



Spatial and Temporal Variability in Early Successional Patterns of an Invertebrate Assemblage at an Offshore Oil Platform

Final Technical Summary

Final Study Report



**U.S. Department of the Interior
Minerals Management Service
Pacific OCS Region**

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FINAL TECHNICAL SUMMARY

STUDY TITLE: Early Development of Fouling Communities on Offshore Oil Platforms

REPORT TITLE: Spatial and Temporal Variability in Early Successional Patterns of an Invertebrate Assemblage at an Offshore Oil Platform

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BACKGROUND: The subtidal portions of offshore oil platforms provide a hard attachment site for an assemblage of invertebrates that can reach tens of centimeters in thickness. Many of the species inhabiting platforms off the coast of California are also typically found in local rocky intertidal and subtidal habitats. Interest in the biotic assemblages associated with platforms has increased recently because of the “rigs to reefs” concept. The potential function of such structures as artificial reefs may vary greatly with location, depth and configuration. However, there is a general lack of published information on factors affecting patterns of development or processes that can influence the rate of development and composition of the invertebrate assemblages on offshore platforms.

OBJECTIVES: The objectives of this study were primarily to: 1) test the effects of water depth and time, including time of year and year, on the rate of colonization, species composition, and cover of the invertebrate assemblage at an offshore platform through the manipulation of artificial substrata (tiles) attached to the structure, 2) explore the potential influence of selected taxa that occur early in the successional sequence on the relative abundance of other colonists, and 3) evaluate the importance of depth and time on the accumulation of invertebrate biomass on the platform structure.

DESCRIPTION: This study was conducted at the oil and natural gas production platform “Houchin” (Pacific Operators Offshore, Inc.), located 6.6 km offshore of Carpinteria, California, in the Santa Barbara Channel (34°20'N, 119°33'W) in a water depth of ~49 m. Just prior to the initiation of this study, invertebrates attached to the platform structure were removed to a depth of 18 m during routine maintenance operations. We used unglazed ceramic tiles to experimentally investigate the effects of depth, time of year, and year on patterns of development of the invertebrate assemblage.

The tiles (15 x 15 cm) were attached to the platform at three depths (6, 12, 18 m), randomly assigned to a length of deployment of either 2, 4, 6, 12, or 24 months, and replaced following retrieval, thus allowing data gathered for each length of deployment to be independent through time. Deployment of tiles was initiated in April 1999 and terminated in April 2001. To explore the effect of selected early colonists and depth on patterns of development of the invertebrate assemblage, we conducted a second experiment from June 2002 through June 2003 in which selected taxa were routinely removed from experimental tiles. In addition, scrapings were collected from the recently cleaned platform surface after designated intervals (2, 4, 6, 12 months) at three depths (6, 12, 18 m) from September 1999 to July 2001, and the more structurally complex tuffys were deployed monthly from May 1999 to April 2001. At an adjacent platform, rates of faunal litterfall of invertebrates from the platform to the benthos were measured.

SIGNIFICANT CONCLUSIONS: The invertebrate assemblage that developed on the tiles submerged at Platform Houchin was composed of taxonomic groups commonly reported from other subtidal hard substrate habitats, including coastal rocky reefs in the Santa Barbara Channel. There was, however, a notable absence of macroalgae on the tiles.

Colonial tunicates were predictable early colonists of the tiles. Colonial tunicates are often considered “opportunistic” and poor competitors and our data suggest that later colonists negatively influenced the rates of recruitment, growth, or survival of tunicates as submersion time increased. Encrusting bryozoans were also early colonists of the tiles, but the cover of this taxon varied less predictably over time than tunicates. With longer submersion times, the overall cover of bryozoans decreased, suggesting that later colonizing taxa also inhibited the recruitment and/ or growth of bryozoans. Other taxa, including tubicolous amphipods, barnacles, and sponges occurred on the 2-month tiles in variable and generally low cover. Among these taxa, the cover of tubicolous amphipods (as amphipod tube mat) was highest, but generally much less than 20%. Since open space was available on the tiles for up to 6 months, the availability of this resource did not appear to limit amphipod recruitment or growth. The mean cover and variability in cover of amphipods generally increased with

increasing submersion time up to 6 months, suggesting that the increase in surface complexity over time provided by other attached organisms could have facilitated the recruitment and/or survival of amphipods. However, in our study, the removal of tunicates, bryozoans, or barnacles did not result in a significant decrease in the cover of amphipods, suggesting that factors other than these early colonists influenced the cover of amphipod tube mat.

Cover of barnacles and sponges on the 2-month tiles was typically very low. Open space was still available after 2 months and there was no evidence to suggest that barnacles or sponges were inhibited from settling or were overgrown by taxa already on the tiles. It is likely that the cover of barnacles and sponges was determined by factors such as larval supply, post-settlement survival, and/or growth rate.

Depth greatly influenced the cover of bryozoans, amphipods, barnacles, sponges, and mussels on the tiles. However, the effect of depth on cover varied among taxa. For example, barnacles appeared earlier (after 2 months) and were present in significantly higher cover at 6 m (55% after 24 months) compared with the deeper depths (<28% after 24 months). In contrast, bryozoans were present in higher cover and persisted longer on tiles at deeper depths. The data from our removal experiment also suggest that depth-related variation in the distribution and cover of species occurring early in the successional sequence (i.e., bryozoans, amphipods, barnacles) was not the result of interspecific interactions. Our results suggest the alternative explanation that the distribution and abundance of these taxa was related to variation in the density of larvae (or juvenile amphipods) available for settlement among depths.

Mussels appeared later in the successional sequence. Mussel recruitment was low during this study; mussels occurred only at 6 m on the 12 and 24-month tiles in 2000-2001 (Figs. 3f, 6d). The lack of mussels on tiles at deeper depths (12 and 18 m) may indicate that mussel larvae were not present. However, mussels have been shown to recruit and grow on platforms in the Santa Barbara Channel to depths exceeding 18 m. The higher cover of barnacles at the shallowest depth (6 m) may have facilitated mussel attachment at this depth by providing a more rugose substrate, whereas the low density of barnacles at 12 and 18 m may have retarded mussel recruitment at those depths.

Some taxa (sponges, barnacles, mussels) occurred in much higher cover (and density for barnacles) on the tiles in 2000-2001 compared with 1999-2000. Rates of recruitment of these taxa may have been influenced by differences in oceanic conditions between the two years. A record coastal upwelling event occurred in Spring 1999 and coastal upwelling continued in the Southern California Bight through Summer 1999.

The development of the invertebrate assemblage on the tiles submerged at Platform Houchin could not be categorized as classical succession, but was clearly not random. Development of this assemblage appears to fit the pattern where a combination of life history of the constituent species, settlement preferences, and responses to spatial and temporal environmental variability create a pattern of early succession that was largely predictable in terms of the sequence of occurrence of dominant species, but variable in rate, depending on time of year or depth of tile submersion.

STUDY RESULTS: A total of 41 invertebrate genera from 6 phyla and unidentified taxa of a seventh phylum (Porifera) colonized the tiles. Colonial tunicates and encrusting bryozoans were consistent early colonists on the tiles across all depths. Tubicolous amphipods were also early colonists of the tiles, but highest cover of this taxon generally occurred after 6 or 12 months. Between 12 and 24 months, the cover of amphipod tube mat remained unchanged or declined slightly at all depths. Barnacles could occur on the tiles at 6 m after 2 months and generally increased in cover over time at all depths, with a much slower increase occurring at 12 and 18 m compared with 6 m. Cover of barnacles was higher on tiles at 6 m compared with 12 and 18 m. Sponges were largely absent from tiles submerged for <12 months, but greatly increased in cover from 12 to 24 months at all depths, with significantly higher cover at 12 and 18 m compared with 6 m at 24 months. Mussels were also later colonists, occurring on the tiles only at a depth of 6 m after 12 months.

In the removal experiment, colonial tunicates, encrusting bryozoans, amphipod tube mat, and barnacles comprised 82-88% of total cover on the controls at each depth after 12 months. In the tunicate removal treatment, the mean cover of amphipod tube mat, encrusting bryozoans, barnacles, and open space did not differ from the control; there was a trend of higher cover of bryozoans in the removal treatment. In the bryozoan removal treatment, only the mean cover of open space was higher than the control. In the barnacle removal treatment, only the cover of bryozoans was significantly higher than the control. A significant effect of depth on the cover of the tile assemblage was found in the barnacle removal treatment where the percent cover of amphipod tube mat decreased with increase in depth. There was a marginally significant increase in the cover of bryozoans in the tunicate removal treatment with increase in depth.

The standing crop biomass of the invertebrates varied significantly with depth, year, and time from scraping. The accumulation of biomass always increased with increased exposure time, was highest at a depth of 6 m, and was greater in 2000-2001 compared with 1999-2000 on both the tiles and on the scraped platform surfaces. The standing crop biomass of the invertebrates on the tuffys also varied significantly with depth. The accumulation of biomass was highest at a depth of 6 m and lowest at the 18 m depth. A marked increase in biomass occurred between April and June of 2000 at all three depths. Most of the biomass found on the tuffys (>99%) was made up of gammarid and caprellid amphipods.

