Succession in a Humboldt Bay Marine Fouling Community: The Role of Exotic Species, Larval Settlement and Winter Storms

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Image credits

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Abstract

The initiation and pattern of succession in a marine "fouling" community was observed on a set of 20 black plastic panels suspended horizontally underneath the docks at Woodley Island Marina, Humboldt Bay, California from August 2001 to May 2003. The role of recruitment in the development of this community was examined using a second set of 20 panels which were scraped clean each month to allow new larvae to settle. Each month, both "undisturbed" and "settlement" panels were digitally photographed, and the percent cover of all species occupying at least 2% cover on each photo was recorded. Approximately 54 species of motile and sessile organisms were identified from these photos, of which roughly 35% were exotic species.

The "undisturbed" fouling community was characterized by seasonal pulses of fast-growing, short-lived species (e.g., colonial tunicates) combined with the persistent accumulation of longer-lived, slower-growing species (e.g., mussels, sponges and tubiculous amphipods). The initial phases of development were dominated by colonial and solitary ascidians, bryozoans and hydroids, almost all of which were introduced to Humboldt Bay. Rainstorms, which brought fresh water and heavy sediment loads into the bay each winter, appeared to lead to the sudden disappearance of many of these suspension feeders. Over time mussels, sponges and tubiculous amphipods gradually increased in their abundance, perhaps due to their tolerance to heavy sediment loads.

In conclusion, the "fouling" community in Humboldt Bay is heavily influenced by non-native taxa, many of which disappear following repeated winter storms, leading to sudden increases in free space. Concurrent increases in sedimentation after winter storms appear to select for slow-growing, tolerant species (e.g., mussels) that may form a "climax" community over a longer temporal scale.

Myxicola infundibulum

Introduction

The intentional or accidental introduction of "exotic" species by humans is one of the leading causes of the biodiversity crisis (Wilcove et al. 1998). The release of larvae from the hulls and ballast tanks of ships from distant ports, the dumping of algal "packing material" (with associated species) when shipping live organisms for human consumption, and the deliberate introduction of non-native shellfish species for aquaculture have all contributed to an accelerated homogenization of species in coastal marine habitats. As a result, estuarine habitats such as San Francisco Bay (Carlton 1979) are among the most threatened ecosystems in the world (Carlton and Geller 1993). Further knowledge of the mechanisms used by exotic species to invade new locales, and whether particular types of communities repel or facilitate their arrival, is clearly needed.

The functional role that successful invaders have on future ecosystem function in marine habitats has been largely unexplored. Invasive species can potentially out-compete native populations and drive them to local extinction. This may in turn affect higher trophic levels (e.g., commercial or sport fisheries), as witnessed by the collapse of the anchovy fishery in the Black Sea from the introduction of an exotic comb jelly (Kideys 2002). Likewise, sessile marine invertebrates attached to ship hulls, docks and other man-made structures often feed on suspended plankton during both their larval and adult phases, and therefore their growth and/or survivorship may reflect changes in planktonic communities within a bay. Benthic-pelagic coupling of communities could have implications for commercial operations, such as the rearing of oysters for human consumption. A baseline study of marine "fouling" communities, for example, might establish important biological indicators of early changes in the "health" of a bay or estuary.

In this study we report on preliminary data from an ongoing effort to monitor the settlement, growth and subsequent establishment of "fouling" communities under the Woodley Island Marina in Humboldt Bay, California. Because of Humboldt Bay's location between San Francisco Bay and Coos Bay, Oregon, it receives substantial shipping traffic from fishing vessels traveling up and down the U.S. West Coast as well as larger, ocean-going vessels traveling from ports as far away as Japan. A study by Boyd et al. (2002) has shown that a substantial number (97) of exotic species currently reside within Humboldt Bay. These exotics represent several major phyla ranging from vascular plants to fish. The largest numbers of invasive species, however, are from various invertebrate taxa including polychaetes (24 species), amphipods (20 species) and bryozoans (8 species). Some of the invasive species identified by Boyd et al. (2002) were likely to have been introduced long ago, from dry ballast or "shingle" on wooden ships in the mid-1800s. The most abundant salt marsh cordgrass, *Spartina densiflora*, was probably introduced in this way to Humboldt Bay from South America sometime in the 1860s. Since its introduction, *S. densiflora* has become the dominant cordgrass species within Humboldt Bay.

For the majority of introduced marine species living in Humboldt Bay, little is known about their natural role within the bay ecosystem. Our work represents one of the first attempts to record the presence of native and exotic species under docks in Humboldt Bay, and to investigate their relative ecological role within fouling communities on man-made structures within the bay.

Man-made structures are increasingly common elements along the shoreline of bays and estuaries and may even represent novel habitats for marine invertebrates (Connell 2000). Many of them, including pier pilings and floating docks, have a luxuriant growth of marine invertebrates on them. These systems are relatively easy to study because of their ease of access, and deployment of experiments and data-gathering methods do not require SCUBA gear. Field experiments can address the ongoing debate concerning factors governing time-dependent patterns of succession, such as whether succession leads to alternative stable states or "climax" communities (Sutherland 1974; Petraitis and Dudgeon 2004). More applied concerns, including whether exotic species affect local fisheries and other commercial activities, can be examined.

Specifically, the goals of this study are to: (1) describe the pattern of settlement and succession in invertebrate "fouling" communities within Humboldt Bay, (2) evaluate the relative importance of native and exotic species as space occupiers within this system, and (3) determine the variability in community structure through time.

Long term goals include (1) identification of water-column factors that might influence community structure and perhaps reflect the "health" of the bay, (2) establish methods for the early detection of exotic species introductions, and (3) field test recently developed theory on the mechanisms of succession in epifaunal marine communities.

