Spatial and temporal variability in early successional patterns of an invertebrate assemblage at an offshore oil platform

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Abstract

The effects of selected physical and biological factors on the early development of a subtidal invertebrate assemblage were examined at an offshore oil platform in the Santa Barbara Channel (California, USA). The effects of date, year, length, and depth of submersion were investigated by replacing sets of ceramic tiles with new tiles at frequencies of 2, 4, 6, 12, and 24 months at three depths (6, 12, and 18 m) over a period of 24 months. The effects of existing colonists and depth were explored in a second experiment by removing selected early colonists from ceramic tiles deployed at the same three depths over a period of 12 months. More than 40 invertebrate taxa from seven phyla colonized the tiles. Colonial tunicates and encrusting bryozoans appeared early in the successional sequence (~2 months), in cover ranging from <5% to 80% and from <5% to 55%, respectively. Tubiculous amphipods, barnacles, and sponges could also appear early, but in low cover (<20%). Composition of the assemblage changed over time with barnacles, sponges, and mussels becoming the principal space holders on tiles submerged for 24 months. When potential competitors were removed monthly, variation in the cover of dominant taxa (i.e., bryozoans, amphipods, barnacles) was maintained to 12 months, suggesting that other factors, such as larval availability or post-settlement mortality, were responsible for these patterns. Development of this assemblage appeared to fit a pattern of early 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.
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1. 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; Colinvaux, 1973). Classical successional theory was originally derived from studies of terrestrial plant associations, and has

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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, 1979a,b; 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, unpublished 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 from 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 develop-

ment, 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.

2. Materials and methods

2.1. Study site

This study was conducted at the oil and natural gas production platform "Houchin" (Pacific Operators Offshore), 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 is 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; *Mytilus 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.

2.2. Development of the assemblage

We used unglazed ceramic tiles (15×15 cm) attached in groups of five to experimental frames to test the first two hypotheses. Each frame (15×105 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 1 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.

During the course of the study, a few large individuals of the anemone, *M. senile*, moved onto a
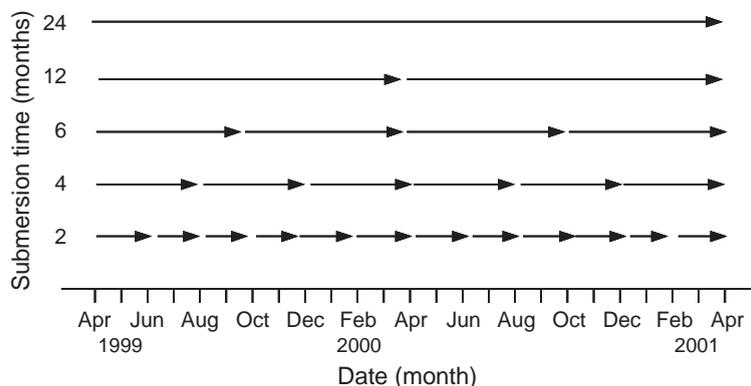

Fig. 1. Arrows indicate the schedule for the deployment and retrieval of tiles submerged in the field for periods of 2, 4, 6, 12, or 24 months at depths of 6, 12, or 18 m. Retrieved tiles were replaced with new tiles (*n*=4 for each depth).

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. Tubiculous 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 (*M. californicus*; *B. 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.

2.3. 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 (15×15 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, *M. 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.

2.4. 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×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).

3. Results

3.1. Development of the assemblage

Invertebrate species from seven 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), tubiculous amphipods (*Ericthonius* sp., Milne-Edwards, 1830), barnacles (*B. trigonus*, *B. pacificus*, and *M. californicus*), and sponges. No macroscopic algae colonized the tiles.

Colonial tunicates (primarily *D. listeranium*) 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×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 a 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×depth interaction, $P>0.1$).

Encrusting bryozoans (primarily *Dendrobeania laxa*) were also early colonizers of the tiles (Fig. 2d). There was a significant date×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. 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 and 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×depth interaction: $P>0.1$, ANOVA).

