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The Development of Subtidal Fouling Assemblages on Artificial Structures in Keelung Harbor, Northern Taiwan

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Hsing-Juh Lin and Kwang-Tsao Shao (2002) The development of subtidal fouling assemblages on artificial structures in Keelung Harbor, Northern Taiwan. *Zoological Studies* **41**(2): 170-182. Effects of substratum, its submersion season, and submersion period on the development of subtidal fouling assemblages were examined for a period of 18 mo in a subtropical harbor. Four types of artificial surfaces, including steel, stainless steel, cathodically protected steel, and concrete, were initially submersed in fall and spring, respectively, and sampled every 3-6 mo. There is little evidence that type of substratum influenced the development of fouling assemblages. However, richer taxa and greater biomass of fouling assemblages occurred on spring-than on fall-submersed plates. Fouling biomass reached a maximum at the end of the study period, but the taxa were richest at the end of 12 months. Classification and ordination analyses show that the species compositions of fouling assemblages were structured by submersion season and submersion period of the substratum, but not by the nature of the substratum itself. The oyster, *Crassostrea gigas*, dominated spring plates throughout the study period, but the assemblages on fall plates were highly variable. This indicates that submersion season and submersion period of the substratum are more important than type of substratum in the development of subtidal fouling assemblages. However, the abundance and species composition on spring and fall plates became less dissimilar by the end of 12 mo. This suggests that development takes the same course even with different seasons of submersion. It is likely that the fouling species acted in individualistic manners, and the assemblages were composed simply of fouling species which arrived at that time. Our results demonstrate that the developmental process is greatly affected by seasonal fluctuations in larval abundance and historical components on a substratum. http://www.sinica.edu.tw/zool/zoolstud/41.2/170.pdf

Key words: Substratum, Submersion season, Submersion period, *Crassostrea gigas*.

Fouling assemblages on artificial substrata have been studied for many decades, not only as a practical problem for biofouling prevention (Holmstrom and Kjelleberg 1994, Abarzua and Jakubowski 1995), but also as empirical models for studying community succession and its underlying mechanisms (Schoener 1974, Mook 1981, Field 1982, Greene et al. 1983, Oshurkov 1992, Anderson and Underwood 1994, Butler and Connolly 1996). Man-made structures, including concrete dikes, artificial reefs, aquaculture cages, undersea storage tanks, offshore platforms, pontoons, retaining walls, and many others, are continuously being added to coastal waters worldwide due to rapid urbanization and large-scale construction. They may produce extra habitat in the form of new surfaces for colonization of fouling organisms. Assemblages on artificial surfaces have been found to differ from those on nearby natural substrata (McGuinness 1989, Glasby 1999). It is imperative to understand how artificial substrata influence abundance and composition of fouling assemblages in urbanized coastal waters (Connell and Glasby 1999).

Fouling assemblages are characterized by continuous changes in species composition in

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response to various biotic and abiotic factors over time, a process referred to as development (Greene and Schoener 1982). The mechanisms underlying the observed sequence of species may involve each species' ability to compete for the available space on a substratum (Quinn 1982, Russ 1982). Osman (1977) found that the development of epifauna living on rocks is greatly affected by earlier species. Connell and Slatyer (1977) proposed 3 biological interactions between earlier species and later colonizers for mechanisms in succession: 1) inhibition; 2) facilitation; and 3) no effect. Little information is available about the development of subtidal fouling assemblages on artificial surfaces.

Artificial structures may constitute different substrata. Various surface characteristics have been found to influence the species and relative abundance of fouling organisms on artificial surfaces, e.g., the texture (Crisp and Ryland 1960), composition (Rittschof et al. 1984, McGuinness 1989, Anderson and Underwood 1994), and interfacial alkalinity (Eashwar et al. 1995) of the substratum. Fouling assemblages on pilings (wood) and concrete have been extensively studied (McGuinness 1989, Anderson and Underwood 1994, Butler and Connolly 1996, Glasby 2000), but far less information is available about the development of fouling assemblages on other common artificial structures, such as steel, stainless steel, and cathodically protected steel.

Most species produce larvae during a limited time. The season in which a substratum is first submersed, and the submersion period it experiences, are expected to affect the colonization of that substratum because of seasonal fluctuations in larval abundances and the proposed biological interactions between earlier arrivals and later invaders. Schoener (1974) showed that the number of fouling species initially increases more rapidly in warmer months than during colder months. Recent studies have suggested the importance of larval supply in regulating the recruitment of sessile assemblages (Minchinton and Scheibling 1991, Bertness et al. 1992). Seasonality has marked effects not only on larval supply, but also on the growth rates of fouling organisms. Most species appear to grow at a maximum rate in warmer months and reach a minimum during colder months. Fouling species with higher growth rates are more capable of invading the available space on a substratum (Osman 1977). Anderson and Underwood (1994) demonstrated that submersion season of a substratum may influence the ensuing development of intertidal sessile assemblages. How submersion season and submersion period interact in the development of fouling assemblages is not known.

It is likely that an artificial substratum, its submersion season and submersion period interact together greatly affecting the development of fouling assemblages. Bertness et al. (1992) found that larval supply is more important than the microhabitat of a substratum in determining the development of fouling assemblages. Anderson and Underwood (1994) also implied that submersion season is more important than type of substratum in structuring the composition of intertidal fouling assemblages. Their relative importance in the development of fouling assemblages is not known. Without an understanding of interactive effects, it may be assumed incorrectly that effects are consistent across all situations.