Methods

Site

Recruitment and community development of fouling invertebrates were observed on artificial plastic panels suspended below the south breakwater dock at Woodley Island Marina, Humboldt Bay, California. Because this marina receives heavy traffic from commercial fishing boats and pleasure craft, it is a likely site for exotic species to first appear within the bay. Woodley Island Marina is the largest marina within Humboldt Bay, comprising a series of nine (30–70 ft) floating docks oriented perpendicular to the shoreline. These large docks extend into North Bay channel, one of two channels connecting North Bay and Eureka Slough with the entrance channel into Humboldt Bay.

Site Characteristics

Precipitation patterns within Humboldt Bay are highly seasonal and rainfall amounts vary from year-to-year (Figure 1). Water temperature within the bay varies daily with tidal flow and cloud cover, and both seasonal and annual patterns are detectable with mean low values ~ 9.0 °C and mean highs ~ 18.0 °C. Intermittent salinity measurements taken at panel-depth along the dock ranged from a low of 19 ‰ during periods of high rainfall, to a high of ~ 34 ‰ during high tides (data not shown). North Bay water surrounding Woodley Island was visibly turbid from sediment loading following periods of high rainfall, and often remained turbid for days at a time, despite tidal flushing.

Fouling panels

Two sets of artificial fouling panels were deployed on rectangular frames constructed of 1-in.-diameter polyvinyl chloride pipe (PVC). Each frame measured 150 x 50 cm, and held 20 (15 x 10 x 0.65 cm) ABS black plastic sheets (panels), individually engraved for identification and attached with stainless steel bolts and wing nuts. The panel replicates were evenly spaced on each frame and randomly reattached to the alternate frame after each sampling.
A vertical section of the frame was affixed to the dock side with galvanized pipe brackets and screws; panels were oriented horizontally, face-down, and submerged directly beneath the "shade" of the dock at a depth of 1 m. Position effects along the dock were avoided by alternating among designated frame-attachment locations.

Settlement

The first frame with 20 panels, deployed February 2001, was designed to record newly arrived recruits of various marine invertebrates. These "settlement" panels were monitored for monthly and seasonal larval settlement and used to detect species introductions as well as reproductive periods of sessile invertebrates in Humboldt Bay. All "settlement" panels were scraped clean and soaked in fresh water after each census to ensure free substrate was continuously available for settlement of marine larvae each month.

Community Development

The second set of 20 panels, deployed July 2001, was designed to follow the development of "undisturbed" sessile marine communities. Panels in this set were sampled in a non-destructive manner by taking photographs to record the settlement, growth and mortality of sessile species through time. Monthly census of this "undisturbed" set coincided with the settlement set. Sampling the two sets simultaneously allowed insights from seasonal time comparisons of recruitment and growth within the developing "undisturbed" community.

Panel Census Methods

Data were recorded at Telonicher Marine Laboratory (TML), Trinidad, California. At 4–6 week intervals, both panel sets were retrieved from the dock and suspended within plastic containers containing fresh seawater. These containers were brought to TML where the panels were maintained face-up in circulating filtered seawater (FSW) tables. Care was taken during the retrieval and handling process to avoid long immersion periods or physical loss of sessile species. Each panel was digitally photographed using Nikon Coolpix 990 or 995 cameras.

Corresponding panel and image numbers were recorded along with notes describing important trends. Photographs captured the whole panel so that species-specific coverage of occupied space could be accounted for in a systematic manner. In addition to whole panel images, "close-up" pictures were taken through an Olympus SZ9 Microscope by a stem-mounted DP11 2.5 mega-pixel digital camera. This helped to identify adults and newly settled individuals and provided a closer look at species interactions during community development. Panels were typically returned to Humboldt Bay within 24 hours of their removal.

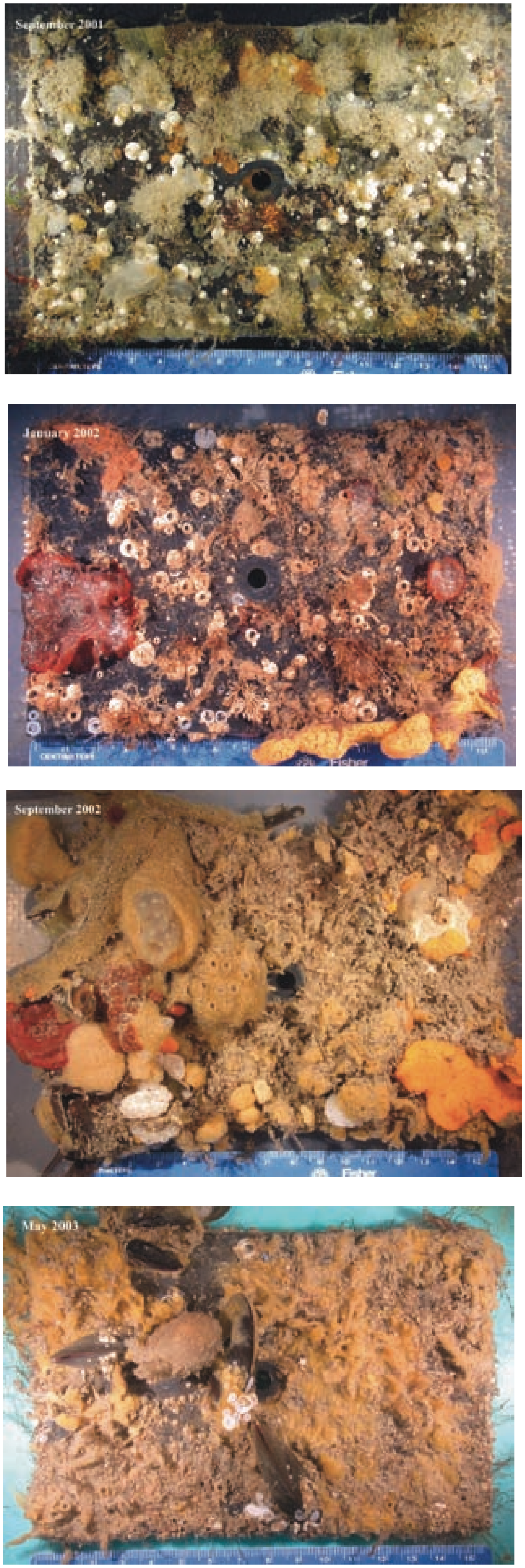
Analysis of Digital Photographs

Photographs of "undisturbed" panels were analyzed by computer. Each digital photo was overlaid with a 5x5 rectangular grid created in Adobe Photoshop 6.0. Percent cover data was recorded for all species occupying at least 2% of observable space. Coverage estimates frequently exceeded 100% due to multi-level growth. Summary statistics and graphs of percent cover data were produced in SigmaPlot 8.0. It should be noted that because some species were cryptically hidden underneath a thick canopy of hydroids, bryozoans and other fouling invertebrates, it is likely that some species were missed.