Tubiculous amphipods could also colonize tiles early but, if present, generally occurred in low cover

Table 1
List of sessile and semi-mobile invertebrates encountered during the study

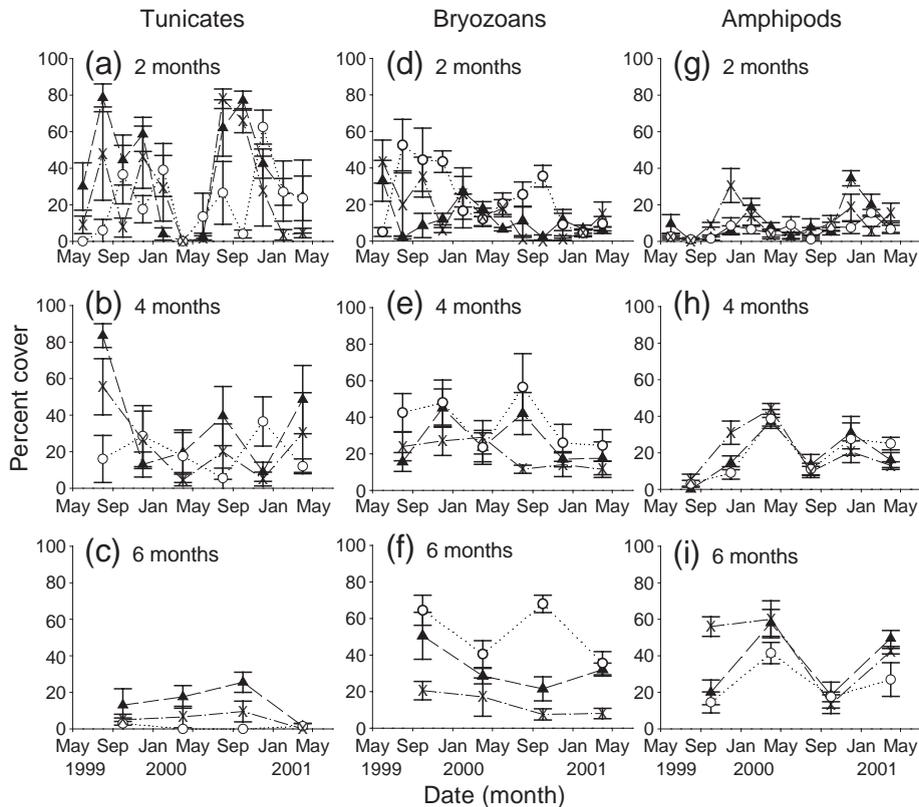| Phylum	Description	Species
Porifera	Sponges	Unidentified
Cnidaria	Anemones	*Corynactis californica* (Carlgren, 1936)
		Epiactis prolifera (Verrill, 1869)
		Metridium senile (Linnaeus, 1761)
	Hydrozoans	*Aglaophenia latirostris* (Nutting, 1900)
		Plumularia sp. (Lamarck, 1816)
		Tubularia crocea (L. Agassiz, 1862)
Ectoprocta	Bryozoans	*Bugula neritina* (Linnaeus, 1758)
		Celleporella brunnea (Hincks, 1884)
		Celleporella hyalina (Linnaeus, 1767)
		Crisulipora occidentalis (Robertson, 1910)
		Dendrobeania laxa (Robertson, 1905)
		Filicrisia franciscana (Robertson, 1910)
		Membranipora serrilamella (Osburn, 1950)
		Rynchozoan rostratum (Busk, 1855)
		Tubulipora pacifica (Robertson, 1910)
		Tubulipora tuba (Gabb and Horn, 1862)
Chordata	Tunicates	*Botrylloides diegense* (Ritter and Forsyth, 1917)
		Diplosoma listerianum (Macdonald, 1859)
		Styela truncata (Ritter, 1901)
Mollusca	Bivalves	*Crassadoma gigantea* (J.E. Gray, 1825)
		Hiatella arctica (Linnaeus, 1767)
		Kellia suborbicularis (Montagu, 1803)
		Mytilus californianus (Conrad, 1837)
		Mytilus galloprovincialis (Lamarck, 1819)
	Gastropods	*Megatebennus bimaculatus* (Dall, 1871)
Annelida	Polychaetes	*Halosydna brevisetosa* (Kinberg, 1855)
		Serpula vermicularis (Linnaeus, 1767)
		Spirorbis sp. (Daudin, 1800)
Arthropoda	Amphipods	*Caprella californica* (Stimpson, 1857)
		Caprella equilbra (Say, 1918)
		Caprella verrucosa (Lamarck, 1801)
		Dulchiella sp. (Stout, 1912)
		Elasmopus sp. (Costa, 1853)
		Ericthonius sp. (Milne-Edwards, 1830)
		Gammaropsis sp. (Liljeborg, 1855)
		Podocerus sp. (Leach, 1814)
		Stenothoe sp. (Dana, 1852)
	Barnacles	*Balanus pacificus* (Pilsbry, 1916)
		Balanus regalis (Pilsbry, 1916)
		Balanus trigonus (Darwin, 1854)
		Megabalanus californicus (Pilsbry, 1916)

