

Influence of adult density on recruitment into soft sediments: a short-term *in situ* sublittoral experiment

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ABSTRACT: Effects of different densities of the ophiuroid *Amphiura filiformis* and of the bivalve *Abra nitida* (both species separately) on initial recruitment were studied *in situ* in a soft-sediment environment at 25 m depth in the Gullmar Fjord (Sweden). Containers with known densities of residents in natural sediment, and some defaunated controls, were exposed for 9 d on the bottom. With both species there was a clear effect on both density and horizontal spatial distribution of recruits in the experimental containers. At high densities (2400 per m²), *A. filiformis* inhibited recruitment of most taxa, whereas the effect of *A. nitida* at medium densities (1400 per m²) was facilitation. Both residents caused a less aggregated distribution of recruits compared with controls. The bioturbation disturbance caused by *A. nitida* seemed to have little negative effect on recruitment. It is suggested that *A. filiformis* may inhibit recruitment by ingesting settlers or newly settled juveniles.

INTRODUCTION

Soft-sediment marine species often have patchy distributions in apparently homogeneous sediment environments (e.g. Angel & Angel 1967, Gage & Geekie 1973, Rosenberg 1974, Gage & Coghill 1977). Woodin (1976) hypothesized that the boundaries observed between discrete, often age-class dominated, infaunal assemblages, and the maintenance of this discreteness, are due to interactions between established individuals and settling larvae. In succession 3 different mechanisms may be involved, namely, facilitation, tolerance and inhibition, as suggested by Connell & Slatyer (1977). They may operate independently, or in various combinations depending on population densities and the particular species. Gallagher et al. (1983) and Whitlatch & Zajac (1985) demonstrated experimental evidence of facilitation, Watzin (1983) and Whitlatch & Zajac (1985) showed evidence of tolerance, and inhibition has been reported in several studies (e.g. Woodin 1976, Peterson 1979, 1982, Williams 1980, Wilson 1980, Luckenbach 1984, Elmgren et al. 1986).

Most experiments on adult-larval interactions have been made over relatively long periods to study successional processes and have often not distinguished between differential settlement and post-settling mortality (but see Luckenbach 1984, Watzin 1986). The latter is indeed a difficult task, but one way to study initial recruitment and reduce successional effects is to keep exposure time to a minimum.

In the experiment reported here, we have studied the effects of 2 quantitatively important species, the ophiuroid *Amphiura filiformis* (O. F. Müller) (hereafter referred to as *Amphiura*) and the bivalve *Abra nitida* (Müller) (hereafter *Abra*), on colonization of sediment in boxes exposed at a muddy-sand locality at 25 m depth in the Gullmar fjord, Sweden, over a 9 d period. The main question we posed was: Does the presence of established adults affect recruitment during a time scale of 1 wk, in terms of both the densities of the recruits and their horizontal spatial distribution?

MATERIAL AND METHODS

Two experiments were undertaken with *Amphiura*, one in mid July and one in mid September 1985 during the period that normally has high juvenile settlement, particularly of bivalves (Schram 1968, Muus 1973). One

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experiment was done with *Abra* in mid July. The experiments were undertaken at a sheltered muddy-sand site at 25 m water depth in the Gullmar Fjord approximately 200 m north-east of Kristineberg Marine Biological Station. This bottom has an *Echinocardium-filiformis* type of assemblage (Molander 1928) in which the 2 test species are commonly found.

Sediment. Sediment (150 l; $20 \times 0.1 \text{ m}^2$ Smith-McIntyre grab samples) was collected from the experimental locality, defaunated by immersion in fresh water for 5 d, and homogenized by sieving through a 5 mm mesh. Large gravel particles and macrofaunal organisms were discarded. Subsamples of the sediment were subsequently sorted, using sieves with a minimum mesh size of 0.107 mm, to check that the sediment was azoic. No living animals were found. The sediment was then filled into 20 plastic containers (17.8 cm long, 12.8 cm broad and 7.5 cm high) to 1 cm below the edge, and allowed to stand in running seawater for several hours prior to addition of the test animals. This water is pumped to the laboratory from 35 m depth close to the experimental site, and normally contains very few larvae (Granmo pers. comm.).

Test species and deployment of experimental boxes.

