surface waters inshore of the foam line were about 0.4ºC warmer than offshore. Surface isotherms bent upwards, contacting the surface at the foam line (Fig. 2.5J). Isohalines and isopycnals did not show much surface structure (Fig. 2.5K, L).

When winds relaxed or shifted to downwelling favorable, the foam line and front typically disappeared and temperature, salinity, and density remained unchanged across the usual front location (~1 km from shore). This is clear on June 29, 2012, when isotherms and isohalines were flat and did not bend upwards at the usual front location (Fig. 2.6A, B). The surface isopycnal bent upward at around 0.8 km, which is inshore of the usual foam line location, but in contrast to when the front was present, the denser surface waters were inshore of the mouth of Sunset Bay (Fig. 2.6C). On this day, winds were from the south and southwest and were light (< 2 m/s).

On one sampling day (August 6) strong downwelling winds (5-7 m/s) and a foam line were present. The foam line was attached at the south end of Sunset Bay, but not the north, and continued past the north end of Sunset Bay (Fig. 2.8). On August 6, temperature, salinity, and density did not change across the location of the foam line; the foam line did not mark a front (Fig. 2.6D-F).

Surface currents (drifters)

I deployed surface drifters across the foam line when it was present on four days with upwelling-favorable winds (Fig. 2.7). When the foam line was present, surface drifters deployed on either side of the foam line were transported directly into the foam line indicating convergent flow on both sides of the front. Once in the convergence, drifters were advected roughly southward. They remained in the foam line until I removed them from the water at the rocky outcropping at the south end of the cove. On July 24 a pair of foam lines was present. Drifters were deployed on either side of the outer foam line, which appeared to be the more conspicuous of the two (i.e., continuous

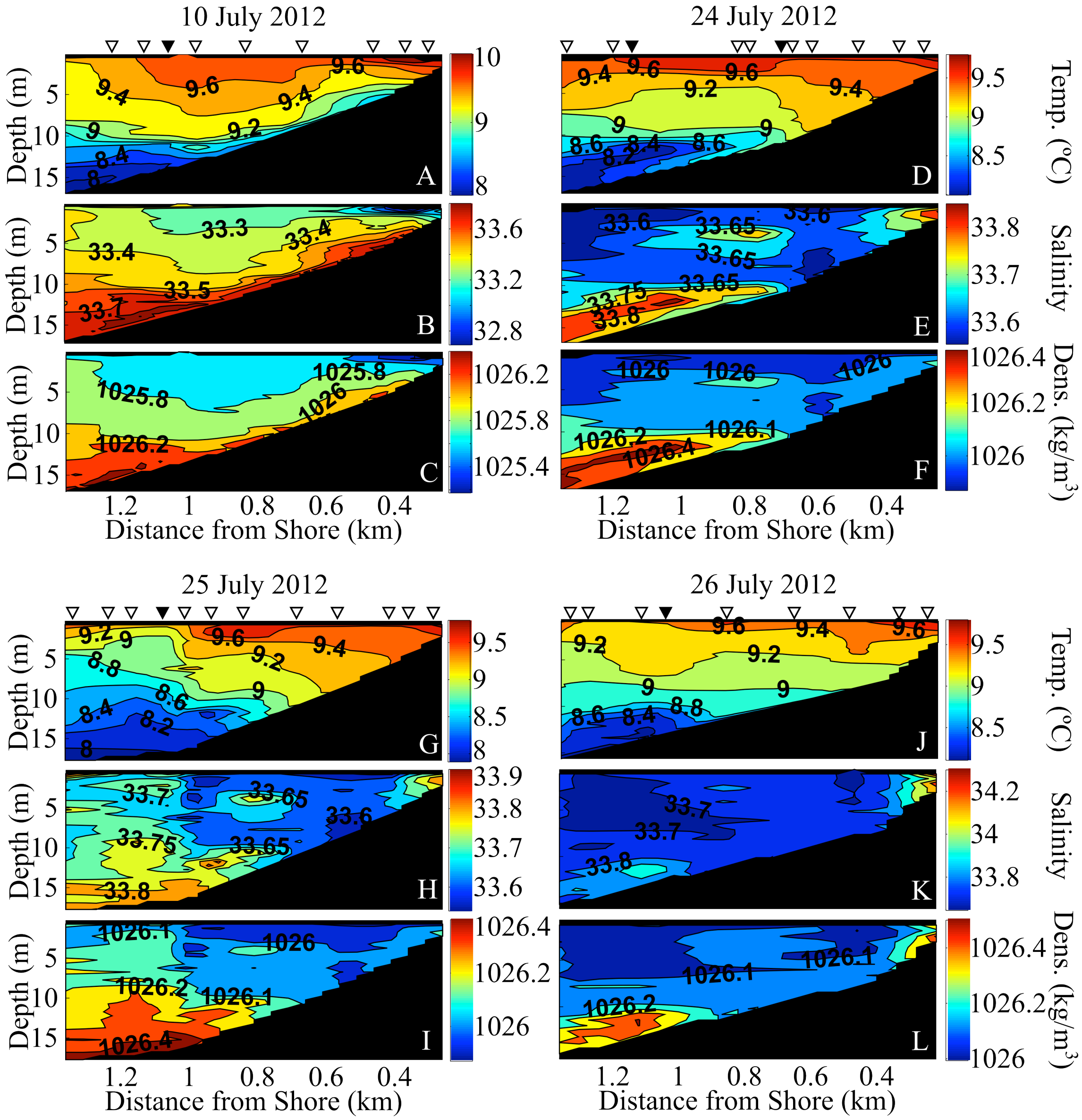

Fig. 2.5. Temperature, salinity, and density contour plots (top, middle, and bottom boxes in each panel, respectively) taken at Sunset Bay on July 10 (A-C), July 24 (D-F), July 25 (G-I), and July 26 (J-L), 2012. On all four days, winds were from the north or northwest (upwelling favorable) and a foam line was present at the mouth of Sunset Bay. White triangles mark the location of CTD casts, and the filled triangles mark the location of the foam line. Isotherms bent up towards the surface near the foam line location, and evidence is seen for a warm lens of water inshore of the foam line; waters landward of the foam line range from about 0.2–1 ºC warmer than waters offshore.

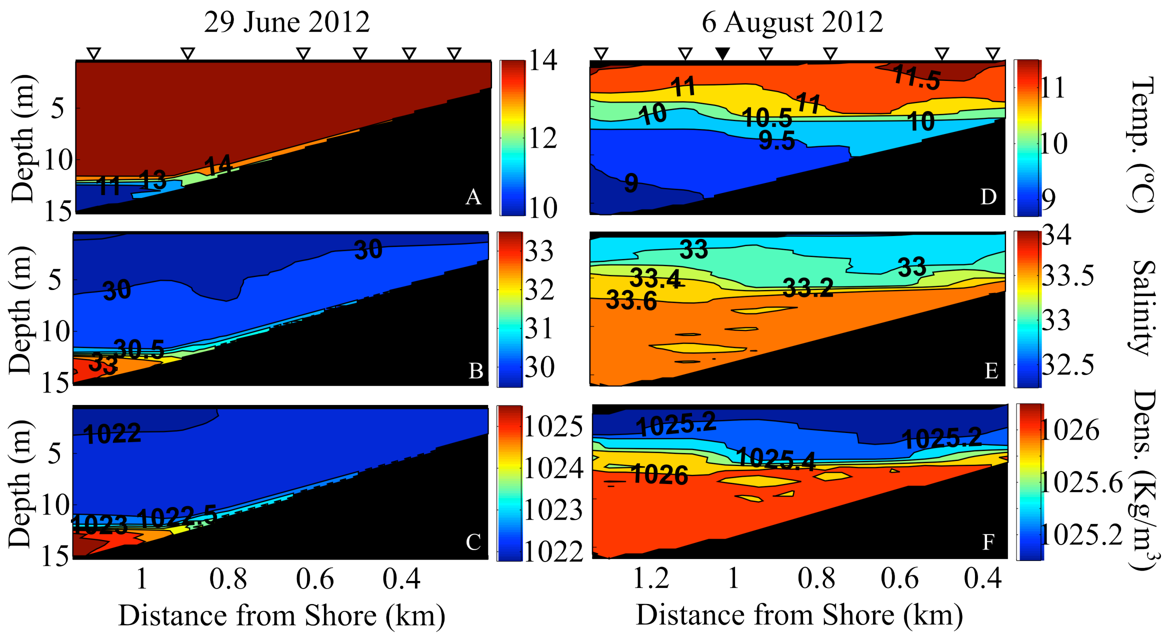

Fig. 2.6. Temperature, salinity, and density contour plots (top, middle, and bottom boxes, respectively) taken at Sunset Bay on June 29 (A-C) and August 6 (D-F), 2012. The CTD malfunctioned on June 25 and no data were collected. On June 29, winds were very light (<2 m/s) and no foam line was present. On August 6, however, strong (5-7 m/s) downwelling-favorable winds were present and a foam line was attached to the south end of Sunset Bay. Isotherms did not bend upwards on either day, suggesting that no front was present.

and with more foam and detritus) and was located at the usual foam line location attached to the seaward end of the rocky outcropping while the inner foam line was farther inshore (Fig. 2.7B). GPS-tracked drifters were used on this day, allowing the calculation of drifter speeds. The seaward drifters converged at a mean speed of 12.8 cm/s (n = 3, SE = 0.7), and the landward drifters (deployed between the two foam lines) converged (toward the outer foam line) at a significantly lower mean speed of 9.3 cm/s (n = 4, SE = 0.6) (t(3.255) = 3.738, p = 0.0145). Drifters deployed landward and seaward of the outer foam line did not differ in mean speed once in the foam line, and traveled at 11.5 cm/s (n = 7, SE = 0.4) (t(4.990) = 0.748, p = 0.244).

I also calculated within-foam line drifter speeds on July 26, which were one-half the speed of July 24: 6.9 cm/s (n = 7, SE = 0.4). On all sampling days, once drifters approached the southern boundary of the cove they appeared to slow. Drifters were calculated on July 26th were slowed significantly to a mean of 3.7 cm/s (n = 8, SE = 0.4); t(13) = 6.293, $p < 0.0001$.

Drifters released on days without a foam line did not converge. Instead, they typically traveled as a cluster with the predominant local surface current during the sampling period or diverged.

Temperature contour plots from CTD transects on the four drifter study days are shown in Fig. 2.6. Although some days with a foam line and convergent flow did not show large differences in surface temperature across the front, the warmest waters were typically found inshore of the foam line on all days.

A foam line was present on Aug 6 during strong downwelling winds. Drifters deployed landward and seaward of the foam line were advected directly and immediately into the foam line indicating a surface convergence. Once in the foam line, drifters traveled in the foam line roughly northward, indicating along-wind flow within the convergence (Fig. 2.8). I did not measure the time to converge or the velocity of drifters within the foam line on this day.

Flow at depth (drogues)

I investigated flow at depth across the front at Sunset Bay on four days when the front was present (Fig. 2.9). On June 21, three drogues were deployed simultaneously about 200 m inshore of the front: two at 1.5 m and one at 5.5 m depth. Although no CTD

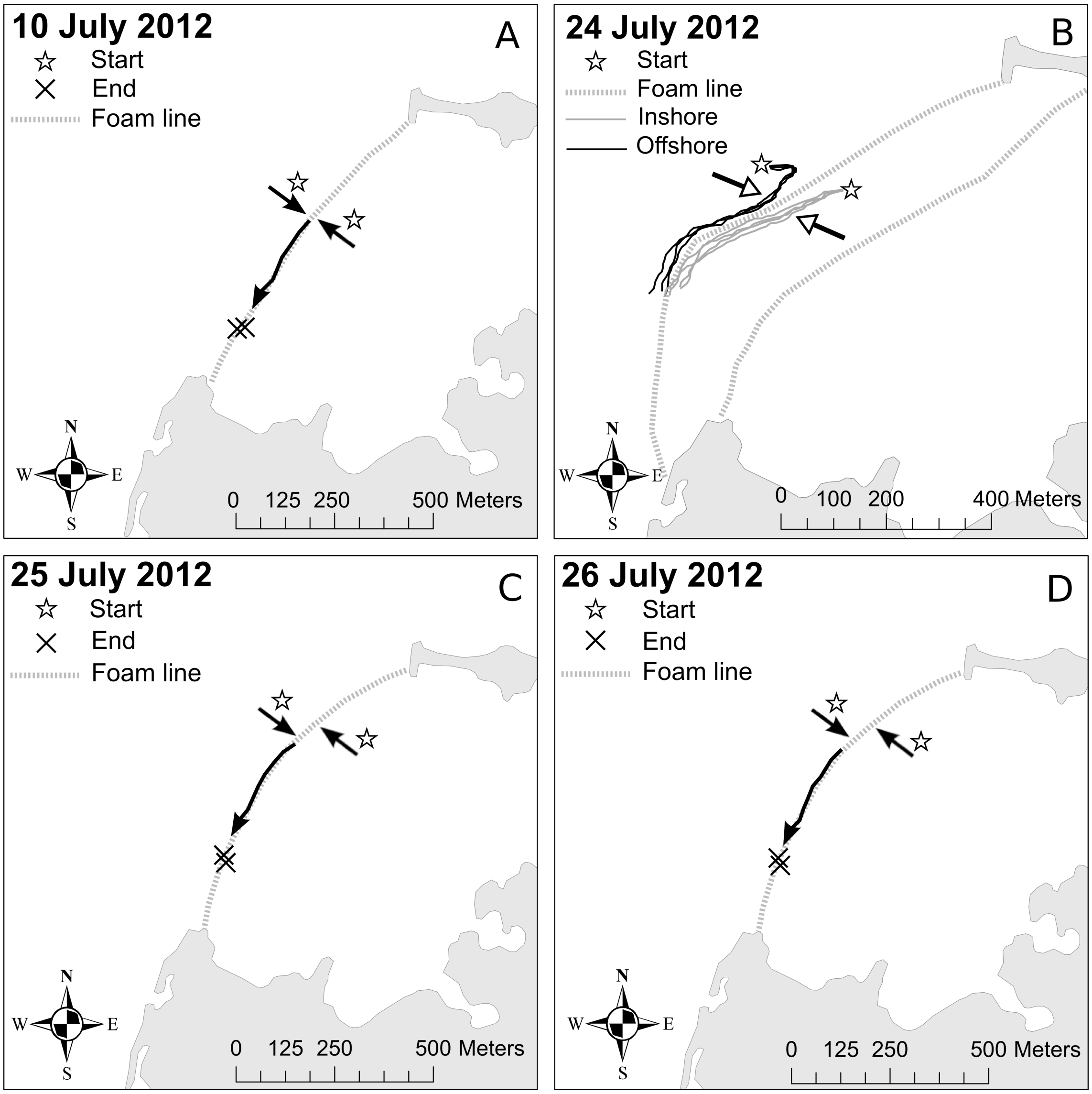

Fig. 2.7. Surface drifter deployments across the front at Sunset Bay when the front was present to test for convergent flow. Observations were made in 2012 on four days with upwelling winds and a visible foam line present at the mouth of Sunset Bay. On July 24, I deployed GPS-tracked drifters, and on the other days I deployed drifters without a GPS and recorded the start and end location of the drifters with a shipboard GPS. A pair of foam lines was present on July 24, with a water color change at the outer foam line located at the mouth of the bay. Drifters were deployed across the outer foam line. On all days, drifters moved directly into the foam line and then traveled in the down wind direction (southwest) in the foam line until we removed them from the water, as shown by black filled arrows. Unfilled arrows indicate the location the drifters entered the foam line on July 24. On July 24, GPS units were set to record position every second. The convergence velocities of seaward and landward drifters were calculated to be 12.8 cm/s and 9.3 cm/s, respectively.

data were available on this sampling date, previous research suggests that the warm lens of water that forms inshore of the front when present was typically 2-5 m thick. Therefore, I assumed that the 1.5 m drogues were within and the 5.5 m drogue beneath the warm lens, respectively. The 1.5 m drogues traveled towards the southeast, and the 5.5 m drogue traveled towards the northeast, indicating a separation of flow with depth inshore of the front. All drogues traveled away from the foam line (Fig. 2.9A).

On July 10 I simultaneously deployed two 1.5 m drogues approximately 100 m both inshore and offshore of the foam line. The inshore drogues moved southwest, eventually encountering the foam line. Once in the foam line, drogues traveled within the foam line southward until they were removed from the water when they approached the rocky shore that makes up the south end of Sunset Bay. The drogues never crossed the foam line. The offshore drogues moved quickly offshore and towards the southwest (Fig. 2.9B).

On July 25, drogues were deployed slightly closer to the front: three 1.5 m and three 5.5 m drogues were released simultaneously about 100 m inshore of the foam line. The 1.5 m drogues traveled as a tight group, moving northwest. The 1.5 m drogues moved towards and eventually into the foam line, and then traveled in the foam line roughly northward until they were removed close to the rocky shore to the north of the bay where the foam line was attached. The 5.5 m drogues traveled as a tight group, moving shoreward (to the west). None of the drogues crossed the foam line (Fig. 2.9C).

On July 26, two 1.5 m and 5.5 m drogues were deployed simultaneously about 250 m inshore of the foam line. Two additional 1.5 m and 5.5 m drogues were deployed immediately thereafter roughly 250 m offshore of the foam line. Both the inshore and offshore 1.5 m drogues moved towards and into the foam line and were then advected roughly northward along the foam line, but never crossed it. Both the inshore and offshore 5.5 m drogues moved offshore and south, with the inshore drogues crossing the foam line (Fig. 2.9D).

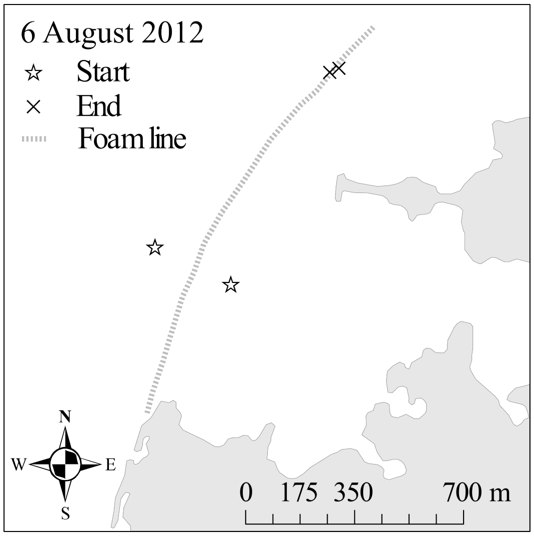

Fig. 2.8. Surface drifters on August 6, 2012 indicated convergent flow at the foam line during strong downwelling-favorable winds at Sunset Bay. Typically no foam line is present at Sunset Bay when winds are from the S or SW. However, on August 6, downwelling winds were strong (roughly 5-7 m/s) during sampling and a foam line was present across the mouth of the bay. The foam line was attached at the south, but not north, end of the bay. Drifters were deployed about 30 m on either side of the foam line and were advected immediately into the foam line, indicating convergent flow. Drifters traveled in the along-wind direction (roughly north) within the foam line until removed from water when approaching rocks. The stars represent seaward and shoreward deployment locations of the drifters, and X's mark the retrieval location. The dotted line marks the location of the foam line on this day.

I investigated flow at depth at Sunset Bay on three days during relaxation or downwelling conditions (Fig. 2.10). On June 25 and 29, winds were light (< 2 m/s) and from the south or southeast, and no foam line was present. On June 25, I simultaneously released two 1.5 m drogues and one 5.5 m drogues approximately 100 m inshore of the usual foam line location when the front is present (~ 1 km from shore). Although no CTD data were

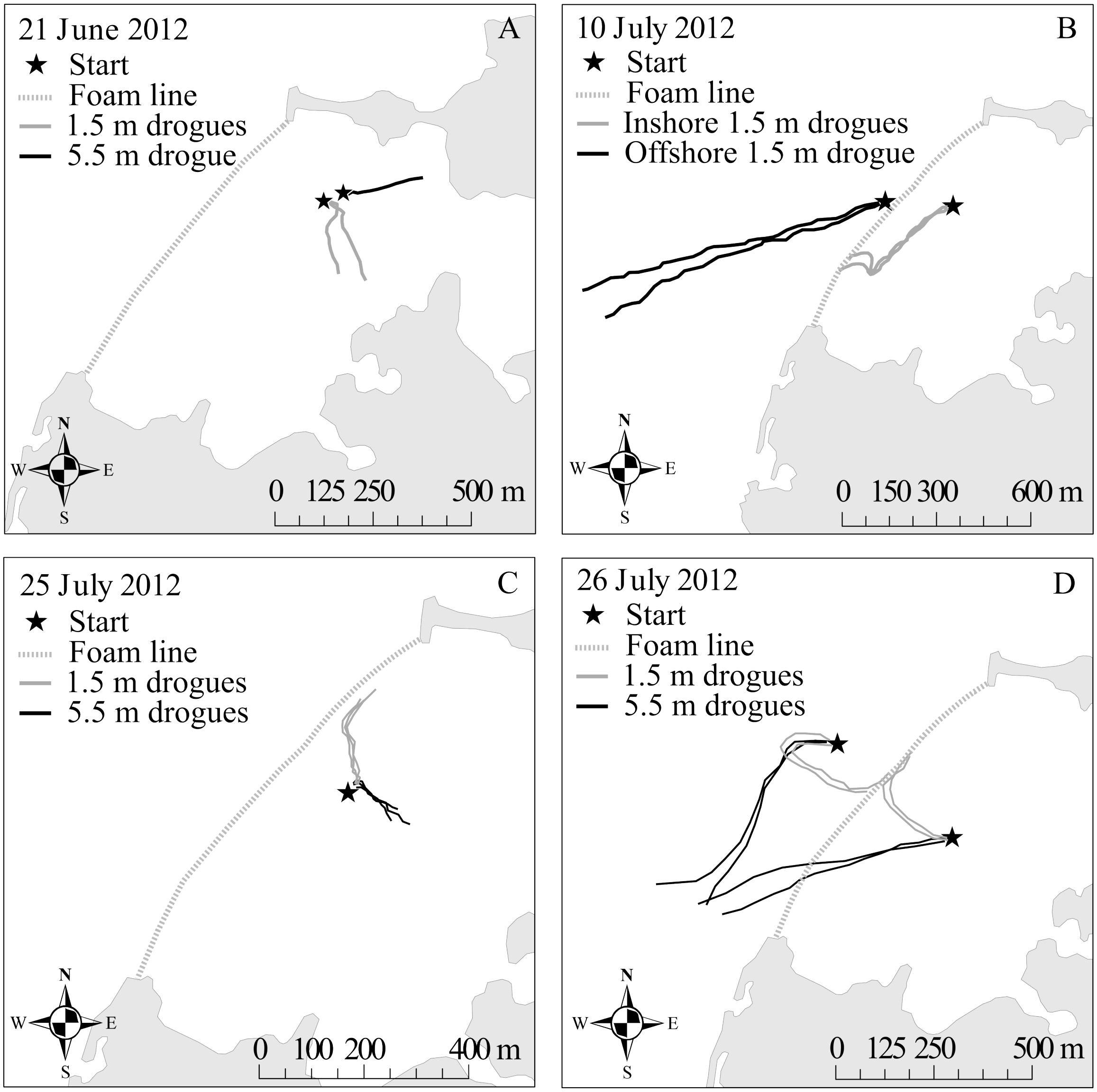

Fig. 2.9. Drogue deployments on days with a front at Sunset Bay. Drogues were deployed at 1.5 m and 5.5 m depths simultaneously on June 21 (A), July 25 (C), and July 26 (D) 2012, and on each of these days indicated separation of flow with depth. On July 10, 2012 (B) all drogues were deployed at 1.5 m depth inshore and offshore of the front. The inshore drogues were entrained in the foam line and traveled in the down-wind direction (the same direction as surface flow in the convergence). On July 25 (C) and July 26 (D) the 1.5 m drogues were also entrained in the foam line, however, they traveled in the opposite direction of the prevailing wind direction suggesting counter flow 1-2 m below the surface on some, but not all (see B) frontal days. Stars indicate starting location of drogues and the dashed line indicates the foam line location.

available on June 25, CTD data from June 29 shows no evidence for a front and temperature was constant throughout most of the water column where the drogues were released (Fig. 2.6A). All three drogues traveled together, moving inshore and southward. There did not appear to be separation of flow with depth on this day, however, as a cautionary note, this was a relatively short deployment (35 min, Fig. 2.10A).

On June 29, I deployed two 1.5 m and two 5.5 m drogues simultaneously about 75 m inshore of the usual foam line location. The 1.5 m drogues initially moved towards the northwest, and then reversed direction once outside of Sunset Bay and traveled southward. It is possible that these drogues were initially in a secondary eddy feature within Sunset Bay, but were caught in offshore flow once out of the bay. The 5.5 m drogues moved southward. Drogue deployments on this day show evidence for separation of flow with depth (Fig. 2.10B).

On Aug 6, winds were strongly downwelling-favorable, and a foam line was present. I deployed two 1.5 m drogues both inshore and offshore of the foam line, and then immediately thereafter, deployed two 5.5 m drogues both inshore and offshore of the foam line. When the 1.5 m drogues approached the north rocks and were removed from the water, I redeployed them from the original start location. The inshore 1.5 m drogues moved eastward, away from the foam line, and did not cross it. The first 1.5 m drogues deployed offshore moved into the foam line and traveled within it northward, without crossing the foam line. When redeployed, these drogues crossed the foam line and then followed the path of the inshore 1.5 m drogues, moving eastward. Both of the 5.5 m drogues moved westward, with the inshore drogues crossing the foam line (Fig. 2.10C).

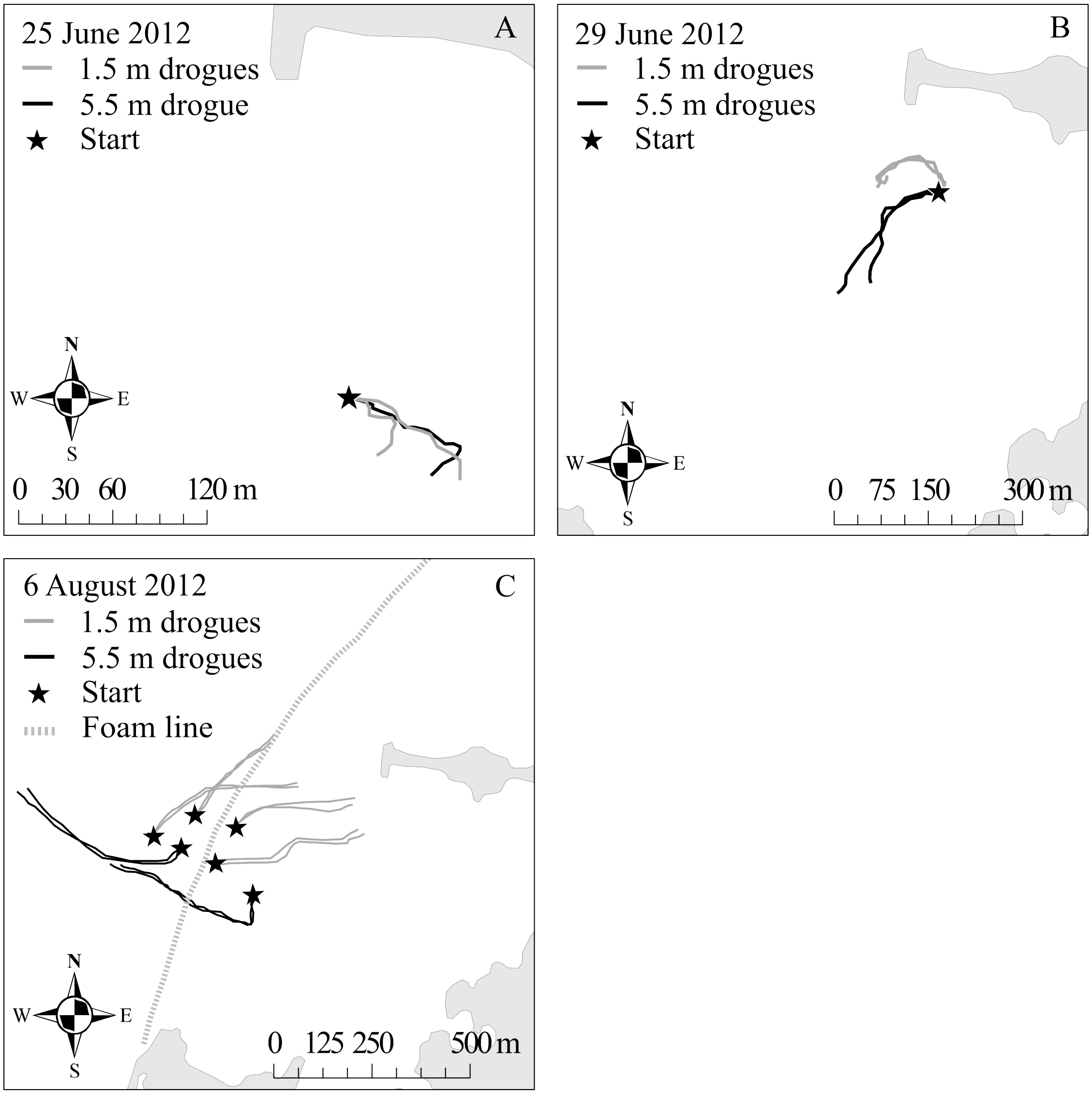

Fig. 2.10. Drogue deployments on days with very light or downwelling-favorable winds. On June 25 (A) and June 29, 2012 (B) winds were very light and no foam line was present. A very short deployment without a foam line present suggested that there may not be separation of flow with depth (A), however, another, longer deployment did show differences in flow with depth (B) as well as on August 6 (C) when there was a foam line present. On August 6, 2012 winds were strongly downwelling favorable (5-7 m/s and from the south) and a foam line was present. Drogues deployed at 1-2 m depth 30 m on either side of the foam line indicated that sub-surface flow was in the down-wind (roughly north) direction. One pair of offshore 1-2 m drogues crossed the foam line and moved in to the bay and northward, while the other pair did not cross the foam line. The inshore 1-2 m drogues moved inshore and northward, and never crossed the foam line. All drogues deployed at 5-6 m depth moved offshore, with the inshore drogues crossing the foam line quickly indicating offshore water sub-surface offshore water flow. Stars indicate starting location of drogues and the dashed line indicates the foam line location, if present.

DISCUSSION

During the summer of 2012 I extensively sampled the water column physical characteristics and flow across the front at Sunset Bay at the surface, 1.5 m, and 5.5 m water depths. To my knowledge, this is the first description of flow at surface and depth across a nearshore, wind-driven topographic front and foam line. The shore-parallel foam line across the mouth of Sunset Bay is the surface expression of a convergent. The kind of topographically-controlled, shore-parallel foam line sampled for this study is a common feature of rocky shorelines, and it is likely that the physics described in this study pertain to similar fronts around the world.

This study demonstrates that the foam line that forms at the surface of the front across the mouth of Sunset Bay is a surface convergence capable of quickly aggregating Lagrangian particles (drifters). Once in the foam line, drifters were advected in the along-wind direction. It is not clear what the eventual fate of particles entrained in the foam line is as drifters were removed from the water as they neared the rocks at the south end of Sunset Bay. Drifters may eventually become grounded on the rocks at the south end of the cove, or move out of the foam line at the surf zone. See Fig. 2.11A for a schematic representation of surface flow across the front.

On the day when two foam lines were present (July 24, 2012), the landward drifters moved toward the outer foam line at a lower speed than the seaward drifters, indicating that the flow between the outer and inner foam lines may be slower. It is likely that when multiple foam lines are present, each acts as a convergence with a divergence zone between the foam lines. As I calculated convergence velocities on only one day, these values should be taken as a sample case; however, they fall within the range (7-26 cm/s) of similar convergences reported in the literature (Pingree et al. 1974, Simpson et al. 1979, Le Fevre 1986, Shanks et al. 2000, Weidberg et al. 2014).

Prior to August 6, 2012, I had not witnessed a front or prominent foam line present during downwelling-favorable winds. Foam lines on downwelling or relaxation days, if present at all, were typically weak and did not extend very far across the mouth of the bay (personal observation, and data in McCulloch 2001). However, on one sampling day (August 6) with strong downwelling-favorable winds (5-7 m/s), a shore-parallel prominent foam line was attached to the southern end of the mouth of Sunset Bay. It is not clear why a prominent foam line was present on this day and not other days with downwelling-favorable winds; it may be because winds were stronger than usual during downwelling conditions (5-7 m/s on August 6). Previous research did not report the wind speeds of downwelling-favorable wind condition observations, so it is not clear whether or not the partial foam lines that have been observed on downwelling days were under lighter winds (McCulloch 2001). Consistent with the foam lines sampled during upwelling-favorable winds, the foam line present on August 6 was a surface convergence with flow within the foam line in the downwind direction. The foam line appeared less prominent, but was still present, when north winds were lighter than about 4 m/s, suggesting that this may be an important threshold in wind speeds necessary for convergence formation.