In the present study, we used multifactorial experiments to determine interactions of an artificial substratum, its submersion season, and submersion period on the development of subtidal fouling assemblages in a subtropical harbor. The purposes of this study are: 1) to compare fouling assemblages on steel, stainless steel, cathodically protected steel, and concrete surfaces in subtropical waters; 2) to elucidate the effects of submersion season on the development of fouling assemblages; 3) to examine the effects of submersion period on the development of fouling assemblages; and 4) to determine their relative importance in the development of fouling assemblages.

MATERIALS AND METHODS

Study site

The experiments were conducted on wharves in Keelung Harbor (25º7'N, 121º42'E), the largest harbor in northern Taiwan. During the study period, the surface water temperature in the harbor exhibited seasonal fluctuations, ranging from a minimum of about 17 ºC in February to a maximum of about 29 ºC in August. The salinity remained at about 33 PSU throughout the year. The water was clear, and the light extinction coefficient remained low (about 0.60 m^{-1}). The coast of the harbor is subjected to a semidiurnal tidal regime with a tidal amplitude of about 0.5-1.0 m.

Experimental design

Four types of artificial substrata were used in this study: steel (FE: AISI 1015 low-carbon mild steel), stainless steel (ST: type 304), cathodically protected steel (CA: AISI 1015 low-carbon mild steel with zinc anodes), and concrete (CO). These substrata are the most commonly used man-made surfaces in Keelung Harbor.

One plate of each substratum measured 20 x 20 cm and was 3 cm thick. Eight plates (duplicates of each substratum) were vertically attached to a steel rack. These plates were arranged in 2 rows, and each row had one of each substratum in random order. Each plate was separated from the rack by an acrylic sheet. Distances between the plates on a row or between rows were 20 cm. The steel racks were positioned beneath fixed docks at a depth of 4 m, which is below the mean low water of spring tides (shallow subtidal zone) according to the tide tables (Chinese Naval Hydrographic and Oceanographic Office). This would minimize the stress of desiccation and rapid temperature changes on the fouling species caused by regular cycles of semidiurnal tides.

Sampling was designed to compare the fouling assemblages on the 4 types of substrata, which were initially submersed in 2 seasons for different periods. Since spring and summer are the settlement seasons of major fouling species such as oysters and barnacles in subtropical Taiwan (Soong et al. 1981), 2 sets of artificial substrata were submersed separately in spring and fall. A set of 12 racks was submersed in the harbor in October 1994 (fall) with 3 racks (24 plates, 6 replicates of each type of substratum) being removed in each of January 1995 (3 months), April 1995 (6 months), October 1995 (12 months), and April 1996 (18 months). The other set of 10 racks was submersed in April 1995 (spring) with 3 racks being removed in each of October 1995 (6 months), April 1996 (12 months), and October 1996 (18 months). Some plates were lost due to damage caused by boats during the study period.

Analysis of fouling assemblages

The plates were removed by slowly lifting the steel racks to the docks using a forklift. Each plate was photographed, and the abundance of each species was estimated. The abundance of solitary animals was determined by counting the number of individuals. The abundance of colonial animals and algae was determined by measuring the percentage cover using a grid of regularly spaced dots and counting the number of dots intersecting a given species. Each plate was equally split into 4 domains. The fouling organisms from the lower-left domain of each plate, measuring 100 cm^2 in area, were then gently removed from the plate surface with a scraper. The scraped samples were brought back to the laboratory for biomass determination and then were fixed in 5% formaldehyde for identification. This enabled a check in the laboratory of the error in distinguishing fouling species in the field.

In the laboratory, the fouling organisms were weighed as wet weight (WW) and identified to the lowest possible taxon using a dissecting microscope, but many could not be identified to species due to the lack of relevant taxonomic literature about those occurring in Taiwan. Therefore, some grouped categories were used for statistical analyses. Despite this, there is evidence that identification to taxonomic levels as high as family and even phylum can lead to the detection of environmental patterns (Clarke and Warwick 1994). Microfouling organisms were not examined because we assumed that their contribution to the total biomass of the assemblage was minor. Dry weight (DW) of the entire fouling assemblage from each plate was measured by drying at 60 °C to constant weight (Aloi 1990). Ash-free dry weight (AFDW) was then determined by subtracting from DW the weight of the associated residue after firing in a 400 °C muffle furnace for 4 h (Biggs 1987). In order to compare our results with those of other studies, the conversion factors for the ratio of AFDW: DW: WW of fouling assemblages were determined to be about 1: 10: 20. The measurements were standardized to weight per 100 cm^2 of plate surface to facilitate comparison among plates.

Statistical analysis

A three-way fixed ANOVA model was used to evaluate whether the number of taxonomic groups, DW, and AFDW of the fouling assemblages collected in the harbor differed significantly among the types of substratum (4 levels), between the submersion seasons (2 levels), or among the submersion periods (4 levels). Before the analyses, DW and AFDW were transformed to square roots to conform to normality and homogeneity of variance assumptions (Fry 1993). If the results of ANOVA indicated significant main effects at the 0.05 probability level, then Scheffé's S test was used to determine which means significantly differed for the unequal numbers of replicates due to the loss of some plates.

In order to reveal the developmental pattern of fouling assemblages caused by the type of substratum, its submersion season, and submersion period, changes in taxonomic groups were studied using multivariate analyses in the PRIMER (v. 5.2) computer package (Clarke and Gorley 2001). The Bray-Curtis coefficient was used to produce a dissimilarity matrix of fouling assemblages between any 2 plates according to the relative abundance of each taxonomic group. In order to combine data of counts and percentage cover to a mixed data set, the relative abundance of each group on each plate was determined by ranking its count or percentage cover according to its range during the study period. The relative abundance of each group on each plate was then recoded as 1-5 to represent the 81%-100%, 61%-80%, 41%-60%, 21%-40%, and 1%-20% levels of ranking. This transformation preserved information in the mixed data set concerning counts or percentage cover across samples, but eliminated any large differences in scale among species. The data matrix consisted of a total of 119 plates with 15 variables representing the relative abundance of each taxonomic group.