The 2 test species (*Amphiura filiformis* and *Abra nitida*) were collected using a modified Ockelmann dredge and separated from the sediment by a 2 mm mesh. For *A. nitida* only specimens with a shell length greater than 5 mm were used. High and medium densities of the test species (Table 1), were established in separate containers, forming 4 replicates of each density treatment for each test species. Four containers with defaunated sediment only were used as controls.

The test species were allowed to establish in the containers for 4 d, whilst kept in running seawater at the laboratory. Afterwards a lid was placed over each container while still submerged. The containers were then quickly (within ca 15 min) transported to the experimental site and distributed on the bottom by a diver. The diver was unaware of how the boxes were related to treatments and test species. After the boxes had been placed on the sediment, the lids were removed. In both experimental runs, the containers were retrieved after 9 d from the sea bottom (covered by lids during transport), and immediately subsampled.

Subsampling. Subsampling of the containers was performed as follows: 8 corers of 1.8 cm internal diameter for *Abra*, and 4 corers of 3.8 cm internal diameter for *Amphiura*, were inserted in the sediment contiguously along the middle length of each container. Different core sizes were used to conform to the different sizes of the test species. The control containers were sampled with both types of corers. Sediments in the top 2 cm, the 2 to 4 cm depth interval, and the remaining 2.5 cm of each core were retained separately in glass jars with

5 % borax buffered formalin stained with rose bengal. In addition to the subsampling, the remainder of the sediment in the containers was sieved through a 1.9 mm mesh and the residue was kept to observe how many of the test animals had survived the experiment and to observe if macroscopic colonists were present.

The material obtained in the top 2 cm of the cores was divided and sorted in 2 fractions of 0.107 to 0.178 mm and > 0.178 mm, respectively. Animals were elutriated from the fine fraction, but manually sorted from the coarse fraction. In all cases animals were sorted out under a microscope at $25 \times$ magnification. Analysis of some of the cores, 4 large and 7 small ones, showed that on average 70 % of the individuals were found in the top 2 cm of the sediment. This is also the region in which both test species would be expected to exert most influence due to their feeding behaviour. Therefore the subsequent analysis was restricted to this sediment zone.

In the first experiment with *Amphiura* and in the *Abra* experiment all 4 boxes were analysed, whereas in the second experiment with *Amphiura*, 3 boxes were analysed in each treatment. In the first experiment with *Amphiura*, 4 cores were analysed from each of the control boxes and the high density boxes. From each of the medium density boxes of this experiment, and from each of all boxes in the second *Amphiura* experiment, 3 cores were analyzed. In the *Abra* experiment 8 cores were analyzed from each of the boxes in the control and the high density treatment, whereas 4 cores were analyzed from each of the boxes from the medium density treatment. Whenever fewer samples were analyzed than the number taken, they were chosen using random numbers from the total number available.

In the analysis of the medium density treatment of *Amphiura* in the second experiment the arenaceous foraminiferans were unfortunately not recorded.

Statistical analysis. Densities of the total and of the numerically dominant recruiting taxa, which occurred in more than 60 % of the cores in each treatment, were statistically analysed for each sampling date separately, using a 1-way nested analysis of variance (SAS Institute 1982) with containers nested within treatments. The hypothesis tested was that there was no difference in recruitment between the treatments. In addition to a significance level for effects of treatments, each test yielded a significance level for the effects of individual containers within treatments, in the following called 'container effect'. Data were not transformed prior to analysis as they complied with the homoscedasticity assumption of ANOVA (Hartley's F-max test; Sokal & Rohlf 1981). Whenever a significant treatment effect was found the differences between means for treatments were tested with the Student-Newman-Keul's test (SAS Institute 1982, Sokal & Rohlf 1969).

The horizontal microdistribution of the established individuals and of the colonists was investigated for several different sample sizes. The medium density treatments and the second experiment with *Amphiura* were excluded because too few cores were analyzed. For the established individuals whole cores were considered, while for the colonists only the top 2 cm. The 8 cores from each *Abra* box were considered as 8 individual samples, then grouped 2 at a time representing 4 samples, and 4 at a time representing 2 samples. The 3 sample sizes actually sampled 2.5 , 5 , and $10 \times 10^{-4} \text{ m}^2$ of sediment.