Fig. 2. Mean percent cover (± 1 S.E., $n=4$) 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 ($\times$), 12 ($\blacktriangle$), or 18 ($\bigcirc$) m. Mean values for each depth in this and subsequent figures are independent of one another, but connected by broken lines to facilitate comparison across sampling dates.

(<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×depth interaction in the mean cover of amphipod tube mat on the 2-, 4-, and 6-month tiles (date×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% to 20% in the fall (October) to 40–60% in the spring (June) after 6 months (Fig. 2i).

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.

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 and 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).

Sponges were present in low cover (generally <10%) through 6 months of submersion and no
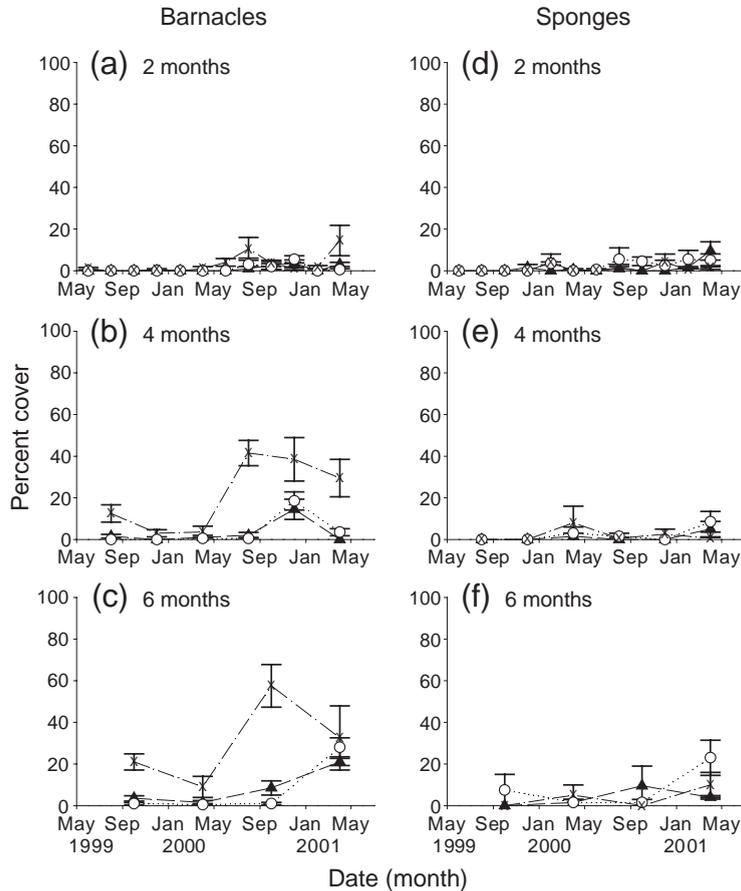
Fig. 3. Mean percent cover (±1 S.E., *n*=4) of barnacles (a–c) and sponges (d–f) after 2, 4, and 6 months of submersion at 6 (×), 12 (▲), or 18 (○) m.

patterns were evident with time-of-year (Fig. 3d–f). Mussels (*M. 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).