Mussels, hydroids, bryozoans, sponges, and barnacles accounted for nearly all (>99%) of the invertebrate biomass in the litterfall traps. Mussels accounted for the greatest biomass of any taxa in all but 3 months. Faunal litterfall tended to be highest in the spring and summer months and lowest in the winter months.

STUDY PRODUCTS:

Presentations:

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Page, H. M. 2001. Ecology of offshore oil platforms and mussel mounds in the Santa Barbara Channel. Invited seminar speaker. Bodega Marine Laboratory.

Publications:

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Bram, J. B., H. M. Page, and J. E. Dugan. *Spatial and temporal variability in early successional patterns of an invertebrate assemblage at an offshore oil platform*. *Journal of Experimental Marine Biology and Ecology*, in press.

FINAL STUDY REPORT

INTRODUCTION

The process of change in species composition during the colonization of open space is defined as succession (Horn, 1974; Connell and Slatyer, 1977). Classical succession is considered to be an orderly and directional process that results from the alteration of the physical environment by the developing community, eventually leading to a climax community (Clements, 1936; Odum, 1969; Colinviaux, 1973). Classical successional theory was originally derived from studies of terrestrial plant associations, and has now been applied to many other types of assemblages, including those in the marine habitat (e.g. Drury and Nisbet, 1973; Connell and Slatyer, 1977). The concept of succession has been used to predict how an assemblage will change over time and to understand processes responsible for these changes. However, in many systems, no single successional model has successfully accounted for changes in community structure over time and descriptions of succession may often involve more than one model (Connell and Slatyer, 1977; Dean and Hurd, 1980, Walker and Chapin, 1987; Farrell, 1991).

The development of epibenthic assemblages on hard substrates in the marine environment has been the subject of numerous investigations (e.g., Scheer, 1945; Sutherland and Karlson, 1977; Greene and Schoener, 1982; Underwood and Anderson, 1994). These assemblages provide useful systems for ecological study because of the presence of an easily defined limiting resource (space), the relative ease of experimental manipulation, and high species turnover over short time spans (Dean and Hurd, 1980). Several studies have found evidence supporting the idea of succession occurring through a predictable progression of species (Scheer, 1945; Sousa, 1979ab; Vance, 1988; Farrell, 1991). However, results from other studies have suggested that succession may be less predictable. For example, patterns of succession in hard-bottom assemblages were found to vary both temporally (Sutherland and Karlson, 1977; Turner and Todd, 1993; Underwood and Anderson, 1994; Chapman, 2002) and with water depth (Ojeda and Dearborn, 1989; Smith and Witman, 1999; Garrabou et al., 2002). Thus, the predictability of successional patterns may vary with the specific habitat or assemblage being studied (Underwood and Anderson, 1994).

The subtidal portions of oil platforms off the coast of California provide habitat for an assemblage of invertebrates that can reach tens of centimeters in thickness (Wolfson et al., 1979; Page et al., 1999). Many of the species attached to platforms are also found in local rocky intertidal and subtidal habitats. However, the physical and biological environment at offshore platforms differs from that of inshore rocky intertidal and subtidal reefs. Platforms in the Santa Barbara Channel are located offshore (>3 km) on soft-bottom in deeper water (>30 m depth). The platform invertebrate assemblage experiences fully oceanic conditions of water temperature, salinity, and current flow, and invertebrate growth rates are rapid compared to inshore habitats (Page, 1986; Page and Hubbard, 1987). In addition, the densities of grazers (e.g., urchins, gastropods), which can reach 10-17 individuals m⁻² on inshore subtidal rocky reefs (Breitburg, 1985), are

much lower on platforms (Page, unpubl. data). Disturbance in the form of storm swell and maintenance operations opens up space for colonization on the platform structure through the dislodgement of invertebrates (Page et al., 1999).

There is little published information on factors affecting patterns of development or processes that can influence the rate of development and composition of the invertebrate assemblage on platforms. However, two studies in natural habitats in the southern California region provide alternative scenarios that could occur during succession on offshore platforms in the Santa Barbara Channel. Vance (1988) found predictable patterns of succession of macroalgae and sessile invertebrates on a subtidal vertical rock wall (~15 m depth) near Santa Catalina Island (30 km south of Los Angeles, California), which with some variation was repeatable from season to season and year to year. In contrast, Breitburg (1985) found species succession to be dominated by macroalgae, particularly encrusting coralline algae, and strongly influenced by grazers on experimental plates deployed at a subtidal rocky reef (~15 m depth) near Santa Barbara, California.

Based on the physical conditions present offshore, and the scarcity of grazers that could influence the course of succession, we predicted that development of the platform assemblage might conform more closely to the successional pattern found by Vance (1988) than the pattern found on local rocky reefs by Breitburg (1985). In addition, early colonists may influence the rate of recruitment or survival of subsequent colonists through inhibitory or facilitative interactions (e.g., Connell and Slatyer, 1977; Sutherland, 1978; Dean and Hurd, 1980; Breitburg, 1985); these interactions could explain temporal and spatial variation in patterns of succession.

In this study, we tested the following hypotheses through the manipulation of artificial substrata (tiles) attached to an offshore platform: 1) development of the platform assemblage occurs through a predictable succession of species or taxa, 2) the rate of development, cover, and composition of the assemblage varies with date, year, length, and depth of submersion, and 3) biotic interactions can modify the cover and composition of the developing assemblage.

MATERIALS AND METHODS

Study Site

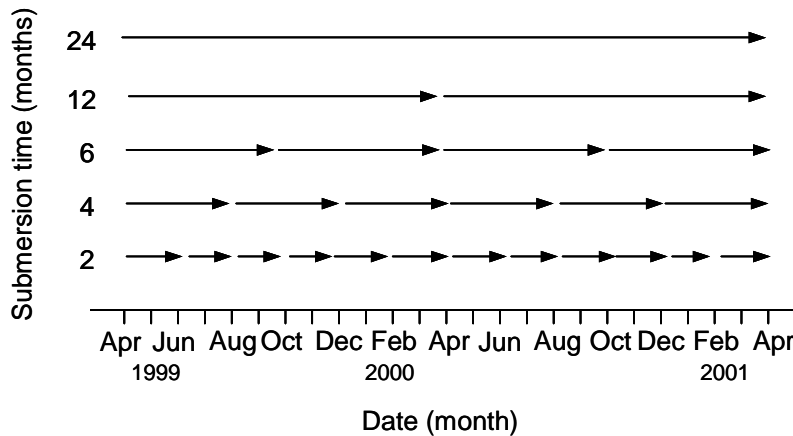
This study was conducted at the oil and natural gas production platform “Houchin” (Pacific Operators Offshore, Inc.), which is located 6.6 km offshore of Carpinteria, California, in the Santa Barbara Channel (34°20'N, 119°33'W) in a water depth of ~49 m. The submerged portion of the platform consists of vertical, oblique, and horizontal cylindrical cross members, which provide support to the structure, and conductor pipes, through which wells are drilled. The assemblage of sessile and semi-mobile invertebrates that colonize the support members and conductor pipes of Platform Houchin are also found on other platforms in southern California (Simpson, 1977; Wolfson et al., 1979;

Page et al., 1999). Invertebrates that are prominent space-holders on the platform at shallow depths (to ~6 m) include mussels (*Mytilus californianus*, Conrad, 1837, *M. galloprovincialis*, Lamarck, 1819), barnacles (e.g. *Megabalanus californicus*, Pilsbry, 1916, *Balanus trigonus*, Darwin, 1854) and the strawberry anemone (*Corynactis californica*, Carlgren, 1936), with encrusting bivalves (*Crassadoma gigantea*, J. E. Gray, 1825) and the white plumed anemone (*Metridium senile*, Linnaeus, 1761) more abundant deeper. Just prior to the initiation of this study, invertebrates attached to the platform structure were removed to a depth of 18 m during routine maintenance operations.

Development of the assemblage

We used unglazed ceramic tiles (15 x 15 cm) attached in groups of five to experimental frames to test the first two hypotheses. Each frame (15 x 105 cm) was constructed of PVC pipe reinforced with rebar. Individual frames, containing five tiles each, were attached to four adjacent vertical conductor pipes at depths of 6, 12, and 18 m (n=4 frames for each depth). Adjacent conductor pipes were located ~1.5 m apart. Each tile in a frame was randomly assigned a submersion time of 2, 4, 6, 12, or 24 months and replaced at the specified time with a new tile (except for the 24 month tiles) (Fig. 1). Each tile was only censused once. Thus, over the 24 month duration of the experiment, data were obtained from 12 sets of tiles submerged for 2 months, 6 sets for 4 months, 4 sets for 6 months, 2 sets for 12 months, and one set for 24 months. Since tiles were replaced with new tiles following retrieval, data gathered for each length of submersion were independent through time (Underwood and Anderson, 1994). The smooth side of each tile was used as the sampling surface and oriented outward from the platform.