The 4 cores of each *Amphiura* box were considered as 4 individual samples, and 2 samples of cores grouped 2 at a time. The 2 sample sizes actually sampled 11.3 and $22.6 \times 10^{-4} \text{ m}^2$. The coefficients of dispersion (variance/mean ratios) were calculated for different block sizes for both the *Abra* and *Amphiura* treatments.

The 95 % limits of the Poisson expectation were calculated. To show the limits between aggregation and random, and between random and even distributions (Angel & Angel 1967) the Monte Carlo method was applied as described in Gage & Coghill (1977).

RESULTS

One d after the test species (*Amphiura filiformis* and *Abra nitida*) were set up in the experimental containers at the laboratory, the entire sediment surfaces were reworked. Containers with *Abra* were clearly dis-

tinguishable from containers with *Amphiura*. The former had the characteristic feeding traces and heaps of pseudofaeces and faecal pellets, while the ones with *Amphiura* showed mounds around the openings for the arms. The test species were exhibiting feeding behaviour. The mean survival levels of the test animals after 9 d on the bottom were relatively high (Table 1). In general 80 to 100 % of the individuals were recovered alive on termination of the experiments. No significant immigration of macrofauna (colonists larger than 2 mm) into the containers was observed (Table 1).

Effects of residents on recruitment

The effects of residents on initial recruitment of the total fauna and of the common colonizing taxa are shown graphically in Fig. 1 to 3.

***Amphiura* treatment: 1st experiment (Fig. 1).** The treatments with *Amphiura* in the first experiment showed a highly significant effect on the total number of colonizers ($p < 0.001$). The medium density showed a increase in recruitment relative to the control, while the high density treatment showed a decrease. This pattern was consistent for 2 of the individual groups, namely Nematoda and Arachnida. An additional 2 groups, Vermes and Copepoda, showed a decrease in the high density treatment relative to the control. Kinorhyncha showed higher recruitment in the medium density treatment relative to both control and high density treatment and Foraminifera showed higher recruitment in both treatments compared to the

Table 1. Initial density and survival of the test animals *Abra nitida* and *Amphiura filiformis*, and mean number of macrofaunal colonists into sediment containers after 9 d at 25 m depth. Expt I was done in July and Expt II in September 1985. 'Medium' and 'High' refer to the 2 density treatments

		Control		Medium		High	
		Expt I	Expt II	Expt I	Expt II	Expt I	Expt II
Initial number of individuals							
<i>Abra</i>	per container	0	–	33	–	66	–
	per m^2	0	–	1447	–	2895	–
<i>Amphiura</i>	per container	0	0	28	28	55	55
	per m^2	0	0	1228	1228	2412	2412
Percent survival at termination							
<i>Abra</i>	%	–	–	87.9	–	74.6	–
	SD	–	–	2.0	–	24.7	–
<i>Amphiura</i>	%	–	–	97.3	87.9	97.8	96.4
	SD	–	–	5.4	3.9	2.3	6.3
Macrofaunal colonists > 2 mm (no. per container)							
Control		2	4.7	–	–	–	–
	SD	1.4	2.5	–	–	–	–
<i>Abra</i> treatment		–	–	2	–	1.5	–
	SD	–	–	4	–	1.9	–
<i>Amphiura</i> treatment		–	–	4	1.7	0.2	2.3
	SD	–	–	2.7	2.1	1.0	1.5

