

## FACILITATION OF SOFT-BOTTOM BENTHIC SUCCESSION BY TUBE BUILDERS<sup>1</sup>

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**Abstract.** Controlled field experiments were used to test the effects of surface-deposit feeders on succession at the Skagit flats, an intertidal sandflat in northern Puget Sound. The tube builders *Hobsonia florida* (Polychaeta, Ampharetidae), *Pseudopolydora kempj japonica* (Polychaeta, Spionidae), and *Tanais* sp. (Crustacea, Peracarida) facilitate the recruitment of other taxa to 10-cm<sup>2</sup> azoic patches. Simulated animal tubes facilitated the immigration of *Tanais* sp. and oligochaetes. *Macoma balthica*, a tellinid bivalve, facilitated the immigration of *H. florida*, while inhibiting that of *Tanais* sp. These experiments clearly documented that facilitation rather than inhibition is the dominant process governing succession in the Skagit community. The facilitation model of succession offers a viable alternate explanation for many soft-bottom benthic processes previously explained by the inhibition model.

**Key words:** community structure; controlled manipulations; facilitation; infauna; polychaetes; succession; tube builders.

### INTRODUCTION

We define succession as the temporal pattern of changes in the specific composition of a community. Watt (1964) reviewed the Clementsian and Gleasonian views of succession; our connotation of the term succession falls between these extremes. The Clementsian view of succession implies an orderly transition from one distinct community, or seral stage, to another. The sequence of communities, or sere, culminates in a stable, environmentally determined, climax community. Much of the recent severe criticism of the concept of succession (e.g., Drury and Nisbet 1973, Peters 1976, Connell and Slatyer 1977) has been levelled at the Clementsian view of succession. The Gleasonian view of succession would classify any temporal change in a community, even fluctuations of population abundances about some mean value, as successional (Gleason 1927). The Gleasonian view is far less susceptible to attack because it makes few explicit predictions about the expected patterns of temporal change or about the causes of the patterns. Our study of succession is in the Gleasonian tradition because it focuses on the patterns of change of local population abundances in response to their environment rather than on changes in abstract indices of community structure (e.g., of diversity or stability). We also draw from the Clementsian tradition in our view that one soft-bottom benthic taxon may alter the effective local environment or microclimate (Allee et al. 1949) experienced by another species in the community. The tubes built by some members of the soft-

bottom benthic community may substantially affect the environmental conditions experienced by other members of the community. These environmental modifications may provide a mechanistic explanation of soft-bottom benthic succession.

Our goal is to explain and predict some of the characteristic patterns of soft-bottom benthic succession. Soft-bottom benthic successional trends are particularly apparent after large-scale defaunations. These defaunations can be caused by storms (Boesch et al. 1976), red tides (Dauer and Simon 1976), low dissolved-oxygen levels (Santos and Simon 1980), and the man-made disturbances of dumping (Rhoads et al. 1978) and organic pollution (Pearson and Rosenberg 1978, Sanders et al. 1980). The practical importance of quickly assessing environmental damage has prompted benthic investigators to search for easily measured parameters to classify soft-bottom successional trends. Changes in the harpacticoid-to-nematode ratio (Parker 1975, Raffaelli 1981, Raffaelli and Mason 1981, Warwick 1981), the log-normal distribution of abundance among infaunal species (Gray 1979, 1980, Gray and Mirza 1979), and community diversity, and the abundances of taxa regarded as "pollution indicators" (Pearson and Rosenberg 1978) have been used to describe successional trends. These methods are strictly empirical and do not provide mechanistic explanations for the characteristic temporal patterns.

While indices of community structure might be found to correlate with successional state, causal explanations of succession are more likely to be determined by studying the responses of individual populations to other members of the community and to their environment. Horn (1971) studied the interactions between trees and their environment by directly measuring the light levels under the canopy of each species of tree in a New England forest. Tree species differ substan-

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tially in the amount of shade cast by their canopies and in the ability of their saplings to tolerate shading. The microclimate created by an adult tree largely determines the types of trees which may replace it, as succession proceeds. Markovian individual-by-individual replacement models of forest succession (Waggoner and Stephens 1970, Horn 1974, 1975, 1981) have been successful in predicting the path of succession because of the strong effects adult trees have on their environment and on the survival of saplings. Species that do not alter their local microclimates or interact strongly with other members of the community could not be modeled easily with Markovian individual-by-individual replacement models. For example, the temporal pattern of change of the Australian thrips documented by Andrewartha and Birch (1954) is almost entirely due to changes in temperature and not to the abundance of any other members of the community (but see Smith [1961] for an alternate view). Such a pattern of temporal change could not be described with an individual-by-individual replacement model and would be termed successional only by the most extreme Gleasonian.

Benthic tube builders are capable of dramatically altering their local environment (Fager 1964, Mills 1969, Rhoads et al. 1977, Eckman et al. 1981). These environmental modifications have profound implications for the mechanisms governing soft-bottom benthic succession. The most generally observed feature of soft-bottom succession after a radical disturbance is the early dominance in the community of shallow-dwelling, tube-building, surface-deposit feeders (the apparent exception being *Capitella* spp., which may surface-deposit feed but do not generally do so [Fauchald and Jumars 1979]). The studies of Grassle and Grassle (1974) and McCall (1977) provide particularly clear demonstrations of this pattern, and these authors document the life history features that separate these opportunistic species from those that eventually replace them. The causes of this replacement are known only poorly. Knowledge of the effects of these deposit feeders on their local environments and on the recruitment of the larval and juvenile stages of other taxa is as yet too meager and contradictory to allow a clear explanation of their role in succession.

To assess the role of deposit feeders in succession, we have adopted the tripartite conceptual model of the mechanisms controlling succession proposed by Connell and Slatyer (1977). These authors described three models of succession: inhibition, tolerance, and facilitation. In the inhibition model of succession, each individual hinders the recruitment of other individuals to its immediate vicinity. This model appears to describe the dominant mode of succession of benthic communities on hard substrata (Sutherland and Karlson 1977, Sousa 1979, Dean and Hurd 1980, Paine and Levin 1981). Sousa (1979) and Dean and Hurd (1980) concluded, on the basis of the evidence presented in Woodin (1976), that inhibition was the dominant

mechanism of succession in soft-bottom benthic communities. It should be noted that Woodin (1976, 1979) predicted inhibition to predominate only in areas of high densities, although such numerical densities have yet to be defined precisely.

In the tolerance model of succession, any species can invade an unoccupied gap in the environment, but there is a distinct hierarchy of species-by-species replacements based on competition or on tolerance to environmental variables. This model is similar to Egler's (1954) initial floristic composition model and Horn's (1981) competitive hierarchy model of succession. The classic example of this type of succession would be the transition to increasingly more shade-tolerant trees during the course of forest succession. McCall (1977) has explained some patterns of soft-bottom benthic succession in terms of the increased tolerance of later succession species.

In the facilitation model, early species prepare the way for later species in the successional sequence but hinder their own recruitment or self-replacement. Both effects are due to modifications of the physical environment. This model of succession, which is similar to the relay floristics model of Egler (1954) and the obligatory succession model of Horn (1981), has been criticized as being inadequate to explain patterns of temporal change in both terrestrial (Egler 1954, Drury and Nisbet 1973) and marine (Sutherland and Karlson 1977, Sousa 1979) communities. Dean and Hurd (1980) found that hydroids "paved the way" for mussel recruitment but were not essential for the mussels to recruit. Sutherland and Karlson (1977), whose definition of succession is more restrictive than ours, stated that succession was not occurring in their community for several reasons, one of which was that fouling organisms do not alter the substratum they occupy, i.e., "prepare" it for later arrivals.

Features of the facilitation model of succession may apply to soft-bottom benthic succession. Deposit feeders do produce profound changes in their local environments through tube building and fecal-pellet production. Tubes may make the environment hospitable to taxa that otherwise would not settle or could not survive in an area (Fager 1964, Mills 1969). The precipitous declines observed in capitellid polychaete populations (Grassle and Grassle 1974) and ampeliscid amphipod populations (Mills 1967, 1969) may be the results of changes in the size composition of surficial sediments caused by their own feeding activities.

There is a crucial difference among the three models of succession, which can be tested readily with controlled manipulations in the field. If the abundance of an early species in the succession sequence is enhanced, only the facilitation model would predict an increase in the immigration rates or survival of other species. The inhibition model would predict a strong decrease, whereas the tolerance model would predict a slight decrease or no change. We tested this crucial distinction among the models by manipulating the

TABLE 1. Descriptions of Skagit taxa. The dimensions are expressed as Corey shape factors (Janke 1966);  $D_L$  is the recruit length, and  $D_T$  is the maximum cross-sectional dimension.  $D_T$  also represents the sieve size that will retain the smallest individuals of each taxon. Approximate adult sizes of the Skagit taxa can be found in Eckman (1979).