The data matrix was classified by hierarchical agglomerative clustering using the unweighted pair group mean arithmetic (UPGMA) linking method and was ordinated using non-metric multidimensional scaling (MDS) techniques. Stress values < 0.2 indicate that a 2-dimensional MDS plot gives a usable summary of sample relationships (Clarke 1993). A two-way crossed ANOSIM (analysis of similarities) was used to determine whether the effects of substratum and submersion season within each level of submersion period on the composition of fouling assemblages were significant by comparing the observed statistic to its permutation distribution for absence of differences (Clarke and Warwick 1994). ANOSIM is a nonparametric analog to a multivariate analysis of variance (MANOVA) without the assumption of multivariate normality. If the results indicated significant main effects at the 0.05 probability level, pairwise comparisons and the Bonferroni correction for the significance level were used to determine which levels differed. Similarity of percentages (SIMPER) was employed to reveal the most representative taxonomic groups in the assemblages over time. A contribution of 15% similarity was used as a cut-off value to determine the most representative groups for each assemblage.

RESULTS

Effects of artificial substrata

During the study period, the values of DW and AFDW were similar, and so only the results of DW are shown here. There was little evidence that the nature of the artificial surface influenced the recruitment or development of subtidal fouling assemblages in Keelung Harbor. There were no significant differences in numbers of taxonomic groups (Table 1) or DW (Table 2) among FE, ST, CA, and CO surfaces. No significant interactions were found between a substratum and its submersion season or between a substratum and its submersion period.

Effects of submersion season

There were significant differences in the numbers of taxonomic groups and DW between fouling assemblages on plates submersed in spring and fall (Tables 1, 2). Taxonomic groups on spring plates were richer than those on fall plates (Fig. 1). The recruitment of fouling organisms was more rapid on spring plates than on fall plates at the end of 6 mo of submersion. At this time, all the space (100%) on spring plates was occupied by fouling

Table 1. Three-way ANOVA (substratum x season x period) of the number of taxonomic groups of fouling assemblages collected in Keelung Harbor. If the result of ANOVA indicated significant treatment effects at the 0.05 probability level (Pr), then Scheffé's S test was used to determine which means significantly differed

Source	*df*	*F* value	Pr > *F*	Separation
Substratum (Sub)	3	0.26	0.85	
Season	1	3.50	0.05	spring > fall
Period	3	31.50	0.0001	12 > 18 = 6 > 3 (mo)
Sub x Season	3	0.96	0.42	
Sub x Period	9	1.15	0.34	
Season x Period	2	5.05	0.008	
Sub x Season x Period	54	0.94	0.59	

organisms. The mean numbers of taxonomic groups on spring plates reached 6.7-8.5 groups per plate. Colonization of fall plates was slower than that of spring plates. About 75% of fall plates were covered by fouling organisms by the end of 6 mo. The mean number of taxonomic groups on fall plates was only 5.3-6.2 groups per plate.

There were significant interactions between submersion season and submersion period (Table 1). At the end of 12 mo, the number of taxonomic groups on fall plates had increased to a maximum of 7.5-9.2 groups per plate, which was comparable to those on spring plates at this time (Fig. 1).

The effects of submersion season on DW between fouling assemblages on spring and fall plates were more evident. DWs on spring plates were significantly greater than those on fall plates (Table 2). At the end of 6 mo, DWs on spring plates were 21-27 g/100 cm^2, compared with 1-2 g/100 cm^2 on fall plates (Fig. 2). Despite the maximum numbers of taxonomic groups occurring on spring and fall plates at the end of 12 mo, DWs continued to increase throughout the study period. At the end of the experiment, DWs on spring plates had reached 68-111 g/100 cm^2. On fall plates, DWs had reached 17-41 g/100 cm^2, which were similar to values on spring plates after 6 mo of submersion. Therefore, significant interactions between submersion season and submersion period were also found on DW (Table 2).

Effects of submersion period

Effects of submersion period on the development of fouling assemblages were significant in terms of the number of taxonomic groups and DW (Tables 1, 2). Taxonomic groups were richer on plates submersed for 12 mo, but were poorer on plates submersed for only 3 mo (Fig. 1). Nevertheless, greater DWs were found on plates submersed for 18 mo (Fig. 2). There were significant interactions of submersion season and submersion period on the number of taxonomic groups and on DW.

Changes in species composition

At least 78 species occurred on the plates during the study period. Fifteen taxonomic groups were aggregated for multivariate analyses, including green algae, red algae, hydroids, corals, upright bryozoans, encrusting bryozoans, flatworms, sedentary polychaetes, errant polychaetes, oysters (*Crassostrea gigas*) and other bivalves, shrimp, barnacles (mostly *Balanus amphitrite*), crabs, isopods, amphipods, colonial tunicates, and solitary tunicates. These fouling species were commonly observed in previous studies along the southwestern coast of mainland China (Huang and Cai 1984).