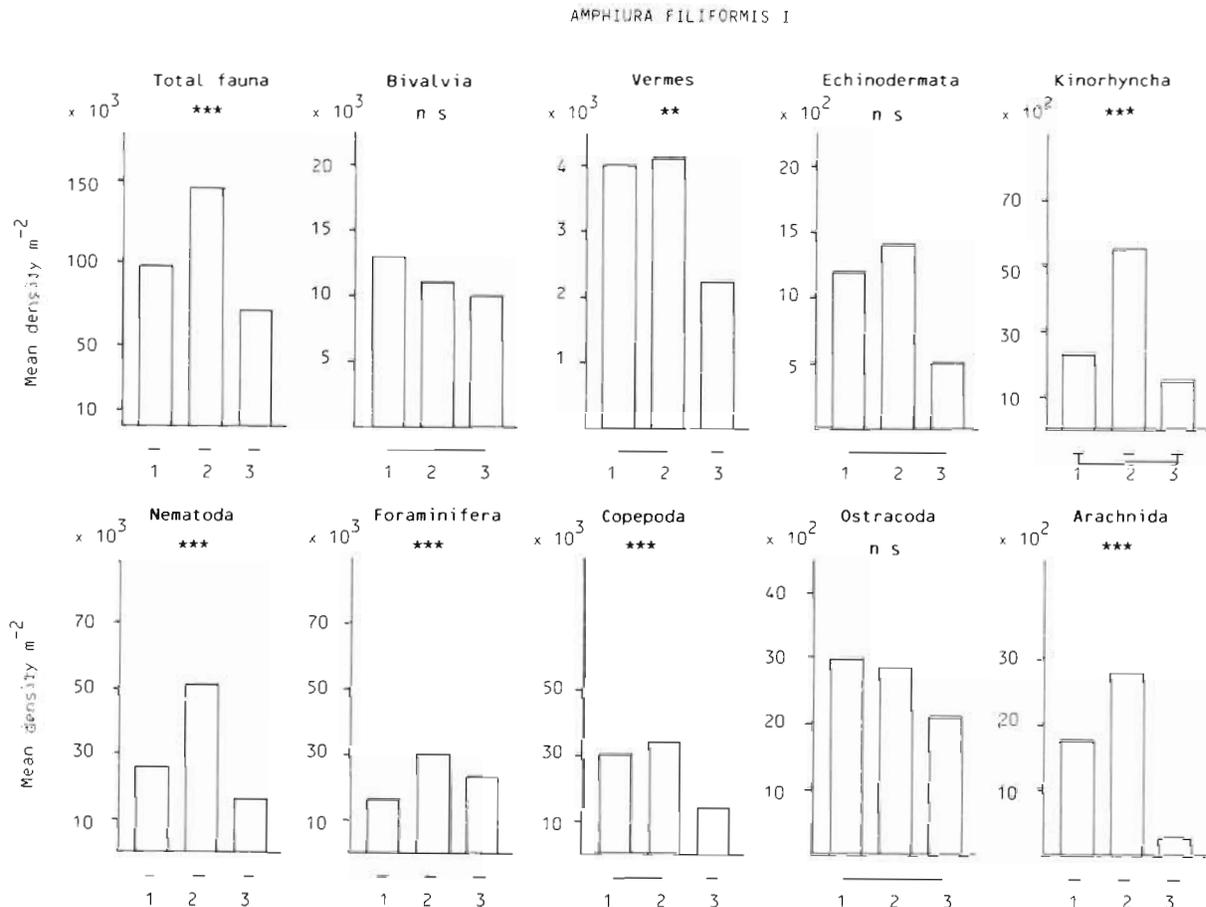


Fig. 1. Histograms showing mean densities of individuals of 10 faunal groups recruiting into sediment-boxes with residents of *Amphiura filiformis*, after 9 d on the sea bottom in mid July (Expt I). Treatments: 1 = control; 2 = medium density; 3 = high density. Significance levels are given for effects of treatment using a 1-way nested ANOVA (***) $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; ns, $p > 0.05$). Differences between means for treatments were tested with the Student Newman Keul's test, and commonly underlined bars are not statistically different ($p > 0.05$)

control. Bivalvia, Ostracoda and Echinodermata showed no significant differences in ANOVA ($p > 0.05$). Except for Vermes, no significant effects caused by the containers were found ($p > 0.05$).

Amphiura treatment: 2nd experiment (Fig. 2). The treatments with *Amphiura* in the second experiment also showed a very significant ($p < 0.01$) effect on the total number of recruits. As in the first experiment the high density treatment showed a significant decrease in recruitment relative to the control, whereas the medium density treatment did not differ significantly from the control. Bivalvia, Copepoda (mainly harpacticoids) and Nematoda showed lower recruitment in both high and medium density treatments compared to the control. Foraminifera showed a higher recruitment in the medium density treatment compared to both control and high density treatment. Other groups – Vermes, Echinodermata, Kinorhyncha, Ostracoda and Arachnida – did not show a significant difference in ANOVA ($p > 0.05$). Except for Foraminifera, no effects caused by the containers were found ($p > 0.05$).