The front at Sunset Bay typically has a warm lens of water inshore of the foam line that ranges from about 2-5 m deep. Drogue deployments suggest that this is due to a lack of water exchange within this layer. A schematic representation of flow at depth across the front at Sunset Bay is presented in Fig. 2.11B. During upwelling-favorable wind conditions, none of the 1.5 meter drogues crossed the foam line. In contrast, drogues released below the depth of the inshore warm lens (5.5 m) were able to cross the foam line. These studies suggest that, when the front is present, water exchange at 1.5 m (within the warm lens) is limited, but that water exchanges across the front at depth. Therefore, it is likely that the warm, less dense, less saline lens of surface water found inshore of the front during upwelling winds is due to limited offshore exchange of surface waters across the front.

A strong convergent foam line was present at Sunset Bay during downwelling-favorable winds on August 6. The CTD profiles, however, did not suggest the presence of a warm lens of water inshore of the foam line or any other indication of a front. It is possible that the front had not been present long enough to allow for the trapped inshore waters to heat up. This does not seem like a likely explanation, however, as downwelling-favorable winds had persisted for about two days prior and I have found that a thermal front is visible in CTD profiles less than a day after upwelling-favorable winds start up again after a relaxation event. An alternate possibility to explain the lack of a front is that the foam line on August 6 did not completely close off Sunset Bay: the foam line was attached at the south, but not north, ends of the bay. This suggests that water may exchange freely when the front was disconnected from shore. This interpretation is supported by the second 1.5 m offshore drogue deployment on August 6: these drogues crossed the foam line, indicating water exchange at that depth. This was not seen in any of the deployments with a front present during upwelling-favorable winds.

Data from drogue deployments indicate that there is separation of flow with depth at Sunset Bay when the front is present: flow at 1.5 m and at 5.5 m water depth is in different directions. I also saw evidence for separation of flow with depth on two of the sampling days when the front was absent (June 29 and August 6), but the surface and deep drogues on another day without a front did not appear to separate much (June 25). This was a particularly short deployment, however. It is possible that separation of flow with depth is not as strong on some days when there is not a front at Sunset Bay, although more deployments would be needed to answer this question. On many days, vertical shear across the front at Sunset Bay can be quite strong.

Surface drogues set to track flow at 1.5 m water depth traveled in different directions on different sampling days. Typically, 1.5 m drogues traveled parallel to the front and foam line suggesting that along-front flow was present at this depth. On three of the four days with a front where I deployed 1.5 m drogues inshore of the front, the drogues become entrained in the foam line. Once entrained, the drogues traveled in the foam line until I retrieved them. On July 10, the 1.5 m drogues traveled in the same direction as the surface convergent flow in the foam line (in the down-wind direction, roughly south), as indicated by the surface drifter deployments (Fig. 2.9B). On both July 25 and 26, however, the 1.5 m drogues traveled in the opposite direction (Fig. 2.9C, D), indicating the presence of a counter current flow (in the up-wind direction) beneath the foam line and surface convergence. My finding of along-front flow in waters immediately adjacent to the front is consistent with other results reported in the literature (e.g., Lwiza et al. 1991, Matthews et al. 1993).

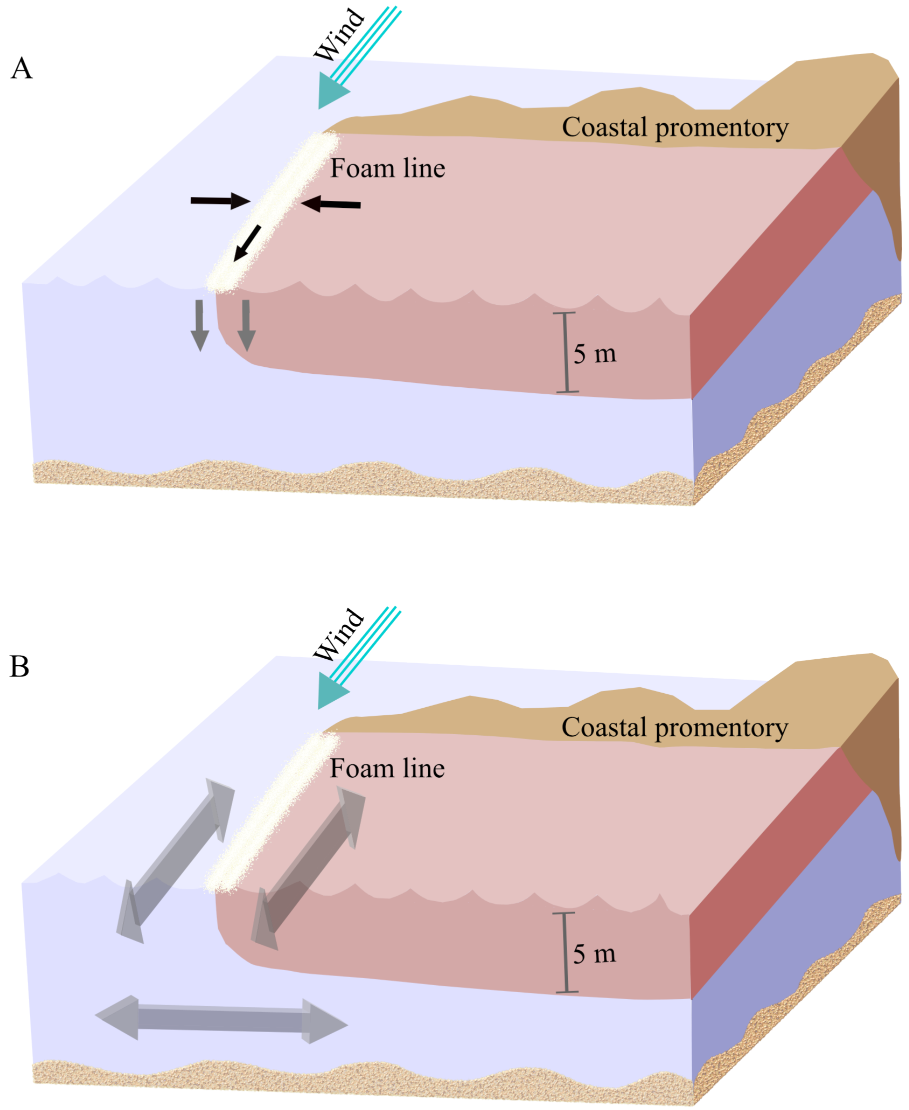

Fig. 2.11. Schematic of flow at the front at Sunset Bay. Winds from the north or northwest (blue arrow) drive alongshore currents in the nearshore that interact with coastal topography and create a front in the lee of the promontory. When the front is present long enough, the inshore surface waters heat up creating a shallow (< 5m) warm lens of water inshore of the front, indicated by the red water color. Diagram of surface convergence (A) includes black arrows that indicate surface (< 20 cm) water movement towards the foam line on both sides of the front. Small black arrow within the foam line indicates along-wind flow within the convergence. Currents indicated by black arrows are from data collected using surface drifters. Gray arrows indicate downwelling at the foam line as indicated by dye studies (Jarvis unpublished data and Shanks et al. 2003c). Diagram of flow at depth (B) summarizes data collected using sub-surface drogues. Top two gray arrows show flow 1-2 m below surface. Drogues at this depth often indicated along-front flow, and never crossed the front. The lower gray arrow shows sub-surface flow from 5-6 m below surface. Drogues at this depth tended to cross the foam line, indicating potential for water exchange below the warm lens of surface water.

The fluid dynamics that account for the formation of the front at Sunset are not well understood. Rocky shores commonly have abrupt topographies such as headlands, coves, bays, and rocky outcroppings, and it is well-known that strong flow past these features can separate from shore to create eddies and fronts in the lee of the topography (Geyer & Signell 1990, Signell & Geyer 1990, 1991). A detailed current study to determine how the front and foam line at Sunset Bay forms would require an array of moored current meters or more detailed surveys: none of which were within the scope of this dissertation. However, the flow patterns created by strong tidal flow around shoreline topography has been studied by several physical oceanographers, and the fluid dynamics of these studies likely pertain to the flow at Sunset Bay. See Fig. 2.12 for a diagrammatic representation of strong flow passed a simplified headland based on modeling and empirical studies (Bowman et al. 1980, Wolanski 1986, Yanagi 1987, Geyer & Signell 1990, Signell & Geyer 1990, 1991, Geyer & Signell 1992, Wolanski et al. 1996). When strong currents encounter a sharp change in topography such as a headland, fluid streamlines become compressed close to the topographical feature and a stagnation area is formed in the lee. The compressed current streamlines curving around the headland act as a pipe with decreasing diameter, similar to the Bernoulli effect (The Bernoulli effect is a phenomenon in fluid dynamics in which flow through a pipe increases in speed as the diameter of the pipe decreases (Vogel 1994)), causing flow to accelerate until the tip of the headland (most seaward end) is reached. As streamlines bend around the headland, centrifugal force produces a decrease in sea surface height at the tip of the headland due (Bowman et al 1980). Current speeds decrease once the tip of the headland is reached, and slow in the lee. This results in a sea surface height difference between the stagnation area and just offshore where the strong current is flowing. This pressure difference between the two areas creates a secondary circulation feature in the transverse direction, resulting in a surface convergence with flow towards the area marked “slick or foam line” (Yanagi 1987).

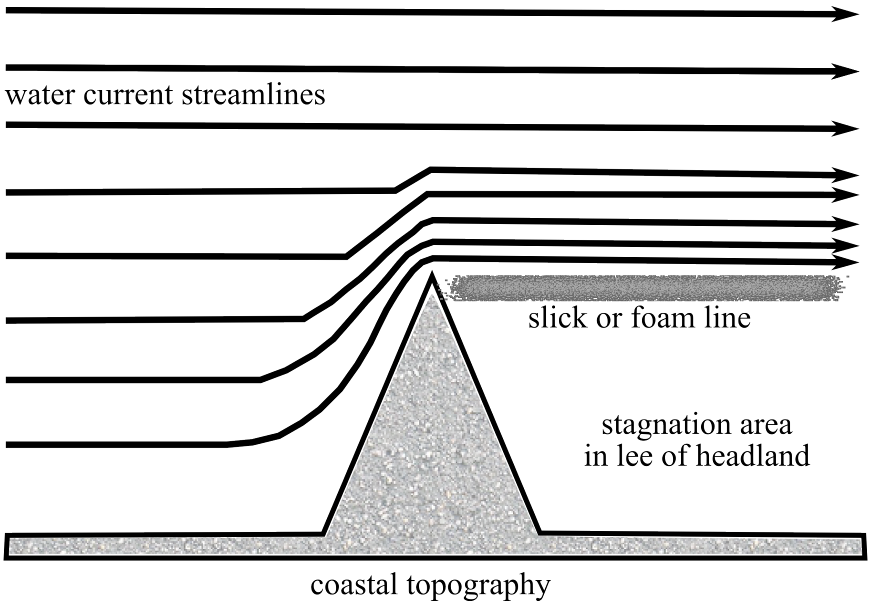

Fig. 2.12. Schematic representation of strong flow around an abrupt change in shoreline topography such as the rocky outcropping at Sunset Bay. View is from above, looking down on a representative headland and the water current streamlines that bend around it. When strong currents encounter a sharp change in topography such as a headland, fluid streamlines become compressed close to the topographical feature and a stagnation area is formed in the lee. Due to the Bernoulli theorem, a sea surface height difference is formed between the stagnation area and just offshore where the strong current is flowing (Yanagi 1987). This pressure difference between the two areas creates a secondary circulation feature in the transverse direction, resulting in a surface convergence with flow towards the area marked “slick or foam line”. The surface convergence typically accumulates foam and floating detritus such as crustacean molts and drifting bits of algae. These kinds of topographic convergences can occur due to the interaction of any coastal current, but most commonly tide- or wind-driven currents, and abrupt changes in shoreline topography including headlands, coves, rocky outcroppings, sea stacks, and islands. Figure adapted from Yanagi 1987.

Topographical fronts only persist as long as the force generating the front continues. In the case of topographical fronts caused by tidal currents, this may only be several hours. Prior studies show that these fronts are capable of trapping or concentrating zooplankton when the front is present, but that zooplankton disperse rapidly with the dissolution of the front as the tide or current changes (Alldredge & Hamner 1980, Wolanksi & Hamner 1988). McCulloch (2003) found that the average duration of the foam line at Sunset Bay during the summer of 2000 was eight days, with a range of 2-20 days and four periods where the foam line (and therefore presumably the front) was present for a week or longer. Upwelling-favorable winds and small waves are common during the spring and summer on the Oregon coast, and McCulloch (2003) found that the foam line was present at least 84% of the summer. If the flow patterns we found persist for the duration of the time the front at Sunset Bay is present (days to weeks), there may be a surface convergence and limited surface water exchange at Sunset Bay for much of the spring and summer.

BRIDGE

In Chapter II, I found strong evidence to support my hypothesis that the foam line at the mouth of Sunset Bay is a surface convergence, with convergent flow on both sides that advected passive particles towards the front. As the foam line is capable of concentrating foam, detritus, and surface drifters, I hypothesized that the foam line would also concentrate some taxa and developmental stages of larvae and other zooplankton. Chapter III tests this hypothesis by comparing concentrations of plankton in surface waters on either side of the front to concentrations within the foam line.

CHAPTER III

FOAM LINES IN THE NEARSHORE: A TOPOGRAPHIC FRONT THAT ACCUMULATES COMPETENT LARVAE AND TRANSPORTS THEM SHOREWARD

This chapter will be submitted for publication with Alan L. Shanks as coauthor. Author contributions: MAJ conceived and designed the study, with input from ALS. MAJ conducted the research and analyzed all data with advice from ALS. MAJ wrote the manuscript.

INTRODUCTION

The vast majority of marine species produce thousands to millions of planktonic larvae that undergo impressive, often complex migrations before metamorphosing and returning to the benthos as relatively sedentary adults. For intertidal and shallow subtidal species, larvae are both released in and must return to nearshore waters where flow is often complex and poorly understood. Nearshore currents interact with coastal headlands, islands, and reefs, generating complex secondary flow features such as upwelling shadows, eddies, and fronts that can aggregate planktonic organisms and increase their retention near coasts (Caffey 1985, Oliver & Willis 1987, Wolanksi & Hamner 1988, Kingsford 1990, Graham & Largier 1997, Wing et al. 1998, Roughan et al. 2005, Morgan et al. 2011).

Although small scale (< 1km) topographic fronts are common on the inner shelf, studies of these kinds of features have generally been limited to those driven by tidal flow, which change position with the tide and are thus unlikely to affect the dispersal of marine larvae that have pelagic larval durations of longer than a few hours (Kingsford 1990). Studies of persistent (days to weeks) topographic fronts often focus on headlands and other larger-scale topographical features along coastlines (Graham et al. 1992, Graham & Largier 1997, Woodson et al. 2012). Similar processes, however, are likely to occur at smaller-scale topographical features such as coves, sea stacks, and rocky outcroppings that very common along coasts worldwide. These small-scale topographic features are often accompanied by foam lines oriented parallel to shore (Fig. 3.1A), at least some of which are fronts caused by multiple physical mechanisms that may be present for weeks at a time and affect plankton distributions (Wolanksi & Hamner 1988, Kingsford 1990, McCulloch & Shanks 2003, Shanks & McCulloch 2003, Shanks et al. 2003b).

One such nearshore front occurs at the mouth of Sunset Bay, a small cove on the southern Oregon coast (McCulloch & Shanks 2003, Shanks & McCulloch 2003, Shanks et al. 2003b). A rocky outcropping extending ~1 km seaward borders the north end of the cove (Fig. 3.1). Upwelling favorable winds (from the N or NW) produce an alongshore, SW-flowing current that encounters this outcropping, creating a foam line in the lee of the headland when waves are < 2 m. Shanks et al. (2003) found that this foam line delineates the surface of a front that separates coastal ocean waters from the cove waters at Sunset Bay. The foam line is present during much of the summer, with an average duration of 6 days (range 1-21 days) (Shanks et al. 2003b). The cove can be isolated from the ocean long enough that a warm surface lens of water (Fig. 3.2A), often low in chlorophyll a (Chl a) (Fig. 3.2C), forms inshore of the front and foam line and the distribution of planktonic organisms differ across the front. Previous work, however, did not investigate plankton within the foam line itself.

When upwelling favorable winds relax or reverse, no foam line is present, and the warm lens typically seen inshore of the front and foam line is either absent or the temperature difference between the waters in the bay and offshore is much reduced (Fig. 3.2B). On multiple occasions, we have witnessed the foam line moving shoreward when upwelling winds relax (Jarvis & Shanks, unpublished data). If competent larvae are concentrated in the foam line, they may be transported shoreward during upwelling relaxation events if the dissipating foam line acts as a moving convergence. This study had the following aims: 1) to test the hypotheses that the front at Sunset Bay has convergent flow at the surface and 2) that the foam line concentrates zooplankters. Fortuitous sampling on one occasion during an upwelling relaxation event allowed us to also investigate 3) whether competent meroplankton remain concentrated in the foam line as it propagates shoreward during a relaxation or wind reversal event.

MATERIALS AND METHODS

During the summers of 2011 and 2012, I sampled a transect at Sunset Bay, a small cove at Cape Arago on the southern Oregon coast (43.3334º N, 124.3718º W) (Fig. 3.1). An inner, protected cove is partially cut off from the outer bay and coast by a rocky constriction ~300 m from shore. All biological sampling occurred in the outer bay and offshore (Fig. 3.1). To test the hypothesis that the foam line at the mouth of Sunset Bay was a convergence, I deployed surface drifters on four days during July 2012. I released four to five drifters ~30 m both seaward and shoreward of the foam line and retrieved

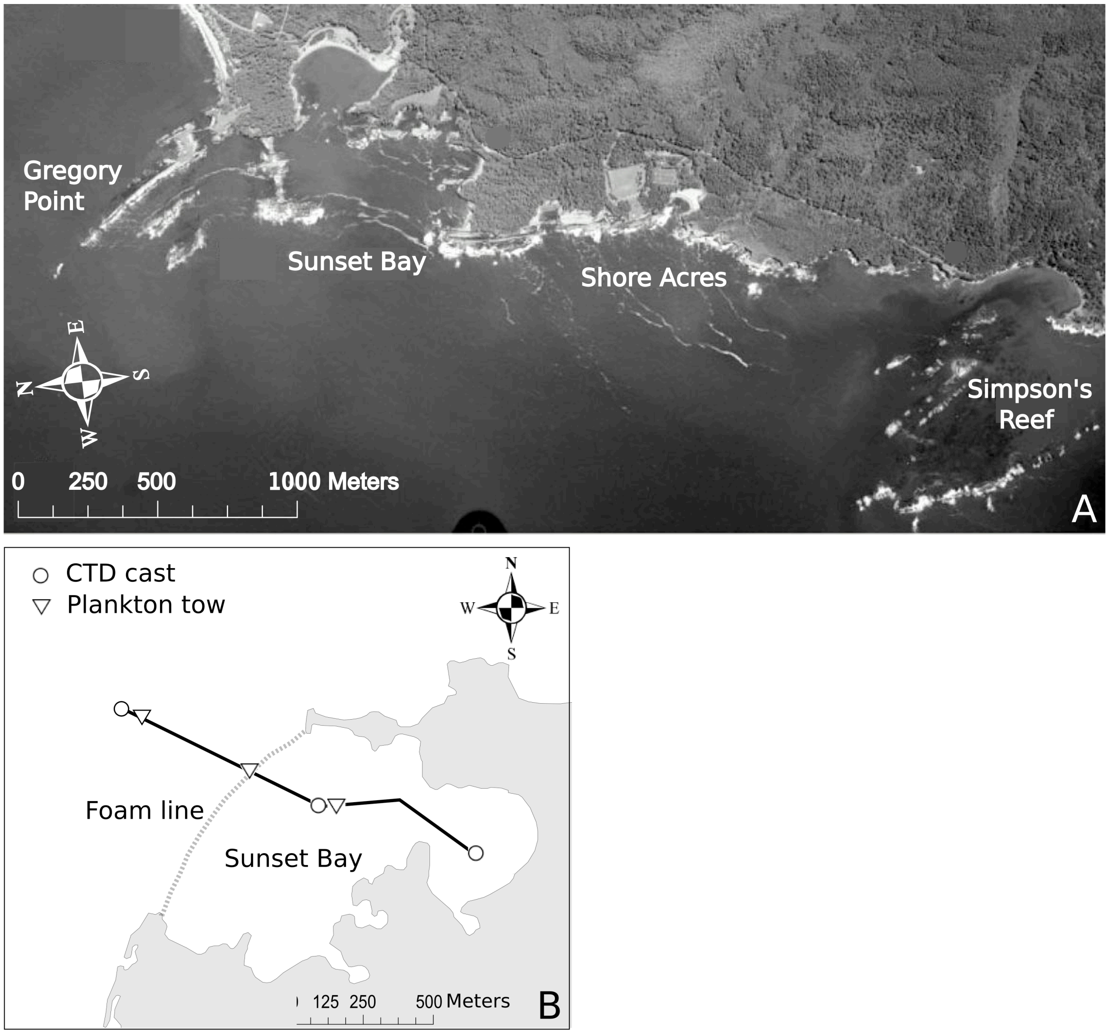

Fig. 3.1. Foam lines along Cape Arago, Oregon, as viewed from above (A) and map of the Sunset Bay, Oregon study site (B). Foam lines (or slicks) can mark the surface of very nearshore fronts caused by at least three mechanisms (Shanks et al. 2003). The foam line at Sunset Bay marks the surface convergence of a topographical, wind-driven front present during upwelling favorable winds and small waves; often a large percentage of the spring and summer. Biological (plankton tows, triangles) and physical data (CTD casts, circles) were taken at stations along a transect roughly perpendicular to shore (solid line). Transects crossed the mouth of Sunset Bay where the topographical foam line (dashed line) and front set up during upwelling favorable winds. In 2012, more CTD stations were added in between marked stations to increase resolution. Fig. 1a adapted from Shanks et al. 2003.

them when they drifted near the rocky shore. On July 10, 25, and 26, drifters consisted of 30 cm long, 1.5 cm diameter dowels fitted with a small float and weight at opposing ends. In the water, the top ~20 cm of the dowel was visible, and the weight and the float were submerged so that the drifters tracked the top ~10 cm of water. I recorded the time and location of the drifters using a hand-held GPS (Garmen Etrex H) upon release and retrieval, and on July 26, at several time points while in the foam line to test if drifter velocities slow as the foam line approaches the rocky boundary at the south end of the cove. On July 24, drifters consisted of 6 x 8 x 15 cm waterproof plastic cases (OtterBox™) enclosing a GPS unit. On this day, two parallel foam lines were present: one at the usual location at the mouth of Sunset Bay and one just inshore, with a water color change at the outer foam line; I deployed drifters around the outer foam line. GPS units in each drifter (n=4 both seaward and landward) were set to record position every second, allowing me to calculate the time it took the drifters to converge at the foam line from either side. Tracks and waypoints were downloaded and visualized using ArcGIS (ESRI).

I measured temperature, salinity, density, and relative Chl a levels with a Seabird model 19 CTD equipped with a WetStar™ fluorometer (not available in 2012). In 2011, I took CTD casts at three stations: inshore (<300 meters from shore), in the outer bay, just inshore of the front (~600-700 meters from shore) and offshore of the front (~1.5 km from shore) (Fig. 3.1B). I increased the number of CTD stations in 2012 for finer resolution. Contour plots were created using Matlab (Mathworks, R2011a). I obtained wind direction and speed from the NOAA Cape Arago weather station (CARO3), located about 0.5 km north of Sunset Bay on Gregory point and calculated hourly alongshore pseudo-wind stress using the standard equation and a constant drag coefficient (Pedlosky 1987). I collected zooplankters at each of three stations: offshore and inshore of the front and within the foam line (Fig. 3.1B). I took neuston plankton tows (~2 minutes, n=3) at each station using a 0.5 m diameter, 153 µm mesh plankton net equipped with a flow meter and floats to sample the top ~30 cm of water. I drove the boat in a zig-zag to sample waters adjacent to the boat rather than in the ship's wake.

On August 10, 2011, the prevailing upwelling winds relaxed during sampling. The first plankton tow was completed near the usual front location at the mouth of the bay, but the last two tows were completed successively closer to shore as the foam line propagated shoreward and dissipated. I compared concentrations of select taxa between each of the three tows to test the hypothesis that plankters remained concentrated in the foam line as it propagated shoreward, an indication that they were likely transported with the moving foam line. All zooplankton samples were preserved in 5% buffered formalin.

Zooplankters were enumerated and identified (Shanks 2001) with the aid of a dissecting microscope. Samples were first washed free of formalin on a 125 µm sieve and transferred to a 400 ml beaker. With the aid of a balance, fresh water was added for a final volume of ~200 ml. Ten ml aliquots were taken using a Stempel pipette (Omori & Ikeda 1984) after mechanically homogenizing the sample by haphazard stirring. Subsamples were counted until at least 200 of the target organisms were enumerated, yielding a sample standard deviation of ~10% for common organisms and ~20% error for the less abundant organisms (Venrick 1978).

I enumerated seventeen taxonomic and developmental groups of plankton. To protect against random significance of multiple comparisons, I divided taxa into groups (i.e., crustacean larvae, ciliated larvae, etc.) and tested groups for differences using a MANOVA. Euphausiid nauplii were 4^{th}-root(x+1) transformed, platyhelminthes juveniles were converted to ranks, and all other data were Box-Cox(x+1) transformed to meet

ANOVA assumptions of equal variance and normality of the residuals. If the MANOVA found significant differences between groups, I then investigated further by testing each taxon within the MANOVA group with a two-way, fixed-effects ANOVA with both sampling date and station as factors. I tested data separately for days with and without a front separately. I used a Bonferroni correction to adjust the alpha to 0.0015 to protect against type-I errors with multiple tests. Uncorrected P-values are reported, and an asterisk indicates significance at the adjusted alpha.

RESULTS

Physical data

When the foam line was present, surface drifters deployed on either side of the foam line were transported directly into the foam line indicating convergent flow on both sides of the front. Once in the convergence, drifters were advected roughly southward, remaining in the shore-parallel foam line until they were removed from the water at the rocky outcropping at the south end of the cove, indicating that Lagrangian particles were carried along the foam line once entrained (Fig. 2.7 in Chapter II). On July 24, when a pair of foam lines was present and drifters were deployed on either side of the outer foam line, the inshore drifters deployed between the two foam lines converged at lower velocities than the drifters deployed offshore of the outer foam line (Fig. 2.7B in Chapter II). The seaward drifters converged at a mean velocity of 12.8 cm/s ($n = 3$, $SE = 0.7$), and the landward drifters converged at a significantly lower mean velocity of 9.3 cm/s ($n = 4$, $SE = 0.6$) ($t(3.255) = 3.738$, $p = 0.015$). The landward drifters moved toward the outer foam line at a lower velocity than the seaward drifters, indicating that the flow between the outer and inner foam lines may be slower. It is likely that when multiple foam lines are present, each acts as a convergence with a weak divergence zone between the foam lines. As I calculated convergence velocities on only one day, these values should be taken as a sample case: however, they fall within the range (7-26 cm/s) of similar converging current speeds reported in the literature (Pingree et al. 1974, Simpson et al. 1979, Le Fevre 1986, Shanks et al. 2000, Weidberg et al. 2014).

On July 24, drifters deployed landward and seaward of the outer foam line did not differ in mean velocity once in the foam line, and traveled at 11.5 cm/s (n = 7, SE = 0.4) ($t(4.990) = 0.748$, $p = 0.244$). I also calculated within-foam line velocities on July 26, which were slightly lower than on July 24: 6.9 cm/s (n = 7, SE = 0.4). Once drifters approached the southern boundary of the cove, velocities visually slowed and were calculated on July 26th to slow significantly to a mean of 3.7 cm/s (n = 8, SE = 0.4) ($t(13) = 6.293$, $p < 0.0001$). Drifters released on days without a foam line did not converge. Instead, then typically traveled as a cluster with the predominant local surface current or diverged. Temperature contour plots from CTD transects on the four drifter study days are shown in Fig. 3.2E-H. Although some days with a foam line and convergent flow did not show large differences in surface temperature across the front, the warmest waters were typically found inshore of the foam line on all days.

I sampled multiple days within a single frontal event, which can last days or weeks as long as the winds continue upwelling-favorable. To insure independence of biological data, I randomly selected a single day within each frontal event to analyze; in 2011 I used data from August 5, 10, and 17. The two non-front sampling days, Aug 22 and Sept 12, 2011 were separated by a frontal event and were analyzed as independent samples. Due to CTD failures, I obtained complete CTD transects on only two of the five sampling days in 2011; one day when winds were upwelling favorable (Aug 10, Fig. 3.2A, C) and one day of downwelling/relaxation (Aug 22, Fig. 3.2B, D), however, prior research has shown that the foam line at the mouth of Sunset Bay marks the surface of a front present whenever the waves are small (<2 m) and winds are from the N or NW (Shanks et al. 2003b). If these conditions were met and a foam line was visible, I assumed the front was present. Salinity varied less than 0.3 each day; only Chl a (when available) and temperature contour plots are reported. On August 10, when the foam line was present, shoreward of the foam line I observed the characteristic warm surface lens of water with low relative Chl a concentrations (Fig. 3.2A, C). Water inside Sunset Bay was 1ºC warmer and Chl a concentrations were about half that of waters on the seaward side of the foam line; the foam line delineated a front. On August 22, water at the head of the bay was only slightly warmer (0.4ºC) than offshore waters, and Chl a concentrations did not change across the usual front location. The highest relative Chl a concentrations were found inside the bay on August 22, in contrast to August 10 when the reverse was true (Fig. 3.2).

Zooplankton distributions

Four patterns of zooplankton distribution were present on days when a foam line was present. ANOVA tables for days when the front was present and absent are reported in Tables A.1-4 in Appendix A. Taxa at significantly higher concentrations in the foam line than to either side were cyprids of *Balanus glandula,* and *Cthamalus dalli,* all crab megalopae (includes *Cancer magister, Pachycheles* spp*.,* and Pagurid crabs), the

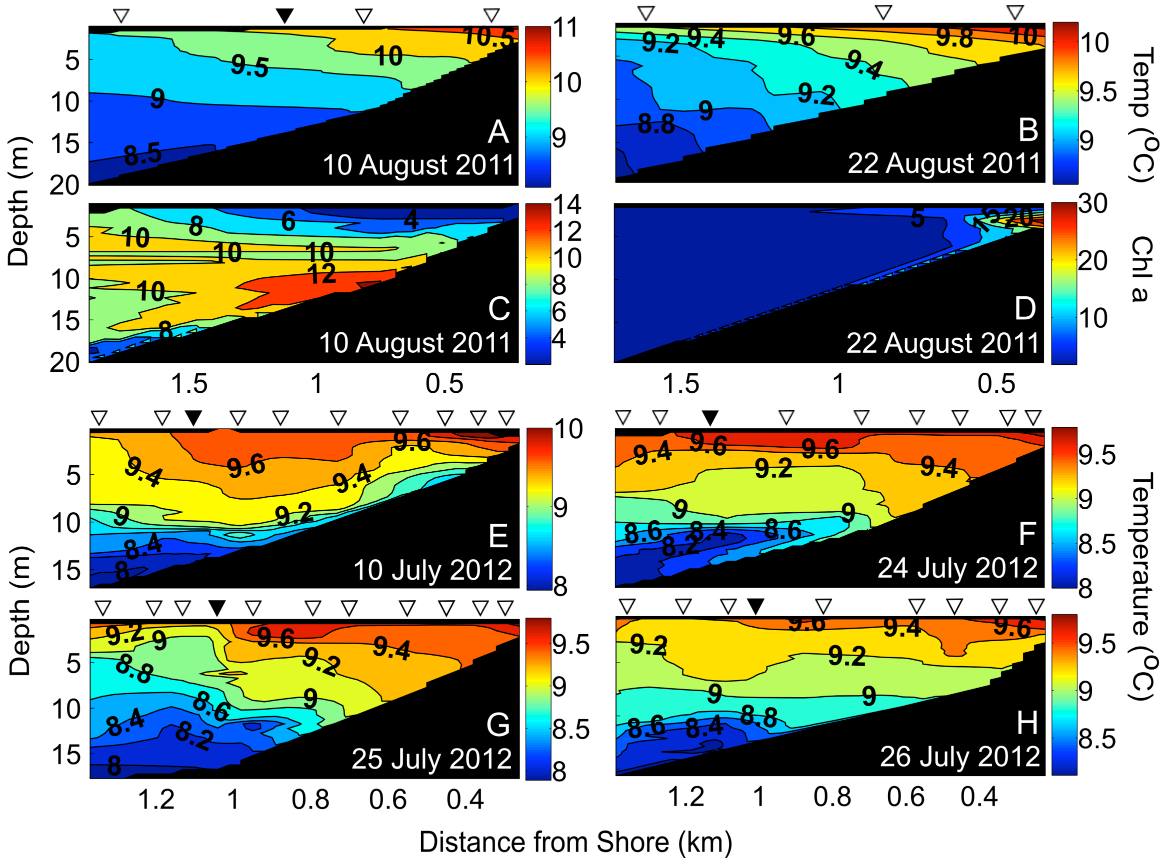

Fig. 3.2. Temperature and chlorophyll a (Chl a) contour plots for 10 Aug (A and C) and 22 Aug 2011 (B and D) at Sunset Bay. On 10 Aug winds were from the north (upwelling favorable) and a foam line was present at the mouth of Sunset Bay. On 22 Aug winds were from the south (downwelling favorable), and no foam line was visible. Open triangles mark the location of CTD casts, and the filled triangle marks the foam line location if present. On 10 Aug, isotherms bent up towards the surface near the foam line location. Temperature and Chl a contour plots both show evidence for the warm, chlorophyll-poor surface lens of water that is characteristic of the water landward of the topographical front at Sunset Bay. On 22 Aug, the warmest waters were in the inner bay, but the difference in surface temperature across the front was ~0.2ºC, in contrast to a ~0.8ºC difference on Aug 10 when the foam line was present. Temperature contour plots for drifter study days completed on July 10, 24, 25, and 26 in 2012 are shown in panels E-H. On all four days, winds were from the north (upwelling favorable) and a foam line was present at the mouth of Sunset Bay. Isotherms bent up towards the surface near the foam line location, and evidence is seen for a warm lens of water inshore of the foam line; waters landward of the foam line range from ~0.2–1ºC warmer than waters offshore.

combined total zoea (includes Porcellanids*,* *Cancer spp.,* Pinnotherids*,* and Grapsid crabs), polychaete worm larvae, platyhelminthes juveniles, isopods, amphipods, harpacticoid copepods, and fish eggs (Group #1, Fig. 3.3**,** Table 1 in Appendix A). Calanoid copepods were significantly more concentrated at the offshore station (Group #2, Fig. 3.4, Table 2 in Appendix A), and barnacle nauplii stages I-III were significantly more concentrated at the inshore station (Group #3, Fig. 3.5, Table 3 in Appendix A). The distributions of copepod nauplii, euphausiid nauplii, and barnacle nauplii stages IV-VI did not vary relative to the foam line (Group #4, Fig. 3.6**,** Table 4 in Appendix A).