Taxon	Trophic type	Reproduction	Dimensions of smallest recruits ( $\mu\text{m}$ ) ( $D_T \times D_L$ )
<i>Hobsonia florida</i>	tube-building, surface-deposit feeding polychaete	tube brooding, planktonic (?) larvae	90 $\times$ 220
<i>Pseudopolydora kempji japonica</i>	tube-building, surface-deposit feeding, suspension feeding polychaete	tube brooding, planktonic larvae	120 $\times$ 400
<i>Tanais</i> sp.	crustacean tube-building, particle browsing peracarid	brooding	130 $\times$ 500
<i>Macoma blathica</i>	bivalve burrowing, surface-deposit feeding tellinid	planktonic larvae	400 $\times$ 500
<i>Manayunkia aestuarina</i>	tube-building, surface-deposit feeding, suspension feeding polychaete	tube brooding, benthic juveniles	100 $\times$ 400
Oligochaetes	burrowing deposit feeders	—	70 $\times$ 300
<i>Corophium slamonis</i>	crustacean tube-building, surface-deposit feeding peracarid	brooding	200 $\times$ 750
<i>Pygospio elegans</i>	tube-building, surface-deposit feeding, suspension feeding polychaete	asexual fission	200 $\times$ 1300

abundances of surface-deposit feeders in the field and monitoring the effects on the recruitment of other taxa.

We conducted our tests of succession on an infaunal community inhabiting the intertidal zone of the Skagit flats. This area at the mouth of the north fork of the Skagit River in northern Puget Sound consists of an extensive intertidal flat composed of medium- to fine-grained sand (median grain size = 120  $\mu\text{m}$  [Eckman 1979]). Our experiments were performed 200 m seaward of a fringing tidal marsh of the bulrush *Scirpus americanus* ( $\approx 1.5$  m tidal elevation above MLLW). The community is dominated by surface-deposit feeders (Table 1). Earlier studies of this community, particularly those of Smith (1980) and Eckman (1979), provided the requisite information to design experiments on the appropriate spatial and temporal scales. We chose to study succession in initially defaunated 10-cm<sup>2</sup> patches for the following reasons. First, 18–30% of the spatial extent of the flats has usually been affected within the previous month by disturbances of this small scale, caused by the feeding activities of dabbling ducks and demersal fishes (Smith 1980). Second, the initial abundances of infauna can be manipulated more readily in small rather than in large patches. Finally, more powerful statistical tests can be performed on data obtained from numerous small patches rather than data obtained by subsampling the same large plots through time. Hierarchical statistical designs (Sokal and Rohlf 1969; chapter 10) are not needed to separate the effects of deposit feeder manipulations from the plot-to-plot variability.

We chose to use extremely fine-meshed (63- $\mu\text{m}$ ) sieves to process our samples in order to sample ad-

equately the larvae and juveniles of several taxa that would pass readily through the larger sieves used in most other benthic studies (Table 1). Understanding the processes affecting the immigration and survival of larvae and juveniles is required to explain the mechanism of soft-bottom benthic succession fully. As discussed by Woodin (1981), a tube builder may affect both the rate of larval immigration and the survival rate of the larvae, once settled. It would be extremely difficult to separate these two effects in the Skagit community with a coarse-meshed (e.g., 1-mm) sieve. The juveniles of the ampharetid polychaete *Hobsonia florida* and several other taxa will not be retained by a 1-mm mesh sieve until nearly a month after settlement, and the adults of several taxa enumerated in this study (oligochaetes and the sabellid polychaete *Manayunkia aestuarina*) are rarely retained on a 1-mm mesh sieve.

Most of the deposit feeders larger than 1 mm enumerated in this study were quick-frozen on dry ice in the field so that the proteins in their guts could be analyzed. Although we will not report on gut contents analyses in this paper, the presence of larval proteins in the guts of suspected predators can be documented using antisera to the members of the Skagit community, which we have developed (Feller et al. 1979).

## METHODS

### Field manipulations

The six field experiments were designed to study succession in defaunated 10-cm<sup>2</sup> patches to which we had added various species of surface-deposit feeders or simulated animal tubes. In four experiments con-

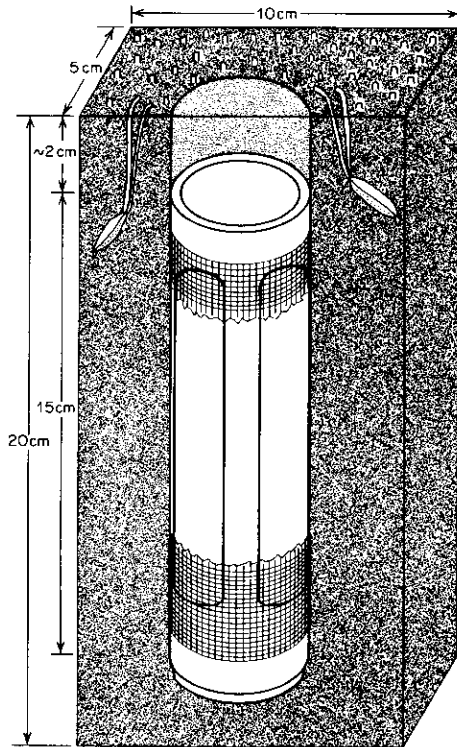


FIG. 1. A cut-away view of a PVC core and azoic sand patch in place within natural sediments. Most of the side surface of the PVC core was removed using a router and replaced with 1.1-mm mesh window screening. (The PVC core was 15 cm long  $\times$  3.7 cm internal diameter.)

ducted in 1979, the defaunated patches were randomly located within  $1 \times 1$  m plots, which had been randomly positioned within a  $30 \times 30$  m area. In two experiments conducted in 1980, the defaunated patches were located within  $1 \times 5$  m plots whose long axes were oriented cross-stream to the incoming tide. These plots were positioned randomly within a  $30 \times 30$  m area located 50 m seaward of the 1979 experimental site.

We created the defaunated patches by first removing a  $10 \text{ cm}^2 \times 20 \text{ cm}$  deep cylindrical plug of natural sediment and then inserting a mesh-covered PVC core filled with clean foundry sand (Fig. 1). The surface of the foundry sand patch was made flush with that of the natural substratum. This commercially available foundry sand (120 mesh [ $\approx 125\text{-}\mu\text{m}$ ] olivine) consists predominantly of quartz grains with a median grain size closely matching that of the natural sediment. At the start of each experiment, the foundry sand in these patches was virtually devoid of organic coatings or microbial populations. Within one or two tidal cycles, the uppermost few centimetres of each patch consisted of dark, natural sediment, which presumably had been transported as bedload. The PVC cores were designed to allow the passage of pore water and to mark the defaunated patches for subsequent sampling.

The experimental designs of the six successional ex-

periments are listed in Table 2. The abundances of the Skagit infaunal populations prior to the initiation of the six successional experiments are provided in Table 3. At the start of each experiment, we randomly selected the patches which were to receive transplanted members of the infauna, simulated animal tubes (sticks), or no initial additions (controls). In 1979 we manipulated three surface-deposit feeders: the ampharetid polychaete *Hobsonia florida* and the spionid polychaete *Pseudopolydora kempji japonica* (both of which are tube builders), and the tellinid bivalve *Macoma balthica*. In 1980 we manipulated simulated animal tubes, *H. florida*, and the peracarid crustacean *Tanais* sp., a tube builder which feeds by particle browsing. The animals had been collected 2 d prior to the start of each experiment using 1-mm mesh sieves. They were sorted to taxon in the lab and placed in containers with clean foundry sand, which the tube builders used to construct new tubes.

With one exception (the 10 *Macoma balthica* treatment in the *Macoma/Pseudopolydora* [MAPS] experiment), the numbers of individuals of each taxon added to the defaunated patches were within the range of abundances of large adults in the natural community. The increasing numbers of *H. florida* added per defaunated patch in later experiments (Table 2) reflect our improved ability to sort and transplant healthy worms and our desire to be able to maintain demonstrably enhanced numbers of worms for greater lengths of time. By inspecting each tube with the aid of a dissecting microscope set up in the field, we ensured that it contained a worm before we inserted the tube (with forceps) within a defaunated patch. We placed the *M. balthica* individuals just beneath the sediment surface within the patches. We manipulated the initial abundances of *Tanais* sp. by first encircling the perimeter of each  $10\text{-cm}^2$  patch with 500- $\mu\text{m}$  Nitex<sup>®</sup> screening to prevent initial flight. We then added 40 tanais to each patch. The Nitex<sup>®</sup> screening was removed 4 h later, before the return of the tide but after tube building had commenced. In 1980 we added simulated tubes to some patches as a control to assess the purely hydrodynamic effects of tubes (Eckman 1979, Eckman et al. 1981). The simulated tubes, which mimicked the tubes of *H. florida* in size, were cylindrical wooden applicator sticks, 21 mm in length and 2 mm in diameter. We inserted the simulated tubes in haphazard arrays within the  $10\text{-cm}^2$  patches, with their tops protruding several millimetres from the sediment surface.