Abra treatment: (1 experiment only) (Fig. 3). *Abra* densities had a highly significant effect on the total number of recruits ($p < 0.001$). The medium density treatment showed significantly higher recruitment than the control and the high density treatment, while the high density treatment was slightly higher than the control. An identical pattern was shown by Nematoda, whereas Bivalvia, Foraminifera and Copepoda showed a higher recruitment in the medium density treatment compared to both the control and the high density treatment. Vermes did not show a significant difference in ANOVA ($p > 0.05$). There were clear effects caused by the containers for all taxa except Bivalvia and Vermes ($p < 0.05$).

Effects of residents on the microdistribution of recruits

The dispersion of the total number of residents and colonizers from the 1st experiment is depicted in Fig. 4 & 5, respectively. The coefficients of dispersion were

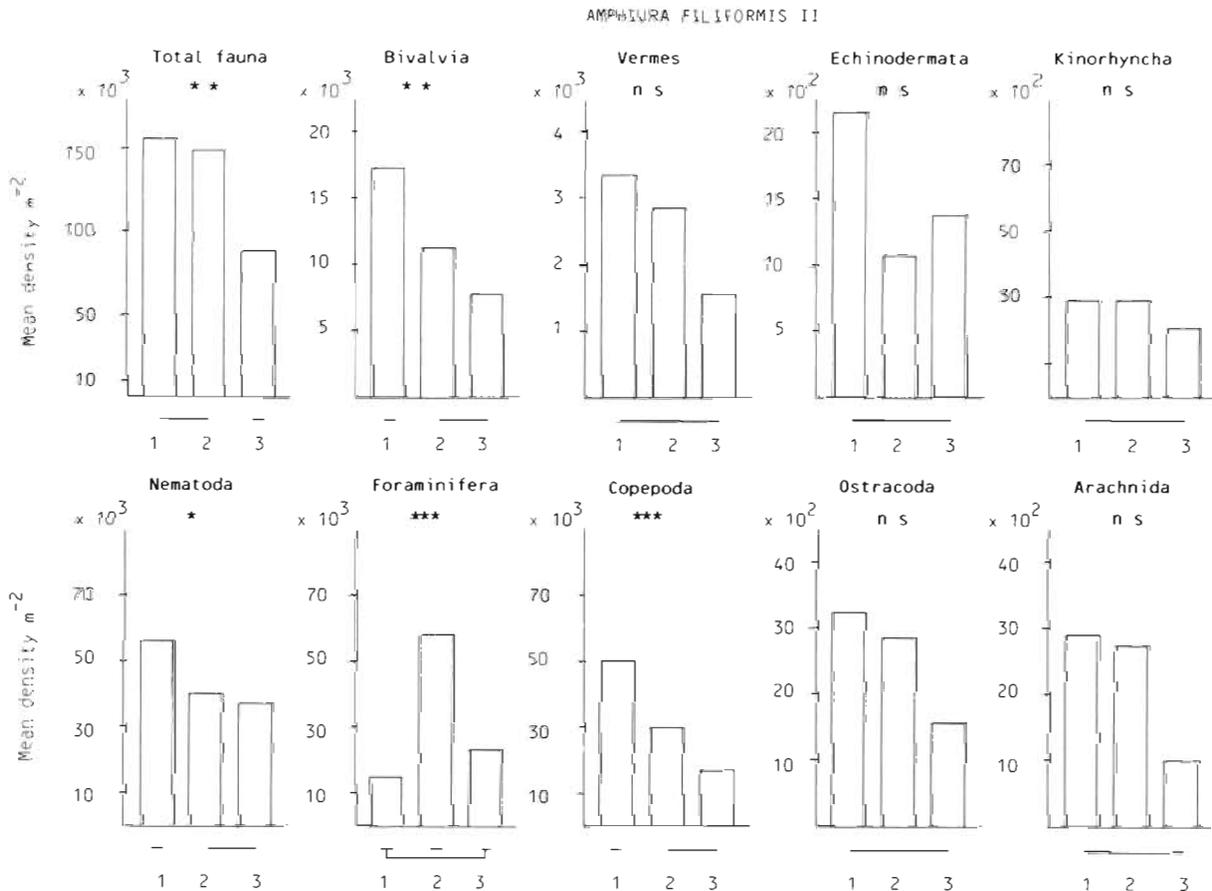


Fig. 2. Histograms showing mean densities of individuals of 10 faunal groups recruiting into sediment-boxes with residents of *Amphiura filiformis* after 9 d on the sea bottom in mid September (Expt II). For explanation see Fig. 1 legend

calculated for different combinations of cores (i.e. sample sizes) within the containers. Comparisons were made only between the high density treatment and the control for the invading taxa, and between the high and medium densities for the resident test species. Both species of residents had a distribution in the containers that showed little deviation from random, the deviation being slightly greater at high densities for *Abra nitida* (Fig. 4). However, the invading recruits in both treatments and controls showed a distribution which deviated from random towards clumping. In the *Abra* treatments the distribution of invading taxa in the controls deviated more from random towards clumping than in the high density treatment (Fig. 5). In the *Amphiura* treatments the distributions of recruits showed a similar pattern, although with greater overlap (Fig. 5).