Figure 1. Arrows indicate the schedule for the deployment and retrieval of tiles submerged in the field for periods of 2, 4, 6, 12, or 24 months at depths of 6, 12, or 18 m. Retrieved tiles were replaced with new tiles (n=4 for each depth).



During the course of the study, a few large individuals of the anemone, *Metridium senile*, moved onto a few of the tiles from the adjacent platform structure, thereby occupying space on the tile and potentially inhibiting the recruitment of other invertebrates. Once a month, SCUBA divers inspected the tiles and all large anemones that had moved onto the tiles were removed. On collection, the tiles were carefully placed in plastic bags *in situ* and transported to the laboratory. In the laboratory, the tiles were photographed to aid in species identification, and then frozen for later analysis. Tiles were first deployed in April 1999 and the experiment was terminated in April 2001.

We identified and measured the percent cover of invertebrates on each tile using point-contact sampling (Underwood and Anderson, 1994). A pin (1 mm diameter) was inserted through each of 50 holes spread uniformly throughout a clear fiberglass grid situated above the tile. All organisms touched by the pin were identified and recorded. The percent cover of each species was determined by multiplying the number of contacts by two. Due to the layering of species on the tile, the pin could contact more than one species and the total cover could exceed 100%. Non-sessile species, such as brittlestars, were removed prior to point contact analysis. Tubicolous amphipods were quantified using percent cover of their tube mat. Due to the difficulty in identifying some of the organisms to species level, data were combined into higher taxonomic categories for statistical analyses.

We also quantified barnacle density by counting individuals on each tile. Four species of barnacles were found during the study (*Megabalanus californicus*, *Balanus trigonus*, *Balanus pacificus*, Pilsbry, 1916, *Balanus regalis*, Pilsbry, 1916). For statistical analysis, all the barnacle data were pooled due to the difficulty of accurately determining the species of new recruits.

Biotic interactions

To test the effect of early colonists and depth on assemblage development, we conducted a second experiment from June 2002 through June 2003 in which selected early colonizing taxa were routinely removed from experimental tiles. Individual frames, each with four unglazed ceramic tiles (15 x 15 cm), were attached to four adjacent conductor pipes at depths of 6, 12, and 18 m (n=4 frames for each depth). Each tile in a frame was randomly assigned to one of four treatments in which either 1) colonial tunicates, 2) encrusting bryozoans, or 3) barnacles were removed, or 4) no taxa were removed (control). The taxa selected for removal were chosen based on their appearance early in the successional sequence in the previous experiment and their potential to affect the rate of colonization, species composition and cover of the developing assemblage. Colonial tunicates can grow rapidly and have been reported to inhibit barnacle recruitment (Young and Gotelli, 1988). Encrusting bryozoans can also inhibit the recruitment and growth of other species (Sutherland and Karlson, 1977). Barnacles have been reported to inhibit the recruitment of tunicates, but facilitate the recruitment of mussels (Dean and Hurd, 1980). As in the preceding experiment, the smooth side of each tile was used as the sampling surface and oriented outward from the platform.

Every 4 weeks, SCUBA divers inspected the tiles and carefully removed the appropriate taxon from each treatment using a small spatula. As described earlier, individuals of the anemone, *Metridium senile*, which migrated onto the tiles, were removed. On termination of the experiment, the tiles were carefully placed in plastic bags *in situ* and transported to the laboratory. The tiles were then frozen for later analysis. We identified and measured the percent cover of invertebrates on each tile using the point-contact sampling method described above.

Statistical analysis

All statistical analyses were conducted using Systat 10 (SPSS). The main effects of date and depth for each length of submersion (first experiment) or the removal of taxa from the tiles and depth (second experiment) on the percent cover of selected taxa (and also density for barnacles) was explored using Analysis of Variance (ANOVA). We tested the main effects using a split plot model where all the tile treatment combinations were present within each “whole plot” (pipe x depth combination); error terms were calculated as in Hicks (1999). The percent cover data were arcsine transformed ($x' = \arcsin \sqrt{x}$) and the barnacle density data were log transformed ($x' = \log_{10}(x + 1)$) prior to analysis (Zar, 1999).

RESULTS

Development of the assemblage

Invertebrate species from 7 phyla colonized the tiles (Table 1). Invertebrate taxa important as space holders included a colonial tunicate (*Diplosoma listerianum*, Macdonald, 1859), encrusting bryozoans (*Dendrobeania laxa*, Robertson, 1905, *Membranipora serrilamella*, Osburn, 1950), tubicolous amphipods (*Erichthonius* sp., Milne-Edwards, 1830), barnacles (*Balanus trigonus*, *Balanus pacificus*, *Megabalanus californicus*), and sponges. No macroscopic algae colonized the tiles.

Colonial tunicates (primarily *Diplosoma listerianum*) were consistently among the first taxa to colonize the tiles. Mean cover of tunicates on the 2-month tiles was highly variable across sampling dates, with a significant date x depth interaction ($P < 0.001$, $F = 3.664$, $df = 22, 66$, ANOVA) (Fig. 2a). Cover of this taxon on the 2-months was highest (62-78%) in late summer and fall (August, October) and lowest (<5%) in spring and early summer (April, June). With increased submersion time, temporal variation in the cover of tunicates became less evident (Fig. 2b), and was not significant ($P > 0.1$) on the 6-month tiles where cover was <25% at 12 m and <10% at 6 and 18 m (Fig. 2c). There was significant effect of depth on the mean cover of colonial tunicates only for the 6-month tiles ($P = 0.003$, $F = 17.953$, $df = 2, 6$, date x depth interaction, $P > 0.1$).

Encrusting bryozoans (primarily *Dendrobeatia laxa*) were also early colonizers of the tiles (Fig. 2d). There was a significant date x depth interaction in the mean cover of bryozoans on the 2-month tiles ($P < 0.001$, $F = 3.558$, $df = 22, 66$, ANOVA) with a suggestion of seasonality at 18 m where highest cover occurred in late summer-early fall.

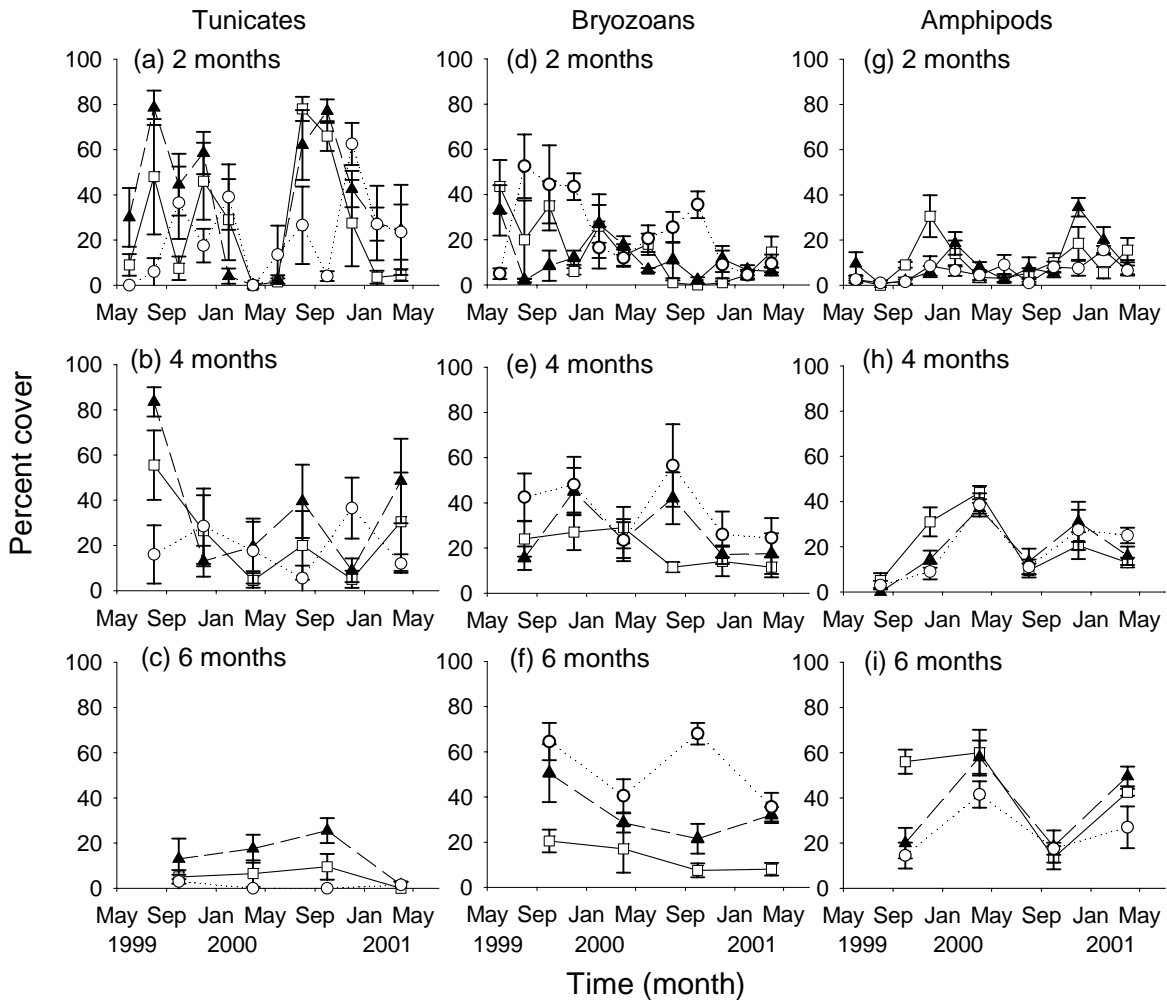
Table 1. List of sessile invertebrates on the settlement plates during the study.