When the front and foam line were absent, no taxa were concentrated at the usual location of the foam line at the mouth of Sunset Bay. Amphipods and Harpacticoid copepods were more concentrated at the inshore station (Fig. 3.7). On these days, the concentrations of most taxa did not vary with station location, including Calanoid copepods and their nauplii, *B. glandula* cyprids, barnacle nauplii stages I-III, polychaete larvae, and bivalve and gastropod veligers (Fig. 3.8**)**. Euphausiid nauplii, crab larvae, *C. dalli* cyprids, barnacle nauplii stages IV-VI, fish eggs and isopods were not caught in high enough numbers to allow statistical analysis on the two days when a front was absent.

On August 10, 2012, winds relaxed while I was sampling, and the foam line began to propagate shoreward. I marked the foam line location with GPS as it moved shoreward, but unfortunately the time did not record correctly. The foam line moved about 250 meters shoreward during the time it took me to take three plankton samples within the moving foam line. I estimate the elapsed time to be about 45 minutes, giving the frontal propagation velocity around 7-8 cm/s. All three plankton tows show very high

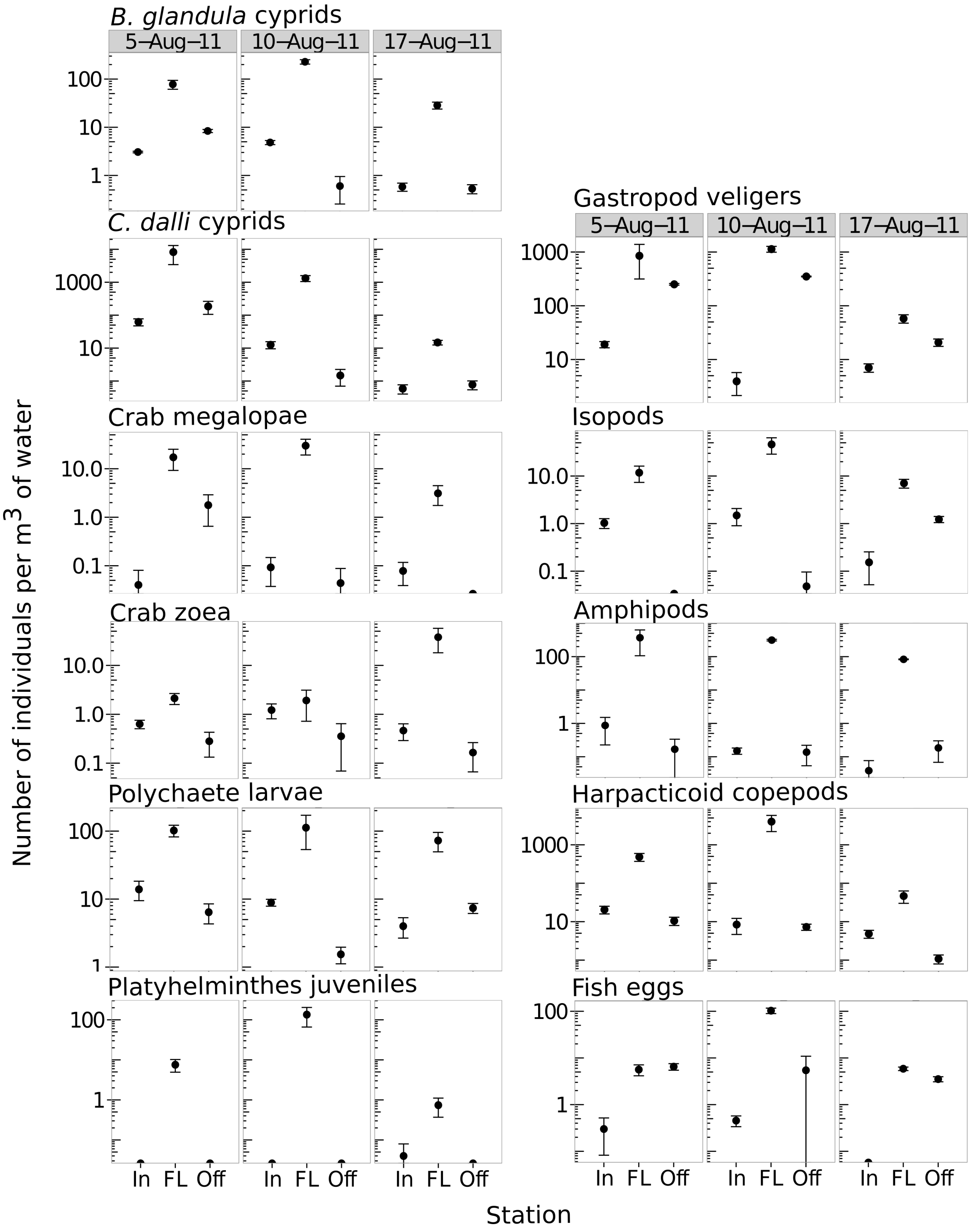

Fig. 3.3. Zooplankton taxa significantly concentrated in the foam line at Sunset Bay. Concentrations (mean, SE) of zooplankton in neuston plankton tows that sampled the top 30 cm of water taken inshore (In), offshore (Off), and in the foam line (FL) on three days with a front present in 2011. Many taxa, including competent (cyprids and megalopae) and ciliated larvae (e.g., polychaete worm larvae and gastropod veligers), were significantly concentrated in the foam line when a front was present at Sunset Bay.

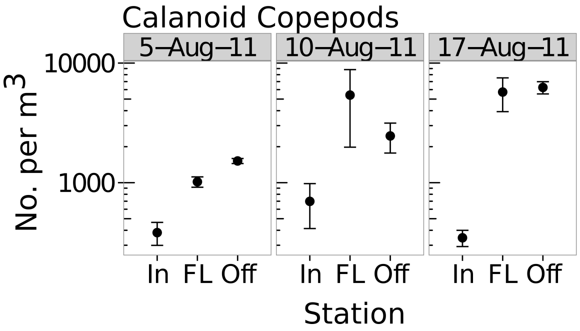

Fig. 3.4. Zooplankton taxa significantly concentrated offshore of the front at Sunset Bay. Concentrations (mean, SE) of calanoid copepods in neuston plankton tows that sampled the top 30 cm of water taken inshore (In), offshore (Off), and in the foam line (FL) on three days with a front present in 2011. Calanoid copepods were found in significantly higher concentrations offshore of the front on days when the front and foam line were present at Sunset Bay.

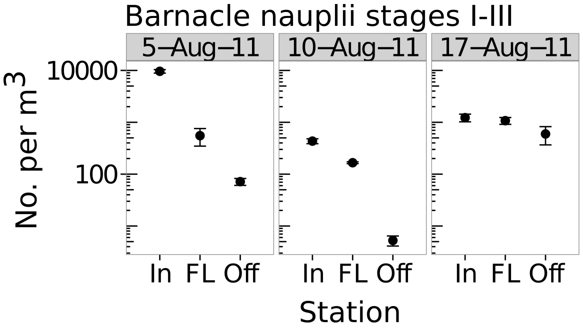

Fig. 3.5. Zooplankton taxa significantly concentrated inshore of the front at Sunset Bay. Concentrations (mean, SE) of early barnacle nauplii (stages I-III) in neuston plankton tows that sampled the top 30 cm of water taken inshore (In), offshore (Off), and in the foam line (FL) on three days with a front present in 2011. Barnacle nauplii stages I-III were found in significantly higher concentrations inshore of the front when the front and foam line were present at Sunset Bay.

concentrations of some meroplankton, including cyprids, megalopae, and gastropod veligers, suggesting that these organisms remained in the foam line as it moved shoreward (Fig. 3.9). Note, however, that this trend did not hold true for all plankters originally concentrated in the foam line: polychaete worm larvae and platyhelminthes juveniles did not appear in high numbers in the third (most shoreward) tow (Fig. 3.9). As tows were taken as the foam line moved, each sample could not be replicated. Foam and visible detritus aggregated in the foam line were patchy, thus sample variance of raw counts tended to be much higher in the foam line than other stations. I do not know if the decrease in polychaete larvae and platyhelminthes juveniles in the third (most inshore) tow on August 10th represents a significant change from the mean or simply part of the large variation we saw in foam line concentrations depending on where in the foam line I sampled.

DISCUSSION

This study demonstrates that the foam line at Sunset Bay is a surface convergence that is capable of concentrating some taxa and developmental stages of invertebrate larvae and other zooplankton. Foam lines are common along coasts, and are often attached to shoreline topographic features such as rocks and headlands, as is the foam line described here. It is likely that similar foam lines mark the surface convergences of fronts as well, and also concentrate some zooplankton taxa. What zooplankters are concentrated will be determined by the current spends at the convergence combined with the swimming abilities and behaviors of the individual zooplankton taxon or developmental stage.

Although most marine invertebrate larvae are likely unable to swim against common horizontal current velocities in the ocean, many larvae are able to swim against slower vertical velocities (Mileikov 1973, Franks 1992) and have an extraordinary amount of behavioral control over their position in the water column using swimming and sensory capabilities and swimming vertically (Chia et al. 1984, Metaxas 2001).

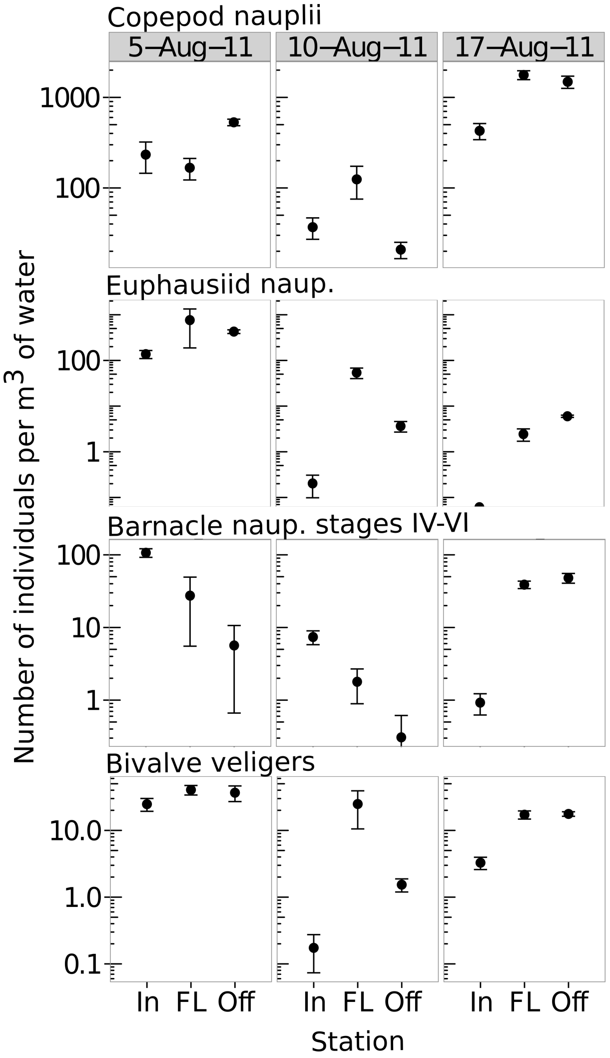

Fig. 3.6. Zooplankton taxa without a significant distribution pattern with respect to the front at Sunset Bay. Concentrations (mean, SE) of zooplankton in neuston plankton tows that sampled the top 30 cm of water taken inshore (In), offshore (Off), and in the foam line (FL) on three days with a front present in 2011. Copepod and euphausiid nauplii, barnacle nauplii stages IV-VI, and bivalve veligers did not have a consistent distribution pattern with respect to the front when it was present at Sunset Bay.

Currents in the ocean often change or reverse direction with a relatively small change in depth. A helpful analogy is given by Bakun, who described the water column as consisting of stacked conveyer belts moving in different directions (1996). Using this analogy, a larva would only have to swim up or down a small distance to encounter a different conveyer belt, or horizontal current, which would result in a much further horizontal distance traveled than if the larva were to simply swim horizontally in the same direction. Therefore, the swimming behaviors and depth preferences of larvae, not just its swimming speeds, can greatly affect their distribution in the ocean, including around a front or convergence.

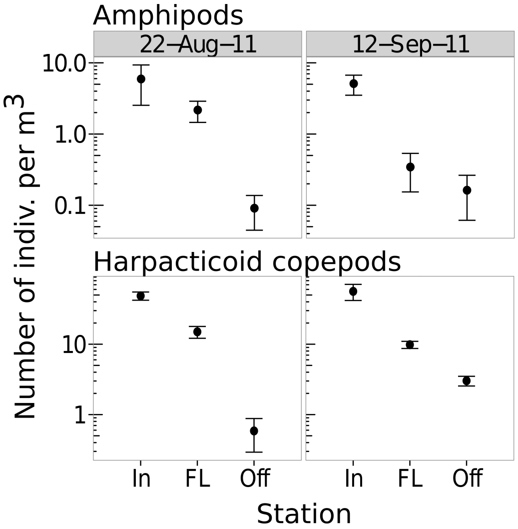

Fig. 3.7. Taxa significantly concentrated inshore of the front at Sunset Bay. Concentrations (mean, SE) of zooplankton in neuston plankton tows that sampled the top 30 cm of water taken inshore (In), offshore (Off), and at the mouth of the bay where the foam line forms when present (FL) on two days when the front was absent in 2011. Amphipods and harpacticoid copepods had significantly higher concentrations at the inshore station on days without a front or foam line present at the mouth of Sunset Bay.

Modeling studies suggest that if larvae behave as passive particles, either through weak swimming ability or lack of depth preference, they will be simply swept through a frontal system. If larvae have a subsurface depth preference or weak upward swimming speeds relative to vertical velocities at the front, they will become diffusely aggregated at depth around the front (Franks 1992, Epstein & Beardsley 2001). If, however, larvae have a preferred depth and have both the behavior and upward swimming capability equal or greater than the downwelling speeds below the convergence, they will become concentrated at the front (Owen 1981, Shanks 1985, Epifanio 1987, Franks 1992, Govoni & Grimes 1992). I found *Balanus glandula* and *Chthamalus dalli* cyprids, crab zoea and megalopae, polychaete larvae, and gastropod larvae concentrated in the surface convergence, which suggests that all of these larvae had behaviors and swimming capabilities to maintain a near-surface and/or neustonic depth preference. Barnacle larvae typically progress through six naupliar stages that feed and develop in the plankton

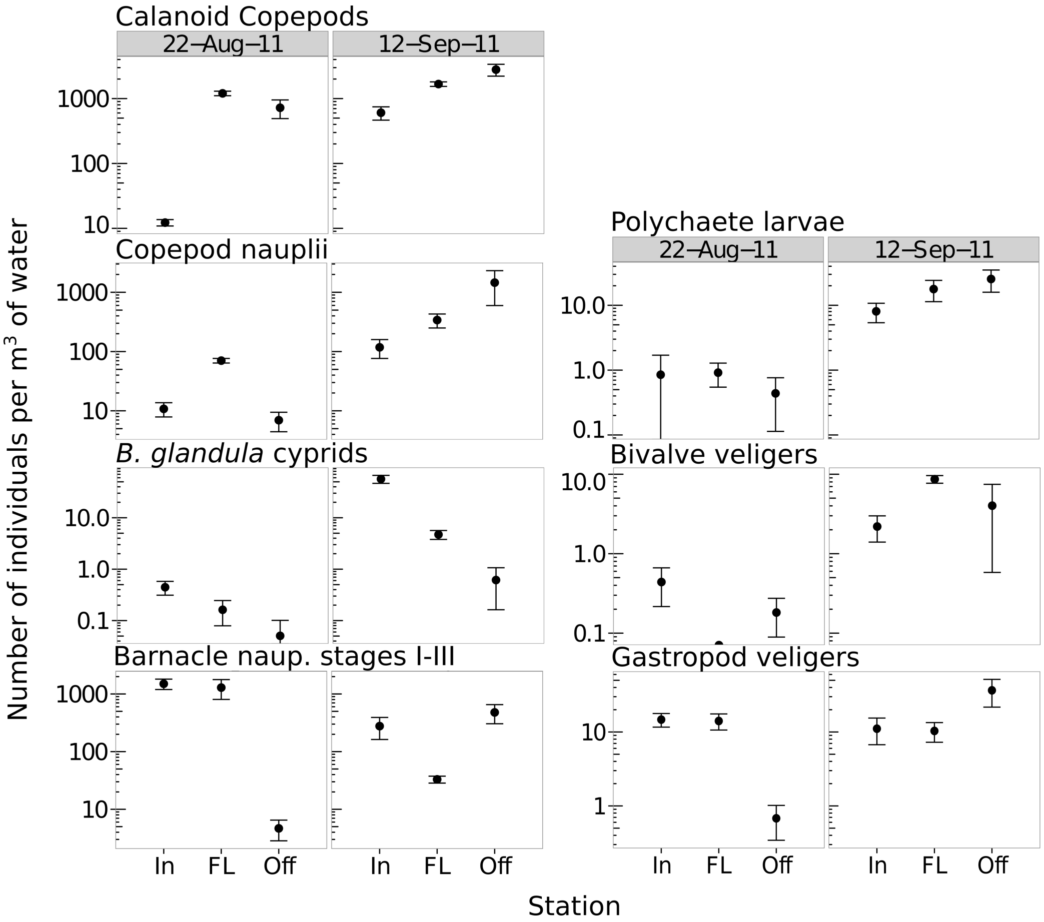

Fig. 3.8. Zooplankton taxa without a significant distribution pattern across the mouth of Sunset Bay when the front was absent. Sunset Bay Concentrations (mean, SE) of zooplankton in neuston plankton tows that sampled the top 30 cm of water taken inshore (In), offshore (Off), and at the mouth of the bay where the foam line forms when present (FL) on two days when the front was absent in 2011. Many taxa did not display a consistent distribution pattern when a front and foam line were absent from the mouth of Sunset Bay. This is in contrast to frontal days in which most of these taxa had significant and consistent distribution patterns with respect to the front.

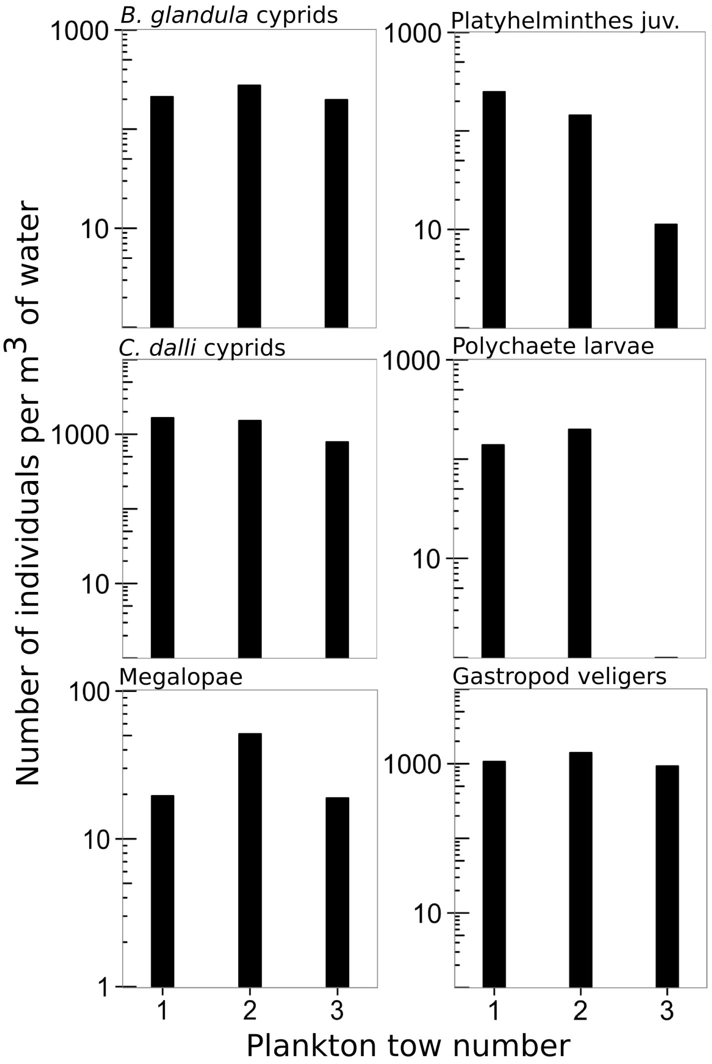

Fig. 3.9. Concentrations of zooplankton in neuston plankton tows that sampled the top 30 cm of water taken in the foam line while it propagated shoreward. On August 10, 2011, the prevailing upwelling winds relaxed while I was sampling. The first plankton tow was completed near the usual front location at the mouth of the bay (1.1 km from shore), but the next two tows were completed successively closer to shore as the foam line propagated shoreward (0.9 km and 0.8 km, respectively). The foam line traveled shoreward at a rate of approximately 7-14 cm/s, moving ~250 meters during the estimated forty-five minutes that it took to take three plankton samples within the moving foam line. Each bar represents concentrations from a single plankton tow. All three plankton tows show very high concentrations of some meroplankton, including the competent cyprids and megalopae, suggesting that these organisms remained in the foam line as it moved shoreward. Polychaete worm larvae and platyhelminthes juveniles did not appear in high numbers in the third (most shoreward) tow, but as these tows could not have replicates we do not know if this change is significant.

before molting into a competent, non-feeding cyprid. Barnacle nauplii, although found in high numbers nearshore, were not concentrated in the surface convergence, whereas cyprids were concentrated by orders of magnitude from waters on either side of the convergence. This change in distribution at the surface convergence between precompetent and competent larval stages could result from either a change in swimming ability or in the swimming behaviors and depth preferences of barnacle larvae as they develop. Although nauplii do appear to be weaker swimmers than the later stage cyprids, gastropod veligers are generally even weaker swimmers and were concentrated in the convergence. Therefore, a difference in swimming ability alone is not sufficient to explain why cyprids, but not nauplii, were concentrated at the convergence. Laboratory behavior studies suggest that barnacles exhibit an ontogenetic change in larval behavior and depth preferences (Knight-Jones & Morgan 1966, Lang et al. 1979), which would likely result in different depth preferences and potentially explain the very different nearshore distributions I found between barnacle nauplii and cyprids.

In addition to having the appropriate behaviors and depth preferences, larvae must have swimming capabilities greater than the vertical velocities at the front for concentration to occur. Downwelling speeds at convergences are difficult (if not impossible) to measure on a scale relevant to a marine invertebrate larva (i.e., < 1 cm from the surface) and Eulerian measurements are generally unable to resolve current velocities within a few meters of boundaries such as the surface. Using an array of Vector Measuring Current Meters (VMCMs) placed at depths ranging from approximately 10-165 m depth beneath convergence zones of Langmuir cells, Weller & Price (1988) measured vertical velocities reaching 20 cm/s or greater at depths of about 20 m below the surface convergence; speeds much faster than invertebrate larval swimming speeds (Chia et al. 1984). Using a plate with an perpendicular, attached measurement stick, Sutcliffe et al (1963) was able to measure near-surface (< 1 m) downwelling speeds by measuring the vertical displacement of the plate below the convergence of Langmuir circulation cells, and found vertical velocities to be generally < 5 cm. Using these same "Sutcliffe floats", Filatove et al. (1981) measured downwelling speeds at depths ranging from 5-70 m below the surface convergences within Langmuir cells in a lake to be 2 – 4 cm/s. Both studies found near-surface velocities to be much lower than the velocities reported by Weller & Price (1988) reported from greater depths. Shanks et al. 2000, using the principles of continuity and conservation of mass, estimated the downwelling speeds below the moving convergence of an upwelling front to be 0.5 mm/s; slower than swimming speeds of most larvae (Chia et al. 1984, Shanks et al. 2000). These limited data suggest that vertical velocities below a convergence decrease as one approaches the surface, and convergences have been found to concentrate very slow swimming zooplankters such as polychaete larvae, gastropod veligers, and even dinoflagellates (Kingsford & Choat 1986, Kiorboe et al. 1988, Ryan et al. 2010). I speculate that downwelling velocities approach zero very close to the surface, which is a condition assumed by models of circulation at frontal convergences (Franks 1992, Epstein & Beardsley 2001), but is difficult to test.

Not only did the foam line at Sunset Bay concentrate some taxa and stages of larvae and other plankton, but, when upwelling-favorable winds relax and the front begins to dissipate, the foam line also appears to maintain high concentrations of many of these taxa and transport them shoreward. In addition to shoreward transport, the foam line (at least when attached) transports Lagrangian particles within the foam line at the surface in the along-front direction, similar to the "larval conduit" surface slicks and foam lines described by Eggleston et al. (1998) that can concentrate and focus the delivery of larvae to nearshore habitats. I did not release drifters around the front as it propagated shoreward on August 10th and thus do not know if the within foam line southward advection seen on days when the foam line was attached continues as the front dissipates and propagates shoreward. Therefore, I do not know if the continued high concentrations of some larvae as the foam line propagated shoreward is the result of the same individuals being maintained within the foam line or if larvae were advected south along the foam line as new larvae are concentrated and added to the north side of the foam line, keeping concentrations high given the appropriate current speeds and plankton swimming capabilities and behaviors.

For a moving convergence to successfully maintain high concentrations of larvae as it travels, larvae must maintain the appropriate upward swimming behaviors, and the propagation speed of the front must be equal or less than the converging velocities. If the propagation speed of the front is greater than the convergence speeds, then larvae with the appropriate behaviors will be concentrated at the front momentarily, and then be left behind as the front travels forward along its trajectory (Shanks et al. 2000). I calculated the inshore and offshore velocities of currents converging on the foam line to be 9.3 and 12.8 cm/s respectively, so given my estimate of the frontal propagation speed as 7-8 cm/s, we would expect the foam line to act as a moving convergence that continues to trap and transport plankton shoreward; our results agree with the conclusions of Shanks et al. 2000 and Franks 1992. I present this conclusion with caution as we were only able to estimate the convergence velocities and propagation velocity of the front on one occasion each, and these velocity measurements were taken on separate days. It is possible that convergence speeds may differ depending on wind speed or other physical variable. I did not quantify convergence speeds on all drifter deployment days, however, personal observations from drifter releases suggest that the converging current speeds were fairly consistent, and drifters were always advected into the foam line from both sides.

Of the zooplankton significantly concentrated in the foam line at Sunset Bay, of particular interest are the barnacle cyprids of *Balanus glandula* and *Cthamalus dalli*, as these species readily settle on experimental plates used to correlate settlement or recruitment with potential cross-shelf transport mechanisms (Pineda 1994, Menge 2000, Connolly et al. 2001, Shanks 2009a, b). If these larvae remain in the foam line as it propagates shoreward, as our data suggests, one should see a settlement spike inshore of such a front when upwelling winds reverse or relax and the foam line dissipates (McChulloch & Shanks 2003). A widely held misconception is that marine invertebrate larvae are swept offshore with the surface Ekman layer during upwelling (Roughgarden et al. 1987, 1992, Alexander & Roughgarden 1996, Farrell et al. 1991, Connolly et al. 2001, Menge et al. 2004). It is often suggested that one should see a spike in settlement during downwelling or relaxation events if larvae are swept offshore by upwelling, thus only settling when the upwelling front relaxes shoreward (Roughgarden et al. 1988, Farrell et al. 1991, Roughgarden et al. 1991, Alexander & Roughgarden 1996, Connolly et al. 2001, Broitman et al. 2005, Broitman et al. 2008). Studies specifically designed to test this hypothesis have found instead that the vast majority of larvae remain well inshore of the upwelling front during both upwelling and downwelling conditions (Morgan et al. 2009, Shanks & Shearman 2009, Fisher et al. 2014), and I too found larvae of many taxa in high numbers landward of 1 km from shore.

While it is highly likely that the vast majority of surviving larvae remain inshore of 3 km in coastal upwelling systems (Morgan et al. 2009, Shanks & Shearman 2009), it is interesting to note that both the upwelling front and the front at Sunset Bay appear to be moving convergences capable of transporting larvae shoreward when upwelling winds cease or reverse (Shanks et al. 2000, this study), and thus a shore-based measure of settlement would be unable to distinguish between the two potential cross-shelf larval delivery mechanisms because both are associated with downwelling events. McCulloch & Shanks (2003) were able to tease apart these two delivery mechanisms by mooring settlement plates on either side of the front at Sunset Bay. They found peaks in barnacle settlement during downwelling only on the plates moored inshore of the front at Sunset Bay, suggesting a very localized delivery event inshore of their seaward plates moored at 1.5 km from shore. If the upwelling front relaxing shoreward was the delivery mechanism for these cyprids, McCulloch & Shanks (2003) would have seen a spike in settlement during downwelling at both stations, which they did not find. My data suggests that the cross-shelf delivery mechanism that resulted in inshore peaks in settlement seen by McCulloch & Shanks (2003) was likely the foam line at Sunset Bay acting as a moving convergence transporting trapped cyprids to shore during a reversal from upwelling favorable winds.

The vast majority of barnacle species in the study area are found at all larval stages deep in the water column during upwelling, completing development inshore of 3 km (Morgan et al. 2009, Shanks & Shearman 2009). Therefore, the majority of their development is within the coastal boundary layer, which is characterized by attenuated current velocities (Nickols et al. 2012). The coastal boundary layer consists of the innermost portion of the continental shelf, including waters from just outside the surf zone to roughly 1-2 km offshore depending on bottom contours, where currents encounter shoreline topography and bathymetry (Nickols et al. 2012). Once in shallow waters, i.e., within the coastal boundary layer, offshore net transport of water during upwelling (Ekman transport) as well as alongshore currents are much reduced, suggesting that larvae that remain within a few km of shore will experience limited dispersal at all water depths (Lentz & Chapman 1989, Largier et al. 1993, Austin & Lentz 2002, Kaplan & Largier 2006, Nickols et al. 2012). This may explain why researchers have reported varying depth preferences for barnacle cyprids in the nearshore. Once within the coastal boundary layer, the vertical distribution of cyprids is unclear, with researchers reporting cyprids near the bottom or below the thermocline (Miron et al. 1995, Morgan et al. 2009, Shanks & Shearman 2009, Tapia et al. 2010), without an obvious depth preference (found throughout the water column; De Wolf 1973, Pineda 1999), and in the neuston (Grosberg 1982, Shanks & Wright 1987, Shanks & Shearman 2009). Internal waves, estuarine plumes, and topographical fronts are common within the coastal boundary layer, and all have surface convergences that can transport drifters and zooplankton shoreward (Zeldis & Jillett 1982, Shanks 1983, Kingsford & Choat 1986, Shanks & Wright 1987, Shanks 1988, Kingsford 1990, Pineda 1994, Grimes & Kingsford 1996, Eggleston et al. 1998). It is possible that cyprids, megalopae, and other late-stage larvae of some species may have evolved to swim upwards once in the coastal boundary layer to take advantage of the prevalence of surface convergences in the nearshore that offer the potential for shoreward transport to reach coastal settlement sites. This hypothesis is supported by the finding that at least one species of cyprid (*Semibalaus balanoides*) swims upwards against downwelling flow up to 7 cm/s in a flume (DiBacco et al. 2011).