For the small core sizes used in the *Abra* treatments (1.8 cm internal diameter) the amount of aggregation noted among the colonizing individuals decreased with increasing block size, both in the control containers and the *Abra* high density boxes (Fig. 5). It can be seen in the graph that the distribution of the fauna was random, or close to it, at block sizes of 4 combined cores

(i.e. with a linear dimension of ca 8 cm). For the larger core sizes of the *Amphiura* treatments (3.8 cm internal diameter) in the high density containers the amount of aggregation observed among the invading taxa decreased with the increase in block size from considering cores singly to combined 2 at a time (i.e. from a block size of approximately 4 to one of 8 cm). However, an increase in aggregation was noted in the control treatments at the larger block size (Fig. 5).

DISCUSSION

Of the 3 models of succession proposed by Connell & Slatyer (1977), the inhibition model best explains the majority of cases of adult-larval interactions in high density soft-sediment communities. This view holds that infaunal adults have a deleterious effect on the recruitment and survival of larvae and juveniles. This effect has in most cases been attributed to predation either by meiofauna (Thorson 1966, Watzin 1983, 1986), deposit-feeding amphipods (Segestråle 1962, Oliver et al. 1982, Elmgren et al. 1986), bivalves

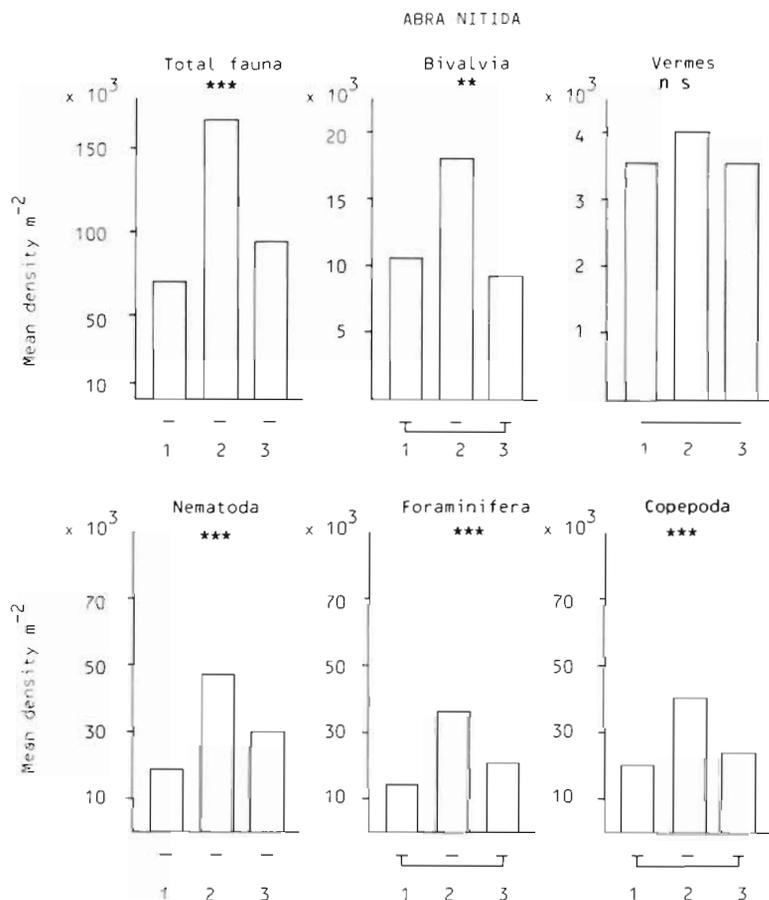


Fig. 3. Histograms showing mean densities of individuals of 6 faunal groups recruiting into sediment-boxes with residents of *Abra nitida* after 9 d on the sea bottom in mid July. For explanation see Fig. 1 legend