Phylum		Species				
Porifera	Sponges	Unidentified				
Cnidaria	Anemones	<i>Corynactis californica</i> <i>Epiactis prolifera</i>				
	Hydrozoans	<i>Aglaophenia latirostris</i> <i>Plumularia</i> sp. <i>Tubularia crocea</i>				
Ectoprocta	Bryozoans	<i>Bugula neritina</i> <i>Celleporella brunnea</i> <i>Celleporella hyalina</i> <i>Crisulipora occidentalis</i> <i>Dendrobeatia laxa</i> <i>Filicrisia franciscana</i> <i>Membranipora serrilamella</i> <i>Rynchozoan rostratum</i> <i>Tubulipora pacifica</i> <i>Tubulipora tuba</i>				
		Chordata	Tunicates	<i>Botrylloides diegensis</i> <i>Diplosoma listerianum</i> <i>Styela truncata</i>		
		Mollusca	Bivalves	<i>Crassodoma giganteus</i> <i>Hiatella arctica</i> <i>Kellia suborbicularis</i> <i>Mytilus californianus</i> <i>Mytilus galloprovincialis</i> <i>Megatebennus bimaculatus</i>		
				Annelida	Gastropods	<i>Halosydna brevisetosa</i>
					Polychaetes	<i>Serpula vermicularis</i> <i>Spirorbis</i> sp.
		Arthropoda	Amphipods	<i>Caprella californica</i> <i>Caprella equilibra</i> <i>Caprella verrucosa</i> <i>Dulchiella</i> sp. <i>Elasmopus</i> sp. <i>Erichthonius</i> sp. <i>Gammeropsus</i> sp. <i>Podacerus</i> sp. <i>Pleustimptes</i> sp. <i>Stenothoe</i> sp.		
				Barnacles	<i>Balanus pacificus</i> <i>Balanus regalis</i> <i>Balanus trigonus</i> <i>Megabalanus californicus</i>	

Unlike the pattern for colonial tunicates, overall cover and temporal variability in the cover of bryozoans did not decrease with increase in submersion time from 4 to 6 months (Fig. 2e, f: $P>0.1$). However, the increase in cover of encrusting bryozoans with depth became pronounced on the 6-month tiles (depth: $P<0.001$, $F=40.861$, $df=2, 6$; date x depth interaction: $P>0.1$, ANOVA).

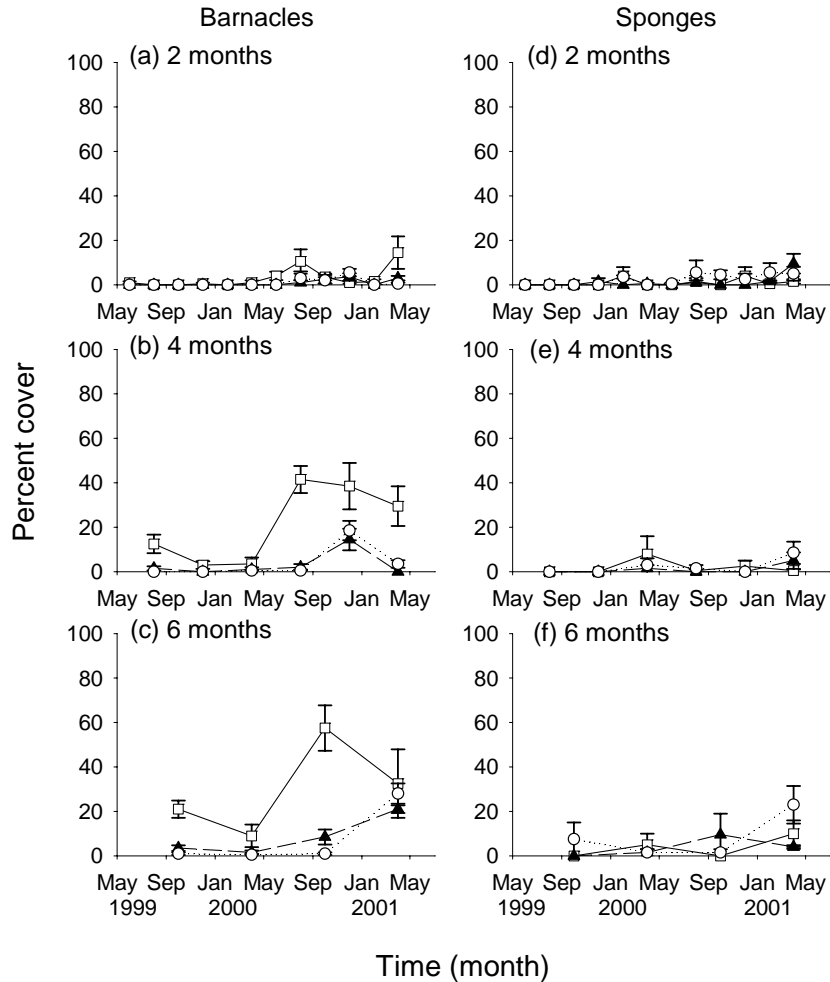
Tubicolous amphipods could also colonize tiles early but, if present, generally occurred in low cover (<10% on 2-month tiles: Fig. 2g). Exceptions were observed in December 1999 at 6 m and in December 2000 at 12 m when the mean cover of amphipod tubes was ~30% on the 2-month tiles. There was a significant date x depth interaction in the mean cover of amphipod tube mat on the 2, 4, and 6-month tiles (date x depth interaction, $P<0.001$, ANOVA) (Fig. 2g-i); peaks in cover occurred in the spring on the 4 and 6-month tiles. The cover of amphipod tube mat increased with time of submersion from 2 to 6-months, and generally ranged from 15-20% in the fall (October) to 40-60% in the spring (June) after 6 months (Fig. 2i).

Figure 2. Mean percent cover (± 1 SE, $n=4$) of colonial tunicates (a-c), encrusting bryozoans (d-f), and amphipod tube mat (g-i) after 2, 4, and 6 months of submersion at 6 (\square), 12 (\blacktriangle), or 18 (\circ) m.



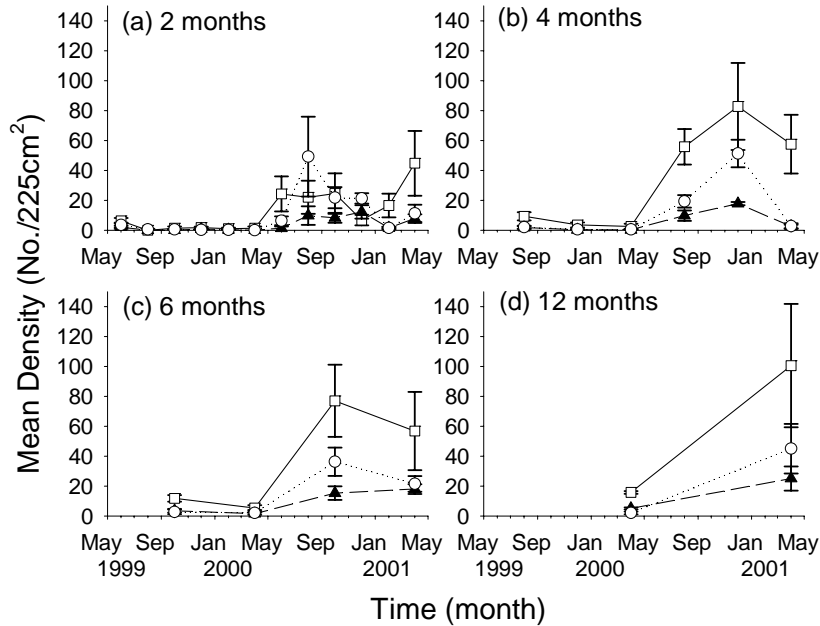
The cover of barnacles was consistently low (generally <10%) on the 2-month tiles at all depths and well-defined seasonality in the cover of this taxon was not evident (Fig. 3a). However, as submersion time increased, the cover of barnacles also increased, particularly during the second year (Fig. 3a-c). Cover of barnacles also varied among depths; highest cover was observed at 6 m on the 4 and 6-month tiles.

Figure 3. Mean percent cover (± 1 SE, n=4) of barnacles (a-c) and sponges (d-f) after 2, 4, and 6 months of submersion at 6 (\square), 12 (\blacktriangle), or 18 (\circ) m.