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×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×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×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).
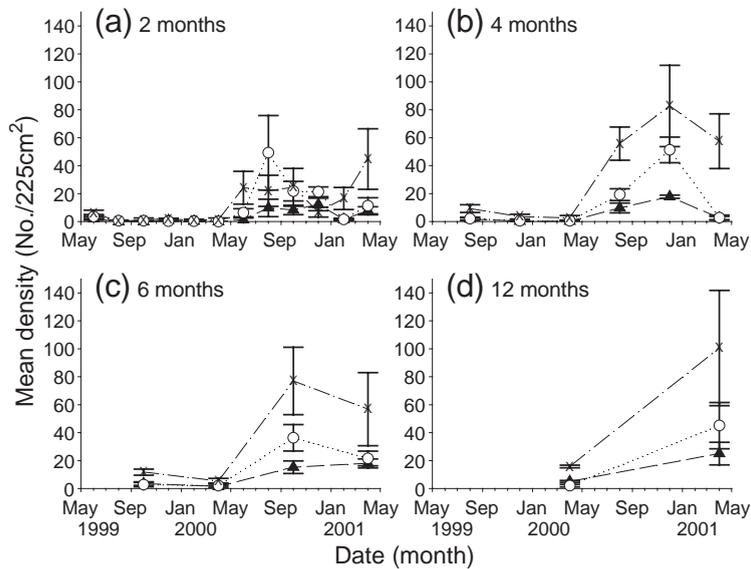
Fig. 4. Mean density (±1 S.E., *n*=4) of barnacles after 2, 4, 6, and 12 months of submersion at 6 (×), 12 (▲), or 18 (○) m.

3.2. 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). Tubiculous amphipods were also early colonists of the tiles, but the 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.

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 (~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).

3.3. 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
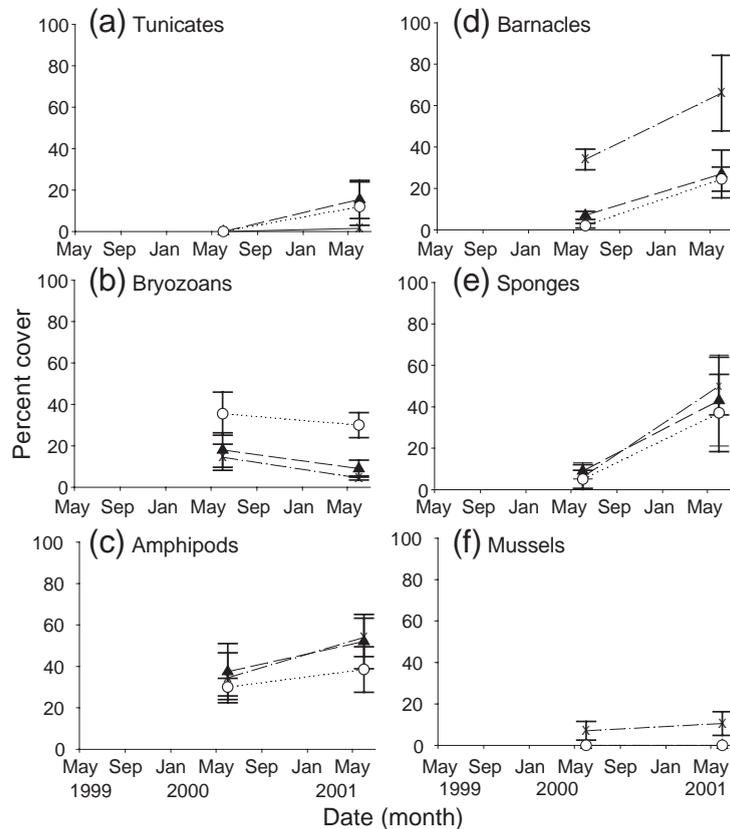
Fig. 5. Mean percent cover ($\pm$1 S.E., n=4) of selected taxa after 12 months of submersion at 6 ($\times$), 12 ($\blacktriangle$), or 18 ($\bigcirc$) m in 1999–2000 and 2000–2001.