(Mileikovski 1974, Williams 1980) and polychaetes (Wilson 1980) or crustaceans (Peterson 1977). Inhibition may also be caused by active behavioural avoidance (Woodin 1985). Woodin (1976) and Peterson (1979) suggested that inhibition was the most important mechanism of succession in soft bottom communities and predicted this to occur only in areas with high densities of residents. However, Gallagher et al. (1983) found that tube builders may facilitate recruitment. They suggested that the mechanism was active habitat-selection by the larvae and juveniles, probably keyed to the small-scale alterations caused by the tubes. On the other hand settlement may be a passive process caused by changed hydrodynamics due to the tube-structures (Eckman 1983, 1987) although not generally applicable (Peterson 1986).

The experiments reported here do not distinguish between the mechanisms behind the observed effects on colonization but it is likely that the residents played at least a dual role. Firstly, when feeding they may reduce survival of the invaders and secondly, they may change the physical and chemical environment (Peterson 1979). Settlement of larvae and immigration of meiofauna may occur either by passive dispersal or by active selection. Active selection may involve a number

of variables such as substratum quality, chemical cues and modification of the physical environment. The presence of adults undoubtedly changes the quality of the chemical and physical properties of the sediment and in the case of *Amphiura* also in the near-bottom water.

Our results show that high densities of *Amphiura* inhibit recruitment into the experimental boxes. This pattern was consistent in both the first and the second experiments and includes both the larval settlers (Bivalvia, Echinodermata, Vermes), as well as the meiofaunal groups representing immigrating species. In the medium density treatments this pattern was less clear (Fig. 1 & 2).

The 'high density' used in our experiments (2412 ind m⁻²) is similar to those recorded in the southern Skagerrak and the northern Kattegatt by Josefson (1986), and lower than those reported for Saltkällefjord by Rosenberg & Möller (1979) where densities of about 4000 ind m⁻² were recorded.

When feeding, *Amphiura* holds 3 or 4 of its arms up into the current flow with a rheotactic response to current direction, trapping both non-living particulate suspended matter and living phytoplankton (Buchanan 1964, Ockelmann & Muus 1978). Hunt (1925) found bottom material detritus, foraminiferans and occasion-

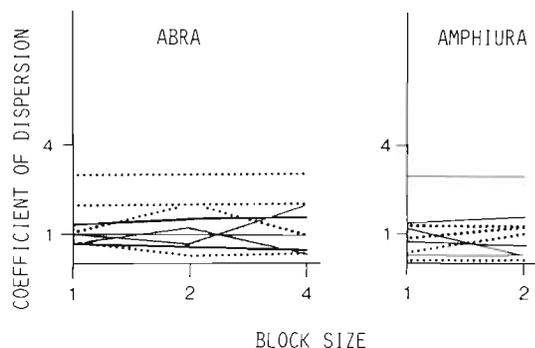


Fig. 4. Coefficients of dispersion for residents in *Abra* and *Amphiura* treatments at various combinations of cores (block sizes) from containers with medium (solid lines) and high (dotted lines) density treatments. Shaded area denotes interval of random expectation

ally small molluscs and worms in the guts of *Amphiura*. The general consensus, however, is that poorly selected bottom detritus constitutes most of the food although occasionally small animals may be ingested (Blegvad 1914, Buchanan 1964). The findings of our experiments may readily be interpreted in the light of the feeding behaviour of *Amphiura*. Thorson (1958) is of the opinion that newly settled larvae may suffer greatly from the feeding activities of *Amphiura*. Our experiments suggest that this may be the case, at least when the density of this species is high enough, and this is in agreement with Woodin (1976, 1979) who

predicted inhibition to predominate in high density assemblages. Another possibility is that colonizers actively avoided containers with *Amphiura* due to some chemical agent emitted by this species (e.g. Woodin 1985). If so, unless dosage-dependent, a similar reaction may be expected also in the medium density treatments. However, no such effect was found. It therefore seems more likely that the inhibitory effect is caused by the feeding activities of *Amphiura*. Another factor of possible importance is the conditioning of the sediment caused by the feeding activity of the residents. A bioturbated sediment may include cues that attract invaders. This may be the reason why the medium density treatments in some cases seemed to facilitate rather than inhibit recruitment. The controls had sediment surfaces virtually without traces of animals. In the high density treatment the detrimental effect of feeding may be strong enough to counterbalance such a conditioning effect and, in the case of *Amphiura*, actually inhibit colonization.