Results

Organisms

More than 54 species of marine invertebrates from seven different phyla were identified from photographs taken during the sampling period. Exotic species accounted for ~ 34% of all species (both motile and sessile) identified from these photos (see Table 1 for a list of sessile species). Motile invertebrates were identified only if they were clearly visible in digital photos; caprellids, chitons, and nudibranchs were regularly observed feeding on sessile organisms attached to the panels, but were often found hidden beneath a canopy of hydroids, bryozoans and feather duster worms. Because photographs only captured the over-story or canopy



(Left) Successive images of a single fouling panel, deployed under the Woodley Island Marina in Humboldt Bay, California, over a period of three years. (Top) In September 2001, this panel is covered by colonial bryozoans (primarily *Bugula californica*) and solitary barnacles (*Balanus crenatus*), with a few encrusting ascidians (*Botrylloides* sp. and *Botryllus tuberatus*) present. (Second) Following winter storms in January 2002, most of the "overstory" in this community (especially colonies of *Bugula*) have disappeared and many of the barnacles have died. However, two colonies of the bright red invasive bryozoan *Watersipora subtorquata* appear. (Third) Eight months later in September 2002, one of these two colonies of *Watersipora* is completely overgrown, while the second is surrounded by colonial ascidians (*Diplosoma macdonaldi* and *Distaplia occidentalis*). At this point, a large percentage of the panel is occupied by sponges and the fine, muddy tubes of *Corphium*. (Bottom) Another eight months later, in May 2003, these colonial ascidians have disappeared, leaving the panel primarily covered with sponges (through which some of the original barnacles can be seen) and a few large mussels.

layer of fouling communities that developed on our panels, total species richness is underestimated. Destructive sampling of several fouling panels each month is needed to produce a more complete species list. This would require a much larger number of fouling panels in the "undisturbed" treatment.

Settlement

Several of the most conspicuous species displayed seasonal pulses of settlement varying dramatically within and between years (Figure 2). Recruitment levels were higher during summer and fall; little or no settlement was observed during winter months.

The hydroid *Obelia dichotoma* and bryozoan *Celleporella hyalina*, both exotic species, were present most months of the study. *Obelia* peaked in abundance in May 2001 and again in March 2003. *Celleporella* settled in 2001 during the months of May, August and November, and peaked in abundance on settlement panels in October 2002. Colonial tunicates demonstrated comparatively strong settlement during summer and early fall months (Figure 2). *Botrylloides* settled heaviest from June through August 2001 and again from July through September 2002. *Botryllus* settled in the early fall months of October 2001 and September 2002, although it did not comprise more than 10% cover on any occasion. In 2001, both *Distaplia occidentalis* (July) and *Diplosoma macdonaldi* (October) recruited heavily, dominating nearly half the space on settlement panels. Nevertheless, recruitment levels for these 2 species resulted in less than 20% cover during the same months in 2002. In contrast, settlement numbers were low for the solitary tunicate *Ciona intestinalis* during fall 2001 and 2002.

Two large pulses of recruitment from the barnacle *Balanus crenatus* occurred during October 2002 and May 2003 (Figure 2). These peaks, representing close to 40% cover, are remarkable given that a newly metamorphosed barnacle comprises less than 0.5% cover. Prior to these peaks settlement of *B. crenatus* was extremely low, even during the same months in 2001.

The barnacle, *Balanus crenatus.*

Community Development

The initial composition of the "undisturbed" panel set, deployed in July 2001, was characterized by a steady accumulation of competitive, fast growing colonial tunicates (Figure 3). *Diplosoma macdonaldi* and *Botrylloides* sp. dominated most of the space after two months of development. *Diplosoma* peaked in abundance at 30% cover in September and then rapidly declined in October, failing to reach that level in any of the remaining months of the study. As *Diplosoma* growth subsided there was a rise in the abundance of *Botrylloides* (in October) that lasted until December. *Ciona intestinalis*, originally from the East Coast of the United States, followed on the heels of these two species, peaking at almost 25% cover in November. This peak in *Ciona* coverage resulted from dramatic growth of a few individuals, with some reaching 5 in. or more in length and covering a substantial portion of the fouling panels.

The encrusting bryozoan *Watersipora subtorquata*, a recently observed introduction to Humboldt Bay, settled and expanded on the panels from October through November 2001. *Watersipora* maintained up to 10% coverage through March 2002. We have observed this species forming large (6–8 in.-diameter) lettuce-like "heads" on the new Eureka municipal docks located across the channel from Woodley Island Marina. *Watersipora* declined rapidly in abundance after April 2002 at the study site.

Winter months were characterized by heavy rain, sedimentation, and turbid waters with decreased settlement and growth of any new individuals in the fouling community. There was a noticeable increase in free space on the panels following large storm events (Figure 1), resulting from the disappearance of *Botrylloides*, *Ciona* and other tunicates. The hydroid *Obelia dichotoma* appeared soon after these storms and colonized any available space. *Obelia* maintained ~18% coverage from January 2002 through July 2002.