Interestingly, new evidence suggests that, if residing in the neuston while in the coastal boundary layer, cyprids of intertidal species must change their vertical distribution yet again to cross the surf zone to their intertidal settlement sites. The surf zone is the last stretch of ocean that must be crossed by the larvae of intertidal species prior to metamorphosing and settling in their adult habitat. Recent research suggests that the surf zone is a semi-permeable barrier to larval transport, with onshore flow modeled only at the very bottom of the water column within the surf zone (Fujimura et al. 2014). If cyprids have evolved to swim upward and maintain a near-surface distribution nearshore in order to take advantage of shoreward transport within surface convergences, they must change their distribution and swim down to cross the surf zone to the intertidal. The limited data available suggest that cyprids can change their vertical distribution under particular physical cues such as a passing internal tidal bore front (Pineda 1999), therefore it is not unlikely that cyprids can respond to turbulence at the surf zone edge and respond accordingly. However, much of this is speculation as the vertical distribution and behaviors of cyprids and other competent larvae have not been measured in any detail and certainly warrant further research.

In this study we discuss the role of foam lines and associated circulation features as a mechanism for accumulating high concentrations of competent larvae, including cyprids, and transporting them shoreward during downwelling or relaxation events.

Foam lines along coasts are common, many of which likely delineate fronts that may concentrate larvae in surface convergences. It is common to think of nearshore waters as a ‘larval pool’, with a well-mixed bath of zooplankton contacting the shore; given an appropriate settlement substrate, the settlement of intertidal or shallow subtidal organisms should vary with the abundance of competent larvae in nearshore waters. If my findings hold true for even a small percentage of the foam lines ubiquitous along rocky shores, however, then larval concentrations are likely quite patchy in the nearshore. Even if a competent larva successfully returns to very nearshore waters, settlement may vary from site to site dependent in part on small-scale hydrographic features such as the convergence described here. It is common in marine ecology to measure settlement of a species of interest at a single site as a proxy for a larger region. I suggest that one consider very nearshore hydrodynamics (<1 km from shore) in selecting field sites with the goal of comparing settlement or recruitment. Due to the small scale of the topographical features that generate foam lines and the convergences they may delineate, there may be large differences in settlement patterns at field sites very close together (even 500 meters apart) if one location has a topographic front and the other does not. In contrast, two sites spaced far apart geographically may have similar settlement patterns if the nearshore hydrodynamics delivering competent larvae to shore are the same.

BRIDGE

In Chapter III, I present data that supports the hypothesis that the foam line at the mouth of Sunset Bay concentrates some taxa and developmental stages of larvae and other zooplankton. Previous research by McCulloch and Shanks (2003) found large peaks in the settlement of intertidal barnacles on plates moored within Sunset Bay only when the front dissipated. My research findings detailed in Chapter III suggest that their result may have been due to high concentrations of cyprids (barnacle larvae competent to settle) present in the foam line as is moves shoreward when the front dissipates. In the following chapter, I present data from a time series of barnacle settlement measured from shore to see if I would find evidence for peaks in settlement associated with downwelling or relaxation events as reported by McCulloch and Shanks (2003) measured on intertidal (rather than moored) settlement plates. Additionally, Chapter IV explores the hypothesis that nearshore hydrodynamic features such as fronts may affect alongshore variations in barnacle settlement.

CHAPTER IV

TIME SERIES OF BARNACLE SETTLEMENT MEASURED EVERY OTHER DAY AT TWO SITES CHARACTERIZED BY DIFFERENT FRONT TYPES

INTRODUCTION

Many coastal marine invertebrates and fish release gametes or larvae into the surrounding seawater that develop for days to months before returning to their nearshore adult habitat. Throughout their development, larvae undergo migrations comparable in size with any on land, interacting with coastal currents and hydrography and exhibiting behaviors that help determine their dispersal trajectories. Although larvae are well equipped with diverse sensory and swimming capabilities that enable them to control their position in the water column, and therefore their trajectories (see Kingsford et al. 2002 for a review), their relative slow swimming speeds (Chia et al. 1984) suggest that most larvae do not recruit by simply swimming ashore. Instead, many larvae have probably evolved appropriate behaviors that enable their transport on currents to carry them shoreward near the end of their larval development (Shanks 1995). Therefore, physical oceanographic mechanisms that deliver competent larvae to their shoreward settlement sites are likely important in determining the abundance and distribution of many costal marine species with planktonic larvae. Settlement measured on shore may be correlated with these currents or other physical mechanisms that deliver larvae to shore.

Intertidal barnacles are often used as model species for questions of settlement and recruitment because the adults are important space occupiers in rocky intertidal habitats, their larvae are often extremely abundant in the plankton, and cyprids readily settle on intertidal experimental plates. Both *Balanus glandula* and *Cthamalus dalli* are highly abundant on the southern Oregon coast, but *B. glandula* tend to make up >98% of settlers on experimental plates at Sunset Bay where this study took place and at nearby Bastendorff Beach (McCulloch 2001, McCulloch & Shanks 2003, Shanks 2009a). *B. glandula* is a small intertidal acorn barnacle found in the high and mid intertidal zone from Baja California to Alaska (Morris et al. 1980). *B. glandula* produces 2-6 broods a year, typically releasing larvae from early spring through summer (Morris et al. 1980, Strathmann 1987). The pelagic larval duration is estimated at 3-6 weeks (Pyefinch 1948, Strathmann et al. 1981, Brown & Roughgarden 1985), and larvae undergo six feeding nauplius stages followed by a non-feeding cyprid stage that is competent to settle. After returning to the intertidal and selecting a suitable substrate, the cyprid settles by undergoing metamorphosis and cementing itself to a rock as a juvenile barnacle.

Barnacle larvae are released in the intertidal and develop over the inner continental shelf, with the vast majority of intertidal species (including *B. glandula and C. dalli*) completing larval development within 3 km of shore (Morgan et al. 2009, Shanks & Shearman 2009). Therefore, most barnacle larvae interact with complex nearshore flow fields throughout much of their pelagic larval duration. Currents in the nearshore collide with the benthic boundary layer and coastal topography to generate complex secondary flow patterns such as eddies and fronts, which are distinct boundaries in the ocean between two different masses of water. One such feature is the front at Sunset Bay, a small cove on the southern Oregon coast. A front stretches across the mouth of the bay whenever winds are upwelling-favorable and waves are small (typically less than about 2 m; Shanks et al. 2003c). A convergence that accumulates foam and detritus marks the surface of this front (see Chapter II). The front and foam line are typically absent during downwelling favorable winds or relaxation events, and the foam line has been seen to propagate shoreward when the front dissipates (Jarvis and Shanks, personal observations; see Chapter III).

In a previous study at this site, McCulloch & Shanks (2003c) measured barnacle settlement every other day for several months on plates moored on either side of the front at Sunset Bay. They found peaks in barnacle settlement during downwelling-favorable winds or relaxation events on the plates moored inshore−but not offshore−of this front, suggesting a very localized delivery event inshore of their seaward plates moored at 1.5 km from shore. The foam line at Sunset Bay is capable of concentrating some taxa and developmental stages of zooplankton, including cyprids of both *B. glandula* and *C. dalli*, orders of magnitude higher than surrounding waters. In addition, the foam line is capable of transporting high concentrations of these cyprids shoreward when upwelling-favorable winds relax (see Chapter III). My data suggests that the cross-shelf delivery mechanism that resulted in inshore peaks in settlement seen by McCulloch & Shanks (2003c) is likely the foam line of the front at Sunset Bay concentrating cyprids and then acting as a moving convergence transporting cyprids to shore during a reversal from upwelling favorable winds.

If the foam line at Sunset Bay does indeed act as a moving convergence that is capable of transporting high concentrations of cyprids to shore, I hypothesized that I would see a settlement spike on intertidal settlement plates when winds relax or reverse, as was seen by McCulloch & Shanks (2003c) on moored plates inside the bay. In this study, my aim was to measure barnacle settlement inshore of the front at Sunset Bay, and compare settlement there with settlement at nearby Shore Acres, an open-coast site that does not have such a front. I hypothesized that I would see a peak in settlement during downwelling or relaxation events at the Sunset Bay site, but not at the Shore Acres site, as the latter is not inshore of the type of wind-driven topographic front present at Sunset Bay.

Shore Acres is inshore of what is likely a boundary mixing front, which occurs when stratified offshore water mix due to waves at a coastal boundary (Shanks et al. 2003c, Appendix B). Boundary mixing fronts are often visible due to a foam line, and sometimes an associated water color change, just outside of the surf zone along rocky shores, benches, sea stacks and small islands (Wolanksi & Hamner 1988, Shanks et al. 2003b). Although data are limited, the boundary mixing front at Shore Acres does not appear to concentrate larvae in the foam line, although it does appear to be a surface convergence capable of concentrating Lagrangian drifters (Appendix B, Friedlander unpublished data). Temperature, salinity, density, and Chl a profiles taken across the front at Shore Acres suggest that water is mixing readily across the front, and most zooplankton taxa and developmental stages do not appear to be blocked (Appendix B, Shanks et al. 2003c). Without a topographical front present at Shore Acres, we expected to see a fortnightly periodicity in settlement, as is often seen in studies that measure daily or every other day settlement of barnacles (Shanks 1983, Shanks 1986, Pineda 1991, Pineda 1994, Shanks 2009b, Shanks et al. 2014).

MATERIALS AND METHODS

Wind, wave height, and SST data were obtained from the Port Orford NOAA data buoy located approximately 80 km southwest of the study site. Wave height data was also obtained from the Umpqua Offshore NOAA data buoy located approximately 50 km northwest of the study site. I used hourly wind data and standard equations (Pedlosky 1987) to calculate a two-day hourly average for alongshore wind stress over each 48-hr sampling period. As a constant drag co-efficient was used, values should be considered pseudo-wind stress as the drag coefficient generally increases with wind speed and sea surface roughness. The primary motivation for calculating alongshore wind stress was to define periods or upwelling- or downwelling-favorable winds, which would not be affected by using pseudo-wind stress. The maximum tidal range, or the maximum range between a high and subsequent low tide, during each 48-hr sampling period was calculated using data from NOAA tide tables. The average wave height and period for each sampling period was calculated using wave data from the Port Orford NOAA buoy.

Observations of barnacle settlement were made from 19 June (Julian day 170) to 12 September (Julian day 225) 2013 (n=28) at two rocky intertidal sites at Sunset Bay (43.3334º N, 124.3718º W) and Shore Acres (43.3237º N, 124.3819º W), separated by roughly 500 m along Cape Arago, Oregon (Fig. 4.1). Settlement collectors were ceramic floor tiles placed at about +1.5 m tidal elevation, where adult barnacles were common at both sites. The tiles were 1 cm thick, unglazed brown tiles (10 x 10 cm), and had a grooved bottom surface. Tiles were ‘seasoned’ by soaking in sea water in a laboratory “sea table” with flow-through seawater for 24 hrs, and then deployed within a few meters of each other (n=3) at each site using Splash Zone™ marine epoxy to glue the tiles to the rock with the grooved side facing upward. Any settlers on the sides of the tile were not counted, however, nearly all cyprids settled within the grooves of the tiles. All settlers on the upward face of the tile were counted in the field using a hand lens with 16x magnification and then scrubbed off with a toothbrush to remove any settlers. Plates were reexamined with the hand lens after scrubbing to make sure all barnacles were removed.

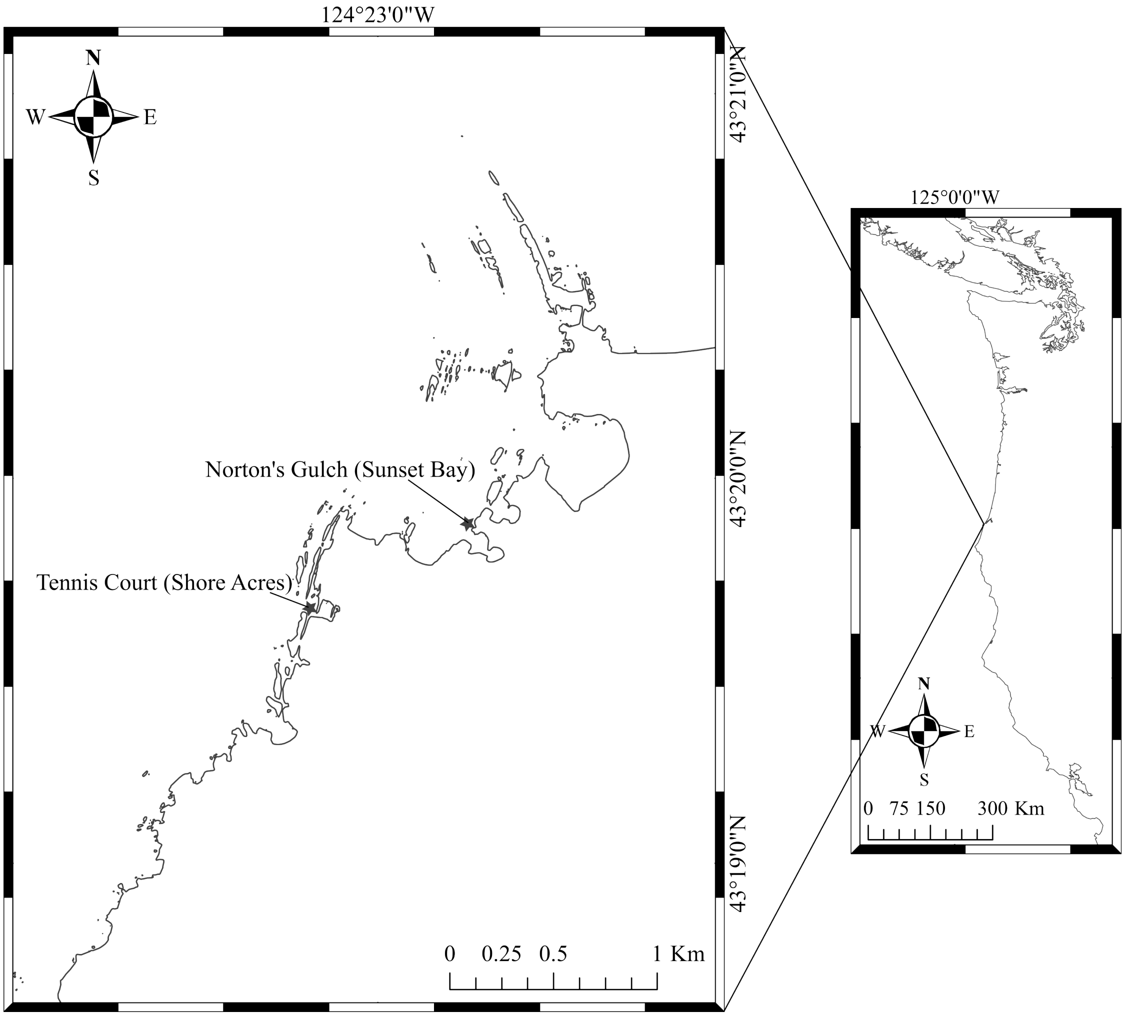

Fig. 4.1. Study sites along Cape Arago on the southern Oregon coast. Barnacle cyprid settlement was measured every other day during the summer of 2013 at two sites as indicated by the black stars.

Time series analysis consisted of a Maximum Entropy Spectral Analysis (MESA) and cross-correlation analysis. MESA fits the data to an autoregressive (AR) stochastic model and uses Fourier analysis of the AR coefficients to find periodicity in the data (Burg 1967). MESA is useful for the analysis of short, noisy, and/or non-stationary time series common in biological data such as settlement time series and is more robust and accurate in defining the period within cyclical time series than autocorrelation and Fourier-transform based techniques (Dowse & Ringo 1989). Cross-correlation analysis was used to for direct comparison of two time series that showed periodicity in the MESA spectra.

Before analysis, time series were de-trended by fitting a line by regression and subtracting it, thus removing the linear trend and the mean (Chatfield 1989, Dowse 2013). No additional preconditioning or filtering (e.g., high- or low- pass filters) was performed on the settlement counts or physical variables prior to spectral analysis. The phase relationship between pairs of time series data was analyzed with a cross-correlation analysis. Plots of cross-correlations held physical variables stationary while lagging the biological settlement time series (1 lag = 48 hrs). Peaks in the cross-correlation analysis that exceed the 95% confidence interval, defined again as $\pm 2/\sqrt{n}$, were considered statistically significant (Chatfield 1989).

RESULTS

The time series of barnacle settlement measured every other day at Sunset Bay and Shore Acres in addition to the time series of the physical variables (maximum daily tidal range, alongshore wind stress, average wave height, and average daily surface seawater temperature [SST]) are plotted over time in Fig. 4.2. During the study, winds were typical of the spring/summer on the Oregon coast, alternating between strong winds from the north or northwest (upwelling favorable) that persisted from several days to weeks and intermittent periods of several days with weaker winds from the south or southeast (relaxation or downwelling favorable). During the sampling period, there were 5 spring and neap tidal series, and 6 upwelling (positive alongshore wind stress) and 3 downwelling (negative wind stress) events.

Warmer SSTs were typically associated with downwelling-favorable winds (negative alongshore wind stress), and cooler SSTs accompanied upwelling-favorable winds (positive alongshore wind stress). This relationship can be seen in the cross-correlation plot between alongshore wind stress and SST; alongshore wind stress was significantly negatively cross-correlated with SST at a lag of 0, −2, and −4 days (Fig. 4.3). The relationship between alongshore wind stress and SST is particularly clear from the start of the study to Julian day 189 where there was a warm event followed by a wind reversal. From Julian days 178−185 winds switched from strongly downwelling-favorable to strongly upwelling-favorable, and SSTs dropped from nearly 15ºC down to around 8ºC. Winds relaxed again on Julian day 199, which was accompanied by a rise in SST from about 8ºC to about 10ºC (Fig. 4.2). In each case, warmer SSTs were associated with wind relaxation or reversal events, as indicated by near zero or negative alongshore wind stress values, respectively. SSTs were not significantly cross-correlated with the maximum daily tidal range or the average wave height.

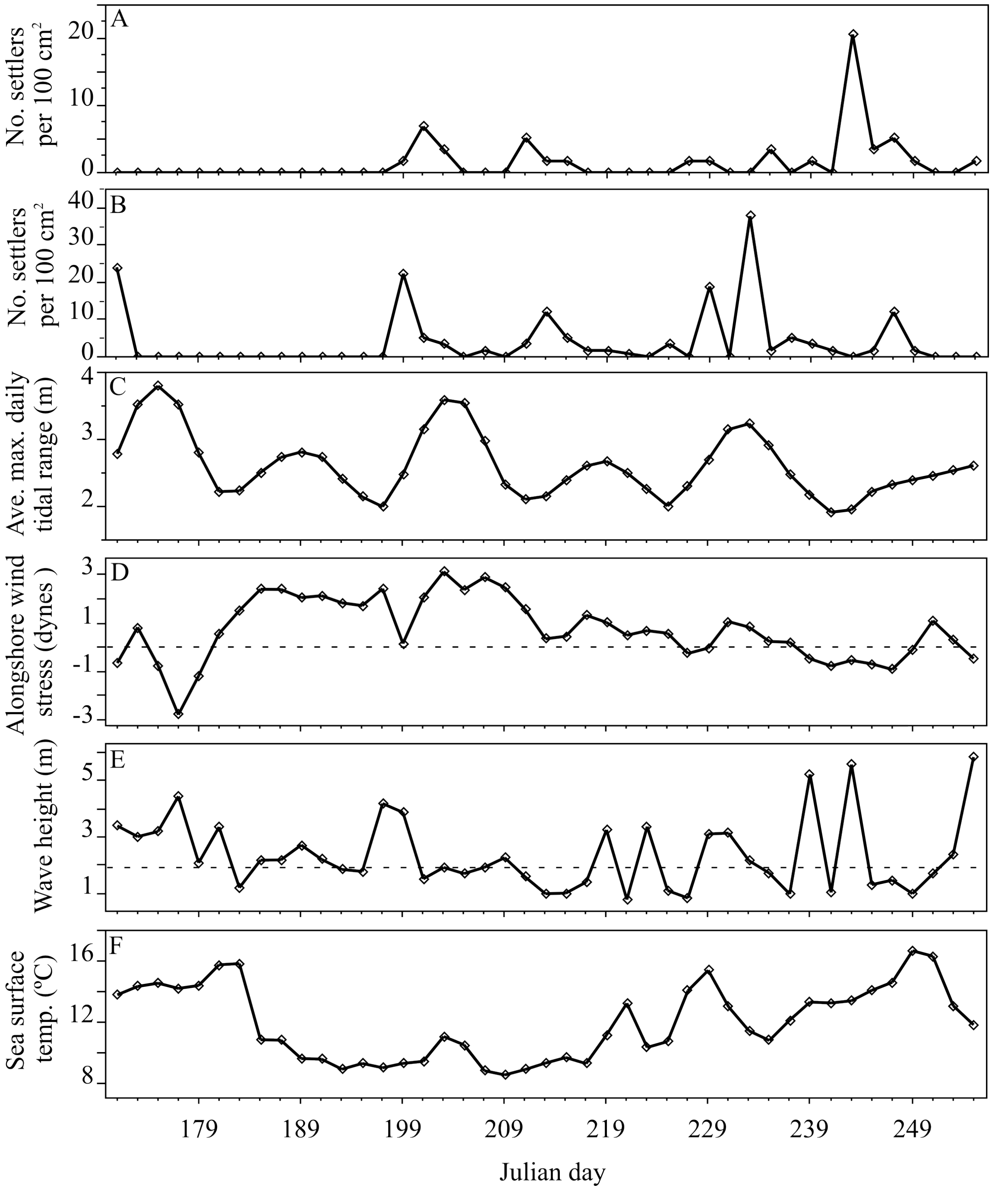

Fig. 4.2. Barnacle settlement measured every other day at Sunset Bay (A) and Shore Acres (B) plotted against Julian day. The average maximum daily tidal range (C), average alongshore wind stress (D), average wave height (E) and the average daily sea surface temperature (F) are plotted against Julian day. Positive and negative wind stress values indicate upwelling- and downwelling-favorable winds, respectively. Dashed line on wind stress plot is at zero dynes: values near or below zero indicate a relaxation or wind reversal event, respectively. Dashed line on wave height plots indicate 1.9 m, which is the value above which personal observations have shown that waves disrupt the front and foam line at Sunset Bay. Data sources detailed in methods section.

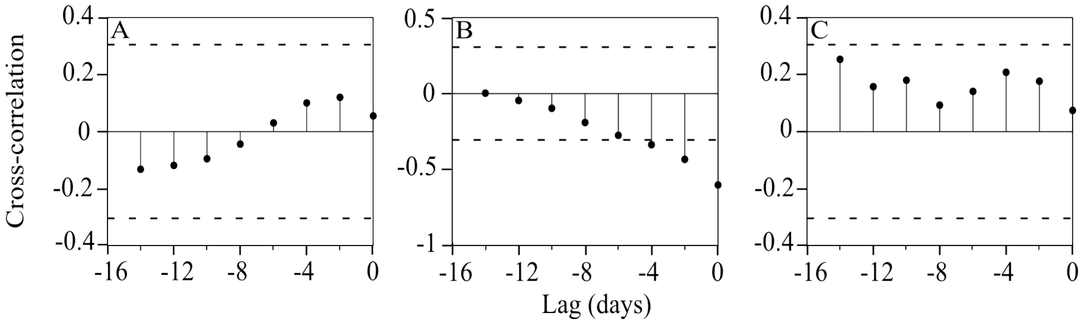

Fig. 4.3. Cross-correlations between average maximum daily tidal range (A), average alongshore wind stress (B), and average wave height (C) with average daily sea surface temperature (SST). Significant cross-correlations were only found between SST and the average alongshore wind stress, at lags of 0, −2, and −4 (B). Y-axis is the r-values for cross-correlations, solid line indicates r = 0, and dashed lines indicate ± 95% confidence interval (± 0.37, defined as ± 2/√n and n=28).

MESA spectral density plots of barnacle settlement and physical time series data are reported in Fig. 4.4. The broader the peak in a MESA spectral density plot, the noisier the data and less clear the exact period of any rhythmicity; the MESA for the maximum daily tidal range shows two sharp peaks with periods of 14.3 and 26.2 days, which gives a relatively high degree of confidence in the period estimate (Fig. 4.4C). The MESA spectrum of the average alongshore wind stress shows a broad dominant peak at a period of around 18.5 days, indicating that the data is noisy, giving a lower degree of confidence in the exact estimate of period length of this peak. The MESA shows a sharp, but smaller, peak at 7.2 days, and additional smaller peaks at periods of 4.6, 5.7, and 10.9 days (Fig. 4.5D). Peaks in the MESA spectrum of the average alongshore wind stress may correspond to synoptic scale atmospheric storms (extratropical cyclones, or ETCs) that typically occur at periods of 2− to 6−day (so-called “weather-band” fluctuations) or to 10− to 100−day intraseasonal oscillations (ISOs) in the atmosphere-ocean system, both of which are important drivers of oceanic primary and secondary production and the cycle of coastal upwelling and downwelling (Lau & Waliser 2005, Bane et al. 2007). The

MESA spectrum for average wave height shows several sharp peaks: the most largest peak is at 14.1 days, followed by one at 4.1 days. Three other smaller, but sharp, peaks are at 5.2, 6.5, and 8.2 days. MESA peaks in average swell height could be related to synoptic storm events as well. The MESA spectrum for sea surface temperature shows a broad peak at around 22.4 days, and a much sharper peak at 10.3 days, with smaller peaks at 7.6, 5.7, and 4.2 days (Fig. 4.4F).

MESA spectral density plots for settlement measured every other day at Sunset Bay and Shore Acres are reported in Fig. 4.4. There is a relatively broad dominant peak in settlement at 14.8 days for Sunset Bay and 15.4 days at Shore Acres, indicating that the data are noisy and that less confidence should be placed in the exact estimation of period. Settlement at Sunset Bay also had MESA peaks at 4.2, 6.9, and 9.1 days while settlement at Shore Acres had additional peaks that are much sharper at 4.3, 5.0, and 6.8 days.

Settlement on all plates was low. At Sunset Bay, many days received zero new settlers, and settlement ranged from 0-15 new settlers per 100cm^2, with the exception of one day that received 41 settlers per 100cm^2. Settlement at Shore Acres was only slightly higher, also with many zeros, but with several peaks in settlement. Settlement at Shore Acres ranged from 0-67 new settlers per 100cm^2. Barnacle settlement measured every other day at both sites was significantly cross-correlated with the average maximum daily tidal range. Settlement at Sunset Bay was significantly negatively cross-correlated with the maximum daily tidal range at a lag of −2 days (1 bi-daily sampling period) (Fig. 4.5A), and settlement at Shore Acres was significantly positively cross-correlated with the maximum daily tidal range at lags of +2 and +4 days (1 and 2 bi-daily sampling periods, respectively) (Fig. 4.5B). Settlement at Sunset Bay was also significantly negatively correlated with average wave height at a lag of −4 days (Fig. 4.5E).

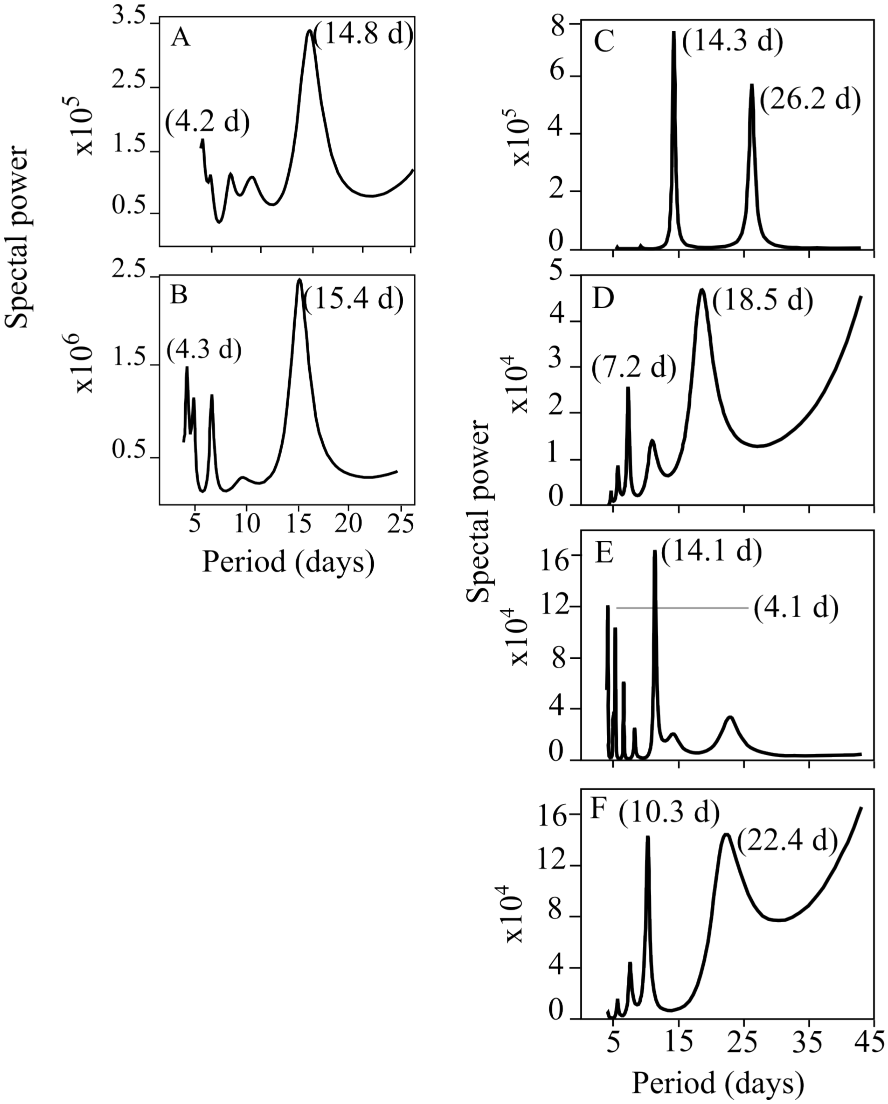

Fig. 4.4. Maximum Entropy Spectral Analysis (MESA) spectral density plots for barnacle settlement measured every other day at Sunset Bay (A) and Shore Acres (B), and the average maximum daily tidal range (C), average alongshore wind stress (D), average wave height (E), and average daily sea surface temperature (F). Period lengths (days) of dominant peaks in the MESA plots are given in parentheses.

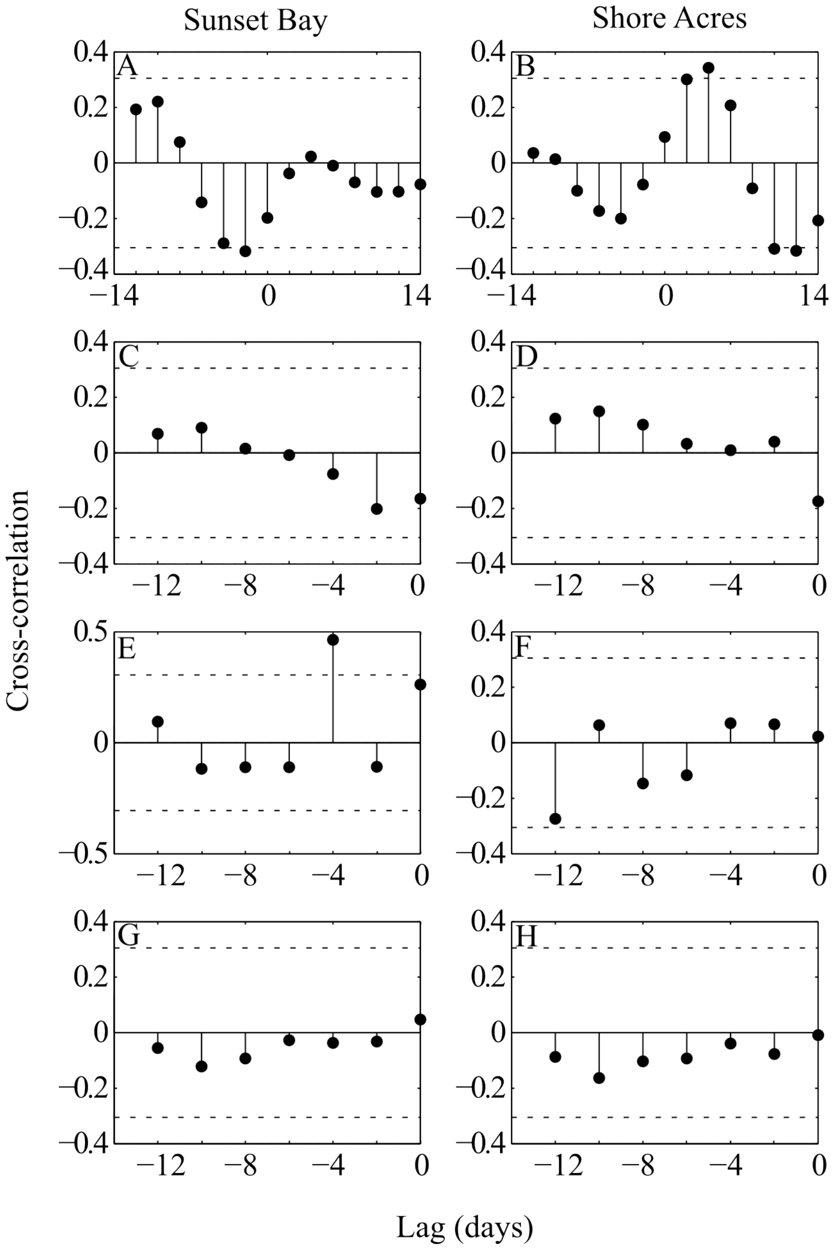

Fig. 4.5. Cross-correlations of average maximum daily tidal range (A, B), average alongshore wind stress (C, D), average wave height (E, F), and average daily sea surface temperature (G, H) with settlement measured every other day at Sunset Bay (left-hand column) and Shore Acres (right-hand column). Settlement at Sunset Bay was significantly negatively cross-correlated with the maximum daily tidal range and average wave height at a lag of −2 (A, E). Settlement at Shore Acres was significantly positively cross-correlated with the maximum daily tidal range at lags of +2 and +4 days (B).