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).

4. Discussion

4.1. 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
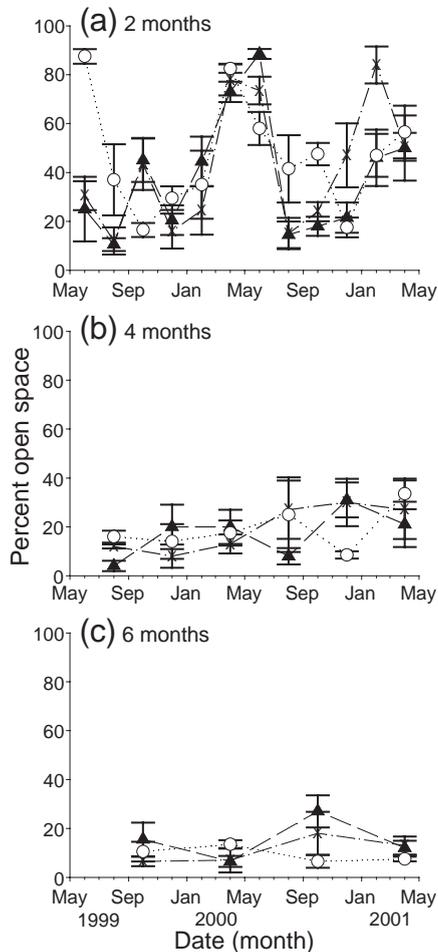
Fig. 6. Mean percent cover (±1 S.E., *n*=4) of open space after 2, 4, and 6 months of submersion at 6 (×), 12 (▲), or 18 (○) m.

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 in the previous 2 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, support this conclusion (Fig. 8).

Other taxa, including tubiculous 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 tubiculous 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 tubiculous amphipod *Ericthonius brasiliensis* was positively associated with the increased habitat
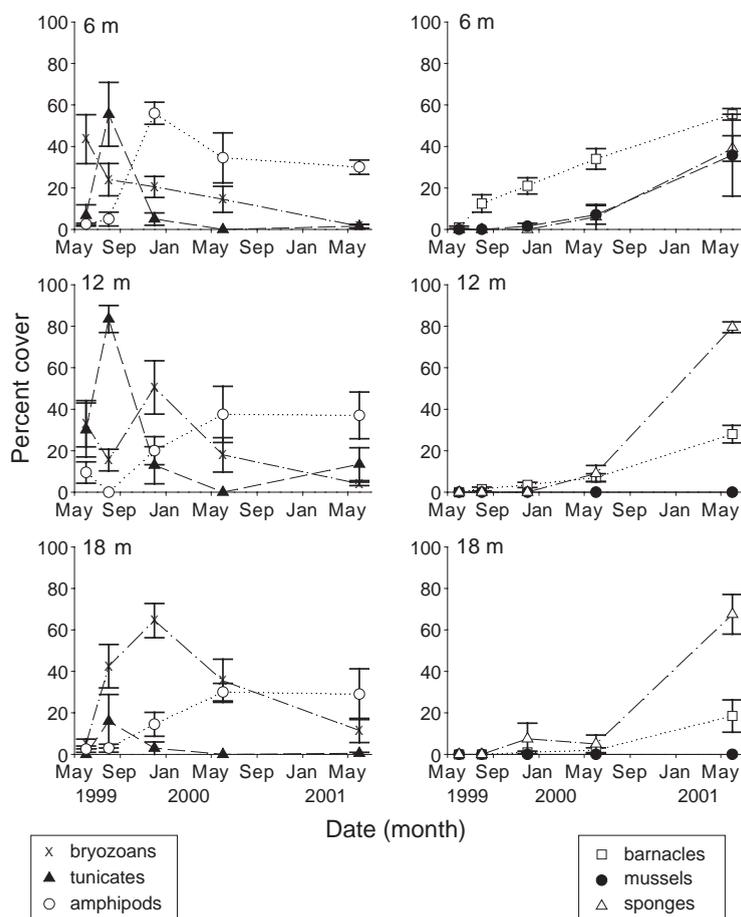
Fig. 7. Mean percent cover (±1 S.E., $n=4$) of selected taxa on tiles submerged in April 1999 at depths of 6, 12, and 18 m after 2, 4, 6, 12, and 24 months of submersion.