During spring months *Balanus crenatus* recruitment to the undisturbed panels was low and never occupied more then 5% cover. Tube-dwelling amphipods, *Corophium* sp., formed clusters of tubes from fine sediment grains accumulating on panel surfaces after winter storms. These crustaceans increased on the panels from January to April 2002 and remained throughout the study. *Botrylloides* reappeared in the spring to occupy 35% of the undisturbed fouling panels. Their rapid peak in abundance was followed by a steady decline through spring 2003.

The sponge *Halichondria bowerbanki*, an exotic species, first appeared in April 2002 on the "undisturbed" panels. Its coverage increased through December 2002, dropped off in January, and recovered in spring of 2003.

There were strong pulses of recruitment and growth from *C. intestinalis*, *W. subtorquata* and a new colonial tunicate, *Distaplia occidentalis*, during the fall of 2002.

Throughout the study, dominant organisms in the community were observed arriving in short pulses of recruitment that typically occurred within a single month. These species were very competitive and overgrew any previous occupants. Beneath these ephemeral species, several disturbance-resistant taxa, including the sponge *Halichondria bowerbanki*, the tube-forming amphipod *Corophium* sp. and the mussel *Mytilus trossulu*s (data not shown) gradually increased their substrate occupancy over time (Figure 3). In contrast to repeated seasonal dominance by fast growing, short-lived species, these durable slow-growing forms were persistent. Recent observations of these same "undisturbed" panels (July, 2004) show continued dominance by the mussel *M. trossulus* and the sponge *H. bowerbanki* (Janiak pers. obs.), demonstrating they are capable of persisting for at least several years on these panels.

Discussion

Roughly 35% of the species identified from this study were introduced from various areas of the worlds' oceans. These introduced species play a critical role in the development of the fouling communities in Humboldt Bay. The initial phases of community development on "undisturbed" panels, for example, were dominated by colonial and solitary ascidians, bryozoans and hydroids, almost all of which were introduced to Humboldt Bay. In addition, some of the late succesional species, including *Watersipora subtorquata* and *Halichondria bowerbanki*, are also introduced. It is therefore impossible to know what the "native" communities within Humboldt Bay should look like.

It is notable that other fouling studies have shown very similar patterns of succession, often with the very same species, in other localities (e.g., Dean 1981; Mook 1981). Most of the hard-substrates available for settlement by sessile marine invertebrates and algae within Humboldt Bay are man-made structures, like those that stabilize the shores within the bay (e.g., rip-rap that lines the entrance channel and other areas within the bay) or those that have been introduced for aquaculture (e.g., the Japanese oyster *Crassostrea gigas*). Studies by Connell (2000, 2001) have shown that within Sydney Harbor, Australia, new urban structures may facilitate the invasion of new taxa. Our own observations on the newly constructed municipal floating docks in Humboldt Bay also suggest this may occur. We have seen greater abundances and much larger colonies of the newly discovered bryozoan *Watersipora subtorquata* at these docks relative to those seen at the Woodley Island Marina. This pattern may represent a temporal correlation between the deployment of these new floating docks and the arrival of *Watersipora*.

Introduced species contributed disproportionately to the development of the fouling community on docks at Woodley Island Marina. This community is characterized by seasonal pulses of fast-growing, short-lived species (e.g., colonial tunicates) combined with the persistent accumulation of longer-lived, slower growing species (e.g., mussels, sponges and tubiculous amphipods). Ephemeral species frequently grew over and on mussels and other longer-lived species, forming a "canopy" layer that showed dramatic changes in percent cover from month to month. Winter storms, which transported both fresh water and heavy sediment loads through the channel adjacent to the Woodley Island Marina, appeared to lead to the sudden disappearance of weedy suspension feeders, including colonial tunicates and bryozoans. Most of these species are exotic and can be found in bays and estuaries on both the Pacific and Atlantic Coasts of the United States, where they inhabit docks and pier pilings in a wide range of salinities. This tolerance of fluctuating salinity makes it more likely that the sudden declines in abundance, following winter storms, may be due to mortality from heavy sedimentation on the "undisturbed" panels. These conditions can effectively clog the suspension feeding organs of many sessile invertebrates (Maughan 2001).

Although both the "undisturbed" and "settlement" panels initially reflected a pulse in settlement by tunicates, later changes in the dominance of species on "undisturbed" panels did not necessarily reflect pulses in recruitment. Initial settlement by the colonial sea squirts *Diplosoma* and *Botrylloides* onto the "undisturbed panels" lead to brief dominance by these species in September and October, whereas fairly low (<5% cover) recruitment by the solitary tunicate *Ciona* was followed by rapid growth, and subsequent dominance by a small number of individuals (25% cover on panels) in November, 2001. A peak in recruitment of the barnacle *Balanus crenatus* seen on "settlement" panels in October 2002 did not result in an increase in percent cover of this species in subsequent months. Osman and Whitlatch (1995) found that the major affect that resident adults have on the recruitment of settling larvae in a developing benthic community is to prevent them from taking over space. In addition, increases in percent cover are not always driven by prior settlement. An increase in the establishment of *Botrylloides* on "undisturbed" panels in May 2002 did not appear to be caused by heavy settlement of this species. Thus, increases in percent cover can be due to apparently "sudden" increases in growth by colonies, which may be present yet hidden below an upper "canopy." In conclusion, dominance on "undisturbed" panels was not always driven by settlement processes, which changed in importance over the course of succession.

Similar studies of marine fouling communities have also shown the importance of settlement changes during the successional process. Field (1982) found that the species that initially settled on panels suspended in the Damariscotta River in Maine were different from those that settled in older, more mature communities. He concluded that species that settled first altered the community, facilitating the recruitment of later species which otherwise may not have invaded.

Chalmer (1982) also found that species selectively settled into different aged fouling communities on asbestos panels immersed near Garden Island, Western Australia. Most species in his study settled on young panels because they had little structure and considerable free space. In contrast, the mussel *Mytilus edulis* was able to settle freely on both young and old panels, and Chalmer (1982) suggested that the ability of *Mytilus* to settle in established communities was the reason for its ultimate dominance as a "climax species."