Spatial and temporal patterns in the density of barnacles were generally similar to those for percent cover with highest densities at 6 m on the 4 and 6-month tiles (Fig. 4b, c). Very little barnacle recruitment occurred in the first year. For example, on the 2-month tiles at 6 m, there was a mean of 1.9 individuals 225 cm⁻² in the first year compared with 23.1 individuals 225 cm⁻² in the second year (Fig. 4a). In the second year, barnacle density was higher at 6 m than 12 and 18 m on the 12-month tiles ($P=0.008$, $F=17.775$, $df=2, 6$, ANOVA, $P<0.05$, Tukey post hoc test). (*Mytilus californianus*, *M. galloprovincialis*) were later colonists, occurring on the tiles in low cover (<10%) only at a depth of 6 m after 12 months (Fig. 5f).

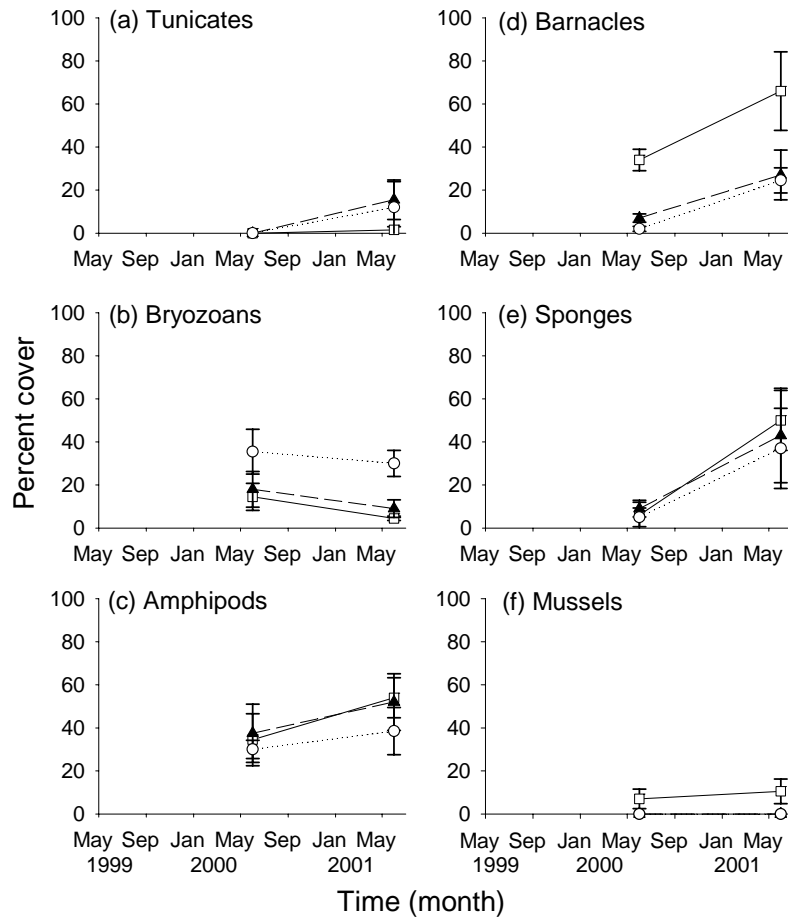
Figure 4. Mean density (± 1 SE, $n=4$) of barnacles after 2, 4, 6, and 12 months of submersion at 6 (\square), 12 (\blacktriangle), or 18 (\circ) m.



There was no difference in the percent cover of colonial tunicates, encrusting bryozoans, or amphipod tube mat between 12-month tiles submerged in April 1999 and April 2000 ($P>0.1$, ANOVA: Fig. 5). There was also no difference ($P>0.1$) in the cover of mussels on the 12-month tiles between years (Fig. 5f). In contrast, barnacles and sponges occurred in significantly higher cover on 12-month tiles submerged in 2000 compared with 1999 (barnacles, $P=0.008$, $F=38.646$, $df=1, 3$; sponges, $P=0.005$, $F=55.359$, $df=1, 3$, year \times depth interaction for both taxa, $P>0.1$: Fig. 5). In addition, there was a significant effect of depth on the cover of barnacles ($P=0.009$, $F=11.231$, $df=2, 6$).

The mean cover of uncolonized or open space on the 2-month tiles was highly variable, ranging from peaks of 60-90% in spring and early summer (April, June) to 15-40% in the late summer and fall (August, October) with a significant date \times depth interaction ($P<0.001$, $F=5.061$, $df=22, 66$, ANOVA: Fig. 6a). The cover of open space decreased with increasing submersion time to generally $<20\%$ at all depths on the 6-month tiles (Fig. 6c). There were no significant date, depth, or date \times depth interaction effects on cover of open space for the 4-month tiles and a significant time effect only for the 6-month tiles ($P=0.009$, $F=7.257$, $df=3, 9$). Cover of open space on the 12-month tiles was $<5\%$ (not shown).

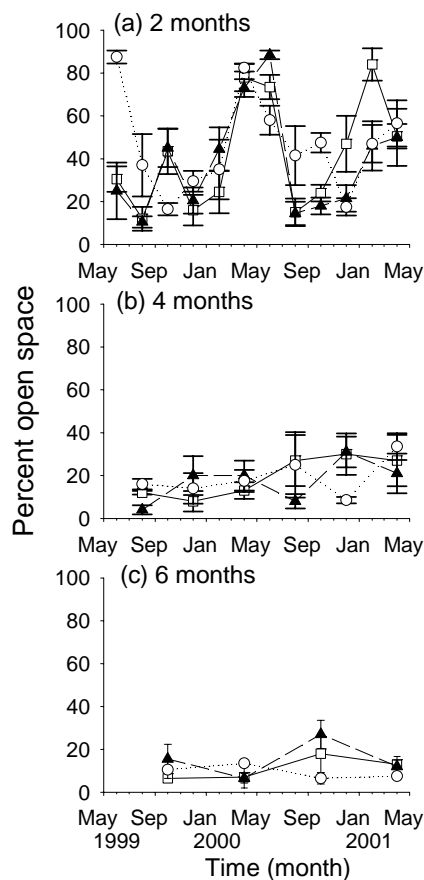
Figure 5. Mean percent cover (± 1 SE, $n=4$) of selected taxa after 12 months of submersion at 6 (\square), 12 (\blacktriangle), or 18 (\circ) m in 1999-2000 and 2000-2001.



Longer-term patterns

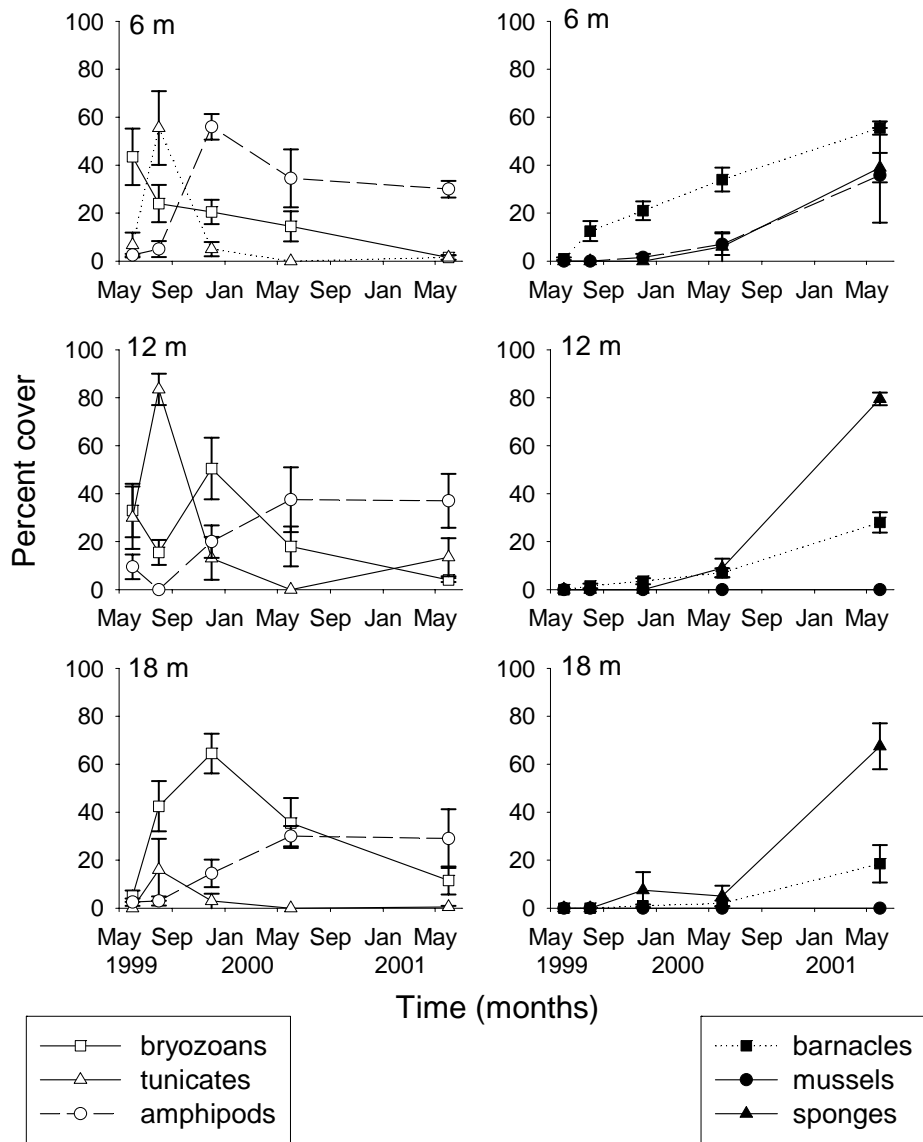
We examined the succession (timing of occurrence and percent cover) of taxa over longer time scales using data from tiles that were submerged in April 1999 and retrieved after 2, 4, 6, 12, and 24 months. Colonial tunicates and encrusting bryozoans were early colonists on the tiles across all depths, but declined to $<15\%$ cover each on the 24-month tiles (Fig. 7). Tubicolous amphipods were also early colonists of the tiles, but highest cover of this taxon generally occurred after 6 or 12 months (Fig. 7). Between 12 and 24 months, the cover of amphipod tube mat remained unchanged or declined slightly at all depths.