#### Field sampling

Within several tidal cycles the locations of the defaunated patches were usually hidden by a thin layer of dark, natural sediment. We located the patches by using a standard dissecting needle to find the tops of the buried PVC cores, which marked the limits of the  $10\text{-cm}^2$  patches. We sampled the patches with a corer having a cross-sectional area of  $5.3 \text{ cm}^2$ . The core sam-

TABLE 2. Experimental designs. The numbers of replicate 5.3-cm<sup>2</sup> samples analyzed for each date are indicated. The number of animals added to the 10-cm<sup>2</sup> patches is indicated in parentheses for each treatment.

Experiment name (date begun)	Treatments (no. of animals added)	Day number												Total samples
		2	5	6	10	11	14	25	27	37	94	121	148	
July <i>Hobsonia florida</i> (12 July 1979)	<i>H. florida</i> (2)			5			5			5			5	20
	Control			5			5			5			5	20
July <i>M. balthica</i> (12 July 1979)	<i>M. balthica</i> (2)			5			5			5			2	17
	Control			5			5			5			2	17
August <i>H. florida</i> (8 August 1979)	<i>H. florida</i> (4)				5				5			5		15
	Control				5				5			5		15
Macoma/Pseudopolydora [MAPS] (8 August 1979)	<i>M. balthica</i> (10)				5				5			5	2	17
	<i>P. kempji japonica</i> (2)				5				5			5	4	19
	Control				5				5			5	5	20
April <i>H. florida</i> (6 April 1980)	<i>H. florida</i> (4)	5	5			5			4					19
	Sticks (4)	5	5			4			4					18
	Control	5	5			5			5					20
Sticks/Hobsonia/Tanais [SHOT] (4 June 1980)	<i>H. florida</i> (6)	5		5		5			5					20
	<i>Tanais</i> sp. (40)	5		5		5			5					20
	Sticks (4)	5		5		5			5					20
	Control	5		5		5			5					20

ple was divided into top 2- and 2-5 cm fractions. In 1979 we fixed both fractions with a 10% formaldehyde solution which had been buffered with sodium borate and included Rose Bengal stain. In 1980 we modified the field sampling program so that we could quick-freeze in the field many of the animals larger than 1 mm. We fixed the 2-5 cm fraction but sieved the top 2-cm fraction with a 1-mm mesh sieve nested over a 63- $\mu$ m mesh sieve. We froze the material retained on the coarse sieve in petri dishes on dry ice and fixed the material retained on the fine sieve. During both

years we used a 10-cm<sup>2</sup> corer to remove the buried PVC core and its contents.

If the buried PVC core was ever observed to be exposed by sediment transport, data from that core were not used in the analysis. As well as providing an unnatural barrier to migration, the exposed lip causes confounding flow and sediment transport effects. Several complete sets of experiments, which we began in March 1980, had to be abandoned because a severe winter storm caused sufficient sediment transport to remove the uppermost several centimetres of sediment

TABLE 3. Abundances of the major taxa in the natural community. Geometric means/5.3 cm<sup>2</sup> and 95% confidence intervals (back transformed) of natural populations prior to the initiation dates of the six succession experiments are presented. The samples were taken randomly from within 1  $\times$  1 m plots randomly positioned within the same 30  $\times$  30 m area as the succession experiments. The samples were processed with a 63- $\mu$ m sieve.

Taxon	Sampling date (Sample size)			
	28 June 1979 (N = 5)	26 July 1979 (N = 5)	24 March 1980 (N = 5)	30 May 1980 (N = 9)
<i>Hobsonia florida</i>	3.5 (1.8, 6.4)	15.8 (12.5, 19.9)	0	30.1 (23.1, 39.1)
<i>Pseudopolydora kempji japonica</i>	0	1.0 (0.2, 2.6)	0	0
<i>Tanais</i> sp.	0	1.2 (0.7, 1.7)	3.1 (2.2, 4.4)	0.5 (0, 1.2)
<i>Macoma balthica</i>	3.2 (1.8, 5.3)	0.3 (0, 1.1)	1.4 (0.4, 3.0)	1.4 (0.8, 2.3)
<i>Manayunkia aestuarina</i>	11.0 (3.0, 35.7)	14.0 (4.8, 38.2)	43.5 (32.4, 58.2)	6.7 (2.8, 14.5)
Oligochaetes	168.1 (104.8, 269.3)	63.0 (33.5, 117.7)	24.9 (20.5, 30.4)	16.9 (12.9, 19.8)
<i>Corophium salmonis</i>	1.5 (0.7, 2.7)	9.0 (3.2, 22.8)	0.9 (0, 3.1)	0.3 (0, 0.8)
<i>Pygospio elegans</i>	7.0 (0.8, 34.2)	11.2 (3.0, 36.4)	0.5 (0, 1.4)	0

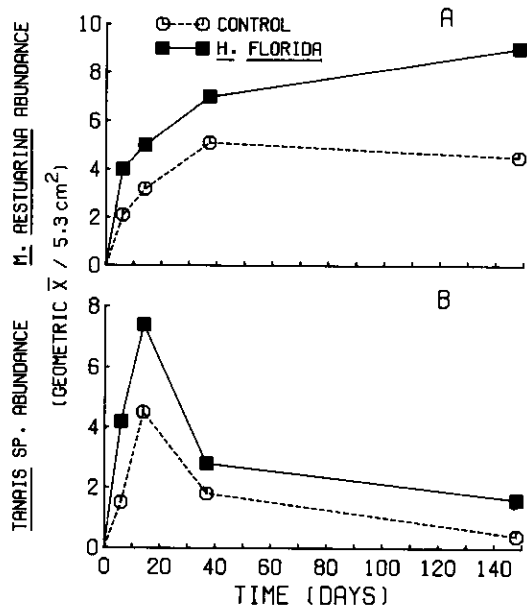


FIG. 2. Results of the July 1979 *Hobsonia florida* experiment. Abundances through time of (A) the sabellid polychaete *Manayunkia aestuarina* and (B) the peracarid crustacean *Tanais* sp. in patches that initially contained either azoic sand plus two *H. florida*, or azoic sand alone (CONTROL). Each mean is based on five replicates (Table 2).

from our entire experimental area, exposing the tops of all of the PVC cores. In the experiments on which we are reporting in this study, we usually created several extra patches of each treatment at the start of an experiment to serve as replacements for patches in which the PVC core had been exposed. Even with these replacement patches, we often had to settle for fewer replicates on the final sampling dates because of the exposure problem.

#### Laboratory sorting

We used a technique developed by Feller (1977) to aid our sorting of the top 2-cm fraction samples. We placed each sediment sample in a 500-mL beaker, rapidly agitated the sediment with a jet of water, allowed the suspension to settle for 3–4 s, and decanted the supernatant solution into a 63- $\mu$ m mesh sieve. This procedure was repeated five times, which removed most of the smaller animals from the sediment. The larger animals, particularly worms in tubes, often remained with the bulk of the sediment in the beaker. We sorted these animals from the sediment at low magnification (6–12 $\times$ ). We sorted the material retained on the 63- $\mu$ m mesh, using higher magnification (12–50 $\times$ ).

Because most small animals occurred in the top 2-cm fraction, a 300- $\mu$ m mesh sieve was used to process the 2–5 cm samples. We analyzed the material passing through the 300- $\mu$ m sieve that was retained on a 63- $\mu$ m sieve in five of the July 1979 samples of the natural

community. The use of the 300- $\mu$ m sieve on these samples resulted in the following underestimates of population abundances: oligochaetes 33.3% and *Manayunkia aestuarina* (a sabellid polychaete) 6.4%. Fewer than 1% of the individuals of the other taxa analyzed in this study passed through the coarse sieve.

We counted only animals with either umbos (*M. balthica*) or anterior ends (all others). We developed an additional criterion for the polychaete *Pygospio elegans* since asexual reproduction in this species results in a variety of morphological states of the anterior. We counted only those individuals with eyespots or palps.

We freeze-dried the frozen samples obtained in 1980. We sorted all of the crustaceans and most of the large polychaetes to species while the samples were desiccated. These animals were then stored in a freezer. Small polychaetes could not be identified while desiccated because we could not remove them from their tubes without breakage. We solved this problem by rehydrating each sample for 24 h with a 10% formaldehyde solution, stained with Rose Bengal. When the animals rehydrated we could sort them readily to species.