Dean (1981) found that mimicking the physical structure supplied by sessile organisms, such as colonial tunicates, hydroids and barnacles, facilitated the settlement of the mussel *Mytilus edulis*, which in turn pre-empted settlement by other species. Observations made in July 2004 of our "undisturbed" panels indicate that the mussel *Mytilus trossulus* is steadily increasing its percent cover over time, along with increases in the sponge *Halichondria bowerbanki* and tubiculous amphipods. Gradual increase in *M. trossulus* abundance, despite any sign of recruitment of this species onto "settlement" panels, may stem from preferential settlement into established communities with preëxisting structure. Alternatively, the relative absence of mussel predators, such as motile crabs and sea stars, may enable mussels to outcompete other species (Enderlein and Wahl 2004). Although mussels may not settle in high numbers, their persistence could be due to their ability to tolerate heavy sedimentation following winter storms, as well as their ability to settle in established communities. We hypothesize that mussels, sponges and tubiculous amphipods will form the eventual "climax community" on our panels if given enough time. These species appear to dominate the floating docks at Woodley Island Marina.

Seasonal declines in abundance, seen in some of the dominant occupiers of space (including *Botrylloides* sp., *Botryllus* sp., *Ciona intestinalis*, *Watersipora subtorquata*, and *Obelia dichotoma*), could be due to either natural history variation or variation in water conditions in the bay. Short life spans, for example, could lead to synchronized senescence amongst a "cohort" of individuals that recruited simultaneously. Such a phenomenon could lead to sudden apparent "mortality" at different times of the year. While we cannot rule out natural senescence as an explanation for the sudden decline in percent cover of *Botrylloides*, *Ciona* and *Halichondria* in January 2002 and 2003, these declines are correlated with high rainfall levels (Figures 1 and 3). It is unclear whether low salinity or increased sedimentation levels from rainstorms are responsible for these sudden disappearances. However, Dybern (1967) showed that *Ciona* is tolerant of a wide range of salinities, and many exotic species have a euryhaline distribution. Therefore, we suggest that deposition of fine sediments, along with reduced salinity from freshwater runoff, are the primary agents of disturbance responsible for the decline of many species in this fouling community. Repeated disturbances may ultimately influence the composition of fouling communities at Woodley Island Marina by favoring "disturbance tolerant" taxa.

In conclusion, this study shows that the diverse community of sessile marine invertebrates that "foul" docks within Humboldt Bay is a highly dynamic system which changes markedly from month-to-month. Pulses of recruitment, rapid growth and sudden mortality characterize this system. Nevertheless, this community may be gradually approaching a less diverse state dominated by a few species, including the mussel *Mytilus trossulus*, the sponge *Halichondria bowerbanki* and the tubiculous amphipod *Corophium* sp. Persistent cover by a few dominant taxa may provide secondary substrate for more opportunistic species to settle on during high recruitment months, masking a stable set of species in the understory.

Because many of the species identified on our panels (~35%) are non-native, it is clear that Humboldt Bay is not immune to invasion by exotic species. In fact, it is likely that this process has been occurring since the mid-

1800s, although it is unclear if the number of exotic species has increased exponentially, as has been seen in San Francisco Bay (Carleton and Geller 1993). Clearly, further study over a longer time span is necessary to determine whether a "climax" community is attained, and whether this community can repel further invasion by exotic species. In addition, the role of sediment deposition in these communities appears to be an important source of disturbance that may drive this system.