Figure 6. Mean percent cover (± 1 SE, $n=4$) of open space after 2, 4, and 6 months of submersion at 6 (\square), 12 (\blacktriangle), or 18 (\circ) m.



Composition of the invertebrate assemblage changed between 12 and 24 months with barnacles, sponges, and mussels becoming the dominant space holders. Barnacles occurred on the tiles at 6 m after 2 months, albeit in very low cover ($\sim 1\%$) in 1999, and generally increased in cover over time at all depths, with a much slower increase occurring at 12 and 18 m ($<10\%$ until 24 months) compared with 6 m ($>20\%$ after 6 months) (Fig. 7). Between 12 and 24 months, cover of barnacles increased 1.6-fold at 6 m, 4-fold at 12 m, and 9-fold at 18 m. Cover of barnacles was higher on tiles at 6 m compared with 12 and 18 m ($P=0.006$, $F=9.786$, $df=2, 9$, One-way ANOVA, $P<0.05$ Tukey post hoc test) on the 24-month tiles. Sponges were largely absent from tiles submerged for <12 months, but greatly increased in cover from 12 to 24 months at all depths, with significantly higher cover at 12 (80%) and 18 m (68%) compared with 6 m (39%) at 24 months ($P=0.011$, $F=7.751$, $df=2, 9$, One-way ANOVA, $P<0.05$, Tukey post hoc test). Cover of mussels also increased greatly (from 7 to 36%) between 12 and 24 months, but only at a depth of 6 m (Fig. 7).

Figure 7. Mean percent cover (± 1 SE, n=4) of selected taxa on tiles submerged in April 1999 at depths of 6, 12, and 18 m after 2, 4, 6, 12, and 24 months of submersion.



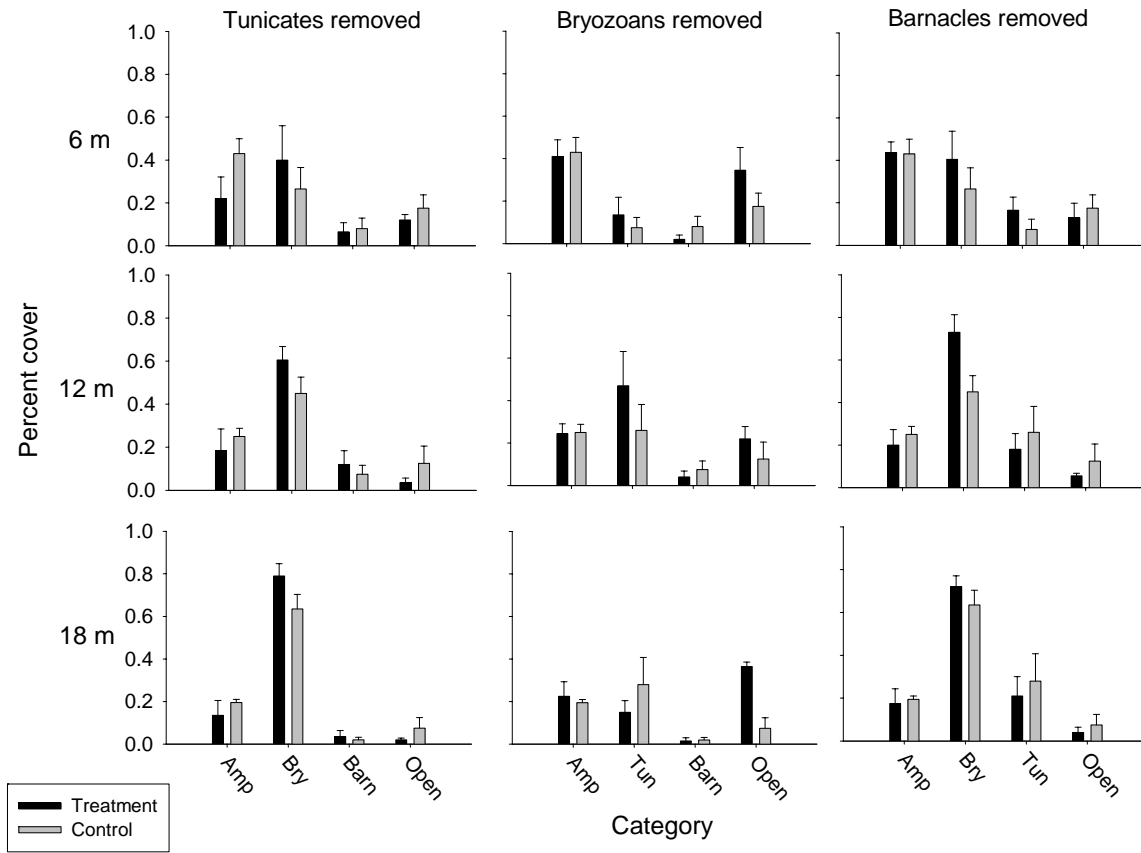
Biotic interactions

In the removal experiment, colonial tunicates, encrusting bryozoans, amphipod tube mat, and barnacles together comprised 82-88% of total cover on the controls at each depth after 12 months (Fig. 8). There were no significant interactions ($P > 0.1$) between removal treatment and depth on the cover of any taxon. In the tunicate removal treatment, the mean cover of amphipod tube mat, encrusting bryozoans, barnacles, and open space did not differ from the control ($P > 0.05$, ANOVA). In the bryozoan removal treatment, only the mean cover of open space was higher than the control ($P = 0.008$, $F = 38.513$, $df = 1, 3$,

ANOVA). In the barnacle removal treatment, only the cover of bryozoans was significantly higher than the control ($P=0.005$, $F=52.606$, $df=1, 3$).

A significant effect of depth on the tile assemblage was found in the barnacle removal treatment where the percent cover of amphipod tube mat decreased with increase in depth ($P=0.02$, $F=4.994$, $df=2, 6$, ANOVA: Fig. 8). There was a trend of increase in the cover of bryozoans in the tunicate removal treatment with increase in depth ($P=0.055$, $F=4.902$, $df=2, 6$: Fig. 8).

Figure 8. Mean percent cover ($\pm 1SE$, $n=4$) of tubicolous amphipods, colonial tunicates, encrusting bryozoans, barnacles, and open space on tiles submerged at depths of 6, 12, or 18 m in which either (a) tunicates, (b) bryozoans, or (c) barnacles were removed monthly for 12 months.



Accumulation of invertebrate biomass on the platform structure

Biomass on conductor pipes and tiles consistently increased with exposure time, was highest at a depth of 6 m, and was higher in 2000-2001 compared with 1999-2000 (Figs. 9, 10). We found no effect of orientation (down current vs. up current) on the accumulation of biomass at the 3 depths.

Figure 9. Mean ($\bar{x} \pm 1SE$, $n=8$) accumulation of biomass at 6 (○), 12 (▲), and 18 m (□) on the surface of conductor pipes on Platform Houchin. Surfaces were initially scraped to remove attached organisms in July 1999.

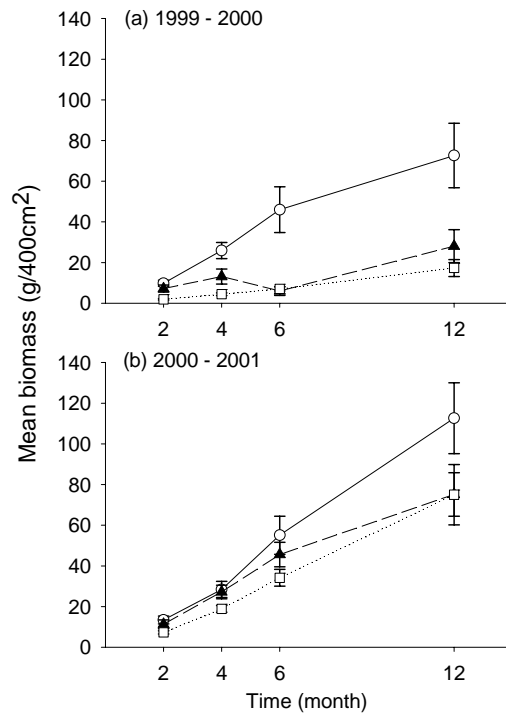


Figure 10. Mean biomass ($\bar{x} \pm 1SE$, $n=8$) of invertebrates on ceramic tiles deployed at depths of 6 (○), 12 (▲), and 18 m (□) for 2, 4, 6 or 12 months at Platform Houchin. The same tiles were used for percent cover estimates (Figs. 2, 3).