#### Statistical analyses

We used the SPSS program ANOVA (Nie et al. 1975) to perform the analyses of variance. Only the seven most abundant macrofaunal taxa (Table 1) and oligochaetes were analyzed. We used a  $\log(x + 1)$  transformation to transform the counts of those taxa whose abundances showed a significant violation of the assumption of homoscedasticity ( $F_{\max}$  test [Sokal and Rohlf 1969]). The transformed counts, reported as the back-transformed  $[(\text{antilog}_{10} \bar{x}) - 1]$  or geometric mean, were distributed such that the assumption of equality of variance was not violated.

We analyzed each experiment with a fixed-effects, two-way ANOVA, with deposit feeder and time as the main effects. When the effects of more than one treatment were being assessed in an experiment, we first tested the overall two-way ANOVA for either significant deposit feeder or deposit feeder  $\times$  time interaction effects. If neither was significant at  $\alpha = .05$ , we stopped testing. If either ratio was significant, we performed separate analyses comparing each treatment with the control, using significance levels conservatively adjusted (by Bonferroni's technique [Miller 1966]) for the proper number of comparisons. For example, if there were three treatment vs. control comparisons, a treatment was judged to be significant at an experimentwise  $\alpha$  of .05 only if the separate two-way ANOVA was significant at an  $\alpha$  of .016.

The analyses of variance were used to provide objective criteria for the classification of the effects of surface-deposit feeders on the recruitment of other taxa. If the presence of a deposit feeder significantly increased the abundance of another taxon, the effect

TABLE 4. Two-way analyses of variance tables for the four 1979 succession experiments. Each subgrouping presents the results of a separate analysis; the total degrees of freedom for each analysis can be obtained by addition. In all but one case, the MAPS experiment, the manipulated taxon is indicated in the experiment name. MAPS = *Macoma balthica* or *Pseudopolydora kempj japonica* manipulations.

Experiment	Manipulated taxon	Affected taxon		Manipulation main effect	Time main effect	Manipulation × time interaction	Residual (error)
a) July <i>Hobsonia florida</i>	<i>H. florida</i>	<i>Manayunkia aestuarina</i> †	df	1	3	3	32
			Mean square	0.511	0.162	0.009	0.058
			F	8.8**	2.8	0.2	
b) July <i>Hobsonia florida</i>	<i>H. florida</i>	<i>Tanais</i> sp.†	df	1	3	3	32
			Mean square	0.476	0.514	0.016	0.094
			F	9.5**	10.2**	0.3	
c) July <i>Macoma balthica</i>	<i>M. balthica</i>	<i>Tanais</i> sp.†	df	1	3	3	26
			Mean square	0.066	0.081	0.362	0.099
			F	0.7	0.8	3.6*	
d) July <i>Macoma balthica</i>	<i>M. balthica</i>	<i>Hobsonia florida</i> †	df	1	3	3	26
			Mean square	0.333	1.411	0.017	0.070
			F	4.8*	20.1***	0.2	
e) August <i>Hobsonia florida</i>	<i>H. florida</i>	<i>Pseudopolydora kempj japonica</i>	df	1	2	2	24
			Mean square	20.831	1.633	8.63	1.5
			F	13.9***	1.1	5.8*	
f) August <i>Hobsonia florida</i>	<i>H. florida</i>	Oligochaetes	df	1	2	2	24
			Mean square	149.6	516.9	787.0	63.12
			F	2.4	8.2**	12.5***	
g) August MAPS	<i>P. kempj japonica</i>	<i>Tanais</i> †	df	1	3	3	31
			Mean square	0.088	0.184	0.305	0.061
			F	1.4	3.0	5.0‡	

\*  $P \leq .05$ ; \*\*  $P \leq .01$ ; \*\*\*  $P \leq .001$ .

† Counts have been transformed to  $\log(x + 1)$ .

‡ Experimentwise  $P \leq .05$ .

was classified as facilitation. If the presence of the deposit feeder led to a decreased abundance of another taxon, the effect was classified as inhibition. As we shall discuss later, the existence of these biological interactions is a necessary but not a sufficient condition for classifying the overall succession as fitting either the facilitation or inhibition models proposed by Connell and Slatyer (1977). The classifications as to facilitation or inhibition in the Results section thus are provisional and will be treated further in the Discussion.

## RESULTS

### July 1979 *Hobsonia florida* experiment

We designed this experiment to assess the effects of the initial addition of two *Hobsonia florida* on succession through a 5-mo period. To estimate how long an enhanced abundance of larger worms persisted, we measured the distance between eyespots of the larger *H. florida* samples within the 10-cm<sup>2</sup> patches. Eyespot separation in *H. florida* is highly correlated with body volume (Self and Jumars 1978). Worms with an eyespot spacing narrower than 250  $\mu\text{m}$  were too small to have been added initially. Though enhanced numbers of large worms persisted through day 37, a statistically significant difference was found only on

day 6 ( $\bar{x}_{\text{treatment}} = 1.2$ ;  $\bar{x}_{\text{control}} = 0.4$ ;  $t$  test,  $P < .05$ ), probably due to the low power of the test.

The immigration of two taxa was enhanced in the patches which contained *H. florida*. Thus, we classified the effects of *H. florida* on succession as facilitation. The two taxa affected were the small sabellid polychaete *Manayunkia aestuarina* (Fig. 2A, Table 4a) and the peracarid crustacean *Tanais* sp. (Fig. 2B, Table 4b). The changes in abundance of these two taxa can be attributed entirely to enhanced immigration rates into the *H. florida* patches relative to the control patches during the 1st wk of this experiment, the period when greater numbers of *H. florida* surely were present. Most of the other taxa which immigrated into the defaunated patches changed in abundance significantly with time but were not affected by the initial presence of *H. florida*.

### July 1979 *Macoma balthica* experiment

Originally we had intended the PVC cores to serve as barriers to the lateral migration of *M. balthica*. However, we discovered that PVC cores which were placed close to the sediment surface were often exposed during periods of active sediment transport (spring tides and storms). The placement of the PVC cores at a depth of  $\approx 2$  cm within the sediment (Fig. 1) permitted the lateral migration of fairly large *M.*

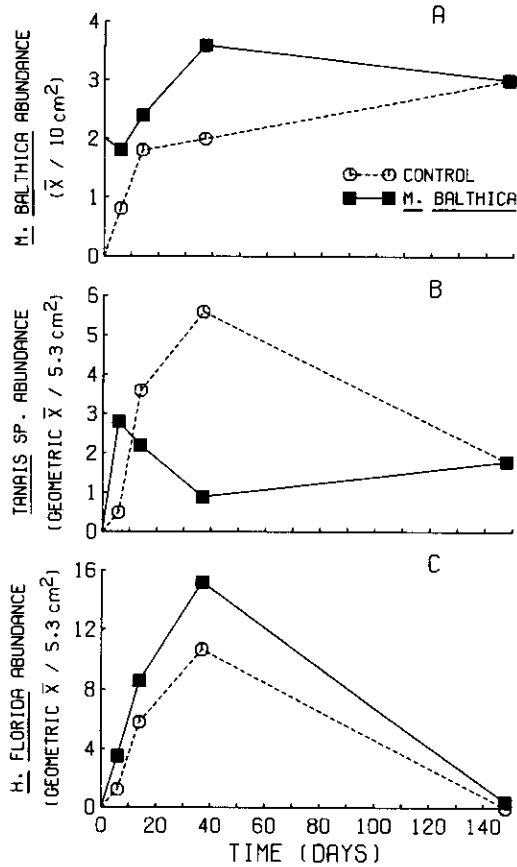


FIG. 3. Results of the July 1979 *Macoma balthica* experiment. Abundances through time of (A) the tellinid bivalve *Macoma balthica*, (B) the peracarid crustacean *Tanais* sp., and (C) the ampharetid polychaete *Hobsonia florida* in patches that initially contained either azoic sand plus two *M. balthica*, or azoic sand alone (CONTROL). The number of replicates for each date is presented in Table 2.

*balthica* into both treatment and control patches (Fig. 3A). We found higher densities of *M. balthica* in the treatment patches through the first 37 d of this experiment. Statistical analyses of the mean abundances on each date revealed that only the day 6 treatment and control means were significantly different at an  $\alpha$  of .05 (*t* test). Several of the PVC cores were exposed in patches which we had intended to sample on day 148; we did not sample these patches. As a consequence, the estimates of animal abundances on day 148 are based on only two *M. balthica* cores and two control patches (Table 2).