The grouping patterns of multivariate analyses were primarily determined by submersion season and submersion period, but not by the substratum itself. Classification of the relative abundance of each taxonomic group from each plate separated the fouling assemblages into 2 major categories (A and B) at a dissimilarity level of 0.52 (Fig. 3). The 1st category (A) contained samples from fall plates submersed for less than 12 mo, and the 2nd category (B) comprised samples from all spring and fall plates submersed for more than 12 mo. Category A was separated further into 3 groups at a dissimilarity level of 0.40, containing mainly samples from fall plates submersed for 3 (category C) and for 6 mo (categories D and E). Category B was separated further into 3 groups at a dissimilarity level of 0.30, comprising samples from fall plates submersed for 12 (F) and 18 mo (H), and all spring plates (G). The fouling assemblages on fall plates submersed for more than 12 mo were more similar to those on spring plates than to those on fall plates submersed for 3 and 6 mo. Samples from spring plates submersed for 12 mo can be separated from other spring plates. Samples collected from spring plates submersed for 6 and 18 mo were very similar and were separated at a dissimilarity level of as low as 0.20. Our results suggest that submersion period is as important as submersion season in structuring the fouling assemblages.

Results of the non-metric MDS ordination paralleled those produced by the classification (stress = 0.19). Non-metric MDS showed that succession of fouling assemblages was evident on fall plates, but not on spring plates (Fig. 4). It also demonstrated that samples from fall plates submersed for less than 12 mo (Fig. 4, right) were distinct from those from all spring plates and from fall plates submersed for more than 12 mo (Fig. 4, left). Samples from fall plates were widely scattered, but samples from spring plates were relatively not well separated, regardless of length of submersion period.

Two-way crossed ANOSIM within each level of submersion period demonstrated that the taxonomic composition of fouling assemblages on spring plates significantly differed from those on fall plates at the 5% significance level, but no significant differences were found among substrata (Table 3). Despite detecting significant differences among types of substratum at the end of 18 mo in the overall test, the observed statistic (*R* value) was only 0.26 compared to the usual range of 0 and 1, indicating that the fouling composition on the substrata is barely separable at all (Clarke and Gorley 2001). The pairwise statistics (*R* values) among substrata were < 0.5 and also showed no clear differences among substrata.

During the study period, more than 1 type of assemblage was observed on fall plates, depending on the length of the submersion period (Fig. 5). SIMPER showed that the most-representative taxonomic groups on fall plates at the end of 3 mo were sedentary polychaetes and encrusting bryozoans. At the end of 6 mo, the fouling assem-

Table 2. Three-way ANOVA (substratum x season x period) of dry weight of fouling assemblages collected in Keelung Harbor. Dry weights were transformed to square roots before analyses. If the result of ANOVA indicated significant treatment effects at the 0.05 probability level (Pr), then Scheffé's S test was used to determine which means significantly differed

Source	*df*	*F* value	Pr > *F*	Separation
Substratum (Sub)	3	1.14	0.34	
Season	1	84.70	0.0001	spring > fall
Period	2	69.70	0.0001	18 > 6 = 12 (mo)
Sub x Season	3	1.07	0.37	
Sub x Period	6	0.84	0.55	
Season x Period	2	15.90	0.0001	
Sub x Season x Period	6	0.91	0.49	

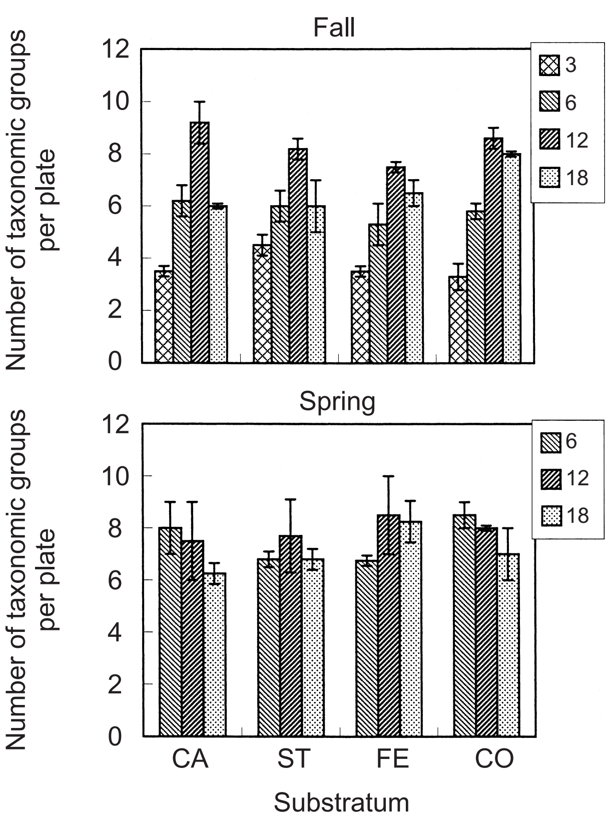

Fig. 1. Mean number (± SE, *n* = 2-6) of taxonomic groups per plate of fouling assemblages on substrata submersed in Keelung Harbor for 3, 6, 12, and 18 mo. Four types of substrata (CA: cathodically protected steel, ST: stainless steel, FE: Steel, CO: concrete) were submersed in fall and spring, respectively.