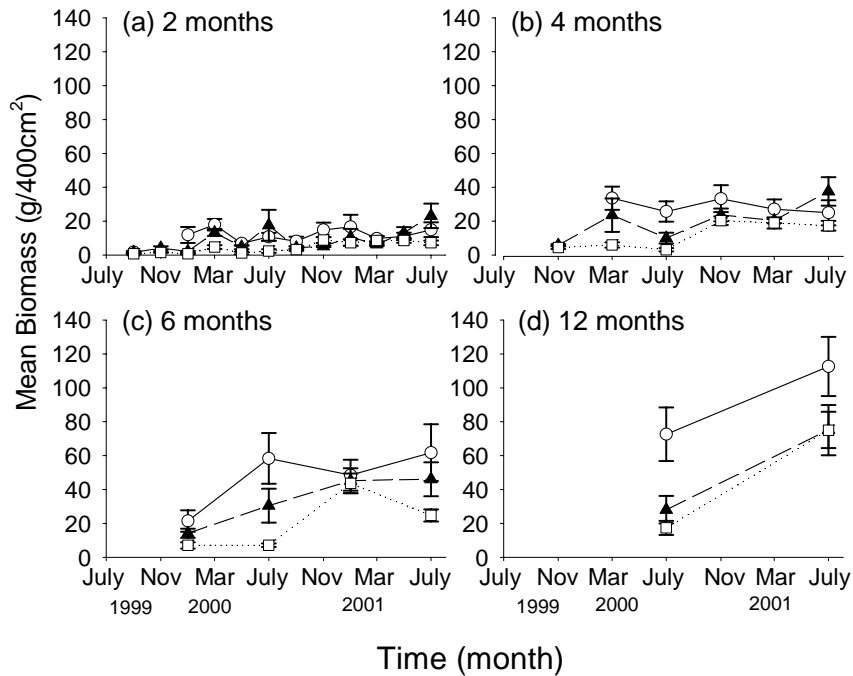
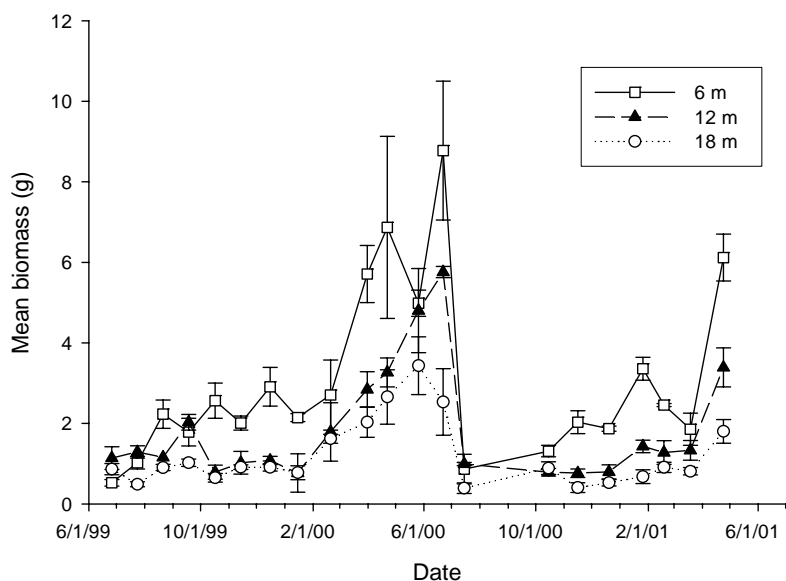


Figure 11. Accumulation of invertebrate biomass in tuffys ($\pm 1SE$, $n=4$) after 1 month of exposure at depths of 6, 12, and 18 m.

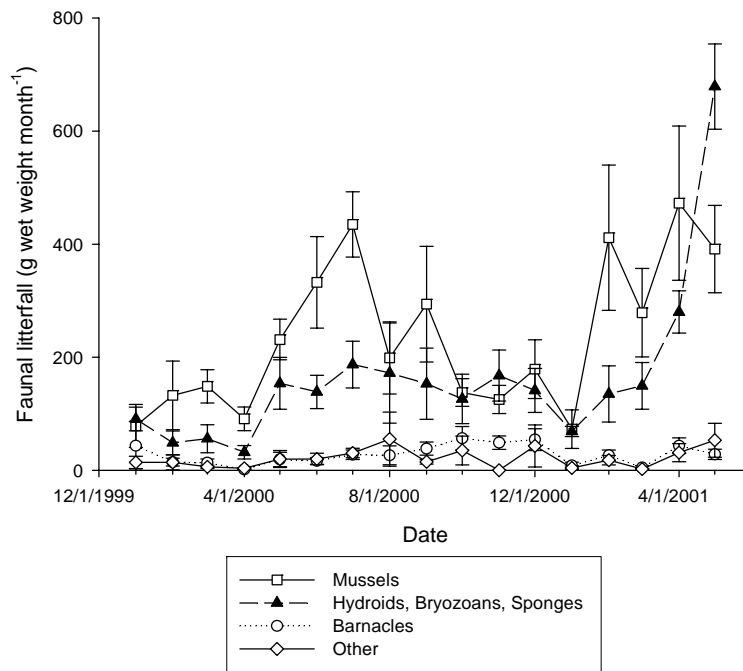


The standing crop biomass of the invertebrates on the tuffys varied significantly with depth ($P < 0.001$, $F = 30.110$, $df = 2$, One-way ANOVA). The accumulation of biomass was highest at a depth of 6 m and lowest at the 18 m depth (Fig. 10). A marked increase in the rate of biomass accumulation occurred between April and June of 2000 at all three depths. Most of the biomass found on the tuffys (>99%) was made up of gammarid and caprellid amphipods.

Composition and rate of faunal litterfall from platform structures

Mussels, hydroids, bryozoans, sponges, and barnacles accounted for nearly all (>99%) of the invertebrate biomass in the litterfall traps (Fig. 11). Mussels accounted for the greatest biomass of any taxa in all but 3 months. Faunal litterfall tended to be highest in the spring and summer months and lowest in the winter months.

Figure 12. Mean biomass (± 1 SE, $n=8$) of invertebrate taxa in faunal litterfall traps deployed at Platform Hogan for 1 month at a depth of 18 m.



DISCUSSION

Development of the assemblage

The invertebrate assemblage that developed on the tiles submerged at Platform Houchin was composed of taxonomic groups commonly reported from other subtidal hard substrate habitats (e.g., Sutherland and Karlson, 1977; Turner and Todd, 1993; Vance, 1988), including coastal rocky reefs in the Santa Barbara Channel (Breitburg, 1985). There was, however, a notable absence of macroalgae on the tiles. Macroalgae are often a conspicuous component of hard substrate assemblages (Sousa, 1984; Breitburg, 1985); however, Bascom et al. (1976) reported that macroalgae were sparse on a platform located ~6 km from our study site. The low abundance of macroalgae on our tiles suggested the possibilities that spores in the plankton were flowing through the platform without settling (Bascom et al., 1976) or that shading provided by the overlying platform superstructure and/or vertical orientation of the conductor pipes negatively influenced algal survival and growth (Baynes, 1999). While we have no data on the availability of algal spores, we have observed filamentous red macroalgae on support members exposed to more direct sunlight around the periphery of the structure, which tends to support the later hypothesis. Forteath et al. (1982) also suggested the importance of light level in influencing the distribution of macroalgae on the legs and support members of a platform (Montrose Alpha) in the North Sea.

The succession of taxa on our tiles generally occurred in a predictable sequence with colonial taxa appearing first. Colonial tunicates occurred in highest cover early in assemblage development (2-month tiles) at all depths (Fig. 2), but comprised only a minor component of the assemblage (<10% cover) on tiles submerged for 12 months. Colonial tunicates are often considered “opportunistic” and poor competitors (Greene et al., 1983, but see Dean and Hurd, 1980; Nandakumar, 1996) and our data support this view by suggesting that later colonists negatively influenced the rates of recruitment, growth, or survival of this taxon as submersion time increased. Interestingly, the cover of tunicates did not increase in response to the experimental removal of potential competitors (encrusting bryozoans, barnacles) (Fig. 8). However, the removal experiment was terminated in June, a month of low tunicate cover the previous two years. Since tunicates occurred in highest cover in the fall and winter months, interactions between this taxon and other early colonists may be greatest in those months when tunicate recruitment/growth was highest. Our experiments thus suggest that season was important in mediating interactions among early colonists on the tiles.

Encrusting bryozoans were also early colonists of the tiles, but occupied higher cover longer than tunicates. This pattern suggested that bryozoans were better competitors for space than tunicates in young assemblages. However, the higher cover of bryozoans with increasing depth on the 6 and 12-month tiles suggests that competitive interactions were important in limiting the cover this taxon at the shallowest depth (6 m) in older assemblages. Results from the removal experiment, in which cover of encrusting bryozoans in 12 month old assemblages was higher than control values when barnacles were removed, supports this conclusion (Fig. 8).