DISCUSSION

The study was relatively short for bi-daily time series, and settlement was low. The MESA spectra supported a fortnightly periodicity in barnacle settlement at both Sunset Bay and Shore Acres, although the MESA peaks in settlement at Sunset Bay were overall quite weak. Settlement at Shore Acres, however, shows clear evidence for a peak near 14 days, which suggests a relationship with the fortnightly spring-neap tidal cycle. The relationship between barnacle settlement and the fortnightly tidal cycle is supported further by the cross-correlation analysis between the two time series. While settlement at Sunset Bay showed weak evidence for periodicity in the MESA spectra and was only significantly cross-correlated with the average maximum daily tidal range at a lag of −2 days, settlement at Shore Acres was significantly cross correlated with average maximum daily tidal range at lags of +2 and +4.

A number of previous studies have found evidence for fortnightly periodicity in barnacle settlement and delivery of cyprids to shore (Shanks 1983, Shanks 1986, Pineda 1991, Shanks 2009b, Shanks et al. 2014). As the tide ebbs and floods across the continental shelf and other sharp changes in bottom topography such as banks, canyons, and reefs, internal waves are generated along the thermocline that propagate shoreward (Haury et al. 1979, Osborne & Burch 1980, Shearman & Lentz 2004). Internal waves can produce surface slicks capable of transporting larvae if the converging speeds at the slick are at least as fast as the speed of the propagating wave (Ewing 1950, Zeldis & Jillett 1982, Shanks 1983). The physical nature of the structure and flow field around a propagating internal wave changes with the amplitude of the surface tides, which vary on a fortnightly spring-neap tidal cycle (Winant 1974, Holloway et al. 1997, Trevorrow

1998). Some of the data in our lab suggests that the conditions that favor landward transport of cyprids might occur around the maximum spring tides, which this study also found (e.g., Shanks 1986, Shanks et al. 2014).

McCulloch and Shanks et al. (2003) measured settlement every other day at moorings inside and offshore of Sunset Bay and found fortnightly periodicity in settlement at the offshore site, but not within the bay. The settlement plates moored within the bay had large peaks in settlement that correlated with wind reversal events from upwelling- to downwelling-favorable winds. Their study, however, did not measure settlement onshore in the intertidal, as done in this study. The peaks in settlement within Sunset Bay seen by McCulloch and Shanks (2003) were hypothesized to be a result of cyprids delivered to shore in the foam line of the front at Sunset Bay acting as a moving convergence when winds relax or reverse. However, when I measured settlement every other day at an intertidal site within Sunset Bay in this study, I did not see peaks in settlement that corresponded with wind reversal or relaxation events. It is possible that settlement was too low during the sampling period to detect a settlement pattern with respect to wind reversals.

Settlement at both sites was low during the entire study; this was particularly true at Sunset Bay where only 36 barnacles settled throughout the entire study. In contrast, I have seen settlement events of hundreds to thousands of barnacles on a single plate in a 24 hr period in previous years at nearby sites using the same ceramic tiles installed at the same tidal height. Settlement at Shore Acres in 2013 was not much better than at Sunset Bay, with 98 barnacles settling throughout the entire study. It may be that, for an unknown reason, 2013 was a poor year for the return of barnacle cyprids at these study sites and thus settlement was too low to pick up a pattern in the data. In addition, the relatively short time series may not have captured enough cycles of whatever mechanism deliver cyprids shoreward at Sunset Bay for the analysis to be able to detect a signal. Visual inspection of the settlement data at Sunset Bay shows one large peak and two smaller peaks in settlement (Fig. 4.2A). The largest peak occurs at Julian day 245 during a period of downwelling favorable winds (negative wind stress values, Fig. 4.2D) and no simultaneous peak was seen at Shore Acres (Fig. 4.2B). Additionally, the two second-largest peaks in settlement at Sunset Bay on Julian days 204 and 212 correspond with wind relaxation events (wind stress values near zero dynes, Fig. 4.2A, D). It is possible that future studies that incorporate longer time series and have higher rates of settlement may see significant peaks of settlement that correspond to downwelling or relaxation winds.

Sunset Bay and Shore Acres, sites less than 2 km apart along Cape Arago, differed in their settlement patterns of barnacle cyprids. Settlement at Shore Acres clearly had a fortnightly periodicity in settlement, likely driven by the fortnightly spring-neap internal wave cycle as seen by others. In contrast, evidence of fortnightly periodicity in settlement was much weaker at Sunset Bay. There are many differences in hydrodynamics between the Sunset Bay and Shore Acres sites that may drive this difference. In addition to having different types of fronts, Sunset Bay is a protected cove, while Shore Acres is a high wave energy open coast site, and thus the sites are completely different with regards to the physics that govern shoreward transport of water and larvae. Many studies cite retention and larval accumulation in the lee of headlands and in bays resulting in higher settlement or recruitment (Lagos et al. 2005, Roughan et al. 2005). In contrast, I found lower levels of settlement inside a bay than at an open coast site. Studies that measured the settlement of crabs and barnacles at both a bay and open coast site simultaneously found a fortnightly periodicity in settlement at the open coast site, but that settlement was driven by multiple factors within the bay (Shanks 1988, Olmi 1995, Miller & Shanks 2004). Therefore, it appears likely that internal waves deliver cyprids and megalopae to shore where they can settle at open coast sites, but that other factors such as winds and coastal fronts may be important for the ingress of these larvae into bays. The data presented here supports the hypothesis that settlement patterns can vary at very nearby sites with different nearshore hydrodynamics. Additional work is needed to test specific hypotheses about which of the numerous differences between the sites at Sunset Bay and Shore Acres contribute to the observed differences in settlement patterns reported here.

BRIDGE

In Chapter IV, I presented data on the settlement of a coastal marine species with a relatively long pelagic larval duration (barnacles, about several weeks) at two sites characterized by different nearshore hydrodynamics. In Chapter V, I explore potential mechanisms that may drive the settlement of the spores of crustose coralline algae, with are thought to settle out of the water column within a day.

CHAPTER V

THE EFFECTS OF NEARSHORE HYDRODYNAMICS ON THE SETTLEMENT OF THE SPORES OF CRUSTOSE CORALLINE ALGAE

INTRODUCTION

A defining goal in population ecology is to elucidate the various mechanisms that affect the abundance and distribution of organisms. The dispersal of young away from their parents and the supply of recruits are of particular importance in structuring marine populations due to the dominance of complex life cycles in the ocean. Many marine organisms reproduce by releasing thousands to millions of propagules such as larvae or spores into the surrounding seawater that are left to develop for hours to months in the plankton before returning to the intertidal or sea floor. Although the discussion of the importance of dispersal in shaping marine populations dates back prior to the now-classic work of Hjort (1926) and Thorson (1946, 1950) and is not new by any means (Young 1987, 1990), so called “supply-side” ecology has seen an incredible burst of activity since the 1980’s (Gaines & Roughgarden 1985, Lewin 1986, Underwood & Keough 2001). Little of this research, however, has focused on the dispersal of algae.

Most seaweeds reproduce with dispersive propagules called spores that are analogous to larvae in many ways. The spores of some taxa have flagella and can swim, and many have sensory capabilities that allow spores to select appropriate settlement substrates and respond to light and other cues (Reed et al. 1992, Callow & Callow 2000, Amsler 2008). Although questions of dispersal, sinking or swimming behavior, and hydrodynamics are important factors that can alter supply and structure populations in all species with planktonic propagules, very few researchers interested in “larval dispersal” consider algae in their work other than a cursory citation or two in an introduction or discussion to a paper. Most of what is known about the ecology and recruitment of algal spores comes from phycologists interested in the organismal biology of a specific species (i.e., Johansen 1981, but see Reed et al. 1988, Gaylord et al. 2002, Opazo & Otaiza 2007). Information on settlement and dispersal of most macroalgae (with several notable exceptions, including the kelp forest-forming species *Macrocystis pyrifera* and the commercially-harvested edible genus *Porphyra*) is remarkably scarce.

For this discussion, it is important to distinguish clearly what I mean by the terms “settlement” and “recruitment”. For an organism with a planktonic larva or spore, settlement can be defined as the transition from a pelagic to benthic habitat via metamorphosis (Scheltema 1974). A “settler”, therefore, is an individual that has just metamorphosed and become attached or associated with the benthos. A “recruit” into a population is defined as a juvenile that has survived any post-settlement mortality events associated with predation, competition, resource limitation, etc. for a defined length of time (commonly a week or month) after settlement. This distinction is essential to make for researchers interested in correlating settlement with potential hydrodynamic mechanisms hypothesized to deliver propagules to shore. Population size can be altered by many factors throughout the life history of an organism, and a measure of recruitment would not be able to test if variability in the number of recruits is due to pre- or post-settlement mechanisms (see Shanks 2009a for a useful discussion of this topic).

Researchers interested in quantifying settlement must be able to identify the organism of interest soon after the spore or larva attaches to the substrate. This can be relatively easy for some marine invertebrates and fishes, but not so for many macroalgal spores because they are commonly morphologically nondescript and therefore difficult to identify for weeks to months after the spore settles, limiting researchers to measures of recruitment. The coralline algae, however, have spores that readily settle on experimental plates and are easily identifiable (at least to the group-level) using the aid of a dissecting microscope within 48 hours after settlement. In this chapter, I hope to convince the reader that the crustose coralline algae as a group make a useful alternative species to work with for questions of settlement. First, I will give a brief overview of the life history and reproduction in this group. Then, I will detail my findings on settlement of coralline algae at two sites on the southern Oregon coast, discuss hypothesized delivery mechanisms, and provide suggestions for methodology improvements and future work.

The coralline algae (Rhodophyta, Corallinaceae) are one of the most abundant marine organisms on rocky substrates within the intertidal and shallow subtidal environments. Coralline algae crusts are found world-wide at a broad range of habitats ranging from the tropics to Antarctica, and from the rocky intertidal to water depths of at least 200 m (Littler et al. 1985, Steneck 1986). Coralline algae are named for their ability to incorporate calcium carbonate from seawater into their cell walls, and they can play an important role in tropical reef building. Coralline algae, along with their associated bacterial communities, play an important ecological role as a settlement cue for a number of marine invertebrate larvae (Huggett et al. 2006, Williams et al. 2008). The coralline algae are typically divided into two groups based on growth morphology: the articulated coralline algae, which are erect and typically leafy and/or branched, and the crustose coralline algae that are non-articulated and grow in low-profile encrusting turfs on hard substrates or as epibionts on animals or other algae. This study focuses on the later group.

Like most macroalgae, the life history of coralline algae is quite complex (see Fig. 5.1). The life cycle typically alternates between three stages: the sporophyte, gametophyte, and carposporophyte. Two of these stages, the sporophyte and the carposporophyte, release spores into the water column. Although the spores are internally different, the spores are very similar in outward appearance, and the crusts that they form (the sporophyte and gametophyte) are isomeric and thus very difficult to distinguish from one another morphologically without dissecting the adult reproductive tissues (Johansen 1981). The diploid sporophyte (Fig. 5.1A) produces haploid tetraspores (each tetraspore is a single unit composed of four spores released together), or occasionally bispores or trispores (Fig. 5.1C). Tetraspores are produced within specialized structures called conceptacles, which are chambers on the surface of the algal crust that open to the surrounding seawater through pores (Fig. 5.1B). Tetraspores grow into male or female gametophytes that produce haploid gametes (Fig. 5.1D) (Johansen 1981, Cole & Sheath 1990). Male spermatia, or non-motile sperm, travel through seawater to the female conceptacle pores (Fig. 5.1E) where gametes combine to create a zygote within the female gametophyte (Johansen 1981, Rosas-Alquicira et al. 2013). The zygote develops into the carposporophyte (diploid), which lives within the female gametophyte as a parasite (F). While within the female gametophyte, the carposporophyte produces diploid carpospores (Fig. 5.1H) within conceptacles (Fig. 5.1G) that are released into the water

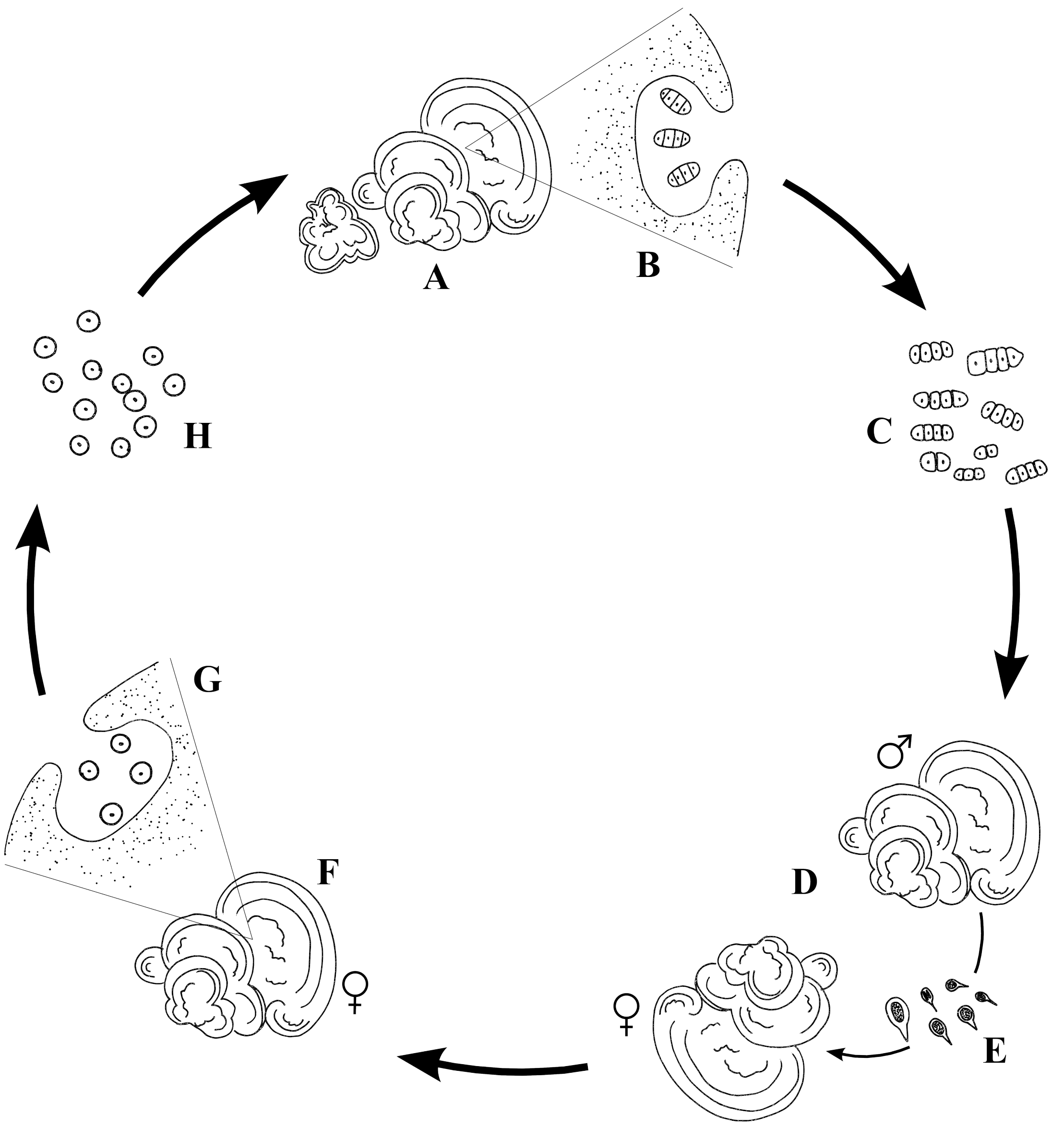

Fig. 5.1 Generalized life cycle of coralline algae. The diploid sporophyte (A) produces haploid tetraspores (C) within specialized pores on the algal crusts called conceptacles (B). Tetraspores grow into male or female gametophytes (D) and produce haploid gametes. Male spermatia, or non-motile sperm, travel through seawater to female (E). Gametes combine to create a zygote within the female gametophyte and the zygote develops into the carposporophyte (diploid), which lives within the female gametophyte as a parasite (F). The carposporophyte produces diploid carpospores within conceptacles (G) that are released into the water column (H). Carpospores settle onto substrate and grow into sporophytes. Although this is considered a typical coralline life cycle, there are many variations on this theme, and reproduction in this group is not well studied. Life cycle information from Johansen 1981, Cole & Sheath 1990, Rosas-Alquicira et al. 2013. Drawings not to scale.

column. Carpospores settle onto substrate and grow into sporophytes (Johansen 1981, Cole & Sheath 1990).

Although the above description is considered a typical coralline life cycle, there are many variations on this theme. It is not well known, however, how often variations take place and exactly which species deviate from this pathway. Additionally, the number of spores (tetraspore, trispore, bispore, etc.) as well as nuclei per spore can very between species, and it is not known for all species. Corallines can undergo asexual reproduction where tetraspores, trispores, or bispores can become sporophytes again rather than becoming gametophytes (Johansen 1981, Cole & Sheath 1990). Coralline algae life histories have not been well studied since the 1980's (see Rosas-Alquicira et al. 2013 and references within) and many questions remain about reproduction in this fascinating group of organisms.

Algal spores vary widely in buoyancy, size, height that spores are released in the water column, and sinking or behavioral characteristics including taxis, kinesis, and swimming abilities, which are all factors that can greatly affect dispersal potential. Crustose coralline algae form low-lying crusts that project often only a few mm from the rocky substrate. As such, their spores are released very close to the sea floor or rocky substrate, and thus within the benthic boundary layer (at least under low current speeds), which may limit their dispersal. It is not known how long coralline algae spores remain viable. However, most macroalgal spores are competent to settle immediately upon release and are thought to attach to substrate within hours to days (Santelices 1990). Johansen (1981) reported that, in the lab, coralline algae spores sank in seawater and became attached to surfaces such as microscope slides, typically germinating in a matter of hours. All of these observations suggest a limited dispersal distance for coralline algae spores, which is supported by Opazo & Otaiza (2007) who found a sharp decline in the number of coralline algae spores in water samples around 900 m from shore. It seems reasonable to assume, therefore, that the majority of spores complete their pelagic duration within nearshore waters, roughly within 1 km of shore. Very view studies, however, have attempted to correlate population ecology of any macroalgae with nearshore hydrodynamics that likely affect the delivery of spores to intertidal and nearshore settlement sites (but see Reed et al. 1988, Gaylord et al. 2002, and Opazo & Otaiza 2007).

Hydrodynamics in the nearshore are notoriously complex, as ocean currents interact with the benthic boundary layer of the sea floor and coastal topography, creating secondary flow features such as eddies as well as the fronts present at Sunset Bay (see Chapter II) and Shore Acres (see Appendix B). Briefly, the front at Sunset Bay occurs at the mouth of a small cove and is present during upwelling-favorable winds and small waves and traps surface waters inshore of the front when present. The front at Shore Acres, a neighboring (<2 km away) open-coast site, is caused by a different mechanism (likely boundary mixing), and results from stratified offshore waters mixing upon contact with the rough boundary (rocky shore) to create a frontal boundary between well-mixed inshore waters and stratified offshore waters. Although data are limited, it appears that the front at Shore Acres does not limit water flow, unlike the wind-generated topographic front at Sunset Bay. I hypothesized that the difference in water flow across these two different front types may result in different patterns in settlement of organisms with pelagic propagules such as larvae or spores.

If a front is present at Sunset Bay when coralline algae spores are released, it is likely that they will complete their pelagic development entirely within a period with a front present at the mouth of Sunset Bay as spores are thought to settle within hours. I hypothesized that I would see higher numbers of coralline algae spores settling on plates inshore of the front at Sunset Bay, but not at Shore Acres, during periods of time when the front at Sunset Bay was stable due to the potential for increased water retention (see Chapter II). Due to the difference in nearshore hydrodynamics at Shore Acres, I hypothesized I would see a different pattern in settlement.

MATERIALS AND METHODS

I used hourly-averaged wind data obtained from the Port Orford NOAA data buoy, located about 80 km SW of the study sites, and standard equations (Pedlosky 1987) to calculate a two-day average for alongshore wind stress over each 48-hr sampling period. As a constant drag co-efficient was used, values should be considered as pseudo-wind stress as the drag coefficient generally increases with wind speed and sea surface roughness. My primary motivation for calculating alongshore wind stress was to define periods or upwelling- or downwelling-favorable wind, however, which would not be affected by using pseudo-wind stress. Using tide information from NOAA tide tables for Charleston, OR, I calculated the maximum tidal range, or the maximum range between a high and subsequent low tide, during each 48-hour sampling period. Using wave data from the NOAA Port Orford weather buoy, I calculated the average wave height for each sampling period. In May and June 2014, I made fourteen observations of wave height estimated from shore at the Sunset Bay and Shore Acres field sites to assess the relationship between nearshore, in situ wave heights at wave height data taken from NOAA buoys. In situ wave height estimates were made from road-side overlooks above settlement sampling sites at both Sunset Bay and Shore Acres within a half our of each other. I used temperature data recorded by in situ Onset Hobo™ temperature loggers that recorded temperature every ten minutes within 1 m of the biological sampling apparatus at each site to calculate the average temperature for the hour around each high tide over each 48-hr sampling period.

Newly-settled coralline algae spores were identified with the aid of a compound microscope with epifluorescence and polarized light capabilities, which provided evidence for photopigment type and cell wall presence and composition. In a preliminary study, newly settled spores on plates were identified in the lab, and then marked using a grease pencil on the back side of the plate and returned to the field to grown until they could be easily identified. No attempt was made to speciate the spores in this study.

Observations of crustose coralline algae settlement were made during eight 48-hr deployments starting on July 9, 20, 22, 24, and Aug 5, 7, 18 and 20, 2013 at two rocky intertidal sites: Camel Humps within Sunset Bay (43.3334º N, 124.3718º W), and at Pack Trail near Shore Acres (43.3237º N, 124.3819º W). Sites were located about 2 km apart along Cape Arago on the southern Oregon coast (Fig. 5.2). Settlement collectors were modified Hester-Dendy multi-plate samplers, and consisted of stacks of four settlement plates with spacers in between each plate (Fig. 5.3). Stacks were mounted with two bolts: one to stabilize the individual plates from spinning when hit with waves, and a longer bolt to install stack into the rocky intertidal. Settlement plates consisted of 0.4 cm thick, clear, 10 x 10 cm acrylic squares that were sanded on one side with 36-grit sand paper.

Stacks were deployed so that the sanded side faced down (towards the rock), and an opaque tile was placed on top so as to shade the settling plates from direct sun as corallines as a group typically do not do well at high light intensity (Johansen 1981). Three stacks were installed within meters of each other at both sites.

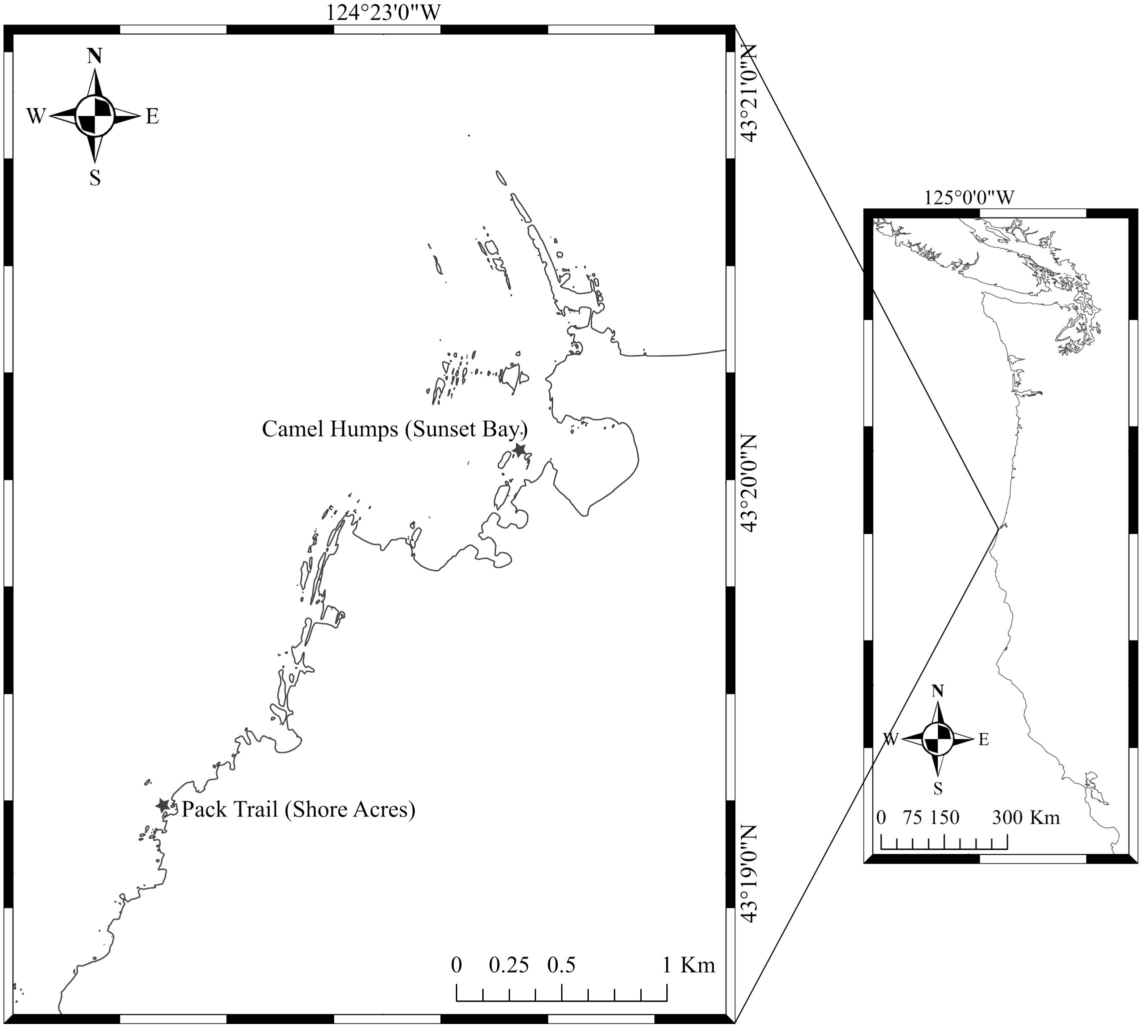

Fig. 5.2. Study sites along Cape Arago on the southern Oregon coast. Coralline algae settlement was measured during eight 48-hr deployment periods during the summer of 2013 at two sites as indicated by the black stars.

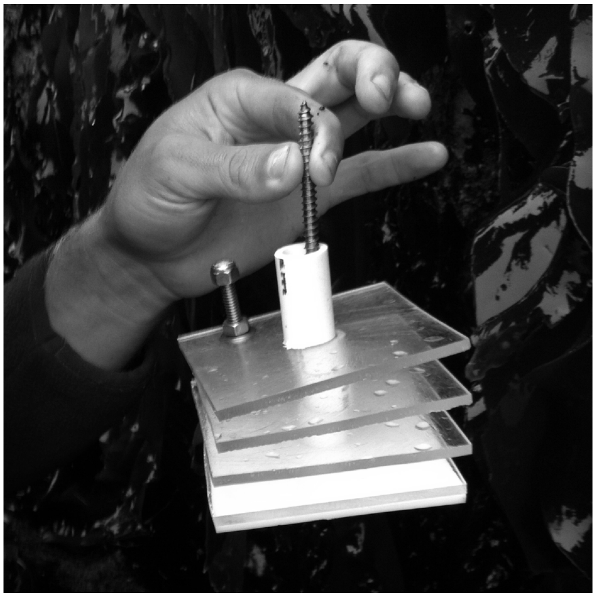

Fig. 5.3. Modified Hester Dendy samplers to collect coralline algae spores. Samplers consisted of stacks of four clear acrylic settlement plates sanded on one side, with PVC spacers between each plate. Stacks were bolted into the rocky intertidal substrate upside-down from the pictured orientation, with the sanded surface of the plates facing the rock. A shorter bolt was used to stabilize individual plates from spinning when hit by waves. An opaque tile was placed on top of stack so as to shade the settlement plates from direct sunlight. Stacks were pre-conditioned for 48 hrs in a flow-through seawater table and then three stacks were deployed within several meters of each other at both sites (Sunset Bay and Shore Acres) at 0 m tidal height where coralline algae crusts were common. Stacks were changed and censused for new settlers after 48 hrs.

Stacks were preconditioned in a flow-through seawater table for 48 hours prior to deployment and then installed in the intertidal at 0 m tidal height where crustose coralline algae crusts were common at both sites. Because the tidal height of the settlement plates was lower than I could access daily, I was unable to take daily time series measurements of settlement. Instead, I made observations of settlement during 48-hr deployment periods when low tides allowed. Each deployment lasted for 48 hours, and then stacks were collected and immediately transferred to the lab in individual buckets of seawater and the settlers counted. If the next 48-hr low tides were < 0 m and allowed access to study sites, new stacks were deployed. When switching out stacks, metal screw anchors remained installed in the rock, allowing stacks to be redeployed at the exact intertidal location for each 48-hr interval. In the lab, all new settlers on each sanded surface of the four settlement plates were counted using a dissecting microscope. The opaque top plates and unsanded sides of plates were not censused. Counts for each plate represent the number of newly settled algae spores/100cm^2 per stack (n=3) at each site.

On the deployment from August 7-9th, settlement spiked on a few of the stacks, causing two high values at Sunset Bay and one high value at Shore Acres that, left untransformed, would be very influential data points in the analysis. To reduce the influence of these few high settlement counts, data were $\log_{10}(x)$ transformed, which also helped data meet assumptions of normality and equal variances. Many of the explanatory variables we measured were highly collinear. We used the variance inflation factor (VIF) to determine which explanatory variables to leave in the model as detailed in Zuur et al. (2010). VIFs were calculated for each explanatory variable, sequentially dropping the covariate with the highest VIF and then recalculating for the remaining explanatory variables until all VIFs were below 3. This is a conservative estimate of collinearity recommended when ecological signals are weak, which is often the case in measurements of settlement. Based on this procedure, I chose to include the percentage of time the front was present at Sunset Bay (% Front), average in situ logger temperature Shore Acres or Sunset Bay (depending on whether we were modeling settlement at Shore Acres or Sunset Bay, TempSA or TempSB), average wave height from Port Orford (Waves), Julian day (Julian), and the average maximum daily tidal range (Tide). Cross-correlations (Pearson correlation coefficients, *r*) among explanatory variables selected using VIFs as detailed above are reported in Table 5.1.

Table 5.1. Cross-correlations (Pearson correlation coefficients, *r*) among selected explanatory variables that were used in model selection to explain settlement ($\log_{10}$) of coralline algae at Sunset Bay and Shore Acres. Variables include the average wave height taken from the NOAA Port Orford data buoys (Waves PO), the in situ temperature taken from data loggers at Sunset Bay and Shore Acres (Temp. SB, Temp. SA, respectively), the percentage of the deployment that had conditions favorable for a front at Sunset Bay (% Front), and the start date of the deployment period (Date). Note that variables Temp. SB and Temp. SA were not used in the same model. All variables used in a model had $r < 0.65$ and variance inflation factors (VIFs) < 2. All explanatory variables were untransformed.

