

Effects of Adult Suspension- and Deposit-Feeding Bivalves on Recruitment of Estuarine Infauna

by

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Abstract. A variety of theories, especially functional-group theories, have proposed that adult infauna may regulate community composition by affecting the survival or behavior of settling larvae and juveniles. The influence of adult suspension- and deposit-feeding bivalves (*Macoma balthica* and *Mya arenaria*) on infaunal recruitment was studied to observe the potential importance of such interactions. The two clams were transplanted at various densities into buckets of defaunated sediment during the spring of two years. Both species had generally similar effects on the densities of other fauna. Total macrofaunal abundance was reduced by both *Mya arenaria* and *Macoma balthica*, with the greatest decline occurring at highest clam densities. The densities of individual species were also affected, but the influence of the two clams varied among taxa and between years. The results suggest that *Macoma balthica* and *Mya arenaria* may alter community composition through a variety of direct and indirect effects upon recruitment. However, the pattern of effects is not consistent with that predicted by functional-group theories of faunal interactions in soft substrates. Indirect effects of the clams, resulting from their influence on one or two dominant taxa, may be more important on short time scales in determining the abundances of certain fauna.

INTRODUCTION

Recruitment success of infauna has been proposed as a potentially important process regulating the composition of soft-substrate benthic communities. Local hydrodynamic patterns, substrate characteristics, larval behavior, and predation by resident infauna may all act to determine larval settlement and subsequent survival (COMMITO, 1982; ECKMAN, 1983; WATZIN, 1983; WEINBERG, 1984; BUTMAN, 1986; WOODIN, 1986). Similarly, several functional-group hypotheses also have proposed that high densities of certain infauna may inhibit recruitment of organisms with specific ecological attributes. The adult-larval interaction hypothesis (WOODIN, 1976) suggests that discrete, dense assemblages of deposit feeders, tube dwellers, and suspension-feeding bivalves may be maintained through interactions between established adults and settling larvae or juveniles. Deposit feeders can ingest larvae in near-surface sediments or disrupt larvae and juveniles while searching for detrital food. Tube builders will pre-empt space otherwise avail-

able for settlement and can ingest larvae on the substrate surface. Suspension feeders can filter out planktonic larvae before they reach the bottom. The trophic-group amensalism hypothesis (RHOADS & YOUNG, 1970) predicts that deposit feeders can inhibit both adult and juvenile suspension feeders by resuspending large quantities of particulates, thereby clogging filtering appendages and organs. The mobility-mode hypothesis (BRENCHLEY, 1981, 1982) predicts that mobile species can prevent the establishment of sedentary organisms by destabilizing (often fluidizing) substrates and disrupting permanent tubes, burrows, or rhizome systems. Sedentary taxa, in turn, may bind sediments, inhibiting burrowing by mobile animals.

The actual importance of functional-group interactions to settlement patterns and community composition has been debated. Recruitment may be affected by a wide variety of physical and biological factors that may overwhelm functional-group effects (COMMITO, 1982; ECKMAN, 1983; BUTMAN, 1986). Substrate characteristics are well known

to be correlated with faunal distributions (ALLEN, 1899; PETERSON, 1913; SANDERS, 1956, 1958) and the influence of wave and tidal disturbance of sediments can be many times that due to biogenic reworking (GRANT, 1983). Small variations in hydrodynamic regimes can also have a significant effect on the ability of larvae to settle (BUTMAN, 1986; BUTMAN *et al.*, 1988). Predation may strongly affect survivorship of infauna (PETERSON, 1979, 1982), while the intensity and impact of biological activities, such as suspension feeding, bioturbation, or deposit feeding, may depend upon species characteristics or overall faunal densities (HUNT *et al.*, 1987; POSEY, 1987).

Despite the influence of these other factors, several studies have suggested that functional-group interactions between adult infauna and recruits can alter the local species composition of benthic communities. An important area of research in benthic ecology is to determine if and when such interactions become a dominant factor in structuring these habitats. The present study examines the effects of two infaunal bivalves, the suspension-feeding *Mya arenaria* L. and the deposit-feeding *Macoma balthica* L., on recruitment of other species. This study has three primary objectives: (1) determine whether varying the densities of these large and trophically different species can affect recruitment and short-term community development, (2) if so, observe whether their effects are consistent with the predictions of functional-group hypotheses, and (3) observe whether effects may vary annually with variations in settlement intensity.