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
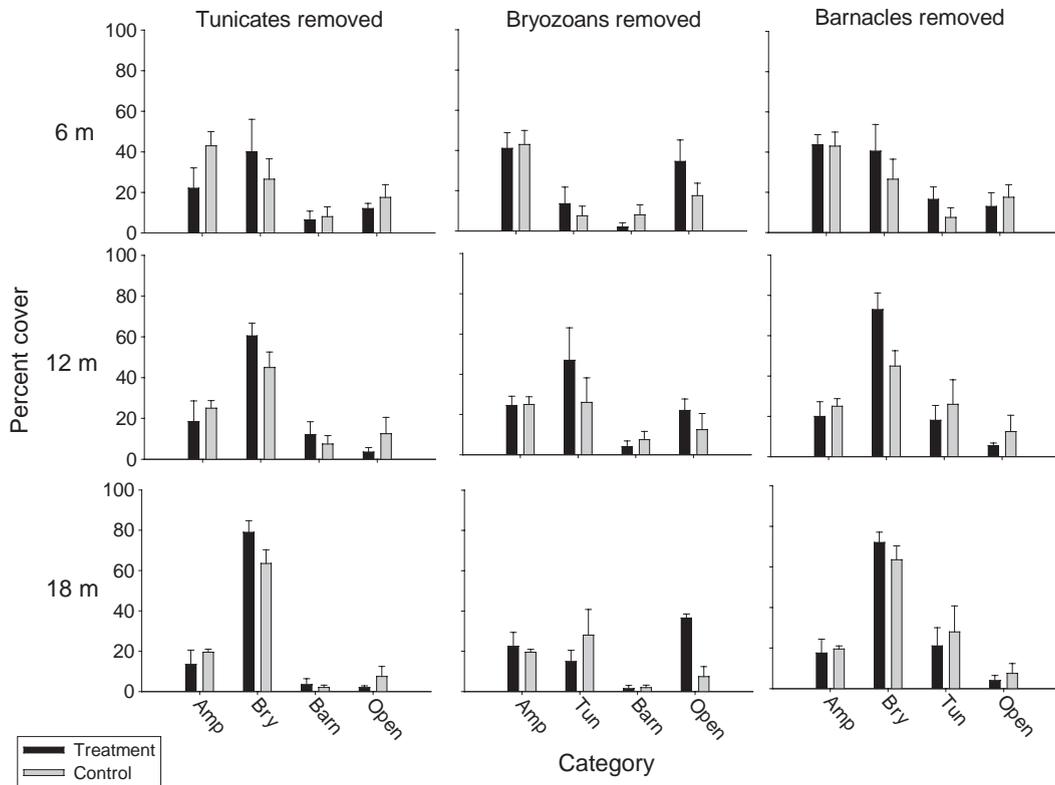
Fig. 8. Mean percent cover (±1 S.E., *n*=4) of tubiculous amphipods (Amp), colonial tunicates (Tun), encrusting bryozoans (Bry), barnacles (Barn), and open space (Open) on tiles submerged at depths of 6, 12, or 18 m in which either (a) tunicates, (b) bryozoans, or (c) barnacles were removed monthly for 12 months.

(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).

4.2. 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 Niña" conditions persisted through Spring 2000, with ocean temperatures cooler than normal (Bograd et al., 2000). Although April 2000–April 2001 was also a La Niña 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 Niña 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 Niña conditions (Schwing et al., 2000).

4.3. 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 2 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.

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