Variable	Date	% Front	Waves PO	Temp. SB	Temp. SA
Date	1.00				
% Front	-0.27	1.00			
Waves PO	0.62	-0.21	1.00		
Temp. SB	-0.29	0.48	0.042	1.00	
Temp. SA	-0.32	0.48	-0.021	0.99	1.00

I modeled settlement measured at Shore Acres and Sunset Bay individually using multiple linear regressions. I selected the best explanatory model using forward stepwise selection using AICc. AICc is the Akaike's Information Criterion, which allows for a model selection criteria that addresses the trade off between goodness of fit of the model with the data and the complexity of the model by penalizing the model for the number of variables included (Burnham & Anderson 2002). Typically the model with the lowest AIC score is selected as the best model to explain the data. AICc is AIC with a correction for small sample sizes.

RESULTS

The time series of select physical variables (average wave height from the Umpqua Offshore and Port Orford NOAA buoys and the average alongshore wind stress) are plotted in Fig. 5.4. During the study, winds were typical of the summer on the Oregon coast, alternating between strong winds form the north or northwest (upwelling favorable) persisting from several days to weeks and intermittent periods of several days of weaker winds from the south or southeast (relaxation or downwelling favorable).

I found that wave heights measured at 1.9 m at the Umpqua buoy were high enough to disrupt the foam line at Sunset Bay. In addition, previous research found that the front and foam line are also not present at Sunset Bay when winds switch from upwelling- to downwelling-favorable. Using this information, I calculated the percent of each deployment with a front present using by the presence of negative (or near-zero) alongshore wind stress and/or waves larger than 1.9 m recorded at the Umpqua buoy to signify front absence. For each 48-hour deployment period, I calculated the percentage of time that the front was likely present given these criteria. The percentage of time with conditions favorable for a front at Sunset Bay ranged from about 30% to 100% of the deployment period. Only one deployment period had conditions favorable for a front for the entire duration, and no deployment period experienced conditions unfavorable for a front for the entire duration.

In May and June 2014, I made fourteen observations of wave height estimated from shore at the Sunset Bay and Shore Acres field sites. Estimated in situ wave heights at Sunset Bay were well correlated with wave height from the Umpqua Offshore NOAA buoy ($R^2=1$, $P<0.0001$, Fig. 5.5E). Using this regression equation and wave height data from the Umpqua buoy, I calculated in situ wave height estimates during the deployment periods at Sunset Bay. Wave height observations made from land at Shore Acres, however, were not well correlated with wave data from the Port Orford (Fig. 5.5D) or Umpqua Offshore (Fig. 5.5F) data buoys, or with in situ estimates of wave height at

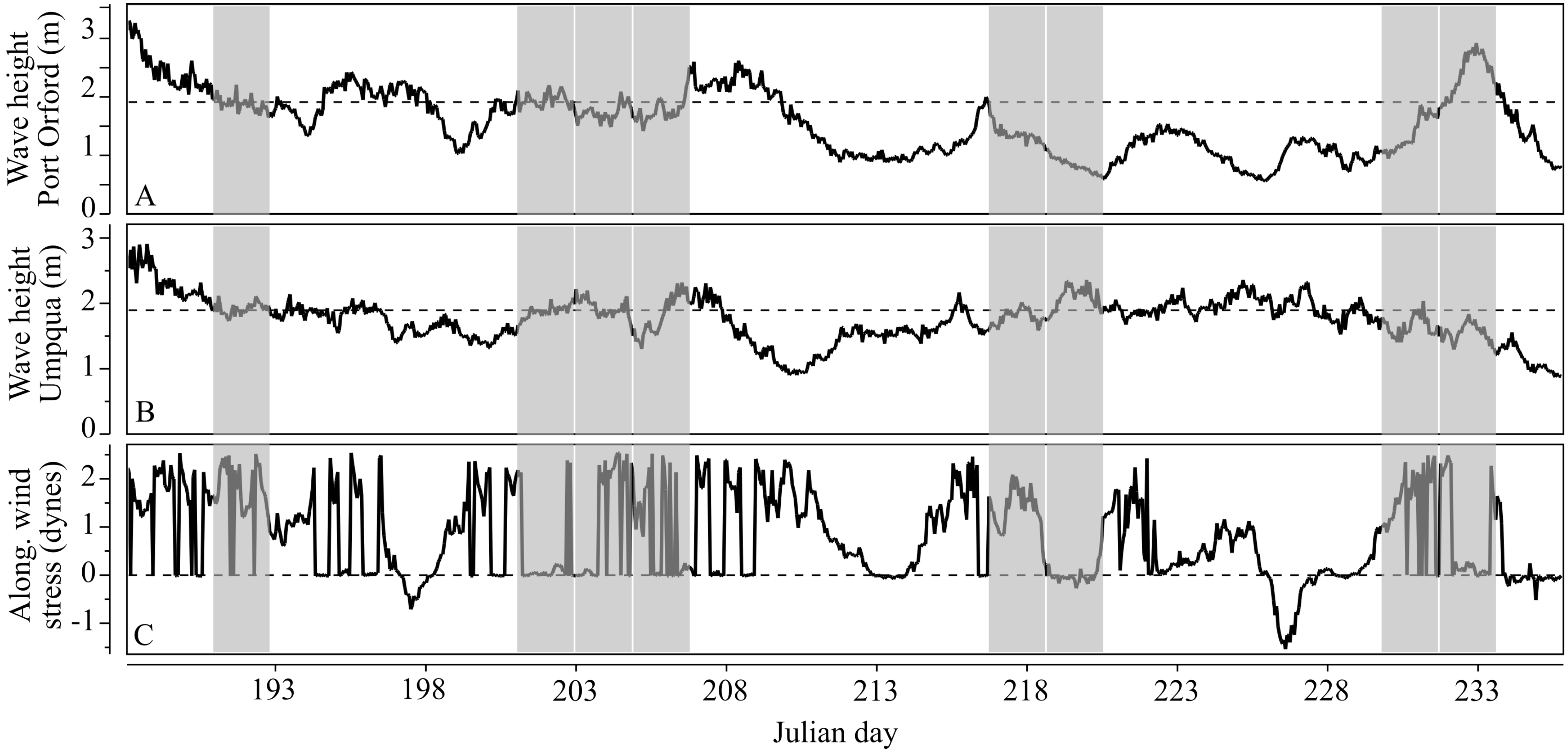

Fig. 5.4. Average wave height (m) measured at both the Port Orford (A) and Umpqua Offshore (B) NOAA buoys and average alongshore wind stress (dynes) measured at the Port Orford buoy (C) plotted against Julian day. Positive wind stress values indicate upwelling favorable winds and negative values indicate downwelling favorable winds. Dashed line on wind stress plot is at zero dynes: values near or below zero indicate a relaxation or wind reversal event, respectively. Dashed line on wave height plots indicate 1.9 m, which is the value above which personal observations show that waves disrupt the front and foam line at Sunset Bay. Previous research has demonstrated that the front and foam line at Sunset Bay is consistently present and complete only during upwelling favorable winds and small waves. From these data, we calculated the percent of time during the 48- hr deployment of the settlement plates that the front was likely present at Sunset Bay. Gray bars indicate times when settlement collectors were in the field with fine white lines indicated individual 48-hr deployment period.

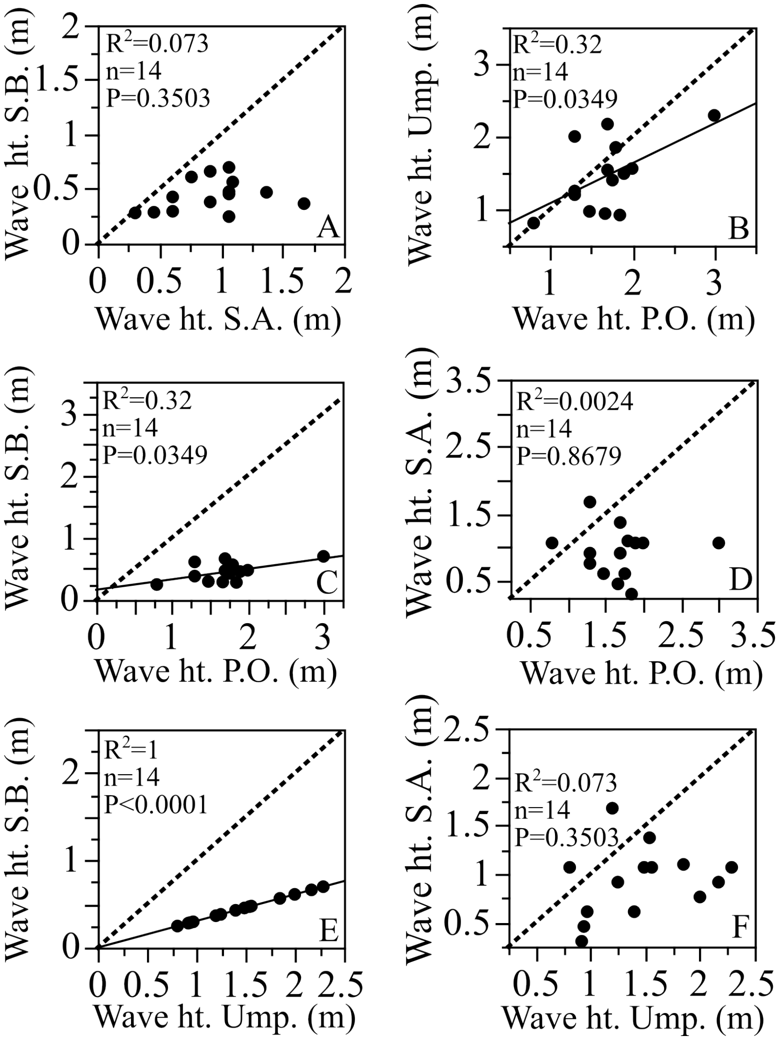

Fig. 5.5. Wave height (ht.) estimates made from land at Sunset Bay (S.B.) are plotted against land-based estimates at Shore Acres (S.A.) (A). Wave height data from the NOAA Umpqua Offshore (Ump.) buoy plotted against the Port Orford (P.O.) buoy (B). Wave height data from the Port Orford buoy are plotted against wave height estimates taken from land at Sunset Bay and Shore Acres (C-D, respectively). Wave height data from the Umpqua buoy are plotted against estimates of wave height made at Sunset Bay and Shore Acres (E-F, respectively). Solid lines and statistical results are from linear correlations between variables. Dotted line represents a one to one relationship between the variables; points that fall above this line indicate larger waves in the Y-axis variable and points that fall below this line indicate larger waves in the X-axis variable.

Sunset Bay (all R^2 values were less than 0.1, and no relationships were significant), and therefore I was unable to calculate estimate in situ wave heights during the deployment periods at Shore Acres.

The average in situ temperatures measured using data loggers at Sunset Bay and Shore Acres are reported in Fig. 5.6. There is no trend between deployment date and temperature at either site. In situ temperatures at both sites are strongly correlated.

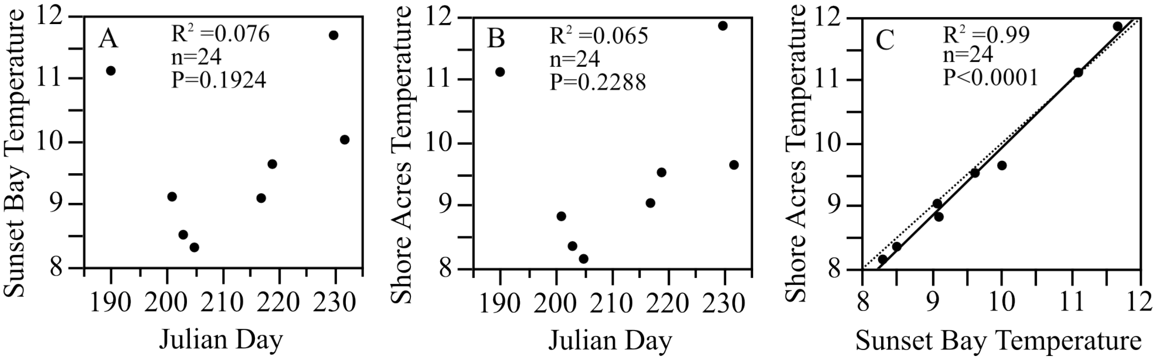

Fig. 5.6. In situ average temperature measured at both Sunset Bay (A) and Shore Acres (B) using temperature loggers (ºC) plotted against Julian day of the start of each deployment. There is not a significant trend of temperature with Julian day at either Sunset Bay (R^2=0.076, n=24, P=0.1924) or Shore Acres (R^2=0.065, n=24, P=0.2288). In situ temperatures measured by loggers were highly correlated at the two sites (C) (R^2=0.99, n=24, P<0.0001). Solid line and statistical results are from linear correlations between variables. Dotted line represents a one to one relationship between the variables; note that average temperature at the two sites is nearly equal.

Spores were easily recognizable 24 hrs after settlement by their pink or pale red color, calcium carbonate enriched cell walls that appear white, and uniquely symmetrical cell division pattern of the young juvenile before significant lateral growth is achieved (see Fig. 5.7). Using an epifluorescence microscope, newly settled spores appeared yellow under a GFPPlus (blue light) filter, and red under green light. This indicates that the juvenile likely contained phycoerythrin, which is found in cyanobacteria and red algae (Oswald et al. 2007, C. Trowbridge and G. Hansen personal communication). In addition, the cell walls of the juveniles appeared to "glow" under polarized light, and the structure seemed brittle and cracked when I tried to remove it from the plate with a razor blade, suggesting that the cell walls were calcified. Coralline algae spores are delicate and uncalcified, but cell walls are impregnated with calcium carbonate within several hours after settlement (Johansen 1981). Cell walls were clearly visible as white lines that separate distinctive pink-red pigment of cells (Fig. 5.7). Spore identification was confirmed with an out-planting study where newly settled spores suspected to be coralline algae were marked and grown in the field until they could be identified. After about a month and a half, sporelings developed into clear coralline algae crusts, displaying the unique lateral and scalloped growth patterns of some members of the group (Fig. 5.7D, E).

Spores (includes tetraspores, bispores, and carpospores) are approximately spherical cells that are dispersed through the water. Once attached to the substrate, the cell is domed and convex in appearance (Fig. 5.7A-C). The first 16 cell divisions in a newly settled coralline algae sporelings are contained within the original spore wall (Fig. 5.7A-C). Cell division follows one of at least seven possible patterns that correspond to taxonomic groupings (Cabioch 1972, Chihara 1974b, Notoya 1976, Johansen 1981, Cabioch 1988). Multiple species often share the same cell division pattern, however, so the taxonomic level to which one can identify a sporelings based on cell division patterns will depend on which species are present locally (Johansen 1981, Cabioch 1988). After sporelings begin to grow in thickness in a few days to a week after settlement, they form marginal meristems (specialized growth centers) and expand over the substrate through lateral growth (Johansen 1981, Fig. 5.7D, E).

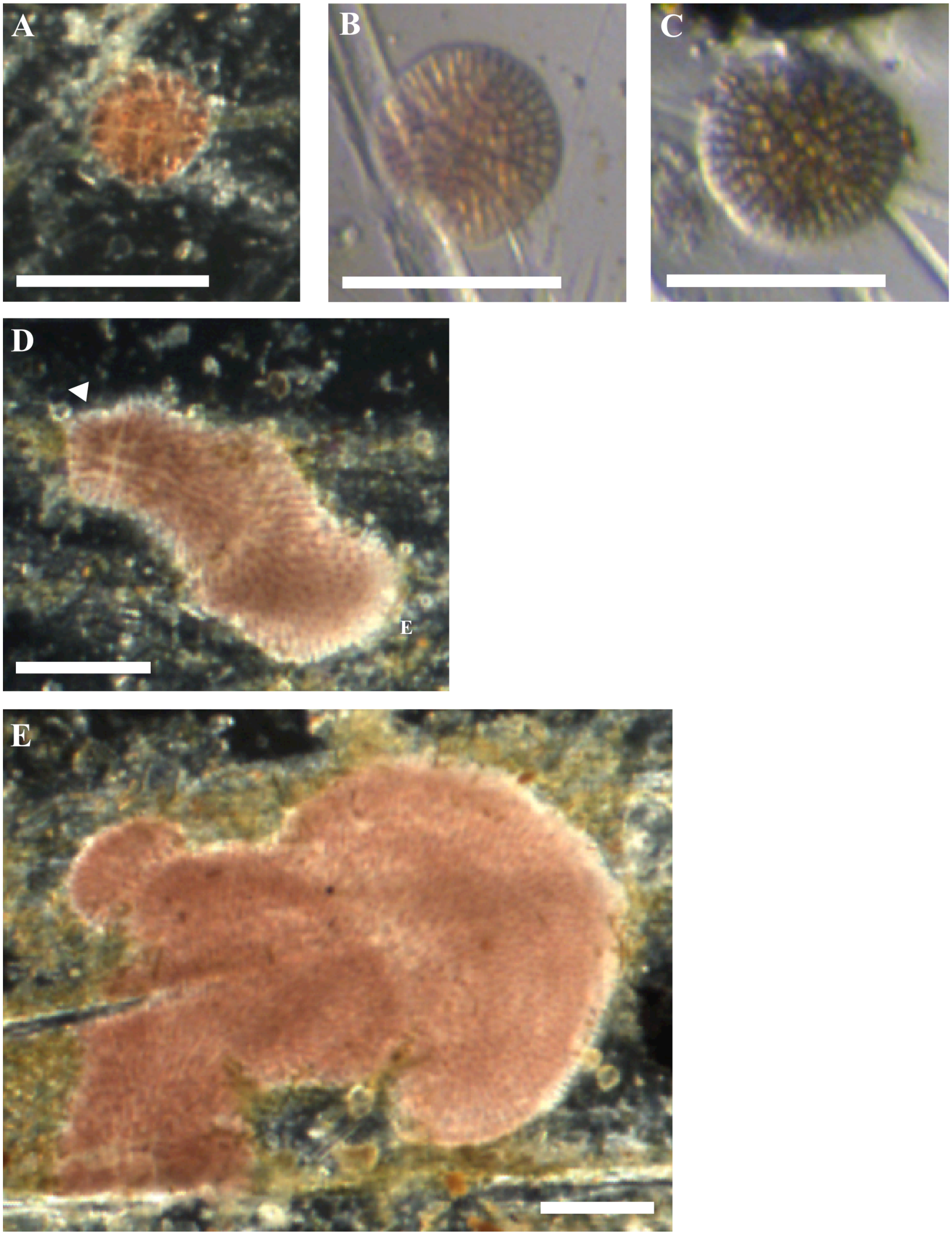

Fig. 5.7. Coralline algae juveniles within 48 hrs of settling (A-C) and growth in the field (D-E). Coralline algae spores are easily recognized after settling due to their pale red/pink color, white calcified cell walls, and unique cell division and growth patterns. The spore undergoes a number of cell divisions within the first few days of settling (variable by species) and then growth typically occurs laterally. The initial spore maintains its convex domed shape and remains visible after lateral growth of the algae begins (D). Scale bar in all images is 100 µm.

Log_{10} settlement of coralline algae at Sunset Bay was not significantly correlated with any physical variable, including the deployment start date (Fig. 5.8A), average wave height measured at the Port Orford (Fig. 5.9A) or Umpqua Offshore (Fig. 5.9C) data buoys or estimated from shore-based observations (Fig. 5.9I), in situ average temperature (Fig. 5.10A), average alongshore wind stress (Fig. 5.9E) or the average maximum daily tidal range (Fig. 5.9G). Models evaluated in the model selection process are reported in Table 5.2. None of the multiple linear regression models I tested were significant to explain the $\log_{10}$ of settlement measured at Sunset Bay except for the full model that included all four variables (in situ temperature, average wave height, the percentage of the deployment period with conditions favorable for a front, and the start date of the deployment). This model was not highly significant ($P=0.0386$), and if I used a Bonferroni correction to adjust for the multiple tests for each model, it was not statistically significant.

Settlement at Shore Acres, in contrast, was significantly negatively correlated with several physical variables, including the average wave height from both the Port Orford ($n=8$, $R^2=0.76$, $P=0.0049$; Fig. 5.9B) and Umpqua Offshore ($n=8$, $R^2=0.65$, $P=0.015$; Fig. 5.9D) data buoys, as well as the average alongshore wind stress ($n=8$, $R^2=0.60$, $P=0.024$; Fig. 5.9F). Models evaluated in the model selection process are reported in Table 5.3. The best model (lowest AICc) to explain $\log_{10}$ settlement at Shore Acres was the average wave height from Port Orford, which explained 76% of the variability (Fig. 5.9B). A selection method using backward selection gave the same results. This model is statistically significant even with a Bonferroni correction to the alpha level for significance to $\alpha = 0.0071$. The "best" models to explain $\log_{10}$ of the settlement of coralline algae measured at both sites are reported in Table 5.4.

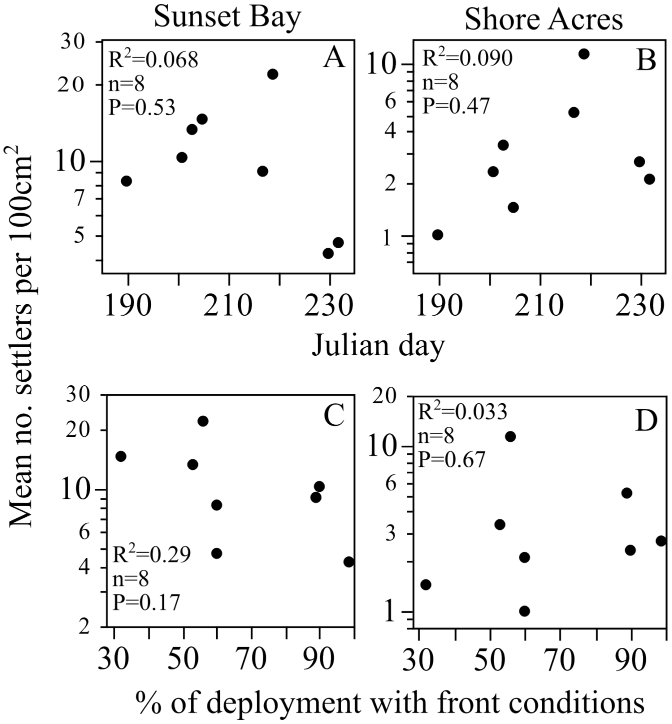

Fig. 5.8. Mean number of coralline algae settlers (per 100 cm^2) for each 48-hr deployment at Sunset Bay (left boxes) and Shore Acres (right boxes) plotted against the start date of each deployment in Julian day (A, B) and the percentage of the deployment time with conditions favorable for a front at Sunset Bay (C, D). There are no trends between settlement at either site and deployment date. Settlement at Sunset Bay has a negative, but not significant, trend with the percent of time with conditions favorable for a front at Sunset Bay, which explains 29% of the variability. As a control, I correlated settlement at Shore Acres with the percentage of time with conditions favorable for a front and there was no trend. Statistical results are from linear correlations between variables.

The front at Sunset Bay was present from 32-100% of the time during the eight deployments. We found no significant relationships between settlement and conditions favorable for a front (Fig. 5.8). Not only was there not higher settlement during the deployment with a front present 100% of the time than when a front was present only 32% of time, but we found a slightly negative trend in settlement measured at Sunset Bay

Table 5.2. Models evaluated to explain ($\log_{10}$) settlement of coralline algae at Sunset Bay using forwards stepwise selection and AICc. AICc is the Akaike's Information Criterion, which allows for a model selection criteria that addresses the trade off between goodness of fit of the model with the data and the complexity of the model by penalizing the model for the number of variables included. Typically the model with the lowest AIC score is selected as the best model to explain the data. AICc is AIC with a correction for small sample sizes. Variables include the average wave height taken from the NOAA Port Orford data buoys (Waves PO), the in situ temperature taken from data loggers at Sunset Bay (Temp. SB), the percentage of the deployment that had conditions favorable for a front at Sunset Bay (% Front), and the start date of the deployment period (Date). Asterisk indicates statistical significance at $\alpha = 0.05$. Model 2 has the lowest AICc. However, model 2 was not statistically significant. The only model that was statistically significant was the model that included all variables and had the highest AICc. A Bonferroni correction for the 10 tests gives an adjusted alpha for significance at $\alpha = 0.0050$: using this adjusted alpha, not even model 10 is significant. Although none of the models do a good job of explaining the data, the best model seems to be Temp. SB, which explains 43% of the variability in settlement of coralline algae at Sunset Bay, but is not statistically significant.

Model No.	Log_{10} settlement at Sunset Bay (*SB*) models	AICc	R^2	Adjusted R^2	P-value
1	*SB* = Waves PO	8.72	0.25	0.12	0.2108
2	*SB* = Temp. SB	6.45	0.43	0.34	0.0761
3	*SB* = % Front	8.20	0.29	0.18	0.1650
4	*SB* = Date	9.06	0.21	0.083	0.2485
5	*SB* = Temp. SB + Waves PO	11.85	0.65	0.51	0.0708
6	*SB* = Temp. SB + Date	14.47	0.52	0.33	0.1609
7	*SB* = Temp. SB + % Front	14.76	0.50	0.30	0.1761
8	*SB* = Temp. SB + Waves PO + % Front	25.73	0.81	0.67	0.0637
9	*SB* = Temp. SB + Waves PO + Date	24.92	0.83	0.70	0.0523
10	*SB* = Temp. SB + Waves PO + % Front + Date	72.96	0.94	0.85	0.0386*

with the percentage of the deployment with conditions favorable for a front (Fig. 5.8C). We also hypothesized that there would be significantly more settlement at Sunset Bay than Shore Acres only on days that a front was present at Sunset Bay. Overall, the average number of settlers per 100 cm^2 was significantly higher at Sunset Bay (n=8, M=9.44, SE=1.02) than at Shore Acres (n=8, M=2.79, SE=1.02); t-test, t(15)=2.99, p=0.0097 (Fig. 5.11). It did not matter what percentage of time the front was present at Sunset Bay for a particular deployment; this pattern held for each deployment period if tested independently. A Bonferroni correction for eight tests sets the significance level at p=0.00625, and all deployment periods yielded a p-value of less than 0.001.

Table 5.3. Models evaluated to explain ($\log_{10}$) settlement of coralline algae at Shore Acres using forwards stepwise selection and AICc. AICc is the Akaike's Information Criterion, which allows for a model selection criteria that addresses the trade off between goodness of fit of the model with the data and the complexity of the model by penalizing the model for the number of variables included. Typically the model with the lowest AIC score is selected as the best model to explain the data. AICc is AIC with a correction for small sample sizes. Variables include the average wave height taken from the NOAA Port Orford data buoys (Waves PO), the in situ temperature taken from data loggers at Shore Acres (Temp. SA), the percentage of the deployment that had conditions favorable for a front at Sunset Bay (% Front), and the start date of the deployment period (Date). Asterisk indicates statistical significance at $\alpha = 0.05$. A Bonferroni correction for the 7 tests gives an adjusted alpha for significance at $\alpha = 0.0071$. The best model (lowest AICc) is Waves PO, which is also significant at the adjusted alpha and explains 75% of the variability in settlement of coralline algae at Shore Acres.

Model No.	$\log_{10}$ settlement at Shore Acres (*SA*) models	AICc	R^2	Adjusted R^2	P-value
1	*SA* = Waves PO	4.39	0.76	0.72	0.0049*
2	*SA* = Temp. SA	15.49	0.022	-0.13	0.6659
3	*SA* = % Front	15.49	0.033	-0.13	0.6658
4	*SA* = Date	14.07	0.19	0.055	0.2799
5	*SA* = Waves PO + Temp. SA	12.26	0.80	0.72	0.0181*
6	*SA* = Waves PO + % Front	13.72	0.76	0.66	0.0286*
7	*SA* = Waves PO + Date	11.30	0.82	0.75	0.0134*

Fig. 5.9 (next page). Mean number of coralline algae settlers (per 100 cm^2) at Sunset Bay (left boxes) and Shore Acres (right boxes) plotted against average wave height from the Port Orford (A, B) and Umpqua Offshore (C, D) NOAA buoys, the average alongshore wind stress (E, F), and the average maximum daily tidal range (G, H). Mean number of coralline algae settlers at Sunset Bay is also plotted against in situ land-based wave height estimates at Sunset Bay (I). There were no significant trends between settlement at Sunset Bay and any of the explanatory variables. Settlement at Shore Acres was significantly negatively correlated with average wave height measured at both buoys as well as the average alongshore wind stress, with the most variability in settlement explained by average wave height from Port Orford (76%). The average maximum daily tidal range did not appear to affect settlement at either site. Solid lines and statistical results are from linear correlations between variables.

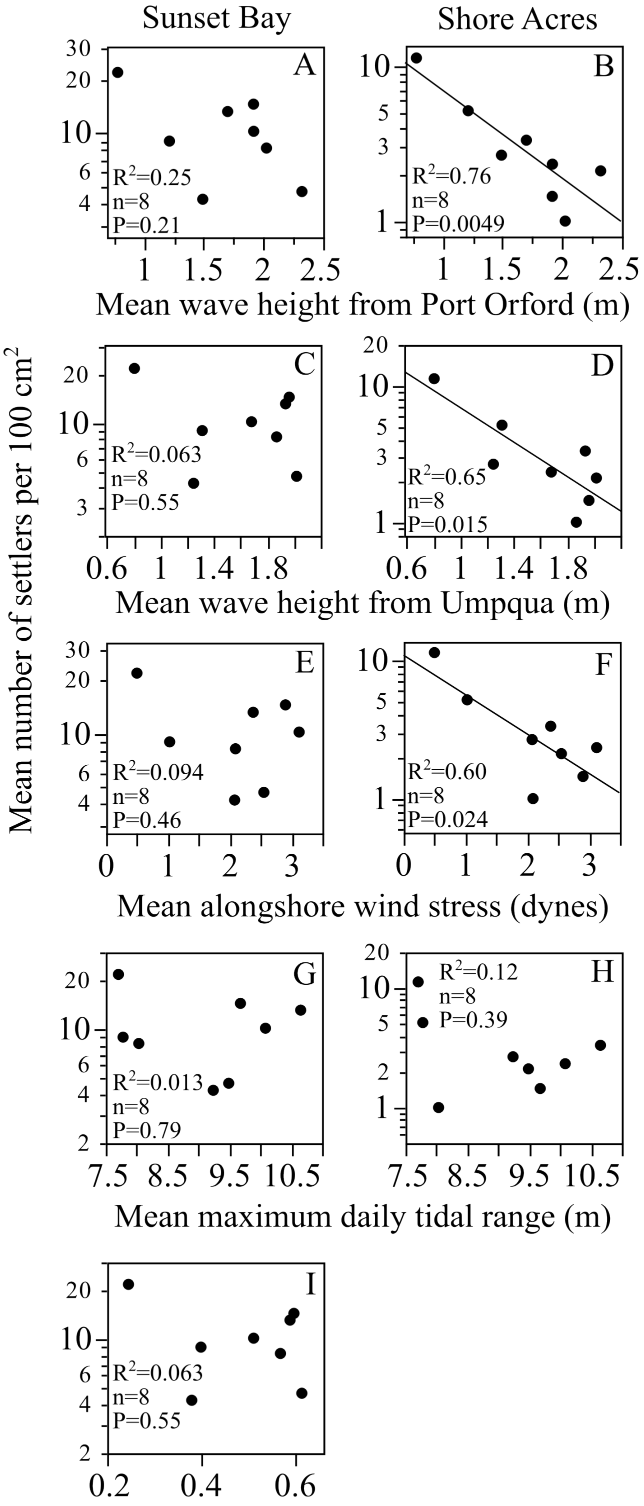
Sunset Bay
Shore Acres
A
R^2=0.25
n=8
P=0.21
B
R^2=0.76
n=8
P=0.0049
Mean wave height from Port Orford (m)
C
R^2=0.063
n=8
P=0.55
D
R^2=0.65
n=8
P=0.015
Mean wave height from Umpqua (m)
E
R^2=0.094
n=8
P=0.46
F
R^2=0.60
n=8
P=0.024
Mean alongshore wind stress (dynes)
G
R^2=0.013
n=8
P=0.79
H
R^2=0.12
n=8
P=0.39
Mean maximum daily tidal range (m)
I
R^2=0.063
n=8
P=0.55
Mean in situ wave ht.
estimate at Sunset Bay (m)
Mean number of settlers per 100 cm^2
1
1.5
2
2.5
0.6
1
1.4
1.8
0
1
2
3
7.5
8.5
9.5
10.5
0.2
0.4
0.6
30
20
10
6
4
2
5
3
1

Table 5.4. Best models of $\log_{10}$ settlement of coralline algae at Sunset Bay and Shore Acres selected using forward selection and AICc. AICc is the Akaike's Information Criterion, which allows for a model selection criteria that addresses the trade off between goodness of fit of the model with the data and the complexity of the model by penalizing the model for the number of variables included. Typically the model with the lowest AIC score is selected as the best model to explain the data. AICc is AIC with a correction for small sample sizes. Variables include the average wave height taken from the NOAA Port Orford data buoys (Waves PO), the in situ temperature taken from data loggers at Sunset Bay and Shore Acres (Temp. SB and Temp. SA, respectively), the percentage of the deployment that had conditions favorable for a front at Sunset Bay (% Front), and the start date of the deployment period (Date). Asterisk indicates statistical significance at $\alpha = 0.05$. Note, however, that the "best" model for settlement at Sunset Bay is not actually significant. No models explained the settlement data at Sunset Bay very well.