The soft-shell clam, *Mya arenaria*, and the balthic clam, *Macoma balthica*, are common inhabitants of intertidal and shallow subtidal fine sands along both the Atlantic and Pacific coasts of North America. *Mya arenaria* is a deep-burrowing, sedentary suspension feeder (PURCHON, 1968) while *Macoma balthica* is a deep-burrowing, surface deposit feeder that may facultatively suspension feed under restricted conditions (BRAFIELD & NEWELL, 1961; MAURER, 1967). *Macoma balthica* can produce a fluid, fecal-rich layer on the sediment surface as a result of its feeding activities (RHODS & YOUNG, 1970; RISK & MOFFAT, 1977).

Both *Mya arenaria* and *Macoma balthica* may be expected to regulate community composition by affecting patterns of faunal recruitment. Functional-group hypotheses predict that a suspension-feeding bivalve, such as *Mya arenaria*, will negatively affect the recruitment of species with small planktonic larvae by removing them before they reach the substrate surface (adult-larval interactions; WOODIN, 1976). Several studies have indicated that suspension feeders may remove significant quantities of particulates and larvae from the water column (BRESE & PHIBBS, 1972; MILEIKOVSKY, 1974; PETERSON, 1979; WILLIAMS, 1980; FRITHSEN & DOERING, 1986). Surface deposit feeders, such as *Macoma balthica*, may ingest or disrupt surface-dwelling taxa whose larvae do not possess a depth refuge from their feeding activities (adult-larval interactions; WOODIN, 1976), prevent the establishment of sedentary

species that are subject to bioturbation (mobility-mode interactions; BRENCHLEY, 1981; POSEY, 1987), or inhibit feeding by suspension-feeding taxa through increased re-suspension of sediments (trophic-group amensalism; RHODS & YOUNG, 1970; ALLER & DODGE, 1974).

MATERIALS AND METHODS

The effects of *Macoma balthica* and *Mya arenaria* on community development were examined using transplants near the mouth of the Rhode River, Maryland, in the lower mesohaline zone of the western shore of the Chesapeake Bay (36°51'N, 78°32'W; see HINES & COMTOIS, 1985, for description). Salinities range from a spring low of 4–7‰ to a high of 11–15‰ in late summer and fall (HINES & COMTOIS, 1985; HINES *et al.*, 1987). Most recruitment into the infaunal community occurs in the spring from March through May. Infaunal densities decline sharply in summer, apparently in response to a seasonal increase in the densities of predatory fish and crabs (VIRNSTEIN, 1977; HOLLAND *et al.*, 1980; HINES *et al.*, 1987).

To examine the influence of *Mya arenaria* and *Macoma balthica* on this recruitment, both species were planted separately into buckets of defaunated sediment during the spring of 1981 and 1982. Sediment from an area adjacent to the experimental site was collected in December 1980 and 1981 and subsequently placed in buckets on shore to freeze during winter. Collecting fresh sediment each year increased similarity between buckets and ambient sediments, reflecting natural fluctuations in sediment composition that may occur over the course of a year. Immediately prior to the start of each experiment in March, the frozen and thawed sediment was pooled into a large tub and thoroughly mixed. The sediment was then sieved through a 7-mm screen to remove large shells and large dead clams and was then placed into plastic buckets (0.06 m² surface area × 35 cm deep). Examination of the sediment under a dissecting microscope confirmed the lack of living macrofauna and meiofauna at the start of experiments. Sediments used during the two years were similar, consisted of 35% silt and clay, 50% fine to medium sand (80–500 μm), and 15% coarse sand (>500 μm).

The buckets of sediment were assigned to five treatments: (1) zero clams, $n = 7$ in 1981 and $n = 10$ in 1982; (2) high *Mya arenaria* density (50 live clams per bucket), $n = 6$ in 1981 and $n = 10$ in 1982; (3) low *Mya arenaria* density (12 clams), $n = 6$ in 1981 and $n = 10$ in 1982; (4) high *Macoma balthica* density (50 clams), $n = 5$ in 1981 and $n = 10$ in 1982; and (5) low *Macoma balthica* density (12 clams), $n = 5$ in 1981 and $n = 10$ in 1982. Low density treatments for both clams approximate natural densities in the Rhode River (HINES & COMTOIS, 1985). High density treatments are within the range of high densities reported for these species by other authors (RHODS & YOUNG, 1970; OLAFSSON, 1986; EMERSON *et al.*, 1988). *Mya arenaria* was obtained from local commercial fishermen operating escalator dredges near the mouth of the

Rhode River, while *Macoma balthica* was collected from hand-operated box cores in the Rhode River. *Mya arenaria* is a larger species than *Macoma balthica* and this natural size difference was reflected in the individuals used in this experiment (mean *Mya arenaria* shell length: 65.5 ± 7.5 mm; mean *Macoma balthica* shell length: 27.6 ± 2.3 mm).