*M. balthica* did not have a uniform effect on all subsequently recruiting species. Even though the presence of *M. balthica* resulted in an initially increased abundance of *Tanais* sp., the later and quantitatively dominant effect was a decreased tanaid abundance in *M. balthica* patches relative to control patches (Fig. 3B). The changing influence with time is reflected in a significant interaction effect between *M. balthica* presence and time in the two-way ANOVA

of tanaid abundances (Table 4c). We classify it, due to the dominant decrease, as inhibition. The immigration of *H. florida*, on the other hand, was enhanced consistently by the presence of *M. balthica* (Fig. 3C, Table 4d). We classified this effect as facilitation.

August 1979 *Hobsonia florida* experiment

We could detect enhanced numbers of large *H. florida* (eyespot spacing > 250  $\mu\text{m}$ ) in patches to which we had added four individuals through the first 10 d of this experiment ( $\bar{x}_{\text{treatment}} = 3.2$ ,  $\bar{x}_{\text{control}} = 1.0$ ; *t* test,  $P < .05$ ). The initial addition of large *H. florida* at the onset of succession in the defaunated patches resulted in long-lasting effects on the abundance of the spionid polychaete *Pseudopolydora kempji japonica*. The increased abundances of *P. kempji japonica* in *H. florida* patches (Fig. 4A, Table 4e), were classified as examples of facilitation.

The initial recruitment of oligochaetes was inhibited strongly by the presence of *H. florida* (Fig. 4B, Table 4f). The effect of our manipulation on oligochaetes was not long lasting, but since we could only document that significantly enhanced levels of large *H. florida* were present during the first sampling date, the data appear to justify classifying the effect as inhibition.

August *Macoma/Pseudopolydora* (MAPS) experiment

In this experiment we manipulated the abundance of both *P. kempji japonica* and *M. balthica*, each in separate patches. Both species are capable of active

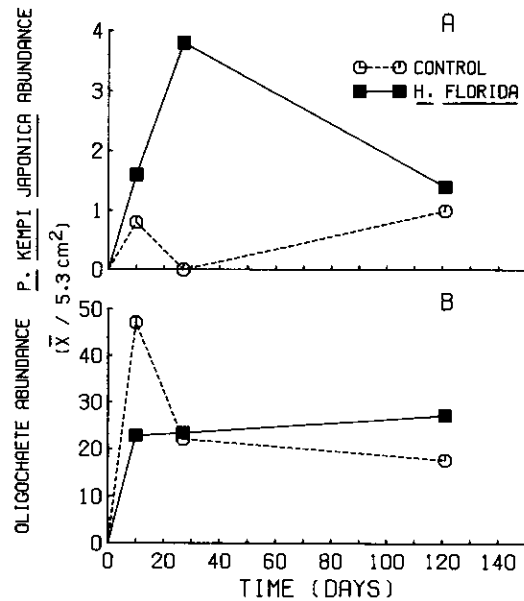


FIG. 4. Results of the August 1979 *Hobsonia florida* experiment. Abundances through time of (A) the spionid polychaete *Pseudopolydora kempji japonica* and (B) oligochaetes, in patches that initially contained either azoic sand plus four *Hobsonia florida*, or azoic sand alone (CONTROL). The number of replicates for each date is presented in Table 2.

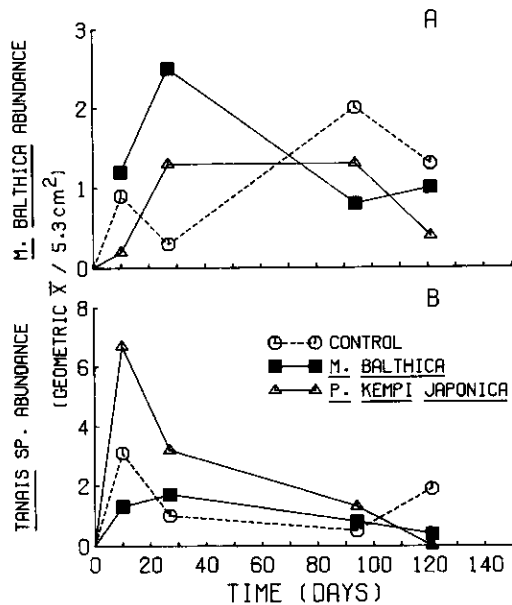


FIG. 5. Results of the August 1979 *Macoma/Pseudopolydora* [MAPS] experiment. Abundances through time of (A) the tellinid bivalve *Macoma balthica* and (B) the peracarid crustacean *Tanais* sp., in patches that initially contained either azoic sand plus *M. balthica* or *P. kempji japonica*, or azoic sand alone (CONTROL). The numbers of manipulated animals added and the number of replicates for each date are presented in Table 2.

migration as adults, which may account for our inability to detect large *P. kempji* in the patches to which they had been added and for the rapidly changing abundances of *M. balthica* in treatment and control cores (Fig. 5A). A two-way ANOVA revealed significant differences in *M. balthica* abundances between the treatment and control patches (treatment  $\times$  time interaction,  $P < .05$ ), but  $t$  tests revealed significantly enhanced densities of *M. balthica* in the *M. balthica* patches relative to the control patches only on day 27. Our manipulation of *P. kempji japonica* (or perhaps only their remaining tubes) had a striking effect on the recruitment of *Tanais* sp. (Fig. 5B). Separate analyses of variance confirmed that the tanaid abundances were affected by the *P. kempji* manipulation (Table 4g) but not by the *M. balthica* manipulation (ANOVA table not included). We tentatively classified this effect as facilitation due to the presence of polychaete tubes. We rigorously tested this interpretation with the controlled experiments conducted in 1980.

#### April 1980 *Hobsonia florida* experiment

We designed this experiment to test the effects of *H. florida* and the effects of simulated *H. florida* tubes on succession. April through May is the period when the seasonal abundances of most Skagit taxa are at their nadir (Smith 1980, E. D. Gallagher, P. A. Jumars, and D. D. Trueblood, *personal observation*). While the low numbers of *H. florida* recruits responding to

our defaunated patches allowed us to detect readily the *H. florida* we had added (Fig. 6A, Table 5a), there were few available recruits of the taxa affected in our previous *H. florida* experiments. For example, the mean abundances of *M. aestuarina* and *Tanais* sp. per 5.3 cm<sup>2</sup> were 2.1 and 1.2, respectively, in the treatment and control patches.

The abundance of oligochaetes clearly was increased by the presence of simulated worm tubes (Fig. 6B, Table 5b). *H. florida*, on the other hand, did not appear to affect oligochaete recruitment when compared to the defaunated controls. If we assume that the simulated-tube patches provide an accurate mimic of *H. florida* tubes, then these data may support the hypothesis that the animals had a deleterious effect on oligochaetes once they had immigrated to the *H. florida* patches. Our present knowledge of the processes affecting the immigration and survival of oligochaetes is too scanty to allow us to explain the mechanisms of the *H. florida*-oligochaete interaction.

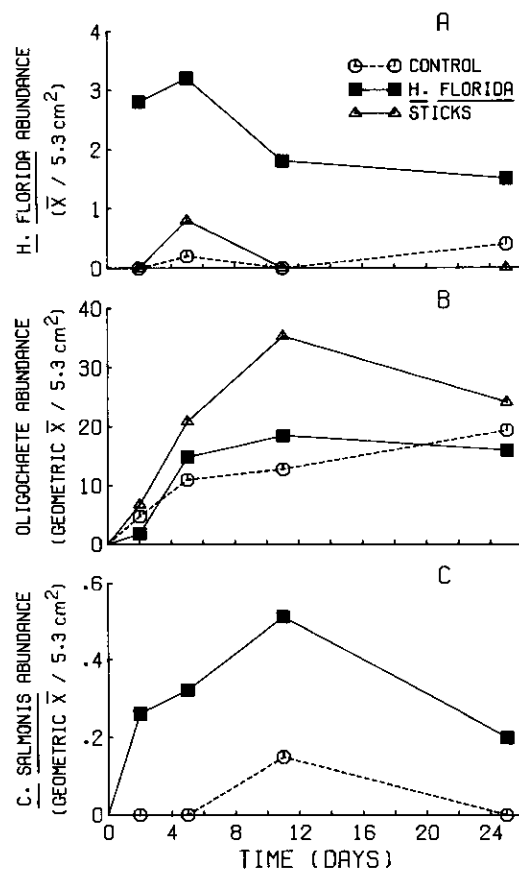


FIG. 6. Results of the April 1980 *Hobsonia florida* experiment. Abundances through time of (A) the ampharetid polychaete *Hobsonia florida* (adults only), (B) oligochaetes, or (C) the gammaridean amphipod *Corophium salmonis*, in patches that initially contained either azoic sand plus *H. florida* or simulated animal tubes (STICKS), or azoic sand alone (CONTROL). The number of replicates for each date is presented in Table 2.