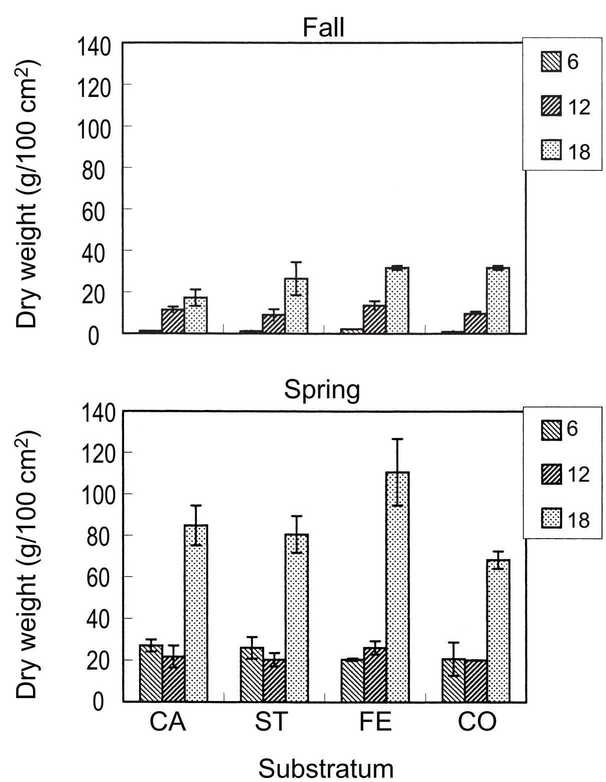

Fig. 2. Mean (± SE, *n* = 2-6) dry weight (g/100 cm^2) of fouling assemblages on substrata submersed in Keelung Harbor for 3, 6, 12, and 18 mo. Four types of substrata (CA: cathodically protected steel, ST: stainless steel, FE: steel, CO: concrete) were submersed in fall and spring, respectively.

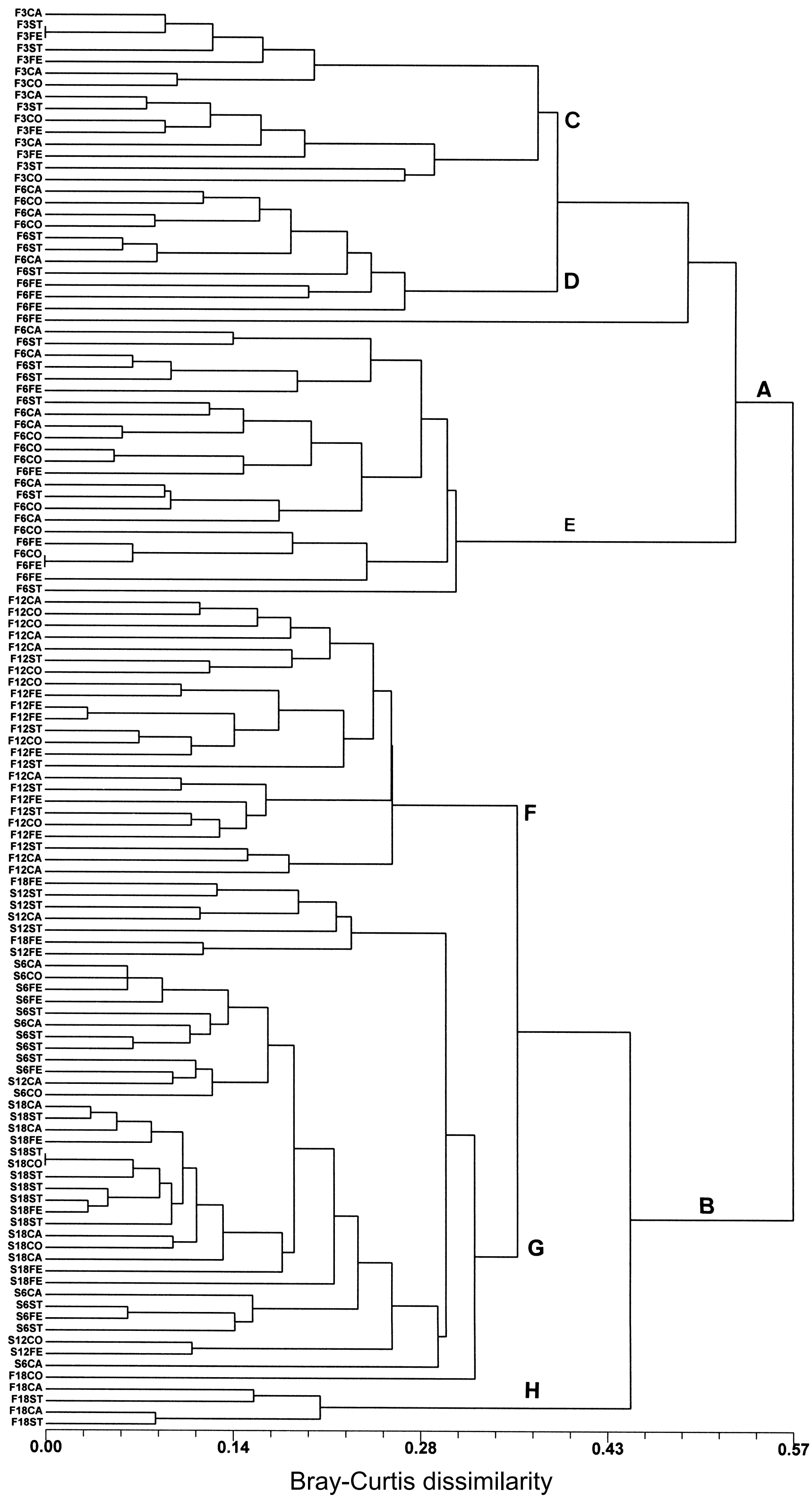

Fig. 3. Classification of abundance data for each group of fouling assemblages on 4 types of substrata submersed in Keelung Harbor for 3, 6, 12, and 18 mo. These substrata were initially submersed in spring and fall, respectively. The label of each sample consists of 3 codes: the lst code is submersion season (F: fall, S: spring); the 2nd code is submersion period in months; the final code is type of substratum (CA: cathodically protected steel ST: stainless steel, FE: steel, CO: concrete).

blages had become more diverse. The relative abundance (average rank) of sedentary polychaetes and encrusting bryozoans had decreased, but green algae occurred on many of the plates at this time. At the end of 12 mo, oysters instead of green algae were frequently observed on fall plates. By the end of 18 mo, barnacles were the most frequently observed group and the most abundant group on fall plates, followed by encrusting bryozoans and oysters.