In the experiment with *Abra* a pattern of facilitation at medium densities was found when considering total fauna (Fig. 3). Of the 2 test species, *Abra* most likely disturbs the sediment surface more. Therefore, our results are unexpected if impact of bioturbation were the important inhibiting factor (Brenchley 1981, Wilson 1981).

Josefson (1982) reported densities of *Abra nitida* up to 2000 ind m^{-2} in the Skagerrak. Here we used densities of 1447 and 2895 ind m^{-2} in the medium and high density treatments, respectively. In both treatments 83 % of the adult *Abra* were recovered in the top 2 cm of the sediment, 17 % in the 2 to 4 cm horizon and none below this. In aquaria, *Abra* were found most commonly between 2.5 and 4.0 cm depth with a low correlation between shell length and burrowing depth (Wikander 1980). However, *Abra* takes all its sediment from the top few millimeters of the sediment, and deposits faecal pellets and pseudofaeces in heaps on the sediment surface (Wikander 1980). Thus, colonizing species are most likely to be present within the feeding region of *Abra*, although some worms may burrow deeper (Woodin 1974). At the end of our experiment, as well as before exposure on the bottom, there was visual evidence of considerable sediment reworking. Assuming that the estimated reworking capacity of *Abra*, determined by Wikander (1981) under laboratory conditions, approximates conditions in the field, then all the top 5 mm of the sediment would have passed through the mantle cavity of *Abra* at least once in the medium density treatment of our experiment, and possibly 2 or 3 times in the high density treatment. Of this sediment only a minor portion (probably < 5 %) is likely to have passed through the digestive system of *Abra* (Wikander 1981). Thus, *Abra* is less likely to exert

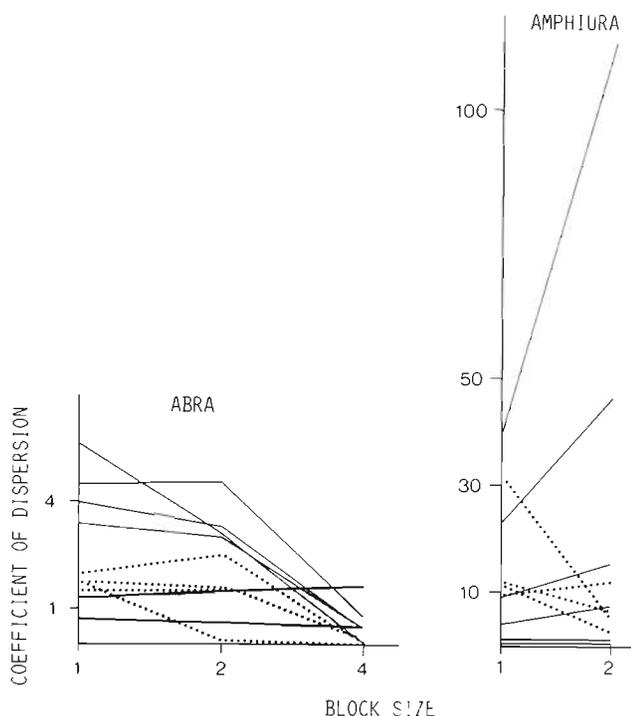


Fig. 5. Coefficients of dispersion for total number of recruits in control containers (solid lines) and containers with high densities of *Abra* and *Amphiura* (dotted lines). Shaded area denotes interval of random expectation

an effect by ingesting colonists. However, it is possible that passage through the mantle cavity of *Abra* represents a mortality agent for potential colonizers and decreases the chance of successful establishment in the bottom substratum. According to Mileikovski (1974), larvae ingested by deposit-feeders have low chances of survival, whereas Hylleberg & Galucci (1975) claimed no such effect on bivalve spat.

In addition to the effects discussed, the residents seemed to affect the horizontal distribution of the invaders. The distribution of the invaders in the controls was less random than in the high density treatments for both species (Fig. 5). This is in agreement with the observation that the residents themselves showed a nearly random distribution (Fig. 4). Apparently the residents prevented aggregation of invaders in the containers, but the mechanism is unknown.

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