TABLE 5. Two-way analyses of variance tables for the two 1980 succession experiments. Each lettered subgrouping presents the results from a separate analysis. Each analysis tests for the effect of one manipulated component relative to the control. The experimentwise  $\alpha$  has been conservatively adjusted for the number of treatment vs. control comparisons. SHOT = manipulations of simulated tubes (sticks), *Hobsonia*, and *Tanais*.

Experiment	Manipulated component	Affected taxon		Manipulation main effect	Time main effect	Manipulation $\times$ time interaction	Residual (error)
a) April <i>Hobsonia florida</i>	<i>H. florida</i>	<i>H. florida</i>	df	1	3	3	31
			Mean square	47.300	1.327	1.863	0.948
			F	49.9***	1.4	2.0	
b) April <i>Hobsonia florida</i>	Sticks	Oligochaetes†	df	1	3	3	30
			Mean square	0.465	0.597	0.050	0.056
			F	8.3*	10.7**	0.9	
c) April <i>Hobsonia florida</i>	<i>H. florida</i>	<i>Corophium salmonis</i> †	df	1	3	3	31
			Mean square	0.104	0.013	0.001	0.017
			F	6.0*	0.8		
d) SHOT	<i>Tanais</i> sp.	<i>Tanais</i> sp.†	df	1	3	3	32
			Mean square	2.806	0.366	0.091	0.145
			F	19.4**	2.5	0.6	
e) SHOT	Sticks	<i>Tanais</i> sp.†	df	1	3	3	32
			Mean square	0.478	0.865	0.421	0.090
			F	5.3	9.6**	4.7*	
f) SHOT	<i>H. florida</i>	<i>Manayunkia aestuarina</i> †	df	1	3	3	32
			Mean square	0.396	0.647	0.044	0.062
			F	4.4*	10.5**	0.7	
g) SHOT	Sticks	Oligochaetes†	df	1	3	3	32
			Mean square	0.332	2.433	0.007	0.049
			F	6.8*	49.7**	0.1	
h) SHOT	<i>H. florida</i>	Oligochaetes†	df	1	3	3	32
			Mean square	0.599	1.584	0.126	0.050
			F	12.0**	31.8**	2.5	
i) SHOT	<i>Tanais</i> sp.	Oligochaetes†	df	1	3	3	32
			Mean square	1.116	1.917	0.049	0.065
			F	17.2**	29.6**	0.8	
j) SHOT	<i>H. florida</i>	<i>Macoma balthica</i> †	df	1	3	3	32
			Mean square	0.602	0.059	0.073	0.059
			F	10.1**	1.0	1.2	
k) SHOT	<i>Tanais</i> sp.	<i>Macoma balthica</i> †	df	1	3	3	32
			Mean square	0.367	0.120	0.090	0.049
			F	12.8**	4.1*	3.1	

\* Experimentwise  $P < .05$ , \*\*  $P \leq .01$ , \*\*\*  $P \leq .001$ .

† Counts have been transformed to  $\log(x + 1)$ .

Though the numbers of the gammaridean amphipod *Corophium salmonis* recruiting to our patches were small, there was a clear pattern of facilitation observed (Fig. 6C, Table 5c). Since few of the samples contained *C. salmonis*, the assumption of equality of variance (Sokol and Rohlf 1969) was not met for parametric ANOVA. A nonparametric Kruskal-Wallis ANOVA (Hollander and Wolfe 1973) also revealed the increased abundance of *C. salmonis* in the *H. florida* treatment to be significant ( $P < .05$ ). The simulated-tube (stick) treatment had no significant effect on *C. salmonis* abundances relative to the control. *Corophium salmonis* was never affected by any of our previous experiments, nor was it affected in our subsequent 1980 experiment.

#### June 1980 stick/Hobsonia/Tanais (SHOT) experiment

We designed the SHOT experiment to test the effects on succession of the tube builders *H. florida* and

*Tanais* sp. as well as the effects of simulated tubes. The abundances of these infaunal taxa (and sticks) were enhanced in separate 10-cm<sup>2</sup> patches. We were able to demonstrate the persistence of these manipulations through the full duration of the experiment. The effectiveness of our tanaid manipulation is evident from the number of tanaids recovered from the manipulated patches during the first few sampling dates (Fig. 7A). There were significantly greater numbers of *H. florida* whose freeze-dried mass was  $>1$  mg sampled in the *H. florida* patches through day 25 ( $t$  test,  $P < .05$ ). Virtually every simulated tube (applicator stick) that we added was recovered during field sampling.

The SHOT experiment provided several striking examples of facilitation by tube builders and by simulated tubes but no examples of inhibition. The abundance of *Tanais* sp. was enhanced by the presence of tanaids, *H. florida*, and simulated tubes (Fig. 7A). It appears that the tanaids did not begin recruiting to this

area of the flats until after day 11. Separate treatment vs. control, two-way analyses of variance revealed that only tanaids (Table 5d) and simulated tubes (Table 5e) facilitated the recruitment of tanaids at an experimentwise  $\alpha$ -level of .05.

The presence of *H. florida* facilitated the immigration of *M. aestuarina* (Fig. 7B, Table 5f). The presence of simulated tubes or tanaids had no apparent effect on this sabellid polychaete.

As in the April 1980 *H. florida* experiment, simulated tubes facilitated the recruitment of oligochaetes (Fig. 8A, Table 5g). The presence of *H. florida* and *Tanais* sp. also facilitated the recruitment of this taxon relative to the control patches (Fig. 8A, Table 5h, i). The numbers of animals found in the patches containing *H. florida* were lower than those found in the simulated-tube patches on the final two sampling dates. These data are consistent with the explanation that *H. florida* tubes stimulated oligochaete immigration but that the animals inhabiting the tubes may have a deleterious effect on the persistence of oligochaetes in the patch.

The abundances of *M. balthica* were greater in patches to which either *H. florida* or *Tanais* sp. had been added (Fig. 8B, Table 5j, k). This effect was particularly distinct on day 6, when we detected no *M. balthica* in the control patches, and is another example of facilitation. During this period of neap tides, we also

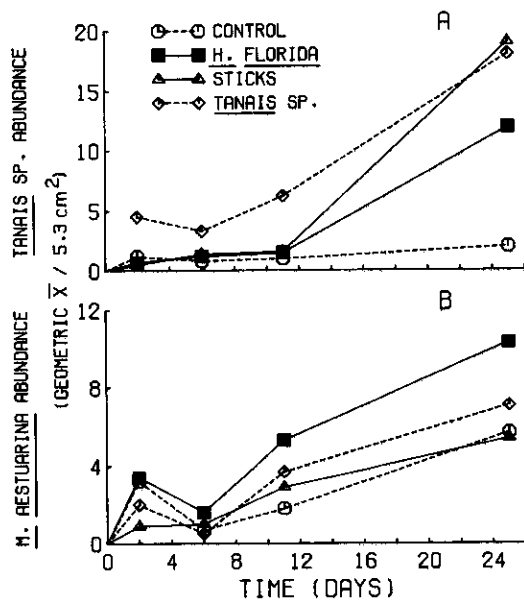


FIG. 7. Results of the June 1980 SHOT experiment. Abundances through time of (A) the peracarid crustacean *Tanais* sp., and (B) the sabellid polychaete *Manayunkia aestuarina*, in patches that initially contained either azoic sand plus *H. florida*, *Tanais* sp., or simulated animal tubes (STICKS), or azoic sand alone (CONTROL). The numbers of manipulated animals or sticks and the number of replicates for each date are presented in Table 2.

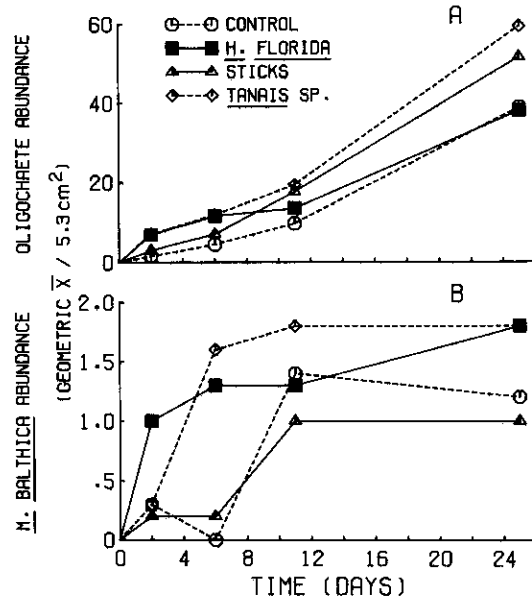


FIG. 8. Results of the June 1980 SHOT experiment. Abundances through time of (A) oligochaetes and (B) the tellinid bivalve *Macoma balthica*, in patches that initially contained either azoic sand plus *H. florida*, *Tanais* sp., or simulated animal tubes (STICKS), or azoic sand alone (CONTROL). The number of manipulated animals or sticks and the number of replicates for each date are presented in Table 2.

observed abrupt declines in *M. aestuarina* (Fig. 7B), but the recruitment of most other taxa (e.g., oligochaetes, Fig. 8A) appeared to be unaffected.