Dependent variable	Predictor	Parameter estimate	Model				
			R^2	Adjusted R^2	df	*F*	*P*
Log_{10} settlement at Sunset Bay	Temp. SB	-0.13	0.43	0.34	7	4.58	0.0761
Log_{10} settlement at Shore Acres.	Waves PO	-0.58	0.76	0.72	7	18.86	0.0049*

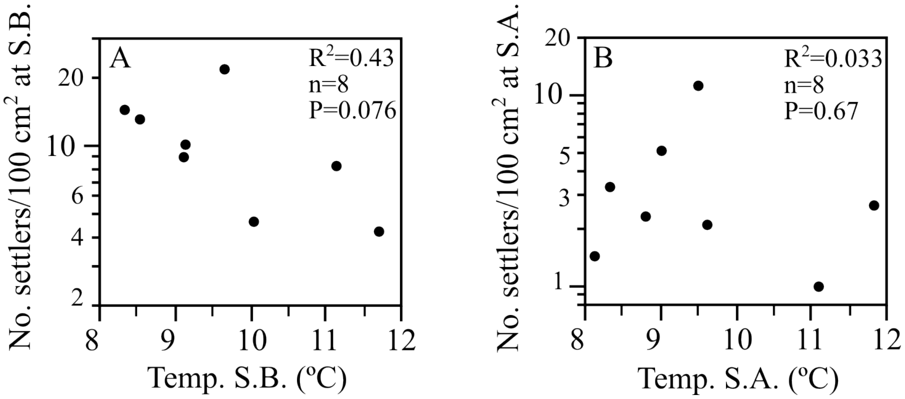

Fig. 5.10. Mean number of coralline algae settlers (per 100 cm^2) at Sunset Bay (A) and Shore Acres (B) plotted against the average in situ temperature taken from data loggers at Sunset Bay and Shore Acres. There were no significant trends between settlement at Sunset Bay and in situ temperature. Statistical results are from linear correlations between variables.

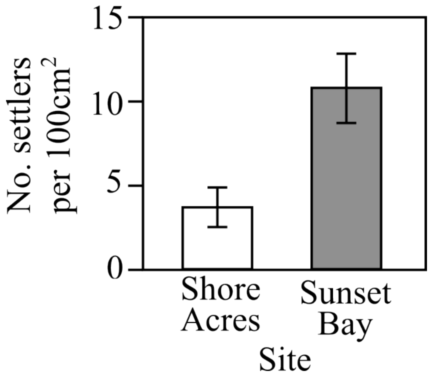

Fig. 5.11. Coralline algae settlers ($\log_{10}$ of the average number per 100 cm^2) at Shore Acres (white bar) and Sunset Bay (gray bar) averaged over all 48-hr deployment periods (n=8). There was significantly higher settlement at Sunset Bay than Shore Acres (t-test, t(15)=2.99, *p*=0.0097). Error bars represent one standard error from the mean.

DISCUSSION

Temperature at Sunset Bay was positively correlated with the percentage of time the front at Sunset Bay was present; this suggests that the temperature within Sunset Bay increases with the presence of the front (supported by data in Chapter II). I hypothesized I would see an increase in coralline algae settlers given the potential for the retention of water, and therefore spores, when a front is present. I found, however, the opposite trend: although not significant, settlement at Sunset Bay had a negative trend with the percent of time a front was present. Furthermore, the lowest settlement at Sunset Bay occurred during the only deployment with conditions favorable for a front throughout the entire 48 hrs. Clearly, the presence of a front at Sunset Bay did not enhance settlement. A dispersal distance of 900 m for coralline algae as a group was estimated by spore counts in water samples collected in a transect perpendicular to shore during calm seas by Opazo & Otaiza (2007). It is possible that the negatively buoyant coralline algae spores remain inshore of the front at Sunset Bay at all times and are not advected offshore when the front is absent.

Settlement of coralline algae at Sunset Bay over the experimental deployments was not well explained by any of the physical variables measured in this study. In contrast, settlement of coralline algae at the Shore Acres site was well explained by the average wave height from Port Orford, which explained 76% of the variability in the data. The largest number of settlers in a deployment occurred in the period with the smallest average wave height (< 1 m at the Port Orford buoy). Settlement measured at Shore Acres was also significantly negatively correlated with the average alongshore wind stress, which was highly collinear with average wave height, likely because strong winds and large waves typically occur together as wind generates waves.

Recent research in our lab has found that the surf zone is a semi-permeable barrier to the exchange of water, phytoplankton, and larvae between the surf zone and waters just offshore that varies predictably with surf zone bathymetry (Shanks et al. 2010, Shanks et al. in review, Morgan et al. in review). Surf zone hydrodynamics result largely from the steepness of the bathymetry that exists as a continuum from relatively flat (dissipative: wide surf zones) to steep (reflective: narrow surf zones). Flow above the boundary layer within the surf zone is offshore, limiting the onshore transport of plankton into the surf zone (Morgan et al. in review). Benthic streaming, or the onshore flow of water near the benthos, occurs on both reflective and dissipative shores during small waves (Longuet-Higgins 1953, Fewings et al. 2008, Lentz et al. 2008, Brown et al. in press). Modeling results suggest that particles such as larvae or spores can cross the surf zone near the bottom of the water column when wave heights are small (Fujimura et al. 2014). Coralline algae spores are negatively buoyant (Johansen 1981): perhaps spores cross the surf zone during small waves, which could potentially explain my finding that the settlement of coralline algae at Shore Acres was significantly negatively correlated with wave height.

In addition to inhibiting the potential benthic streaming cross-surf zone transport mechanism of low density particles (i.e. larvae and spores), large waves could disrupt the settlement of coralline algae in several other ways that would lead to the same negative correlation of settlement with wave height. In a modeling paper, Denny & Shibata (1989) argue that the sinking or swimming speeds of any spore or larva is so small when compared with the turbulent forces within a surf zone that they will have no effect on their distribution within the water column. In other words, large waves increase turbulence within the surf zone to a point where particles such as a negatively buoyant coralline algae spore are no longer functionally negatively buoyant and are continually resuspended in the turbulence. Additionally, it is likely that there is an upper bound on the attachment strength of spores in flow that would decrease the number of spores that attach to the substrate and settle under large waves. In a laboratory flume, spores of *Macrocystis pyrifera* had higher attachment success at currents speeds of 15 cm/s than at higher current speeds of 25 cm/s (unpublished data from Reed and Raimondi, reported in Gaylord et al. 2002).

The hypothesis that coralline algae spores may be more prevalent near the benthos during small waves is also supported by field data collected by Opazo & Otaiza (2007 to investigate the number of coralline algae spores at the surface (0.3 m), mid-water (5 m), and near the sea floor (10 m) during conditions they called “rough seas” and “calm seas”. They did not report the distance from shore that these samples were taken, but as samples were collected by scuba divers within a bay, it seems safe to assume that they were working offshore of the surf zone, but in the nearshore (water depth was only 10m). They indirectly estimated the number of spores at each depth by taking water samples that they then cultured in filtered seawater in the lab for weeks to months until they could identify new algal recruits that had settled out from the water sample. They found that, on calm days, coralline algae recruits were typically more abundant from water samples taken near the sea floor. This result has been found for other red algae spores (Amsler & Searles 1980, Hoffmann & Ugarte 1985, Bobadilla & Santelices 2004), which are typically negatively buoyant and lack many of the neutrally or positively buoyant lipids found in other taxa of macroalgal spores (Reed et al. 1999). On sampling days with larger waves, Opazo & Otaiza (2007) found higher numbers of coralline algae recruits from water samples taken throughout the water column, including the surface, where they had been virtually absent during calm conditions. These data suggest that coralline algae spores are only able to remain near the sea floor during calm conditions, and are resuspended during large waves. This is supported by McNair et al. (1997), whose model found that turbulence can increase the time to hit the bottom within the surf zone for negatively buoyant particles such as coralline algae spores.

An alternate possibility to explain the higher number of spores Opazo & Otaiza (2007) found in water samples taken during large waves is that coralline algae may use the presence of large waves as a cue to release spores into the water column, which could have evolved to increase dispersal potential. Additionally, although many coralline algae are reproductive year round, some species have seasonality in reproduction that could explain the differences in abundances (Chihara 1974a, Johansen 1981).

The Shore Acres site is wave-exposed, and spores may be regularly flushed out of the surf zone and only able to return during small wave events. Sunset Bay, however, typically has much smaller waves, as the bay is shallower and more protected. In situ wave estimates made from land at Sunset Bay were well correlated with the wave data taken from the Umpqua NOAA buoy, so I was able to estimate wave heights inside Sunset Bay during the experimental deployment periods using a linear regression (Fig. 5.5E). I was unable to do this for the Shore Acres site as the in situ estimates of wave height at Shore Acres were not correlated well with wave data from any near-by available data buoy (Fig. 5.5A, D, F). However, in situ land-based estimates of wave height at Shore Acres were consistently much higher than estimates of wave height made within 30 minutes at nearby Sunset Bay (sometimes > 1 m higher). The majority of coralline algae settlement at Shore Acres occurred during the first deployment, when waves measured at the Port Orford data buoy were < 1 m. In 2014 when I made shore-based estimates of wave heights at both Shore Acres and Sunset Bay, almost half of the days had estimated wave heights that exceeded 1 m, whereas the in situ estimates made the same day (within the hour) at Sunset Bay never exceeded 1 m ($n=14$). It is possible that no significant relationship was found between settlement at Sunset Bay and wave height because no deployment periods experienced waves large enough to prevent spores from crossing the surf zone. Less than 3 spores per 100 cm^2 settled on plates at Shore Acres when average wave heights at the Port Orford data buoy were >1.5 m, potentially suggesting that wave heights around 1 m may act as a threshold above which spores are not able to cross the surf zone or settle. Additional deployments that captured a broader range of wave heights could test this hypothesis.

The dispersal of macroalgal spores is influenced by many biological factors such as spore buoyancy, swimming capabilities or behaviors, timing of spore release, the height above the substrate from which spores are released, and the hydrodynamics encountered by the spores such as turbulence, waves, and currents. The data presented here are very limited, as I only have 8 experimental deployments. However, given the limited number of replicates, it is interesting that much of the variability in settlement of coralline algae at the Shore Acres site was explained by wave height alone. Intertidal populations of coralline algae, especially at wave-exposed sites like Shore Acres, may be structured at least in part by wave heights that may act as a barrier to spore delivery to the substrate. In contrast, multiple mechanisms may be important in delivering spores to more protected sites such as Sunset Bay. Future work should measure settlement of coralline algae over a longer period of time and increase the number of replicates to capture higher variability in wave conditions to fully test the hypothesis that settlement of coralline algae decreases larger wave heights, with the greatest settlement occurring at wave heights less than 1 m.

CHAPTER VI

GENERAL CONCLUSIONS

Nearshore hydrodynamics are complex and fascinating. Flow in this region of the ocean encounters coastal topography and the shoaling bottom, creating complex secondary circulation patterns that can have dramatic affects on the distribution of water, nutrients, and plankton. Foam lines are common in the nearshore, and at least some of these foam lines are the surface expression of fronts, or boundaries between different water masses. I found that the front at Sunset Bay, as delineated by a foam line, is a surface convergence capable of concentrating Lagrangian drifters as well as some taxa and developmental stages of zooplankton. In addition, when I observed the front dissipate into the bay when upwelling-favorable winds relaxed, the front carried high concentrations of these zooplankters shoreward with the foam line. It is not clear what the eventual fate of these plankters was. It is possible that competent larvae were transported all the way to shore to settle in pulses that correspond with upwelling relaxation and downwelling events (as seen in McCulloch and Shanks 2003). My data, however, does not support this. Barnacle settlement throughout the study may have been too low to sufficiently test this hypothesis.

Researchers often measure settlement of a species of interest at one site as a proxy for settlement for an entire region (Connolly et al. 2001, Navarrete et al. 2005, Menge et al. 2011). In this study, however, I found that sites that were located very close together geographically (<2 km apart) had different settlement patterns: sites with different nearshore hydrodynamics may differ in larval supply. In comparing the settlement of a species of interest at multiple sites along a latitudinal gradient, it is often assumed that proximity of the sites is what controls the similarity of the settlement patterns (Menge et al. 1997, Connolly et al. 2001, Navarrete et al. 2005). My data, however, suggests that the specific nearshore hydrodynamics of a site may play a larger role in structuring larval supply to shore, and therefore settlement. Sites far apart geographically may have similar settlement patterns if the physical oceanography at the sites is the same. Alternately, as shown in this study, sites close together in space may differ in their settlement patterns if the sites differ in nearshore hydrodynamics.

The data presented here suggests that coralline algae and barnacles are delivered to shore by different mechanisms: barnacles likely by internal waves driven by the spring-neap tidal cycle, and coralline algae by small waves. Patterns of settlement in both taxa were clearly driven by one mechanism at the open coast (Shore Acres) site, but were not well explained by any measured physical variable at the bay (Sunset Bay) site. Studies that have measured the settlement of barnacles and crabs simultaneously at an open coast and bay site have also found evidence for a single delivery mechanism at the open coast site and multiple delivery mechanisms within the bay (Olmi 1995, Shanks 1998, Miller & Shanks 2004). It is possible that multiple mechanisms are responsible for the ingress of larvae and spores into bays, which can make it difficult to tease apart individual delivery mechanisms from a shoreward measurement of settlement.

The coastal ocean is coming under increasing pressure from many uses including wave energy, aquaculture, fishing, and development. Much of our seafood and coastal resources come from this region of the ocean, which is an area of great ecological interest as it encompasses the land-sea interface with its diverse coastal habitats. Many coastal states have implemented various stages of marine reserve initiatives as one strategy for dealing with these pressures. Robust science about the exchange of larvae, spores, nutrients and water between potential marine reserve sites along a coast is essential to make informed and useful management decisions about reserve size, number, and spacing (as reviewed by Gerber et al. 2003). For example, a reserve must be large enough so that larvae spawned within the reserve are retained within the protected area at high enough rates to ensure population persistence within the reserve (Botsford et al. 2001, Kaplan et al. 2006, Kaplan et al. 2009). Alternately, a network of smaller reserves placed close enough together to allow for larval exchange could be used. However, to adequately design a single or network of marine reserves that allows for the population persistence of the communities within a reserve site demands an understanding of flow and larval dispersal within and between reserves. Despite this need, the nearshore remains a relatively new frontier for researchers interested in biological oceanography, larval supply, and population connectivity.

Due to the complexity of flow in the nearshore, the hydrodynamics of the inner shelf have been historically ignored in building the foundational theory of marine reserve design. For example, modeling studies that investigate the potential flow of water and larvae between proposed marine protected area sites have typically assumed a straight coastline (reviewed by White et al. 2010). Recent models that incorporate coastal complexity, however, suggest that topographical features such as headlands and the outcropping at Sunset Bay can increase the persistence of marine invertebrate populations within a reserve (Gaylord & Gaines 2000, White et al. 2010). Clearly, if population persistence of organisms within a protected area is the goal of management efforts, we must incorporate a better understanding of nearshore hydrodynamics into marine reserve design. We are in the beginning stages of research on the nearshore region of the ocean, and have much to learn.

APPENDIX A

ANOVA TABLES FROM CHAPTER III

Table A.1. ANOVA model for Group 1: taxa with higher concentrations in the foam line on days where a front and foam line were present at the mouth of Sunset Bay. No Bonferroni correction has been applied to the values reported. Values that are significant with a Bonferroni correction (P<0.0015 for significance) are shown with an asterisk.

Balanus glandula cyprids – Frontal days					Non-frontal days			
Source	R^2	df	F	P	R^2	df	F	P
Whole model	0.90	5	36.04	<0.0001*	0.83	5	11.44	0.0003*
Day		1	24.64	<0.0001*		1	33.53	<0.0001*
Station		2	76.13	<0.0001*		2	11.023	0.0019
Day x Station		2	1.65	0.2166		2	0.8175	0.4647

Cthamalus dalli cyprids – Frontal days					Non-frontal days			
Source	R^2	df	F	P	R^2	df	F	P
Whole model	0.92	5	46.82	<0.0001*	0.72	5	6.235	0.0045
Day		1	116.8	<0.0001*		1	16.084	0.0017
Station		2	55.79	<0.0001*		2	6.193	0.0142
Day x Station		2	2.87	0.0791		2	1.252	0.2959

Megalopae (total) – Frontal days					Non-frontal days			
Source	R^2	df	F	P	R^2	df	F	P
Whole model	0.89	5	34.58	<0.0001*	0.44	5	1.886	0.1707
Day		1	12.23	0.0021		1	4.543	0.0544
Station		2	75.33	<0.0001*		2	1.393	0.2857
Day x Station		2	5.008	0.0167		2	1.049	0.3803

Zoea (total) – Frontal days					Non-frontal days			
Source	R^2	df	F	P	R^2	df	F	P
Whole model	0.71	5	10.45	<0.0001*	0.71	5	5.77	0.0061
Day		1	0.651	0.4287		1	2.613	0.01320
Station		2	22.58	<0.0001*		2	7.694	0.0071
Day x Station		2	3.21	0.0609		2	5.417	0.0211

Table A.1. (continued)

Polychaete larvae – Frontal days					Non-frontal days			
Source	R^2	df	F	P	R^2	df	F	P
Whole model	0.88	5	31.59	<0.0001*	0.85	5	14.011	<0.0001*
Day		1	2.65	0.1187		1	66.214	<0.0001*
Station		2	75.81	<0.0001*		2	0.976	0.4050
Day x Station		2	1.85	0.1820		2	0.944	0.4160

Platyhelminthes juveniles – Frontal days					Non-frontal days			
Source	R^2	df	F	P	R^2	df	F	P
Whole model	0.94	5	65.08	<0.0001*	0.28	5	0.952	0.4834
Day		1	42.84	<0.0001*		1	0.131	0.7233
Station		2	107.6	<0.0001*		2	1.043	0.3823
Day x Station		2	33.68	<0.0001*		2	1.271	0.3157

Table A.2. ANOVA model for Group 1: taxa with higher concentrations offshore of the front on days where a front and foam line were present at the mouth of Sunset Bay. No Bonferroni correction has been applied to the values reported. Values that are significant with a Bonferroni correction ($P<0.0015$ for significance) are shown with an asterisk.

Calanoid copepods – Frontal days					Non-frontal days			
Source	R^2	df	F	P	R^2	df	F	P
Whole model	0.82	5	18.66	<0.0001*	0.92	5	26.34	<0.0001*
Day		1	9.85	0.0050		1	44.46	<0.0001*
Station		2	38.24	<0.0001*		2	38.62	<0.0001*
Day x Station		2	3.49	0.0493		2	5.00	0.0263

Table A.3. ANOVA model for Group 3: taxa with higher concentrations inshore on days where a front and foam line were present at the mouth of Sunset Bay. No Bonferroni correction has been applied to the values reported. Values that are significant with a Bonferroni correction ($P<0.0015$ for significance) are shown with an asterisk.

Barnacle nauplii stages I-III – Frontal days					Non-frontal days			
Source	R^2	df	F	P	R^2	df	F	P
Whole model	0.67	5	8.39	0.0002*	0.89	5	19.469	<0.0001*
Day		1	0.001	0.9704		1	6.672	0.0240
Station		2	14.88	<0.0001*		2	11.881	0.0014*
Day x Station		2	6.089	0.0082		2	33.456	<0.0001*

Table A.4. ANOVA model for Group 4: taxa with no consistent distribution pattern between days with a front and foam line present at the mouth of Sunset Bay. No Bonferroni correction has been applied to the values reported. Values that are significant with a Bonferroni correction ($P<0.0015$ for significance) are indicated with an asterisk.

Copepod nauplii – Frontal days					Non-frontal days			
Source	R^2	df	F	P	R^2	df	F	P
Whole model	0.49	5	4.065	0.0098	0.75	5	7.088	0.0027
Day		1	13.53	0.0014*		1	19.31	0.0009*
Station		2	1.67	0.2131		2	3.44	0.0659
Day x Station		2	1.73	0.2013		2	4.64	0.0324

Euphausiid nauplii – Frontal days					Non-frontal days			
Source	R^2	df	F	P	R^2	df	F	P
Whole model	0.70	5	9.65	<0.0001*	0.29	5	1.000	0.4582
Day		1	40.72	<0.0001*		1	1.000	0.3370
Station		2	3.29	0.0570		2	1.000	0.3966
Day x Station		2	0.457	0.6392		2	1.000	0.3966

Barnacle nauplii stages IV-VI – Frontal days					Non-frontal days			
Source	R^2	df	F	P	R^2	df	F	P
Whole model	0.57	5	5.67	0.0018	0.74	5	6.878	0.003
Day		1	0.011	0.9165		1	21.112	0.0006*
Station		2	0.919	0.4142		2	2.700	0.1078
Day x Station		2	13.25	0.0002*		2	3.942	0.0483

Bivalve veligers – Frontal days					Non-frontal days			
Source	R^2	df	F	P	R^2	df	F	P
Whole model	0.43	5	3.16	0.0278	0.90	5	7.290	0.0024
Day		1	8.42	0.0085		1	31.25	0.0001*
Station		2	3.61	0.0448		2	0.150	0.8623
Day x Station		2	0.081	0.9221		2	2.450	0.1282

APPENDIX B

WATER COLUMN CHARACTERISTICS AND ZOOPLANKTON DISTRIBUTIONS AT THE BOUNDARY MIXING FRONT AT SHORE ACRES

INTRODUCTION

A front can occur as a result of increased mixing at boundaries, such as the interface between water and shore, especially if the boundary is rugose (e.g., the rocky intertidal; (Wolanksi & Hamner 1988, Shanks et al. 2003a). Rather than a front occurring at the boundary (i.e., the shore), a front can form a few 100s of km from shore, just outside of the surf zone, separating inshore mixed waters from oceanic waters. Inshore of a boundary mixing front, deeper waters are mixed with surface waters to form a mixed water mass of intermediate density at mid depth. Seaward of this front, assuming minimal mixing due to wind or other variables, offshore waters are typically stratified due to solar heating at the surface.

As in other kinds of nearshore fronts, a foam line can delineate the surface of a boundary mixing front. Shanks and coworkers (2003c) characterized the foam line delineated boundary mixing front at Shore Acres, OR, several 100s of meters from Sunset Bay. They completed two CTD transects across the Shore Acres boundary mixing front. In contrast to Sunset Bay, waters landward of the front at Shore Acres were cooler and slightly higher in chlorophyll than waters seaward of the front. The slightly cooler waters landward of the is likely a result of boundary mixing (Shanks et al. 2003a).

According to a review by Wolanksi and Hamner (1988), flow at a boundary mixing front is toward the boundary (the rocky shore) near the bottom and near the surface, while flow of mixed, intermediate waters is away from the boundary in the mid water column. Current direction reverses several times as you move upward through the water as the flow is shoreward at both the bottom and surface but seaward in the middle of the water column, therefore creating vertical shear at the coastal boundary.

However, Shanks and coworkers (2003c) did not find a significant difference in abundance of many larvae across the front using vertical (whole water column) plankton tows.

Given the change in flow direction with depth at a boundary mixing front, the vertical position of larvae in the water column would dramatically affect horizontal or cross-shore distributions of larvae around the front. I attempted to take depth-stratified plankton tows that took discrete plankton samples at each of three depths: within the onshore-flowing surface and bottom waters and within the offshore-flowing mid-water column, as informed by CTD profiles. This data would have been used to test the hypothesis that the depth distribution of larvae at the front would affect their horizontal distribution across the front. This proved, however, logistically challenging at this site. I would recommend that future studies use a plankton pump for depth stratified zooplankton samples. I was unable to obtain fast enough flow with a battery-powered pump to achieve water samples greater than about 1 m^3, however, so I would recommend future studies to find a pumping system that allows greater water flow. Zooplankton taxa that were characteristic of offshore water masses at the wind generated topographical front sites, such as Calanoid copepods, were in relatively high numbers within 200 meters of shore (Shanks et al. 2003a). Perhaps larvae are being mixed across the front, either in surface or deeper waters, but flow around the front has not yet been characterized.

MATERIALS AND METHODS

On May 9, 2013 I sampled along a transect at Shore Acres, an open coast site along Cape Arago on the southern Oregon coast. This site is expected to receive high wave energy, and the bottom does not shoal until close to shore (Fig. B.1). I measured temperature, salinity, density, and relative Chl a levels with a Seabird model 19 CTD equipped with a WetStar™ fluorometer at stations ranging from just seaward of the surf zone (about 100 m from shore) to about 700 m from shore. The transect was perpendicular to shore, and crossed the foam line at Shore Acres, which occurred at 300 m from shore on this date (See Fig. B.1). Contour plots were created using Matlab (Mathworks, R2011a).

Flow at depth was investigated with holey sock type drogues modified for nearshore use. See Chapter II and Fig. 2.4 for a description. Briefly, drogues consisted of a hollow tube of fabric 1 m in length and with holes cut in the fabric to allow water to flow through the drogue. A surface float composed of a waterproof plastic case that housed a handheld GPS unit was attached to the drogue by an adjustable tether so as to deploy the drogue at the desired sampling depth. The increased drag on the drogue compared with the surface float and tether components ensure that the drogue tracks currents at depth rather than at the level of the surface float.

To test the hypothesis that the foam line at Shore Acres was a convergence, I deployed surface drifters several times on May 9. I released four to five drifters ~15 m both seaward and shoreward of the foam line and retrieved them when they drifted near the rocky shore. See Chapter II and Fig. 2.3 for description of the drifters. Briefly, drifters consisted of 30 cm long, 1.5 cm diameter dowels fitted with a small float and weight at opposing ends. The drifters tracked approximately the top 10 cm of water. As the foam line was very close to rocks, deployments were only minutes long, and there was not sufficient time to safely record the time and location of the drifters upon release or retrieval. Therefore, only a visual assessment from the boat of the movement of the drifters was possible.

To test the hypothesis that the foam line concentrated zooplankton, I took plankton tows inshore, within the foam line, and offshore of the foam line. We took neuston plankton tows (2 minutes, n=3) at each station using a 0.5 m diameter, 153 μm mesh plankton net equipped with a flow meter and floats to sample approximately the top 30 cm of water. I used outriggers that held the plankton net out about 2 meters from the side of the boat so as to minimize sampling in waters disturbed by the boat. I would not recommend the use of outriggers for future studies in the nearshore environment as they made the boat difficult to control and steer. Instead, I had much better success in later work using a plankton net attached to the end of a pole that an assistant (I would recommend two additional people) held out in front of the boat while I drove. This kept the net from sampling waters disturbed by the boat, but was easier to control and steer and the net could be easily brought in quickly if I needed to get the boat into deeper waters for safety reasons. This kind of quick maneuvering was much more difficult with the outriggers.

All zooplankton samples were preserved in 5% buffered formalin. Zooplankters were enumerated and identified (Shanks 2001) under a dissecting microscope. Samples were first washed free of formalin on a 125 μm sieve and transferred to a 400 ml beaker. With the aid of a balance, fresh water was added for a final volume of ~200 ml. 10 ml aliquots were taken using a Stempel pipette (Omori & Ikeda 1984) after mechanically homogenizing the sample by haphazard stirring. Subsamples were counted until at least 200 of the target organisms were enumerated, yielding a sample standard deviation of about 10% for common organisms and 20% error for the less abundant organisms (Venrick 1978).

RESULTS AND DISCUSSION

Physical characteristics of the water column

The foam line at Shore Acres delineates the surface of a very nearshore (<400 m from shore) front. Inshore of this front, waters were colder, more dense, more saline, and lower in chlorophyll than waters offshore (Fig. B.1). The physical data supports the hypothesis that this is a boundary mixing front, with waters below the thermocline mixing up with surface waters, creating a well-mixed water column inshore of the front.

The boundary mixing front is caused by mixing by waves. When waves were large, I have observed the foam line to be farther offshore than when waves were small. Future work could characterize the physical characteristics of the water column across the front under different wave conditions to investigate how waves affect the structure of the front. However, it would be very difficult to work this close to shore at this site during large waves.

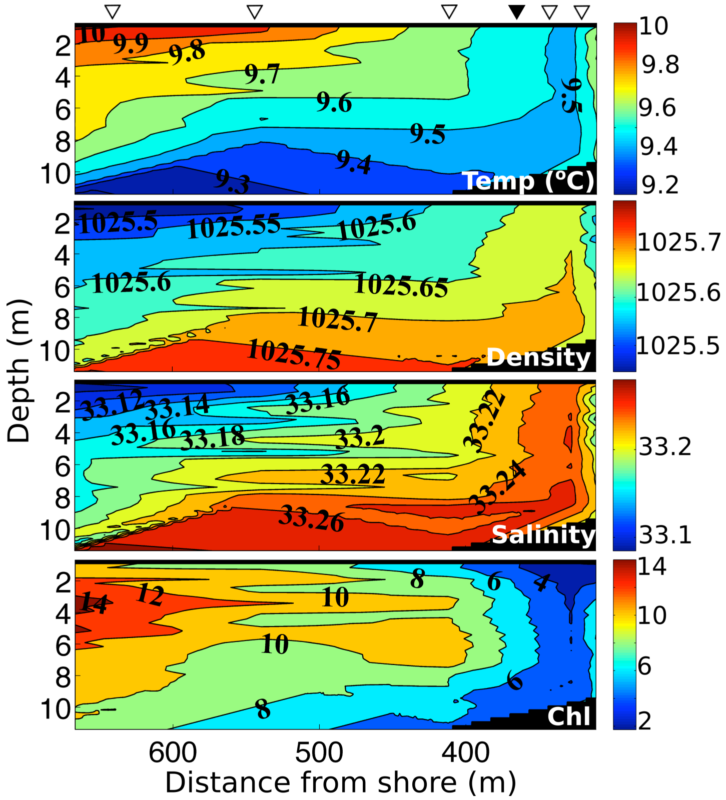

Fig. B.1. Temperature, density, salinity, and chlorophyll a (Chl a) contour plots at Shore Acres (boundary mixing front). CTD casts were taken at the white triangles across the foam line (black triangle) on May 9, 2013. The foam line delineates the surface of a very nearshore (<400 m from shore) front. Inshore of this front, waters are colder, more dense, more saline, and lower in Chl a than waters offshore. The physical data supports the hypothesis that this is a boundary mixing front, with waters below the thermocline mixing up with surface waters, creating a well-mixed water column inshore of the front.

Flow across the boundary mixing front

Some, but not all, of the drifters released on either side of the foam line at Shore Acres were advected into the foam line. Tentatively, the foam line at the boundary mixing front was a convergence, but flow was not as clear as it was at the Sunset Bay convergence. Drifters appeared to travel slower than at the foam line at Sunset Bay, possibly indicating that the convergence speeds at the boundary mixing foam line were lower.

Preliminary work by Friedlander (2014) in our lab has had success measuring surface currents using oranges as disposable surface drifters thrown into the water with a “chuck-it” dog toy throwing stick. Oranges were tracked from triangulated locations on land to determine drifter locations at time intervals. His work suggests that some, but not all, foam lines at Shore Acres are surface convergences that concentrated the oranges. It is not clear what affects the convergence strength of the foam lines. Additional drifter deployments from land under varying conditions would help determine when the boundary mixing foam lines are convergent.

I was only able to successfully deploy two drogues on one day at about 1.5 and 7 meters depth, offshore of the front. The short drogue deployment showed separation of flow offshore of the front on that sampling day (Fig. B.2). Due to the extreme proximity to the rocky shore, I would not recommend drogue deployments inshore of the foam line at the Shore Acres boundary mixing front. There may be separation of flow with depth offshore of the foam line and front at Shore Acres, but more data is needed.

Zooplankton distributions across the front

I tested 20 taxa with a one-way ANOVA with station as a factor. I adjusted my alpha with a Bonferroni correction of 0.05/20 to give an adjusted alpha of 0.0025 as the significance level. Using the adjusted alpha, only four groups showed significant differences in distribution across the front (Fig. B.3). Concentrations for all four groups did not significantly differ between the inshore and foam line station. Nechtochaetes, (late stage polychaete worm larvae with >5 setigers), bivalve veligers, and early Cancer zoea (stages I-III) were found in significantly higher concentrations inshore of the front.

Embryos, in contrast, were found in significantly higher concentrations offshore of the the front.

I recommend that future studies could take plankton tows using the “net on a stick” method I suggest in the methods section at the same time (or at least same day) deployments of oranges in order to determine if the foam line changes in its ability to concentrate drifters and zooplankton under different conditions. I expect the distribution of zooplankton in the very surface waters across the front to vary depending on the strength of the convergence speeds at the foam line.