Clams were held in the laboratory for one day to observe any damage or mortality associated with collection. Live, undamaged individuals were placed into the buckets of sediment with water at the previously described densities and were left until they had burrowed. The buckets were placed on the bottom in 2.5 m of water on 10 March 1981 and on 19 March 1982. All buckets were retrieved on 18 May 1981 and 25 May 1982, respectively. Placement of buckets on the substrate surface was necessitated by the difficulty in burying up to 50 buckets at a time flush with the sediment surface, using SCUBA, and later attempting to recover them in turbid waters. Although the placement of the buckets on, and not dug into, the sediment may affect hydrodynamic characteristics and possibly settlement patterns (ECKMAN, 1983; BUTMAN, 1986), this was not considered a problem in analysis since all comparisons were made between buckets treated in the same manner. However, to observe whether such a placement and the use of defaunated sediments produced significantly different patterns than seen in the ambient community, core samples ($0.01 \text{ m}^2 \times 35 \text{ cm}$ deep) from adjacent areas were compared with the zero clam-density bucket samples.

The macrofauna in each bucket at the end of 1981 experiments was sampled by sieving the entire bucket of sediment through a 0.5-mm mesh. However, this methodology proved time consuming and, in order to increase replication of buckets, the 1982 experiments were sampled by taking a central core of sediment ($0.01 \text{ m}^2 \times 35 \text{ cm}$ deep) from each bucket and then sieving the contents of the core on a 0.5-mm screen. Separate comparisons of faunal density estimates from the two methods, involving the application of both techniques to 10 buckets, indicated that they provide indistinguishable results for all but rare taxa ($P > 0.09$, paired *t*-tests for the 12 most abundant taxa). Counts for the 1981 and 1982 experiments were adjusted for a constant area before statistical analyses. All organisms retained on a 0.5-mm sieve were fixed in 10% formalin solution, stained with rose bengal dye, and identified to species with the aid of a dissecting microscope.

Faunal densities were compared among treatments using three-way analysis of variance. The statistical tests examined the effects of clam density (zero, low, high), clam species (*Mya*, *Macoma*), year (1981, 1982), and interactions between these variables on total faunal abundances as well as the densities of numerically dominant taxa. Data were log-transformed before analysis and a F_{\max} test (SOKAL & ROHLF, 1981) indicated homogeneity of variances after transformations. For statistical analyses, the zero-density control buckets were randomly assigned as control treatments for either the *Mya arenaria* or *Macoma balthica* experiments (4 in 1981 and 5 in 1982 as zero-density *Macoma*

balthica, 3 in 1981 and 5 in 1982 as zero-density *Mya arenaria*).

RESULTS

Most *Mya arenaria* and *Macoma balthica* placed within the buckets survived until the end of experiments. For 1981, percent survivorships (with the mean \pm SD number of clams in parentheses) for each treatment were: high-density *Mya* = 87% (44.3 ± 3.4); low-density *Mya* = 90% (10.8 ± 4.7); high-density *Macoma* = 84% (41.8 ± 3.9); and low-density *Macoma* = 82% (9.8 ± 0.9). For 1982, the percent survivorship of clams was: high-density *Mya* = 95% (47.3 ± 2.6); low-density *Mya* = 92% (11.0 ± 0.9); high-density *Macoma* = 86% (43.0 ± 3.7); and low-density *Macoma* = 97% (11.6 ± 0.4). The surviving clams all appeared healthy at the end of experiments.

The placement of buckets of defaunated sediment on the substrate surface did not produce dramatically different patterns of abundance compared to surrounding areas. Comparison of total macrofaunal densities within the control buckets at the end of experiments compared to an adjacent area showed no significant difference during 1981 (\bar{x} in buckets = $7666.5 \text{ animals/m}^2$ [SE = 2277.2], \bar{x} outside buckets = $8881.2/\text{m}^2$ [SE = 2542.5]; $F = 0.21$, $P > 0.65$), though there were higher densities within buckets during 1982 (\bar{x} in buckets = $1484.6 \text{ animals/m}^2$ [SE = 106.4], \bar{x} outside buckets = $733.22/\text{m}^2$ [SE = 77.1]; $F = 28.62$, $P < 0.001$). During both years, the majority of common species (see below) showed no difference in abundance between control buckets and adjacent areas ($P > 0.05$; 7 of 12 species during 1981, 8 of 12 species during 1982). Given an expectation of some differences in abundance between a community developing from defaunated conditions and one that had not been defaunated, these results suggest minimal artifacts due to experimental design.