#### DISCUSSION

We tentatively have classified the biological interactions observed during our six successional experiments as either facilitation or inhibition (Fig. 9). Interactions classified as facilitation far outnumber those of inhibition. The presence of such interactions provides essential but not sufficient evidence for deciding which of Connell and Slatyer's (1977) models apply to the Skagit succession. We shall review the evidence that we have acquired on the Skagit community which supports or, more important, refutes the applicability of the respective succession models to the Skagit community. Further, we shall discuss the implications that the choice of successional model has on the explanations of several processes believed to control soft-bottom benthic community structure. Finally, we shall discuss several alternate explanations for the patterns observed in the present study.

*Inhibition.*—The key feature of the inhibition model of succession is that an adult inhibits the recruits of its own and other species from settling near it. Of Connell and Slatyer's (1977) three models of succession, the inhibition model is the most in tune with the prevailing view of adult-larval interactions among soft-

EFFECTS

	<i>H. florida</i>	<i>P. kempji japonica</i>	<i>Tanais</i> sp.	<i>M. balthica</i>	<i>M. aestuarina</i>	Oligochaetes	<i>C. salmonis</i>	<i>P. elegans</i>
<i>H. florida</i>	○	+	+	+	+	+ & -	+	○
<i>P. kempji japonica</i>	○	○	+?	○	○	○	○	○
<i>Tanais</i> sp.	○	○	+	+	○	+	○	*
<i>M. balthica</i>	+	○	-	○	○	○	○	○
Simulated Tubes	○	○	+	○	○	+	○	*

FIG. 9. A summary of the effects of our manipulations on succession in the Skagit community. A (+) denotes facilitation and a (-) denotes inhibition. The absence of a sign indicates that no statistically significant effect ( $\alpha = .05$ ) was observed. Asterisks mark manipulations performed only when *Pygospio elegans* was virtually absent from the community (1980). The question mark is included because we could not demonstrate enhanced densities of *P. kempji japonica* due to our manipulation.

bottom benthos. This view holds that infaunal adults have a deleterious effect on the recruitment and survival of larvae and young juveniles. This effect has often been attributed to predation. It has been reported that benthic larvae are consumed by meiofauna (Thorson 1966, Wilson 1968), spionid polychaetes (Breese and Phibbs 1972), terebellid polychaetes (Wilson 1980), deposit-feeding amphipods (Segerstråle 1962), and bivalves (Mileikovsky 1974). While we have been able to document many trophic interactions in the Skagit community which indicate that infauna do consume benthic recruits (Feller et al. 1979), the results of our field experiments have forced us to reject the general applicability of the inhibition model to the Skagit community.

We found only two examples of inhibition in our study (Fig. 9). These instances were an initial inhibition of oligochaete recruitment by *H. florida* in August 1979 (Fig. 4B) and the inhibition of *Tanais* sp. by *M. balthica* in July 1979 (Fig. 3B). The deleterious effect of *H. florida* on oligochaete recruitment may have been due to predation. We doubt, however, that *M. balthica* preyed on the recruits of *Tanais* sp.; tanaid recruits generally are too large to be consumed via the inhalant siphon of *M. balthica*. A more likely explanation is that the decline in tanaid abundance was due to lateral emigration. The inhalant siphon of *M. balthica* is used to scrape and dislodge particles from the sediment surface. This activity may be sufficiently disturbing to cause the tanaids to emigrate.

Dissertation research by Smith (1980) on the dispersion patterns of the Skagit community offered little evidence for the existence of negative interactions in the community. No significant negative correlations but many significant positive correlations were observed between local species' abundances. However, Smith (1980) did find indirect evidence that *H. florida* recruitment may have been reduced in dense mats of *P. elegans* tubes.

*Tolerance.*—We consider the essentials of the tolerance model to be:

- 1) recruits of later succession species are neither facilitated nor inhibited by early-succession species,
- 2) later-succession species are capable of self-replacement, and
- 3) late-succession species are better competitors or are more tolerant of environmental stress.

Connell and Slatyer (1977) found few examples of the tolerance model in the ecological literature. The most straightforward example was the New England forest succession studied by Horn (1975). This forest was eventually dominated by a shade-tolerant beech which reproduced asexually by root saplings.

We found some evidence for the applicability of the tolerance model to the Skagit community. The polychaete *Pygospio elegans*, which was in low abundance in early 1979, became the most abundant taxon in each of the successional experiments begun in that year. The increase in *P. elegans* was almost exclusively due

to asexual reproduction by fission into four or five individuals (Rasmussen 1953, 1973). Male *P. elegans* were found only on the final sampling date in 1979. At an  $\alpha$ -level of .05, we could detect neither facilitation nor inhibition of *P. elegans* recruitment by any of the deposit feeders manipulated (Fig. 10). Asexual reproduction appears to be an ideal reproductive tactic permitting copious self-replacement within small patches while conferring to the progeny whatever advantages (e.g., resistance to predation, enhanced competitive ability) accrue from large size.

This "tolerance model" script was not acted out in the 1980 succession on the Skagit flats. *P. elegans*, which had achieved densities of 150 individuals/5.3-cm<sup>2</sup> sample in December 1979, had declined in abundance to such an extent that only eight *P. elegans* were found in the 137 samples from the two 1980 field experiments reported in this study.

**Facilitation.**—Connell and Slatyer (1977) state, "In the facilitation model the early-succession species modify the environment so that it is more suitable for later-succession species to invade and grow to maturity." In the Skagit community, as in most temperate benthic communities, the timing of recruitment of taxa to defaunated plots is coupled intimately to the seasonal cycles of reproduction of the source populations. In the Skagit succession, *H. florida* is an early-succession species. The seasonal onset of reproduction in this species in May or early June occurs several weeks to a few months before that of any other Skagit macrofaunal taxon (Smith 1980, E. D. Gallagher, P. A. Jumars, and D. D. Trueblood, *personal observation*). Its small larvae are usually the most abundant early colonists of defaunated patches. The presence of *H. florida* in defaunated patches has been demonstrated to facilitate the recruitment of *P. kempji japonica*, *Tanais* sp., *M. balthica*, *M. aestuarina*, and oligochaetes (Fig. 9). In the case of two taxa, *Tanais* sp. and oligochaetes, we have been able to simulate the environmental modification which may cause the observed facilitation, i.e., protruding tubes.

*Tanais* sp. is another "early-succession" taxon which facilitates the recruitment of other taxa (Fig. 9). Tanaids have a seasonal peak in abundance shortly after that of *H. florida* (Smith 1980, E. D. Gallagher, P. A. Jumars, and D. D. Trueblood, *personal observation*), respond quickly to defaunated patches, and once present in a patch facilitate the recruitment of more tanaids, *M. balthica*, and oligochaetes. The presence of *M. balthica* facilitated the recruitment of *H. florida*, and *P. kempji japonica* (or their tubes) facilitated recruitment by *Tanais* sp.

These results clearly indicate that tube builders facilitate the recruitment of other taxa. While facilitation could be inferred from several other benthic studies, and Woodin (1979) predicted tube builders should settle preferentially with other tube builders, our experimental study reveals the pervasiveness of this mech-

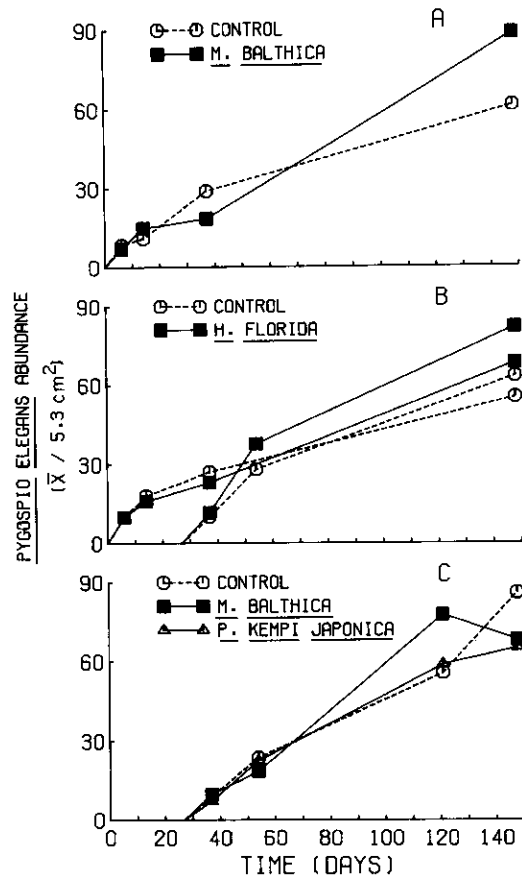


FIG. 10. Abundances of the spionid polychaete *Pygospio elegans* in the four 1979 succession experiments: (A) July *Macoma balthica* experiment, (B) the July (starting on day 0) and August (starting on day 27) *Hobsonia florida* experiments, and (C) the August MAPS experiment. The abundances of *P. elegans* within the initially defaunated patches were not significantly affected ( $\alpha = .05$ ) by any of the manipulated deposit feeders.

anism of succession in a soft-bottom benthic community. Some of the effects which we regard as facilitation can be inferred from earlier studies of the Skagit community. Eckman (1979) discovered that simulated tubes (sewing needles) placed in azoic sediments caused local aggregations of both *M. aestuarina* and *Tanais* sp. Smith (1980) observed that the seven most common Skagit taxa had clumped dispersion patterns and that their abundances were often positively but never negatively correlated with each other. These patterns are consistent with a facilitation model in which larval and juvenile members of the infauna settle preferentially around adult tube builders.