In contrast to the various types of assemblages on fall plates, assemblages on spring plates were dominated by the oyster, *Crassostrea gigas*, regardless of length of submersion period or type of substratum (Fig. 5). The composition of fouling assemblages on spring plates was more diverse than that on fall plates. The assemblages also comprised sedentary polychaetes, barnacles, encrusting bryozoans, and colonial tunicates, but the relative abundance of each taxonomic group changed as time progressed. At the end of 12 mo, barnacles had become the 2nd-most dominant and frequently observed group and continued this dominance until the end of the study period.

DISCUSSION

Quantitative comparisons with fouling assemblages from other harbors are seldom possible since there are few studies using the same sampling techniques and quantitative analyses. Despite using different types of substratum, fouling biomasses in this study were comparable to those from adjacent subtropical harbors. Based on the conversion factor between DW and WW, the WWs of fouling assemblages accumulated on spring plates in Keelung Harbor (25°07'N) by the end of a year were estimated to be 4.2-5.4 kg WW/m^2. These values are within the range reported along the coast of mainland China from Dandong Harbor (40°07'N) to Xisha Harbor (16°45'N) (Huang and Cai 1984). Specifically, when the submersion season and the length of the submersion period were similar, our values were lower than the mean value (17 kg WW/m^2) reported in Xiamen Harbor (24°26'N) (Li et al. 1992), but slightly higher than that (2.8 kg WW/m^2) in Shantou Harbor (23°21'N) (Li et al. 1996).

Despite using different types of substratum, species composition of fouling assemblages

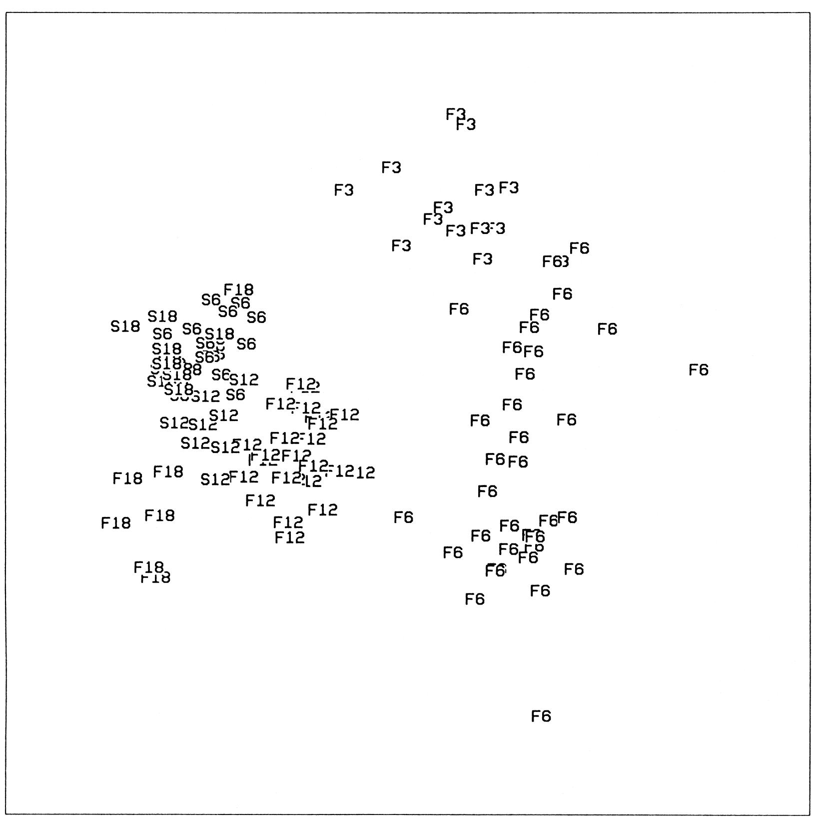

Fig. 4. Non-metric MDS ordination of abundance data for each taxonomic group of fouling assemblages on substrata submersed in Keelung Harbor for 3, 6, 12, and 18 mo. These substrata were initially submersed in spring and fall, respectively. The label of each sample consists of 2 codes: the 1st code is submersion season (F: fall, S: spring) and the 2nd code is submersion period in months.

observed in this study were also similar to those reported in other adjacent subtropical waters. Numbers of fouling species groups per plate observed on plates in Keelung Harbor were similar to those recorded in Dongshan (23º45'N) (Huang and Cai 1984). The dominant taxonomic groups of fouling assemblages in this study were similar to those recorded on submerged artificial concrete reefs off northern Taiwan (Chang et al. 1977) and those from Pingtan (25º30'N), Quanzhqu (24º50'N), Xiamen Harbor, and Dongshan (Huang and Cai 1984). Generally, fouling assemblages along the southwestern coast of mainland China and from Taiwan are gravimetrically dominated by barnacles, oysters, bryozoans, and polychaetes. Quantitative and qualitative comparisons imply that the type of substratum is relatively unimportant in the development of subtidal fouling assemblages in subtropical waters.

It has been widely reported that rough surfaces are more favorable for settlement than are smooth surfaces. Inconsistent with the results of earlier field studies (McGuinness and Underwood 1986, McGuinness 1989, Anderson and Underwood 1994), in this study, concrete surfaces did not result in greater fouling biomass or different compositions of fouling assemblages when compared with FE and ST. The general observation that concrete surfaces attract greater larval settlement than smoother surfaces is largely based on studies of intertidal fouling assemblages (McGuinness and Underwood 1986, McGuinness 1989, Anderson and Underwood 1994). For intertidal assemblages where desiccation is generally a potential stress, organisms might prefer to settle on rough surfaces because of a greater retention of water (McGuinness and Underwood 1986) and lower shear (Bushek 1988). This mechanism is plausible for intertidal assemblages, but not for subtidal assemblages, since plates in subtidal zones are rarely exposed at low tides. This may explain why concrete surfaces in this study did not attract more fouling organisms. On the other hand, Crisp and Ryland (1960) found that many larvae preferentially settle on smooth rather than rough surfaces. Our findings, combined with the experiments of Crisp and Ryland (1960), suggest that marine larvae do not necessarily attach themselves to rough surfaces more readily than to smooth surfaces.