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Figures and Table

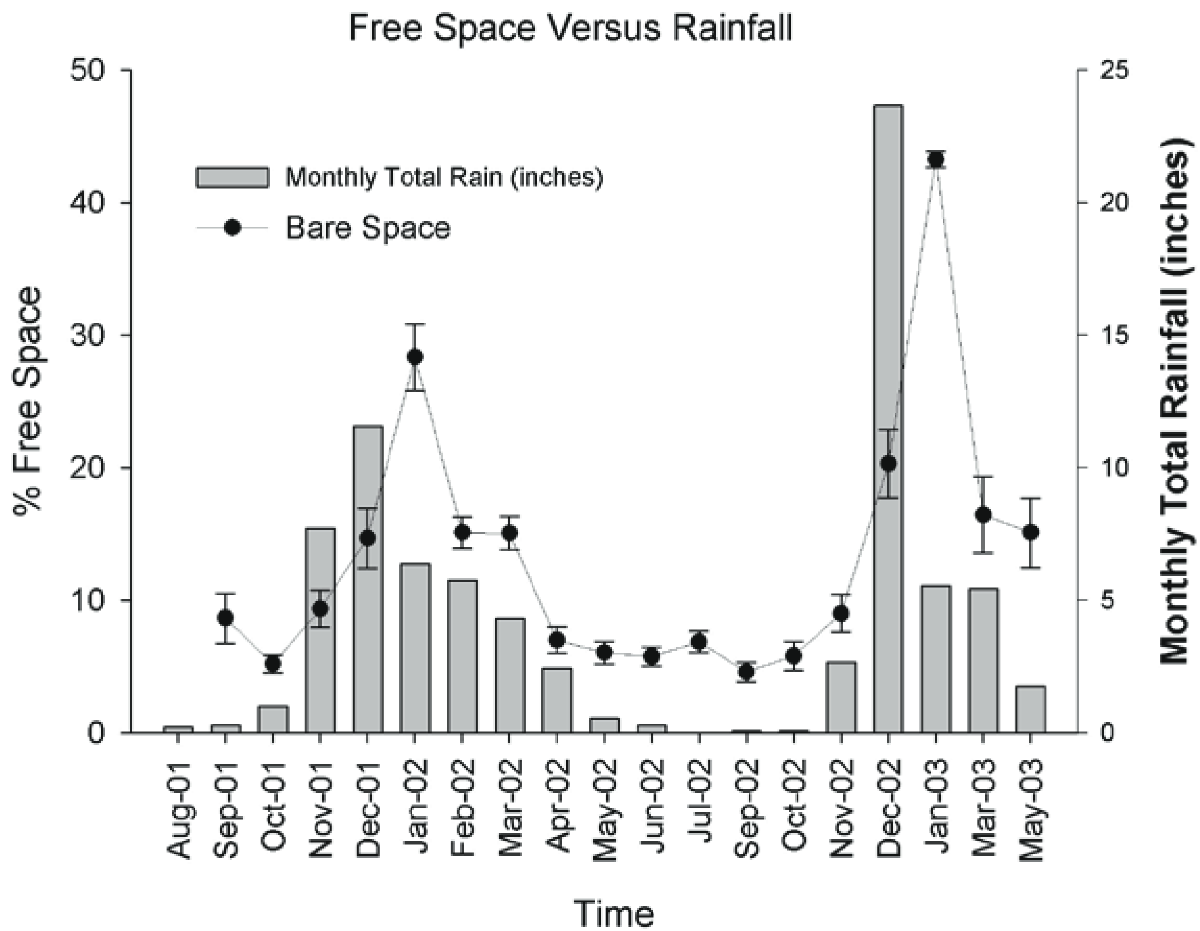

Figure 1. Plot of the average % free space (± 1 S.E.) on "undisturbed" fouling panels at Woodley Island Marina, Humboldt Bay, California. Rainfall data plotted represent the sum of monthly rainfall amounts (in inches) August 2001–May 2003, obtained from the National Weather Service.

a.

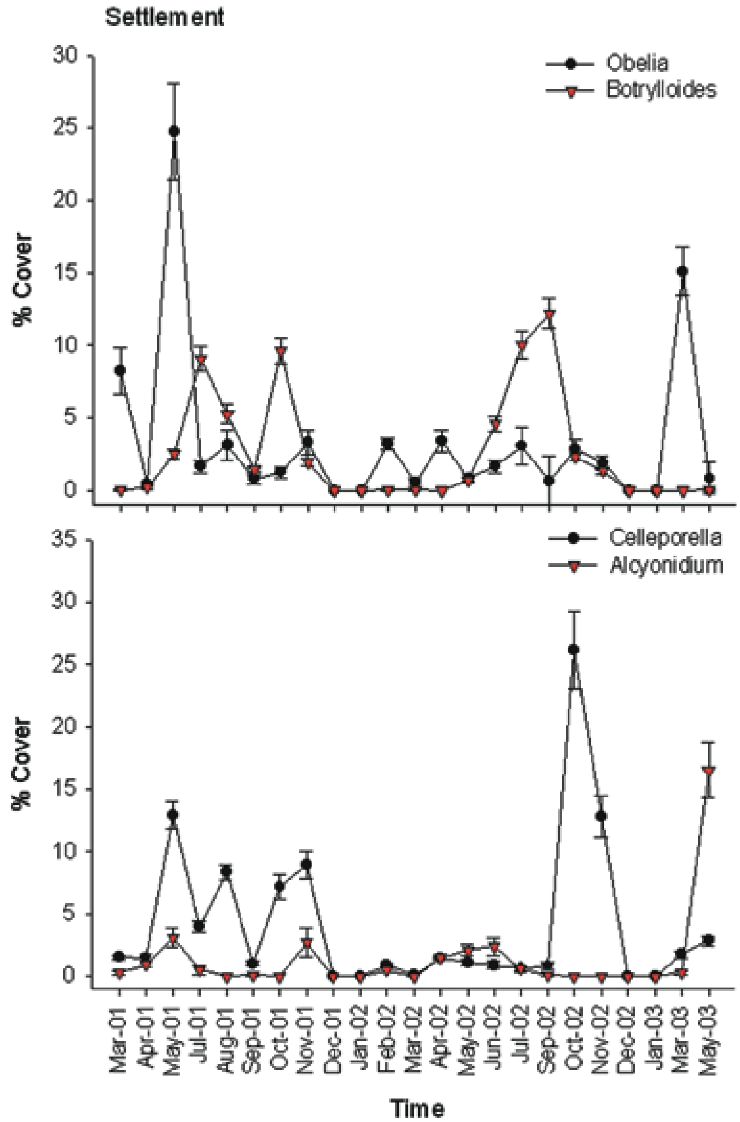

Figure 2a. Mean percent cover (± 1 S.E.) of subtidal invertebrates on settlement panels over time at Woodley Island Marina, Humboldt Bay, California. Graphs present settlement data for frequently recorded species during the sampling period (March 2001–May 2003).

b.