#### Implications for soft-bottom benthic succession

The finding of extensive facilitation in succession in the Skagit community has led us to question some commonly held views of opportunism among benthic

infauna and the effects of cages on soft-bottom benthos. It generally is believed that the species which respond most rapidly after a disturbance, the opportunists, are searching for gaps in the environment. McCall (1977) described this behavior in his opportunistic Group I species, comprised mainly of capitellid polychaetes, ampeliscid amphipods, and spionid polychaetes:

*"Substratum is colonized by Group I opportunists to the extent that it is initially empty of organisms of the same and other species. The highest number of opportunists are found on the most 'empty' substrata."*

Because every species in the Skagit community can be considered a Group I opportunist in terms of size, trophic type, and reproductive strategy, we feel that our data refute the concept that all opportunists are searching for "empty" patches. We believe that the recruits of some species may search actively for a substratum lacking other organisms but that many others settle preferentially adjacent to established tube dwellers. This hypothesis can be tested rigorously as we have demonstrated in this study.

Our findings also have led us to reinterpret many of the results of caging studies of soft-bottom benthos. Most caging studies have been performed on intertidal or shallow subtidal communities dominated by taxa similar to those found on the Skagit flats. These studies most often have used cages to study the effects of predator exclusion on benthic community structure. All too often the effects of the predators cannot be separated from other often unknown effects of cages on larval recruitment. Because even single sewing needles (Eckman 1979) and, in our study, wooden applicator sticks enhance the rates of recruitment of Skagit taxa, we view with incredulity the assumption that the rates of larval recruitment are the same within and outside cages. Sideless and topless cages may allow the identification of effects due merely to the presence of a cage and not the action of predators (Woodin 1981), but they are by no means perfect hydrodynamic mimics. Thus, we concur with those who advise caution in the use and interpretation of caging studies (Dayton and Oliver 1980, Arntz 1981, Hulberg and Oliver 1980).

Many of the results reported from caging studies in the soft-bottom benthos are intriguingly at odds with similar studies performed on rocky intertidal communities. Particularly nettlesome is the finding that while predator exclusion experiments in the rocky intertidal reveal most often that the diversity of the community decreases in response to a lowered predation intensity, Peterson (1979) notes that soft-bottom benthic predator exclusion experiments most often result in increased infaunal diversity. One of the hypotheses for this contrast stressed by Peterson (1979) was that strong negative effects of adults on larval recruitment

kept populations so far below carrying capacity that competitive exclusion did not occur. It is our belief that the differences in the effects of predation on diversity on soft-bottoms vs. the rocky intertidal are due to differences in the mechanisms of succession in the two habitats. Succession in rocky intertidal communities appears to be explained best by Connell and Slatyer's (1977) inhibition model (Sousa 1979, Dean and Hurd 1980), while we feel soft-bottom benthic succession can be explained best by the facilitation model. Horn (1975), Quinn (1979), and Jumars and Gallagher (1982) have modeled the effects of disturbance on diversity, using simple Markovian succession models. Disturbance or predation can have drastically different effects on a community, depending on whether the underlying succession is predominantly facilitation or inhibition. If adults facilitate the settlement of a wide variety of other taxa, as they appear to do in the Skagit community, then offering these adults a refuge from predation will generally lead to an increase in diversity. We pose this hypothesis as a conjecture, one that could be refuted easily by future experiments.

#### *Alternate explanations*

The most likely explanation for the observed patterns of facilitation observed in this study is active habitat selection by the larvae and juveniles of the Skagit community. The behavior of these recruits, which results in preferential settlement near adult deposit feeders, is probably keyed to the small-scale alterations in the local environment caused by either the tubes or feeding activities of the deposit feeders.

One alternate explanation for the patterns we have documented might be that larvae passively accumulate around the deposit feeders and simulated tubes used in this study because of changes in the flow regime. This explanation would be enticing if our manipulations resulted in a reduced boundary shear stress in the patches containing deposit feeders and tubes. While we cannot reject this explanation out of hand, the laboratory investigation of Eckman et al. (1981) appears to refute the main premise of this argument. The density and spacing of tubes used in this study should have led to enhanced overall rates of boundary shear stress in our deposit-feeder and simulated-tube patches relative to our control patches. Thus, even if Skagit larvae and juveniles behaved as passive particles, they would be unlikely to accumulate selectively in our deposit-feeder and simulated-tube patches.

Another alternate explanation for the patterns observed might be that tubes offer larvae and juveniles a refuge from predation or disturbance. The very large robust tubes built by the onuphid polychaete *Diopatra cuprea* offer a refuge from crab predation to the members of the infauna that settle among them (Woodin 1978, 1981). While it is extremely difficult to separate an enhanced immigration rate of recruits from a slight

reduction in mortality rate of recruits over short time intervals, our experiments appear to indicate that facilitation was due to differences in immigration rather than differences in survival. As an example, within a 2-wk period in June 1980 a dramatic increase in tanaid abundance occurred in patches containing tanaids, *H. florida*, or simulated tubes, while virtually no tanaids were found in control patches (Fig. 7A). The effects of predators or disturbance could not have accounted for this difference. The large epifaunal predators, ducks and demersal fish, would be unlikely to be deterred from feeding by small *H. florida* or tanaid tubes, nor could these predators or disturbance have removed nearly 100% of the tanaids without having a more dramatic effect on the abundances of the other taxa in the control patches. The small epifaunal predators found on the Skagit flats, the shrimp *Crangon franciscorum* and the gammaridean amphipod *Eogammarus confervicolus*, are both capable of feeding on tanaids. Enclosure experiments with these predators (E. D. Gallagher, *personal observation*) have revealed that neither predator is effective in reducing natural populations of tanaids, nor was either predator particularly abundant when these experiments were conducted. Thus, the refuge explanation does not appear to apply to the Skagit successional patterns.

Succession in soft-bottom benthic communities in general appears to be governed by mechanisms different from those observed in rocky intertidal communities. There appear to be two major reasons for this difference. Crushing, overgrowth, and the monopolization of space by a few dominant species provide the mechanisms for inhibition in the rocky intertidal, whereas these processes are rarely observed in the soft-bottom benthos (Peterson 1979). While space is at a premium in rocky intertidal communities, it is difficult to identify a resource that is in short supply in shallow-water soft-bottom benthic communities. Second, while substratum modification is rare in the rocky intertidal (Sutherland and Karlson 1977), substratum modification and other alterations of the local environment caused by adult infauna are extremely common in the soft-bottom benthos. Tubes cause dramatic changes in the near-bed flow regime (Eckman et al. 1981). The feeding activities of deposit feeders, particularly fecal pellet production, can substantially alter the size composition of surficial sediments (Grassle and Grassle 1974, Risk and Moffat 1977). The presence of irrigated tubes and burrows produced by the infauna can cause dramatic changes in the processes controlling sediment pore water chemistry (Aller 1980). The depth of aerobic sediments (i.e., the depth to the redox potential discontinuity) increases with time during soft-bottom benthic succession (Pearson and Rosenberg 1978, Rhoads et al. 1978). Enhanced diffusion rates caused by the presence of tubes and animal burrows might reduce levels of toxic metabolites in marine sediments (Aller 1980) or increase rates of microbial

growth, either process possibly providing an adaptive explanation for facilitation by tube builders. Few of the environmental modifications caused by the infauna in soft-bottom benthic communities have direct analogues in rocky intertidal communities. It would be surprising if the mechanisms governing succession were the same in these two habitats.

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