A second assumption is that fouling settlement is greatly enhanced by cathodically protected

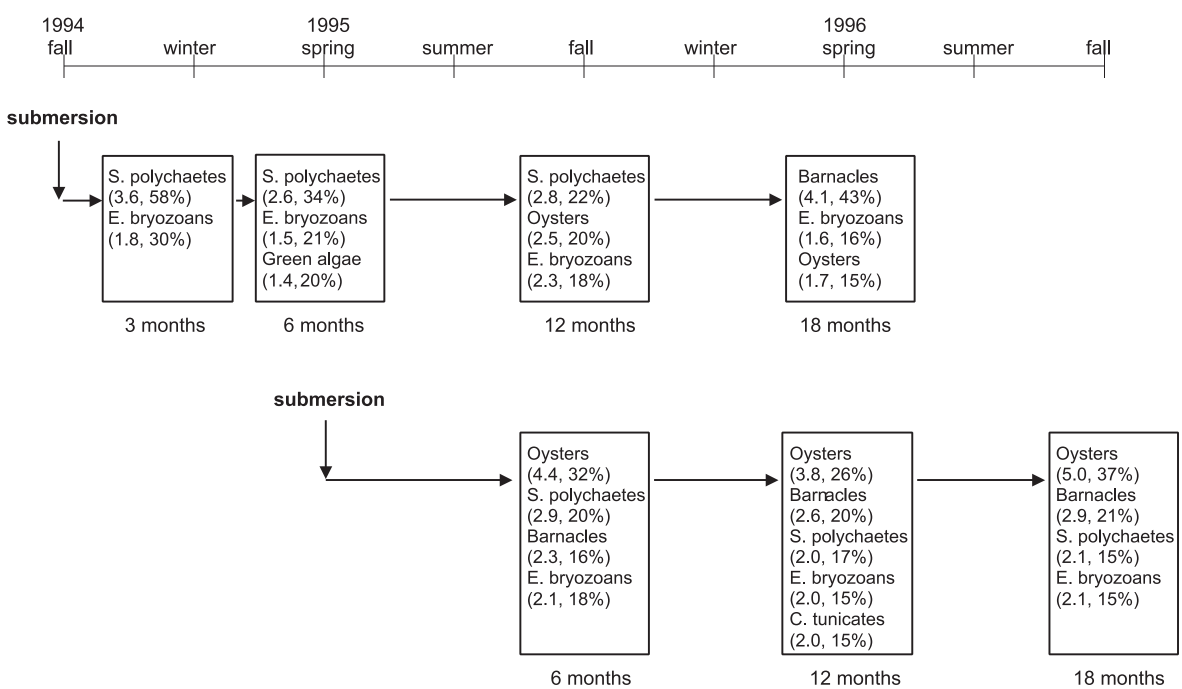

Fig. 5. Changes in composition of fouling assemblages on substrata submersed in Keelung Harbor for 3, 6, 12, and 18 mo. These substrata were initially submersed in spring and fall, respectively. For each taxonomic group, the 1st number in parentheses is the relative abundance, and the 2nd number is the percentage contribution to average similarity within the assemblage. The relative abundance of each group on each plate was coded as 1-5 to represent the 81%-100%, 61%-80%, 41%-60%, 21%-40%, and 1-20% levels of ranking among the ranges during the study period (S. polychaetes: sedentary polychaetes, E. bryozoans: encrusting bryozoans, C. tunicates: colonial tunicates).

surfaces (Eashwar et al. 1995). The enhancement of fouling to interfacial alkalinity and calcareous deposits has been attributed to the transformation of the metal substratum to a more cathodic surface, which may cause considerable roughness providing a more suitable substratum for settlement in intertidal zones (McGuinness and Underwood 1986, Bushek 1988). Since our results from concrete surfaces and the findings of Crisp and Ryland (1960) both suggest that rough surfaces may be no more favorable to settlement than smooth surfaces, the roughening mechanism of cathodically protected surfaces appears not to be applicable to subtidal fouling assemblages in this study. It is not surprising that no significant increase in fouling was detected on surfaces of cathodically protected steel. On the other hand, Perez et al. (1994) found that settlement of cyprids of the barnacle, *Balanus amphitrite*, markedly decreased when surfaces were cathodically protected, but no effects were observed for larvae of the polychaete, *Polydora ligni*. It appears that there is still much controversy with respect to the possible effects of cathodic protection on the development of fouling assemblages or whether such effects exist at all.

The development of subtidal fouling assemblages was greatly influenced by submersion season and submersion period of the substratum, regardless of the type of substratum. The timing of the more diverse group and greater biomass on spring plates closely corresponds with the main settlement season of spring for oysters and barnacles in subtropical Taiwan (Soong et al. 1981), where oysters and barnacles are the major fouling species. In addition, our results show that differences in taxonomic number and biomass between spring and fall plates were more evident before 12 mo of submersion, but less evident after 12 mo (Figs. 1, 2). The decrease in dissimilarity is likely due to increased recruitment of fouling organisms on fall plates during the following spring. This interpretation is supported by the findings that the composition of fouling assemblages on fall plates converged towards that on spring plates with time by the end of a year (Fig. 4). This suggests that development or succession takes the same course even with different seasons of initial submersion. It is likely that the fouling species acted in individualistic manners, and the assemblages were simply composed of those fouling species which arrived at that time.