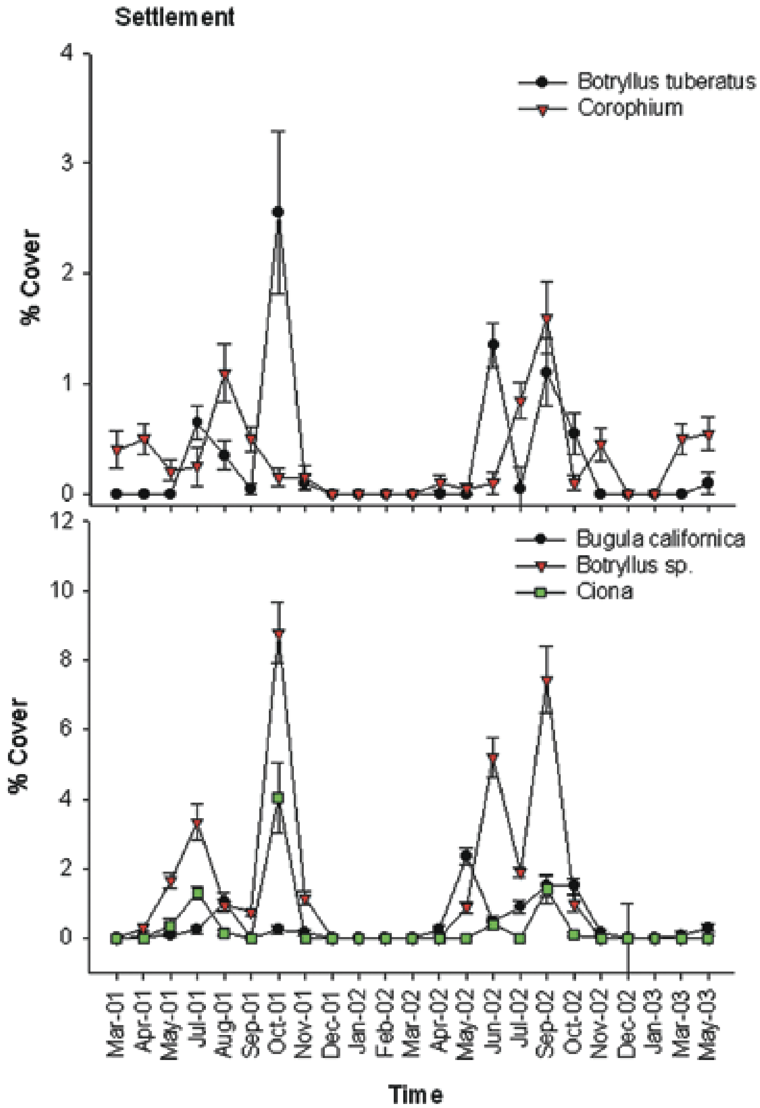

Figure 2b. Mean percent cover (± 1 S.E.) of subtidal invertebrates on settlement panels over time at Woodley Island Marina, Humboldt Bay, California. Graphs present settlement data for frequently recorded species during the sampling period (March 2001–May 2003).

c.

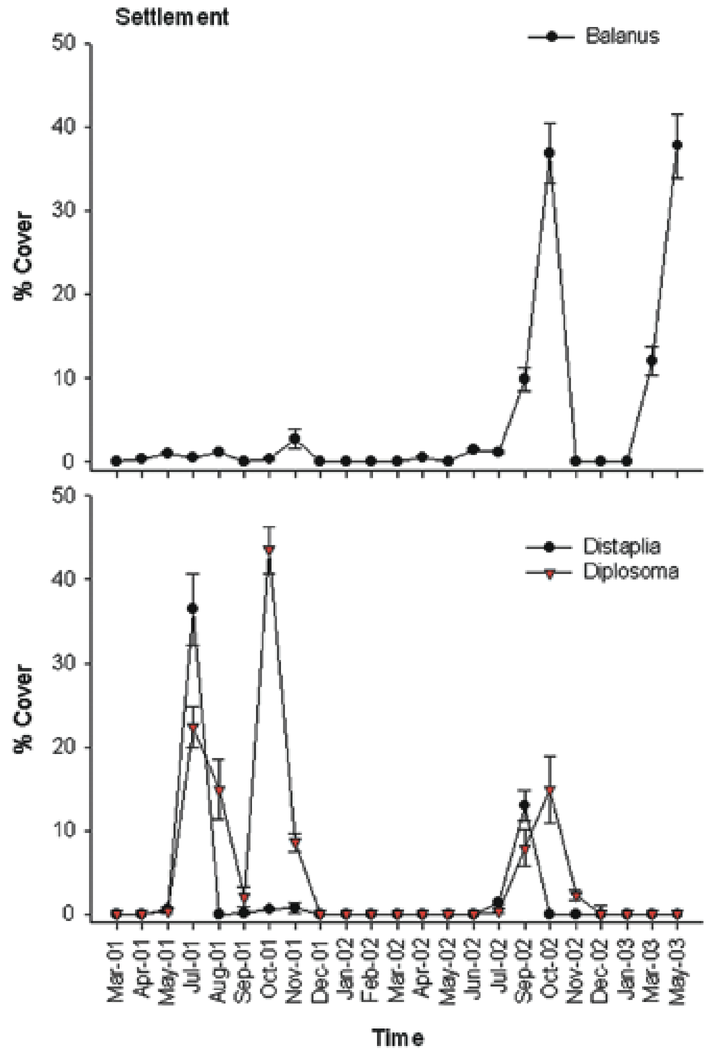

Figure 2c. Mean percent cover (± 1 S.E.) of subtidal invertebrates on settlement panels over time at Woodley Island Marina, Humboldt Bay, California. Graphs present settlement data for frequently recorded species during the sampling period (March 2001–May 2003).

a.