Other taxa, including tubicolous amphipods, barnacles, and sponges also occurred early in assemblage development (on the 2-month tiles), but in variable and generally low cover. Among these taxa, the cover of tubicolous amphipods (as amphipod tube mat) was highest, but generally much less than 20%. Since open space was available on the tiles for up to 6 months, the availability of this resource did not appear to limit amphipod recruitment or growth. The mean cover and variability in cover of amphipods generally increased on tiles as submersion time increased for up to 6 months, suggesting that the increase in surface complexity over time provided by other attached organisms could have facilitated the recruitment and/or survival of amphipods. For example, Bros (1987) reported that the abundance of the tubicolous amphipod *Erichthonius brasiliensis*, was positively associated with the increased habitat heterogeneity provided by barnacle tests. However, in our study, the removal of tunicates, bryozoans, or barnacles did not result in a significant decrease in the cover of amphipods (Fig. 8), suggesting that factors other than these early colonists influenced the cover of amphipod tube mat.

Barnacles and sponges, which reached highest cover later in succession, were also present on the 2-month tiles, but in low cover (<10%). The availability of open space did not appear to limit the recruitment of these taxa because open space was still available after 2 months. In addition, there were no observations to suggest that barnacles or sponges were inhibited from settling or were overgrown by taxa already on the tiles (e.g., Young and Gotelli, 1988; Nandakumar, 1996). The cover of barnacles (Fig. 8) and

sponges (unpublished data) did not increase in response to the experimental removal of early colonists, also suggesting that inhibitory or competitive interactions did not negatively affect the recruitment or growth of these taxa during the experiment. More likely, recruitment of barnacles and sponges was limited by the availability of larvae in the water column. The higher density and/or cover of barnacles and sponges on tiles in 2000-2001 compared with 1999-2000 supports this conclusion (Fig. 4).

Mussels colonized the tiles later (>12 months). Although mussels are abundant on oil platforms in the Santa Barbara Channel (Bascom et al., 1976; Page and Hubbard, 1987), mussel recruitment was low during this study. Mussel pediveligers recruit preferentially onto rugose or filamentous surfaces (Caceres-Martinez and Robledo, 1994; Marsden and Lansky, 2000). The recruitment of mussels can be facilitated by other species, but early colonists are not essential for recruitment (Dean and Hurd, 1980). Thus, we hypothesize that mussel recruitment was low in this study, at least in part, because of a paucity of larvae in the water column (also, see below).

Effect of depth and year on assemblage development

Depth affected the intensity of recruitment, and the distribution and cover of later colonizing species, but not the sequence of early development. Barnacles appeared earlier (after 2 months) and were present in significantly higher cover at 6 m (55% after 24 months) compared with the deeper depths (<28% after 24 months) (Fig. 7). Mussels were also only found on the tiles at 6 m, whereas sponges occurred in highest cover (70-80%) after 24 months at the deeper depths (12 and 18 m).

For barnacles, depth-related variation in density and cover may be related to variation in the density of larvae available for settlement. For example, Grosberg (1982) found that the vertical distribution of adult barnacles on pier pilings and of newly settled spat on settlement plates, reflected the vertical distribution of barnacle cyprids in the water column. The absence of mussels on tiles at deeper depths (12 and 18 m) may indicate that mussel larvae were not present. However, mussels recruit and grow on platforms in the Santa Barbara Channel to depths exceeding 18 m (Page and Hubbard, 1987; Page, unpublished data). Barnacles can enhance mussel recruitment by increasing habitat heterogeneity (Dean and Hurd, 1980; Berlow, 1997). Thus, the higher cover of barnacles at the shallowest depth (6 m) may have facilitated mussel attachment at this depth, whereas the low density of barnacles at 12 and 18 m may have retarded mussel recruitment at those depths. Unfortunately, this possibility was not adequately tested by the removal experiment because of generally low mussel recruitment onto tiles during the experiment. In addition to larval supply, depth-related variation in post-settlement mortality of later colonists, associated with predation or other factors, could also contribute to the observed patterns (e.g., Keough and Downes, 1982). However, predators were not observed feeding at our tiles.

The sequence of appearance of species on the tiles was similar between years, but the cover of barnacles and sponges was much higher (and density for barnacles) on the tiles

in 2000-2001 compared with 1999-2000. Rates of recruitment of these taxa may have been influenced by differences in oceanic conditions between the two years. A record coastal upwelling event occurred in Spring 1999 and coastal upwelling continued in the Southern California Bight through Summer 1999 (Schwing et al., 2000). These “La Nina” conditions persisted through Spring 2000, with ocean temperatures cooler than normal (Bograd et al., 2000). Although April 2000 to April 2001 was also a La Nina year, sea surface temperature measurements indicated that oceanographic conditions were closer to normal than in the preceding year (Durazo et al., 2001).

Water temperature *per se* can affect the development of marine invertebrates and lower water temperatures in 1999-2000 compared to 2000-2001 could have affected the density of larvae in the water column through effects on the reproductive output of adults (Schwing et al., 2000). In addition, upwelling events associated with La Nina conditions could have transported planktonic larvae offshore reducing the supply of larvae available for settlement (Roughgarden et al., 1988; Schwing et al., 2000). It is also possible that larval and post-settlement mortality were higher during La Nina conditions (Schwing et al., 2000).

Patterns of succession at the platform

The absence of macroalgae, including crustose coralline algae, on the tiles at Platform Houchin, and a scarcity of grazers, provided for a very different pattern of succession than found by Breitburg (1985) at an inshore subtidal reef in the Santa Barbara Channel. At the reef site, many sessile invertebrates were inhibited from settling by crustose coralline algae, and were also much more abundant when large grazers were experimentally excluded (total invertebrate cover on grazed plates <2%). Macroalgae were present on the rock wall study site of Vance (1988), but grazers did not appear to influence the pattern of succession, which was generally predictable from season to season and year-to-year and, in this regard, more similar to the results found in the present study. Vance (1988) attributed this regularity to a relatively stable physical environment, in terms of depth, current speed, temperature, and salinity, which could lead to less variable patterns of larval recruitment. Since the offshore physical environment at the platform is more similar to the vertical rock wall site of Vance (1988), than to the inshore reef site of Breitburg (1985), a similar explanation may well apply, at least in part, for patterns of succession found in the present study.

In addition, our results differed from those of other studies (Sutherland and Karlson, 1977; Osman, 1977; Underwood and Anderson, 1994) where strong seasonality in the timing and intensity of recruitment of different species contributed to variation in the pattern of succession, which depended on the time-of-year artificial surfaces were deployed. In the present study, only two taxa (both colonial) dominated early succession and these taxa recruited to the 2-month tiles year round (although the abundance of tunicates varied seasonally). Oceanographic climate may play an important role in influencing the rate of succession since the recruitment of later successional taxa (barnacles, sponges) differed considerably between the two years of the study.

In conclusion, development of the invertebrate assemblage on the tiles submerged at Platform Houchin could not be categorized as classical succession (*sensu* Clements, 1936) because some species/taxa that were present in high cover after 12 and/or 24 months (e.g., barnacles, sponges) could also colonize the tiles early in the successional sequence, albeit in low cover, and did not appear to require the presence of earlier taxa for recruitment. Rather, development of this assemblage appeared to fit a pattern where differences in life history traits among species colonizing the tiles (e.g., production of propagules, growth, longevity), competitive ability, depth-related settlement preferences, and responses to oceanographic climate, create a pattern of succession that was largely predictable in terms of the composition and sequence of occurrence of dominant taxa, but variable in rate of development, depending on date of submersion, year, and depth.

Plate I. Photographs of ceramic tiles submerged for 24 months at depths of 6, 12, and 18 m at Platform Houchin.



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The Department of the Interior Mission

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering sound use of our land and water resources; protecting our fish, wildlife, and biological diversity; preserving the environmental and cultural values of our national parks and historical places; and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people by encouraging stewardship and citizen participation in their care. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.



The Minerals Management Service Mission

As a bureau of the Department of the Interior, the Minerals Management Service's (MMS) primary responsibilities are to manage the mineral resources located on the Nation's Outer Continental Shelf (OCS), collect revenue from the Federal OCS and onshore Federal and Indian lands, and distribute those revenues.

Moreover, in working to meet its responsibilities, the **Offshore Minerals Management Program** administers the OCS competitive leasing program and oversees the safe and environmentally sound exploration and production of our Nation's offshore natural gas, oil and other mineral resources. The **MMS Royalty Management Program** meets its responsibilities by ensuring the efficient, timely and accurate collection and disbursement of revenue from mineral leasing and production due to Indian tribes and allottees, States and the U.S. Treasury.

The MMS strives to fulfill its responsibilities through the general guiding principles of: (1) being responsive to the public's concerns and interests by maintaining a dialogue with all potentially affected parties and (2) carrying out its programs with an emphasis on working to enhance the quality of life for all Americans by lending MMS assistance and expertise to economic development and environmental protection.