Although becoming less dissimilar with time, the compositions of fouling assemblages on spring and fall plates did not converge at all. We found that there were distinct 'spring' and 'fall' assemblages in response to submersion season after a year, although both spring and fall plates were

Table 3. Two-way crossed ANOSIM (analysis of similarities: substratum x submersion season) of fouling assemblages from Keelung Harbor. The significance level was calculated by comparing the observed statistic (sample relationship) to its permutation distribution. Tests were significant at the level of 5% except where indicated by NS. The Bonferroni correction for the pairwise comparisons (n = 6) when α = 0.05 is α' = 0.05/6 = 0.0083 or 0.83% (CA: cathodically protected steel, ST: stainless steel, FE: steel, CO: concrete)

Factor	Observed statistic (R)	Permutations used	Significant statistic	Significance level
6 mo				
Substratum	-0.01	5000	2610	52% (NS)
Season	0.81	5000	0	0.0%
12 mo				
Substratum	0.11	5000	450	9.0% (NS)
Season	0.80	5000	0	0.0%
18 mo				
Substratum	0.26	5000	55	1.1%
Season	1.00	5000	2	0.1%
Pairwise comparisons				
CA vs. ST	0.21	630	49	7.8% (NS)
CA vs. FE	0.48	45	3	6.7% (NS)
CA vs. CO	0.30	105	4	3.8% (NS)
ST vs. FE	-0.02	84	38	45% (NS)
ST vs. CO	0.30	630	15	2.4% (NS)
FE vs. CO	0.27	45	9	20% (NS)

eventually submersed across all seasons. Although spring is the main settlement season for oysters and barnacles in subtropical Taiwan (Soong et al. 1981), the single type of fouling assemblage on spring plates suggests that oysters outcompeted barnacles for the limited bare space and continued their dominance in the subtidal zone throughout the study period. Bushek (1988) attributed the cause of differential settlement between the American oyster and the ivory barnacle to water motion. On the other hand, fall plates were first submersed when larval abundance was declining and initially did not accumulate as many individuals as those on spring plates. More unoccupied space on fall plates might lead to highly variable colonization and an unpredictable type of fouling assemblage, depending on the larval supply in the water column. That may be the reason why samples from fall plates were highly variable (Fig. 4). Thus, the historical components of a substratum are important in determining the resulting composition.

In this study, while fouling biomass reached a maximum at the end of 18 mo, the number of taxonomic groups peaked at the end of 12 mo and subsequently declined. Observed succession of fouling assemblages showed that oysters and barnacles were more abundant at the end of 18 mo than they were at the end of 12 mo (Fig. 5). Qualitative observations also showed that oysters and barnacles at the end of 18 mo were bigger than they were at the end of 12 mo. It may be postulated that the increase in biomass at the end of 18 mo largely occurred through the concomitant increase in growth and aggregation of oysters and barnacles. At this time, the decline in fouling taxa could be attributed to the eventual competitive outcome when space became limiting. Consistent with the findings of Greene and Schoener (1982), patterns on both fall and spring plates showed a steady increase in the dominance of solitary and relatively persistent species (oysters and barnacles) over colonial components (colonial tunicates).

Osman (1977) identified 5 major factors that are important in the development of fouling assemblages in temperate waters: 1) selectivity of sites for attachment; 2) seasonal fluctuations in larval abundance; 3) biological interactions; 4) substratum size; and 5) physical disturbance. He concluded that physical disturbance is probably the most important. In this study, the size was the same for all types of substratum, and these substrata were assumed to be exposed to relatively small physical disturbances in the subtidal zone. Thus, the development of subtidal fouling assemblages can be uncoupled from the effects of substratum size and disturbance. Our results demonstrate that the developmental process is greatly affected by seasonal fluctuations in larval abundance and by historical components. There was little evidence that the type of artificial surface affected the development of subtidal fouling assemblages in Keelung Harbor.

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基隆港水下設施表面附著生物的群聚發展

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我們在基隆港內持續進行了18個月的試版掛放實驗，以了解不同基質、不同掛放季節與時間長短對亞熱帶海域水下附著生物群聚發展的相對重要性。四種基質包括裸鋼、不銹鋼、陰極保護鋼及混凝土，分別於秋季及春季時掛放於水下，每隔3-6個月回收部分試版進行採樣。結果顯示基質並不會影響其附著生物的群聚發展，但是春季掛放試版較秋季掛放試版有較高生物量與較多的附著生物種類生長。春季及秋季試版之生物量在掛放時間18個月時皆達到最高，但是生物種類在12個月時卻是最多。聚類與空間排序分析結果亦顯示附著生物群聚結構會受到掛放季節與掛放時間的影響，但不會因基質而有所不同。在18個月的掛放期間內，巨牡蠣 (*Crassostrea gigas*) 為春季試版的主要優勢種類，但秋季試版的優勢種類則隨掛放時間的長短而改變，因此掛放季節與時間對水下附著生物群聚發展的影響較大。然而春季試版與秋季試版在附著生物量與群聚結構間的差距會在掛放12個月後縮小，顯示即使試版於不同季節時掛放，其附著生物群聚的發展仍會依循類似的途徑，這可能是由於這些群聚的發展是取決當時水中附著生物幼生的量與種類。因此亞熱帶海域水下附著生物群聚的發展過程會同時受到當時水中幼生的種類與數量，以及該基質先前已著生的生物種類的影響。

關鍵詞：基質，掛放季節，掛放時間，巨牡蠣。

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