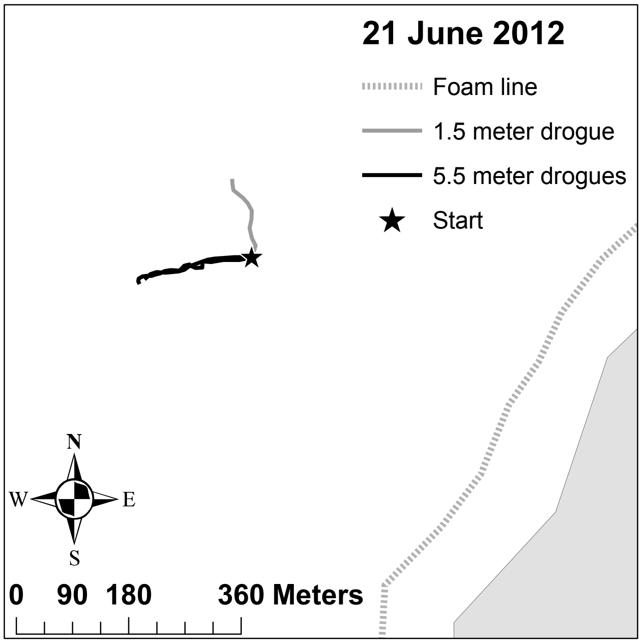

Figure B.2. Separation of flow with depth at Shore Acres, offshore of the boundary mixing front. On 21 June 2012 I released one drogue at 1.5 m and two drogues at 5.5 m depth offshore of the foam line (dashed line) of the boundary mixing front at Shore Acres. Although this was a short deployment (only about 45 min), it shows evidence for separation of flow with depth offshore of the front.

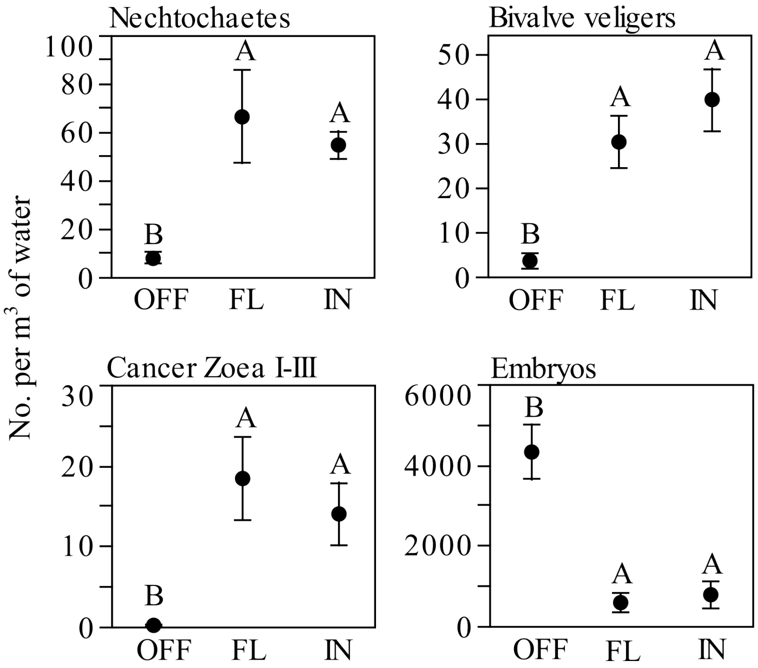

Figure B.3. Surface plankton distributions across the Shore Acres foam line. I sampled the top ~30 cm of water for plankton inshore (IN), offshore (OFF), and in the foam line (FL) that marks the surface of the front at Shore Acres on May 9, 2013. Of the 20 taxa and developmental stages captured in high enough numbers for analysis, only four showed significant differences in concentration across the front. Nechtochaetes (late-stage polychaete larvae), bivalve veligers, and early stage Cancer zoea were all found in significantly higher concentrations inshore of the front. Embryos, in contrast, were found in significantly higher concentrations offshore of the front and foam line. Error bars represent 1 SE from the mean. Means within an individual plot that share a letter are not significantly different from one another.

APPENDIX C

ZOOPLANKTON CONCENTRATIONS WITHIN THE SURF ZONE AND JUST OUTSIDE THE SURF ZONE AT SUNSET BAY AND SHORE ACRES

The following figures show the concentrations (number per m^3 of water) of many taxa of larvae and other zooplankton identified from samples taken within the surf zone and from waters just outside of the surf zone (roughly 200-300 m offshore). Samples were collected simultaneously using two teams: one sampling surf zone waters from shore using a plankton pump, and one sampling offshore waters with a plankton net deployed from a small boat. The pump was powered using a car battery. Water was filtered through a small net, which tended to clog easily with phytoplankton, causing flow to be very slow. We estimated flow of the pump by timing how long it took to fill a 5 gallon bucket three times and using the average. As flow changed with the battery life (the longer we ran the pump, the lower the flow), we re-estimated flow between each replicate to give the most accurate estimate of volume of water sampled possible for each replicate. Flow was disappointingly low with this system (replicates sampled from 0.3–1.6 m^3 of water), and I would recommend a hand-crank (battery-free) pump for future studies.

Offshore plankton samples were taken as close as possible to the surf zone, which ranged from about 200-300 m from shore. The plankton net was mounted with a flow meter, and a small weight on the cod end allowed us to lower the plankton net directly to the bottom. The net sampled from bottom to surface in a vertical tow. This was repeated until at least 5 m^3 of water was sampled.

The following data is from three sampling days: July 17, 24, and 30, 2013. Samples from July 17 and 24 were taken at Shore Acres, near the Tennis Courts cove. Samples from July 30 were taken at Sunset Bay from the outer portion of Norton's Gulch (see Fig. 4.1 in Chapter IV for map of study sites). On July 17, we took three replicate plankton samples at both the surf zone and offshore sites. The three surf zone samples sampled about 0.3, 0.3, and 0.4 m^3 of water and the outside the surf zone samples filtered 7.2, 10.7, and 11.9 m^3 of water. On July 24, only one surf zone sample (1.6 m^3) and two offshore samples (12.8 and 4.4 m^3) were taken. On July 30, seven surf zone samples were taken. The first filtered 1.1 m^3 of water, and then the second filtered 0.6 m^3 of water. The bucket was then lost and no more flow estimates were possible. As the pump outflow visually looked similar to flow during the second replicate's sampling, the flow estimate of 0.6 m^3 of water was used for the remaining surf zone samples. Three replicate plankton samples outside the surf zone were taken, filtering 5.7, 4.0, and 4.9 m^3 of water.

Due to sampling difficulties in the surf zone, these zooplankton samples were the product of very little flow through the net. It is possible, therefore, than some of the low abundances of particular taxa we found were due to our very small volume of water sampled in the surf zone. Work in our lab suggests that zooplankton concentration in surf zones on steep shores (i.e., rocky benches such as my sampling location) can be very low in zooplankton. My data corroborates this finding. The finding of high concentrations of some taxa within the surf zone should be interpreted with caution as it is possible that the plankton pump sampled a small patch of high concentrations of a taxon that is not representative of the whole surf zone. However, it is interesting to note that we found such high concentrations of a few taxa despite the very small amount of water filtered. Of particular interest is the finding of high numbers of cyprids within the surf zone, especially on July 17. Interestingly, there was a peak in barnacle settlement at both the Norton's Gulch and Tennis Court sites July 18-20 that possibly corresponds to the increase in surf zone concentrations of cyprids seen on July 17 (Fig. 4.2, Chapter IV).

I only sampled two days at Shore Acres one day at Sunset Bay. Some taxa showed patterns of distributions that remained constant on all three days and at both sites. However, others zooplankton taxa had different distributions across the surf zone on different sampling days and at the different sites. It is not clear if these differences are caused by day-to-day differences in regional hydrodynamics (i.e., wave height, winds, etc.) or in surf zone hydrodynamics at the two sites.

The following figures (C.1-C.6) show the concentrations (number per m^3 of water) of some of the more common larvae and other zooplankton identified from samples taken within the surf zone and from waters just outside of the surf zone (roughly 200-300 m offshore).

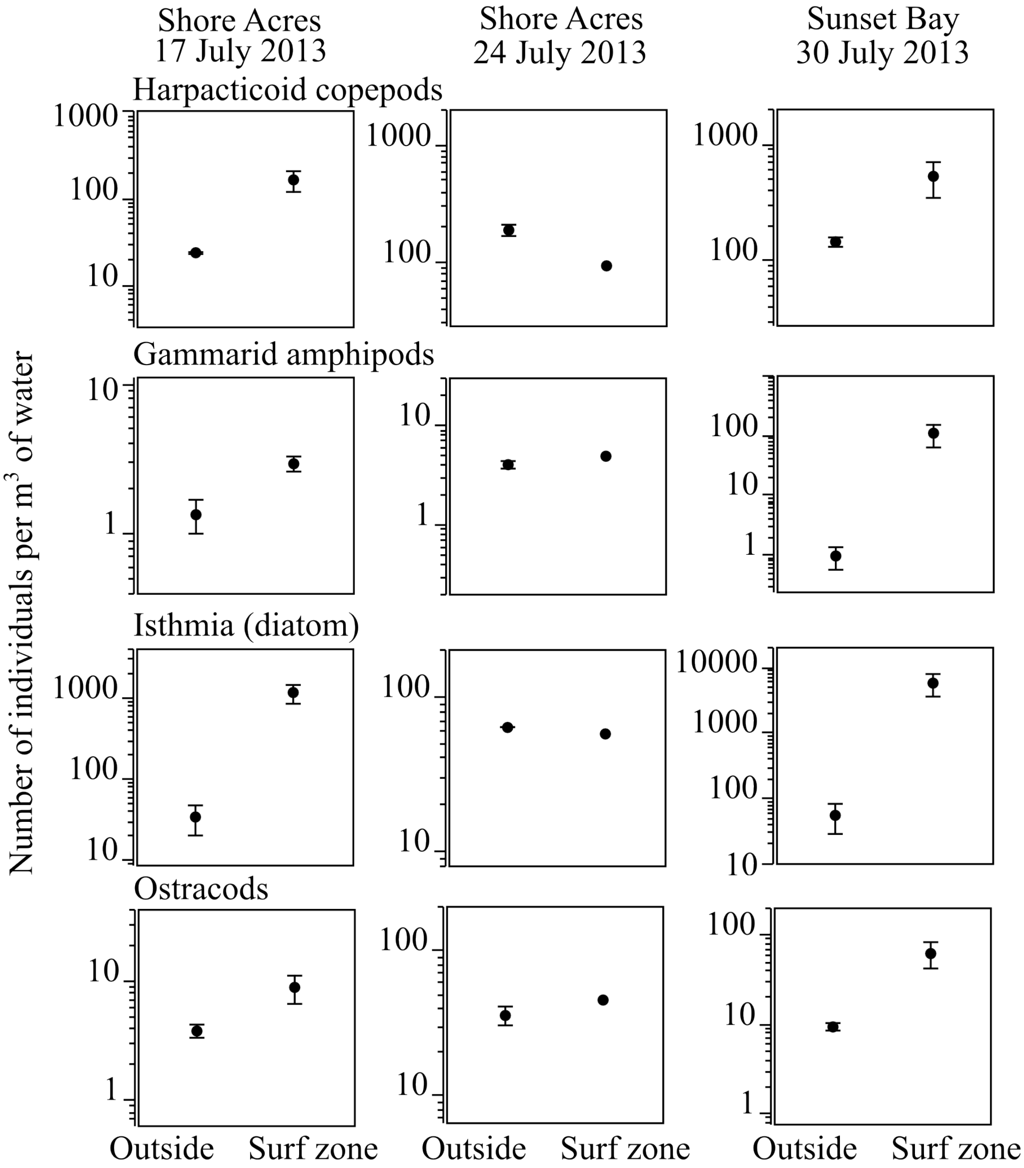

Fig. C.1. Concentrations (mean, SE) of zooplankton in the surf zone and waters 200-300 m outside the surf zone taken on July 17, 24, and 30, 2013 at Shore Acres (first two sampling days, left-hand and middle columns) and Sunset Bay (last sampling day, right-hand column). Surf zone samples were taken with a plankton pump, and offshore samples were taken with vertical plankton tows that sampled the whole water column. These taxa had a trend of higher concentrations within the surf zone than in waters just outside the surf zone.

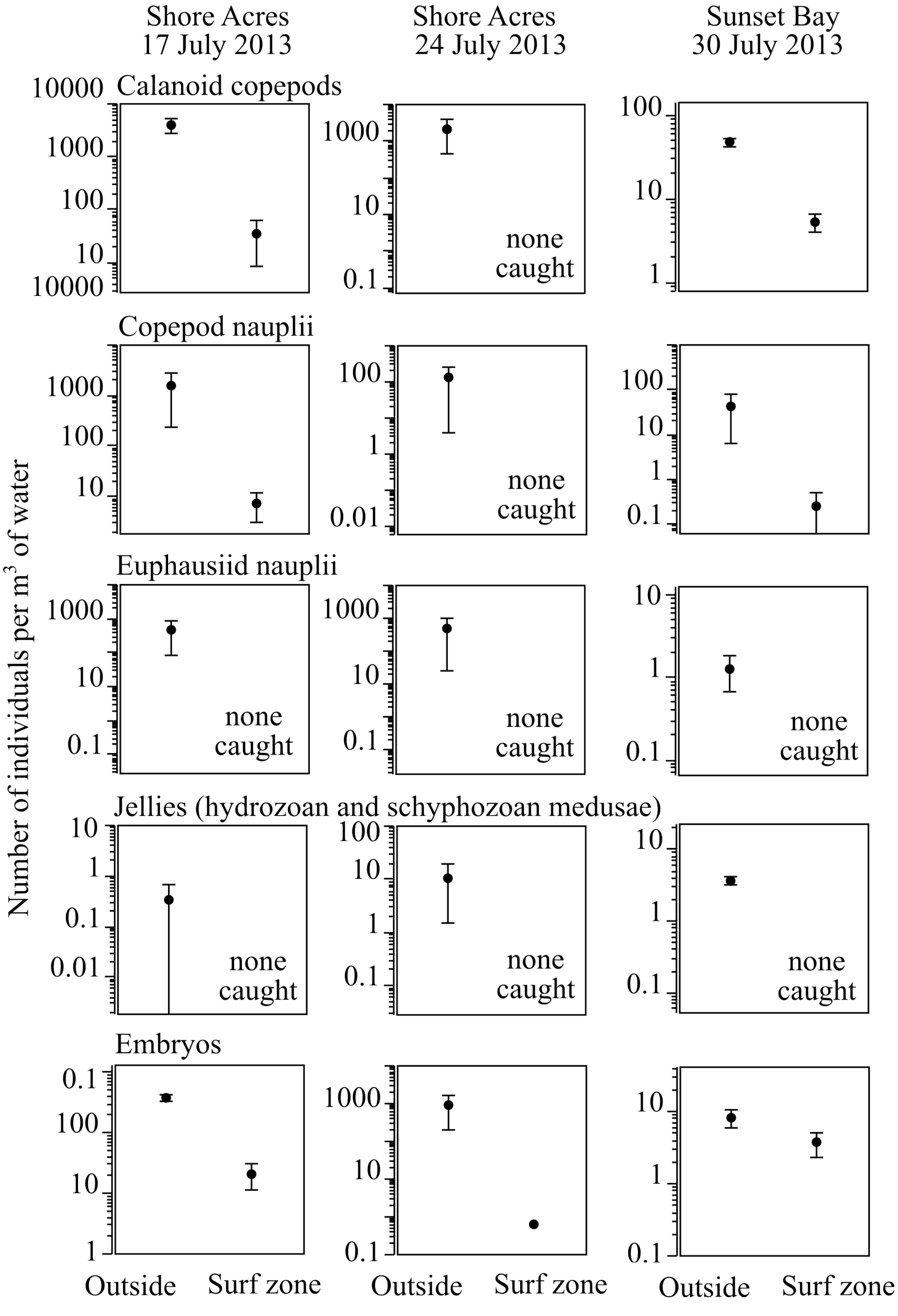

Fig. C.2. Concentrations (mean, SE) of zooplankton in the surf zone and waters 200-300 m outside the surf zone taken on July 17, 24, and 30, 2013 at Shore Acres (first two sampling days, left-hand and middle columns) and Sunset Bay (last sampling day, right-hand column). Surf zone samples were taken with a plankton pump, and offshore samples were taken with vertical plankton tows that sampled the whole water column. Many taxa had a trend of higher concentrations outside the surf zone than within the surf zone.

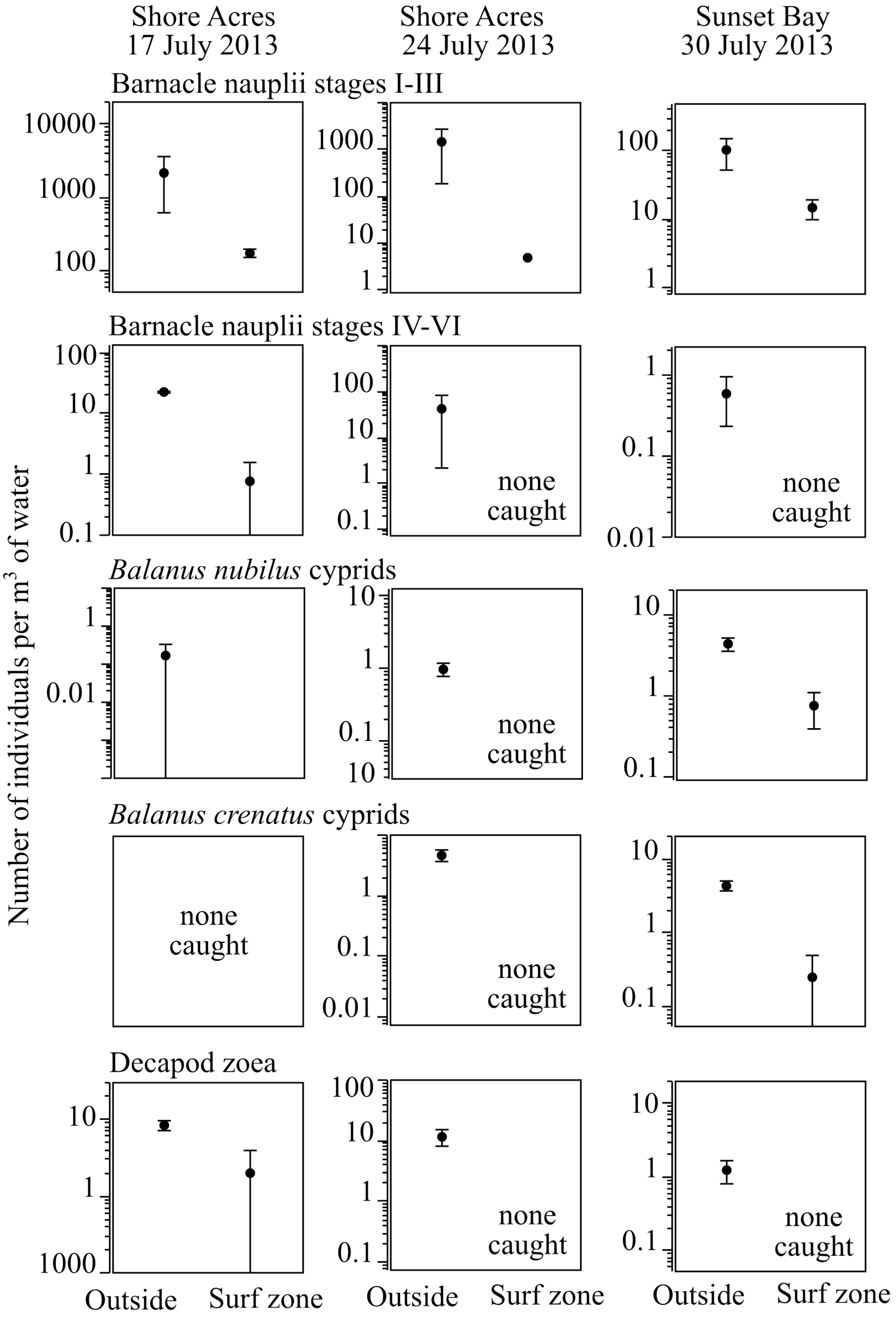

Fig. C.3. Concentrations (mean, SE) of zooplankton in the surf zone and waters 200-300 m outside the surf zone taken on July 17, 24, and 30, 2013 at Shore Acres (first two sampling days, left-hand and middle columns) and Sunset Bay (last sampling day, right-hand column). Surf zone samples were taken with a plankton pump, and offshore samples were taken with vertical plankton tows that sampled the whole water column. Many taxa had a trend of higher concentrations outside the surf zone than within the surf zone.

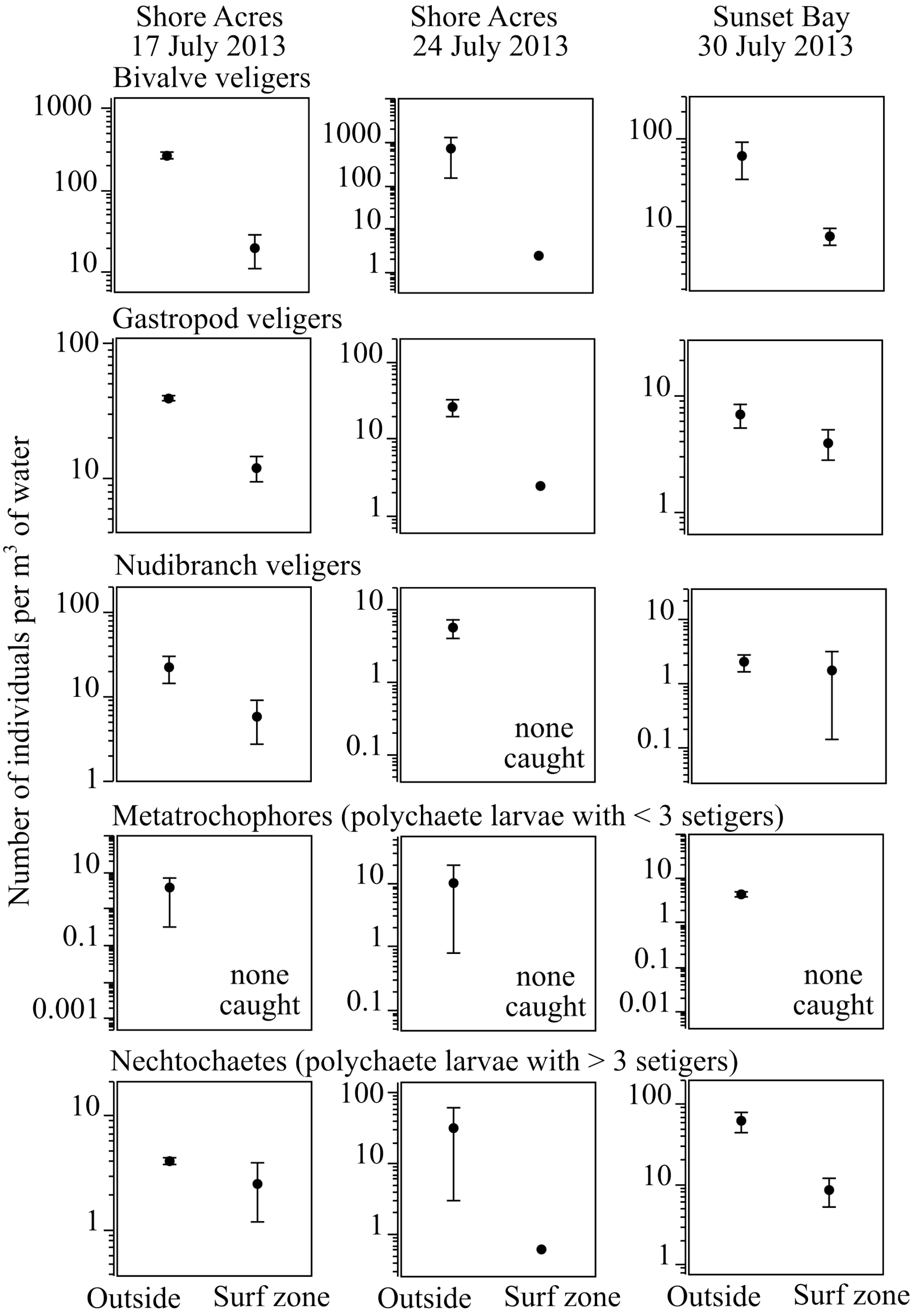

Fig. C.4. Concentrations (mean, SE) of zooplankton in the surf zone and waters 200-300 m outside the surf zone taken on July 17, 24, and 30, 2013 at Shore Acres (first two sampling days, left-hand and middle columns) and Sunset Bay (last sampling day, right-hand column). Surf zone samples were taken with a plankton pump, and offshore samples were taken with vertical plankton tows that sampled the whole water column. Many taxa had a trend of higher concentrations outside the surf zone than within the surf zone.

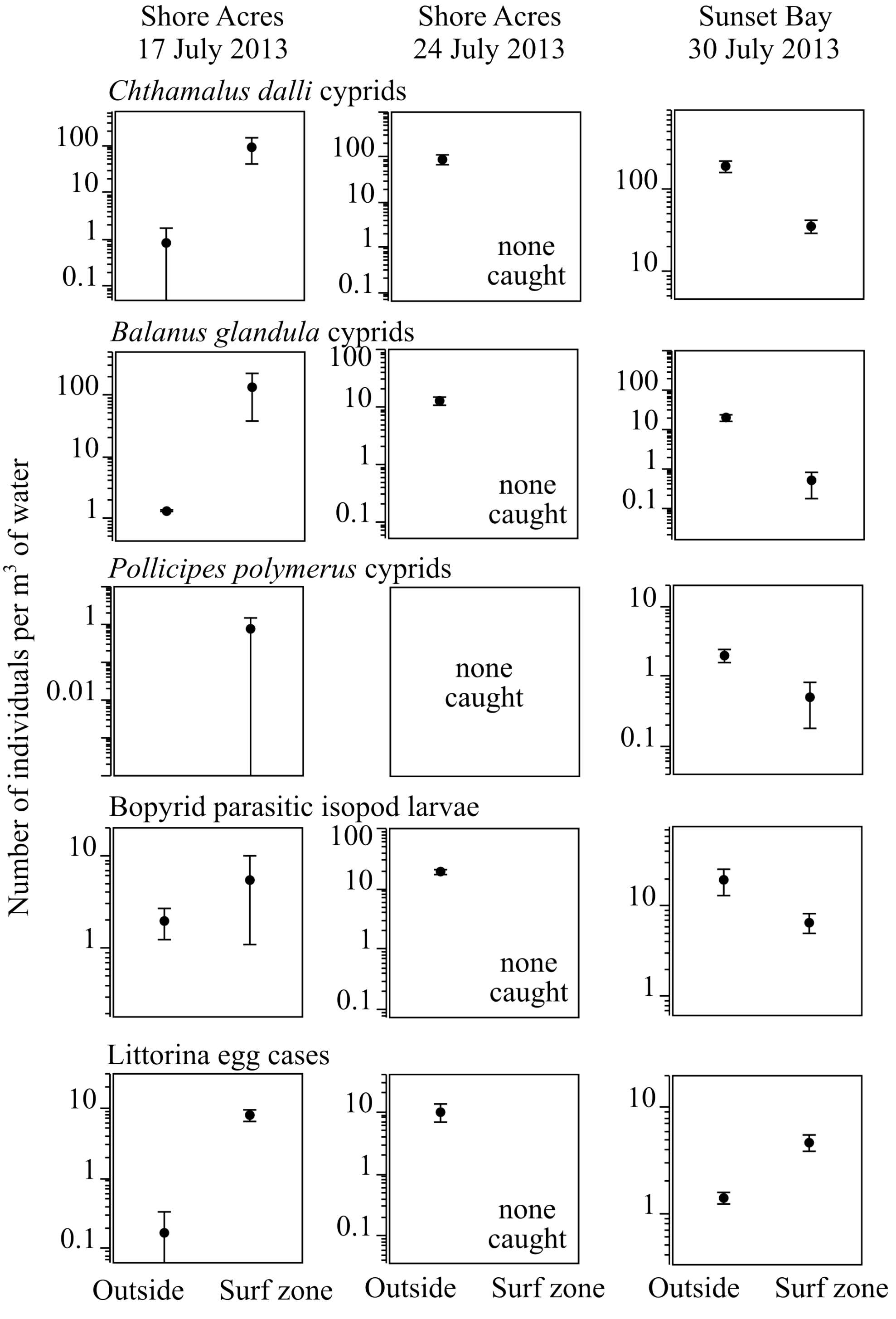

Fig. C.5. Concentrations (mean, SE) of zooplankton in the surf zone and waters 200-300 m outside the surf zone taken on July 17, 24, and 30, 2013 at Shore Acres (first two sampling days, left-hand and middle columns) and Sunset Bay (last sampling day, right-hand column). Surf zone samples were taken with a plankton pump, and offshore samples were taken with vertical plankton tows that sampled the whole water column. Many taxa had distributional trends that changed depending on sampling day and/or site.

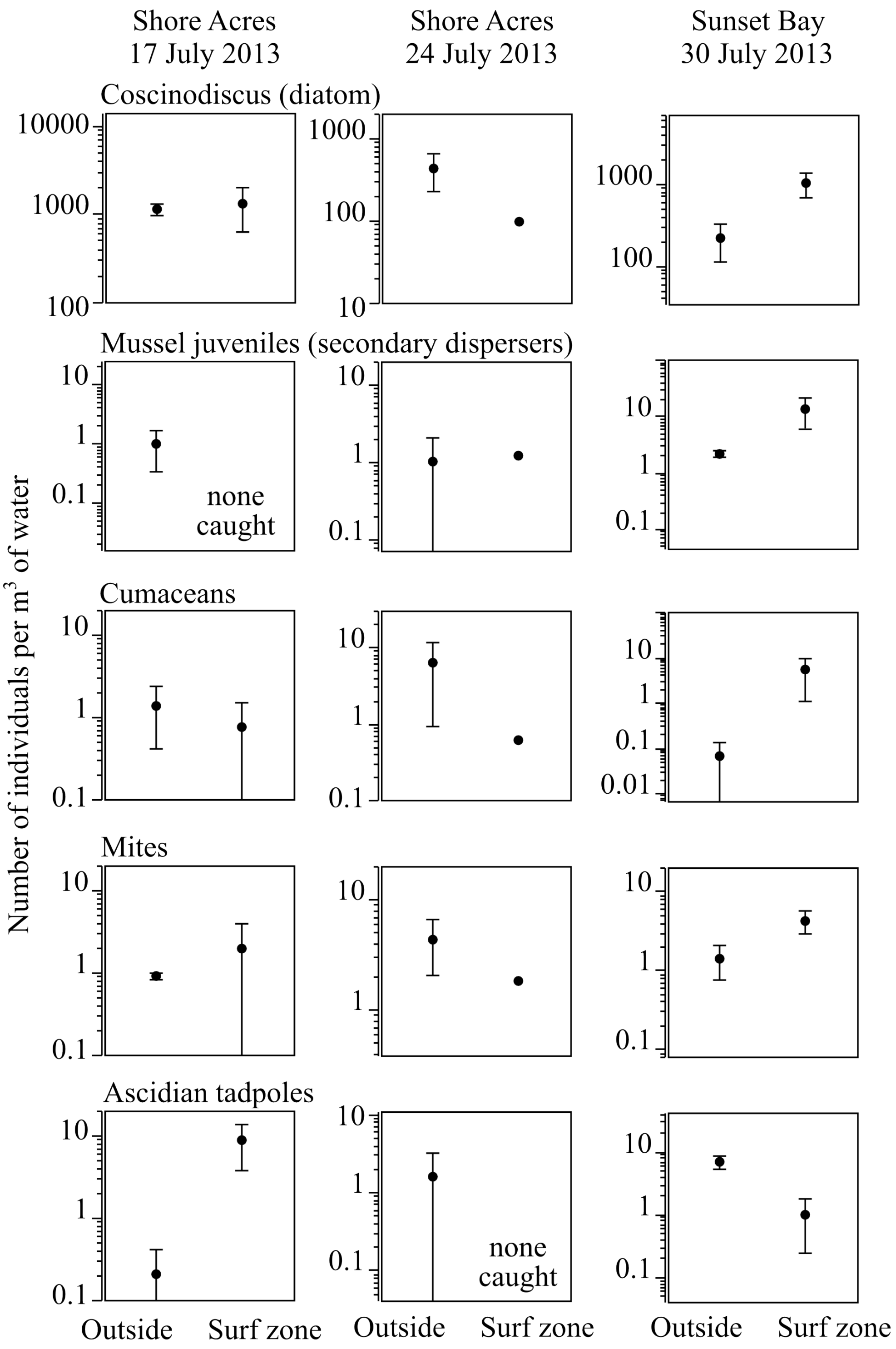

Fig. C.6. Concentrations (mean, SE) of zooplankton in the surf zone and waters 200-300 m outside the surf zone taken on July 17, 24, and 30, 2013 at Shore Acres (first two sampling days, left-hand and middle columns) and Sunset Bay (last sampling day, right-hand column). Surf zone samples were taken with a plankton pump, and offshore samples were taken with vertical plankton tows that sampled the whole water column. Many taxa had distributional trends that changed depending on sampling day and/or site.

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