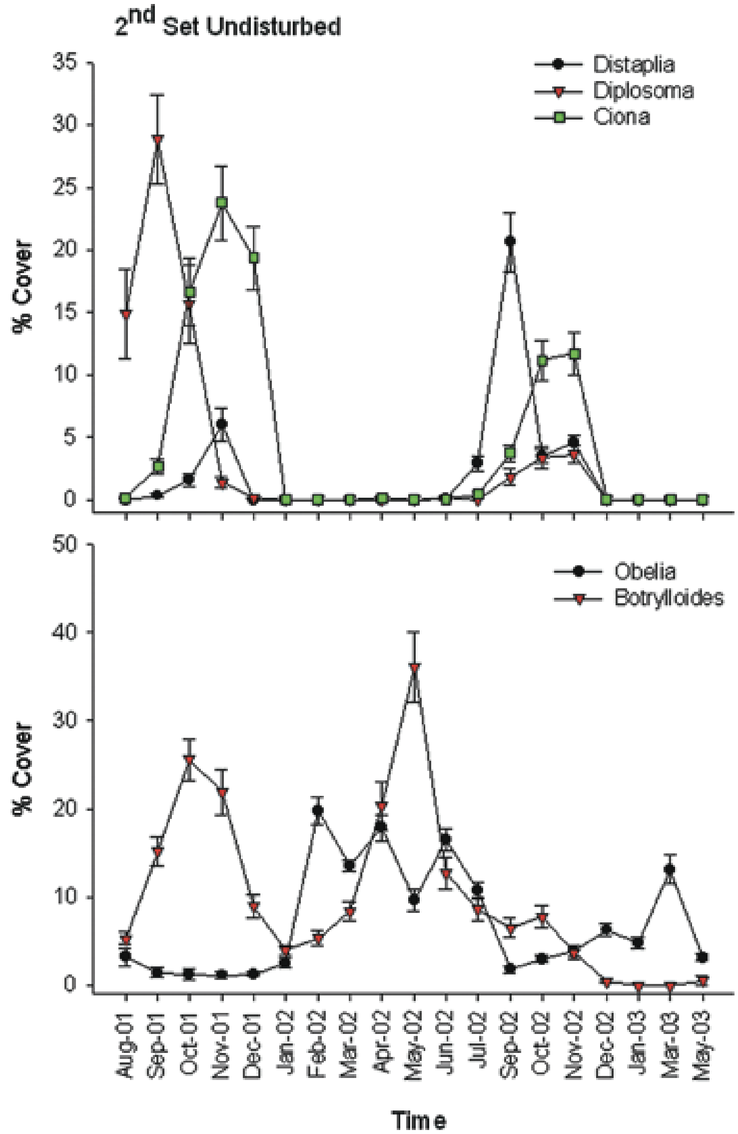

Figure 3a. Mean percent cover (± 1 S.E.) of subtidal invertebrates on undisturbed fouling panels over time at Woodley Island Marina, Humboldt Bay, California. Graphs present the more common species occupying space on panels during the sampling period (August 2001–May 2003).

b.

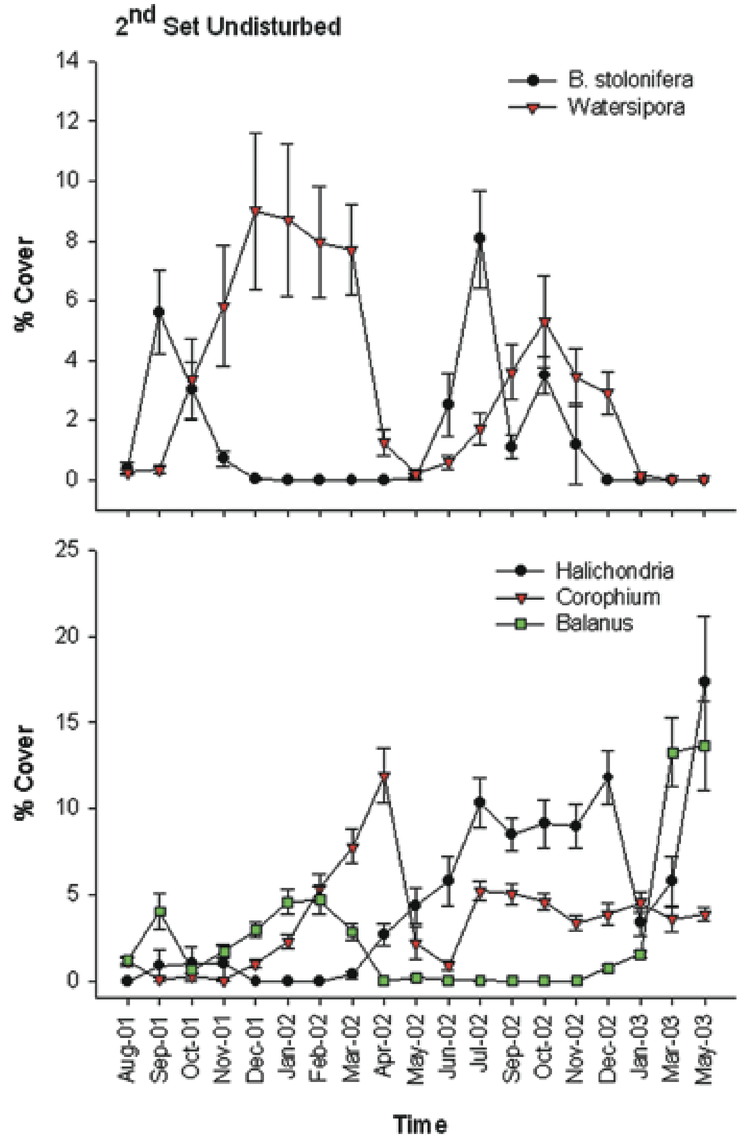

Figure 3b. Mean percent cover (± 1 S.E.) of subtidal invertebrates on undisturbed fouling panels over time at Woodley Island Marina, Humboldt Bay, California. Graphs present the more common species occupying space on panels during the sampling period (August 2001–May 2003).

Table 1. Sessile invertebrate fouling species identified from photographs of panels deployed under the Woodley Island Marina, Humboldt Bay, California. E = Exotic; N = Native. (Note: understory species were not sampled, so this list is not exhaustive)

Porifera		**Bryozoa**	
Halichondria bowerbanki	E	*Alcyonidium polyoum*	E
Haliclona sp.	N	*Celleporella hyalina*	E
Cnidaria		*Bugula californica*	N
Obelia dichotoma	E	*Bugula stolonifera*	N
Tubularia crocea	N	*Bugula neritina*	E
Plumularia setacea	N	*Bowerbankia gracilis*	E
Diadumene leucolena	E	*Watersipora subtorquata*	E
Metridium senile	N	*Schizoporella unicornis*	E
Polychaeta		*Scrupocellaria diagenesis*	N
Schizobranchia insignis	N	**Urochordata**	
Eudistylia vancouveri	N	*Botrylloides* sp.	E
Myxicola infundibulum	E	*Botryllus* sp.	E
Bivalvia		*Botryllus tuberatus*	E
Mytilus trossulus	N	*Ciona intestinalis*	E
Pododesmus cepio	N	*Mogula manhattensis*	E
Crustacea		*Styela clava*	E
Balanus crenatus	N	*Diplosoma macdonaldi*	N
Balanus nubilus	N	*Distaplia occidentalis*	N
		Pyura haustor	N