A three-way analysis of variance (ANOVA) indicated significant effects of clam species (*Mya* vs. *Macoma*), clam density, and year of experiment on total macrofaunal abundance (Table 1). Varying the densities of both *Mya arenaria* and *Macoma balthica* had qualitatively similar effects on total densities, with lower numbers of other macrofauna being associated with high densities of both clam species (Figure 1). There was a marked decline of recruitment into the buckets from 1981 to 1982, as indicated by highly significant variations in total macrofaunal density between years. Such annual variability in recruitment is well documented from temperate estuaries (FLINT & YOUNK, 1983; DAUER, 1984; HINES *et al.*, 1987; POSEY, 1986; HOLLAND *et al.*, 1987). The density effects of both *Mya arenaria* and *Macoma balthica* on total faunal abundances persisted despite these fluctuations in recruitment between years. In addition to significant treatment effects, interactions were significant between clam density and both year and clam species. However, these interactive terms were small relative to the main effects (as indicated by *F*-ratios, Table 1).

Table 1

Influence of clam species (*Macoma* vs. *Mya*), clam density (0, 12, or 50 per 0.06 m²), and annual variability on macrofaunal abundance. Values are *F*-ratios from a three-way analysis of variance.

Taxa	Main effects			Interaction terms			
	Clam species	Clam density	Year	Species* density	Species* year	Density* year	Species* density* year
Bivalvia							
<i>Macoma balthica</i>	0.4 ^{ns}	3.17*	0.03 ^{ns}	6.73**	4.25*	6.15**	0.56 ^{ns}
<i>Macoma mitchelli</i>	0.05 ^{ns}	0.40 ^{ns}	0.08 ^{ns}	1.38 ^{ns}	0.68 ^{ns}	2.42 ^{ns}	1.13 ^{ns}
<i>Mya arenaria</i>	7.94**	10.50****	313.13****	2.46 ^{ns}	3.93 ^{ns}	16.02****	1.25 ^{ns}
Polychaeta							
<i>Heteromastus filiformis</i>	0.22 ^{ns}	12.47****	21.87****	4.37*	5.86*	4.85*	3.01 ^{ns}
<i>Eteone heteropoda</i>	0.01 ^{ns}	0.54 ^{ns}	25.40****	1.91 ^{ns}	3.91 ^{ns}	0.37 ^{ns}	1.37 ^{ns}
<i>Nereis succinea</i>	3.38 ^{ns}	1.09 ^{ns}	30.83****	0.16 ^{ns}	6.59*	0.27 ^{ns}	6.71**
<i>Polydora ligni</i>	0.04 ^{ns}	7.47**	300.29****	8.63***	2.71 ^{ns}	4.37*	0.39 ^{ns}
<i>Scolecoplepides viridis</i>	8.63**	6.42**	215.79****	5.76**	4.76*	12.99****	0.64 ^{ns}
<i>Streblospio benedicti</i>	0.36 ^{ns}	0.28 ^{ns}	25.81****	1.71 ^{ns}	1.03 ^{ns}	5.75**	6.75**
Crustacea							
<i>Cyathura polita</i>	7.79**	7.50**	198.90****	10.72****	7.79**	7.50**	10.72****
<i>Corophium lacustre</i>	9.14**	39.73****	132.88****	3.05 ^{ns}	0.01 ^{ns}	1.20 ^{ns}	1.53 ^{ns}
<i>Leptocheirus plumulosus</i>	0.01 ^{ns}	1.57 ^{ns}	2.28 ^{ns}	0.01 ^{ns}	1.64 ^{ns}	2.47 ^{ns}	0.96 ^{ns}
Total macrofauna	10.37**	52.60****	320.87****	5.29**	0.70 ^{ns}	3.19*	2.01 ^{ns}

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ****, $P < 0.0001$.

Twenty-two species constituted the macrofauna in the experimental buckets during the two years. However, only 12 species had mean densities per bucket that were significantly greater than zero for two or more treatments (Students *t*-tests, $P < 0.05$); and only the densities of these common species were compared among treatments. These species included a variety of taxa (polychaetes, crustaceans, and bivalves) as well as a variety of trophic, mobility, and developmental patterns (Table 2). All 12 species are dominant members of the naturally established infaunal communities of the Rhode River (HINES & COMTOIS, 1985; HINES *et al.*, 1987). None of the species that occurred in the buckets but were not considered in the analyses had a mean density greater than four individuals per bucket in any treatment.

The densities of seven of these 12 common species were affected by variations in clam density and four showed differences in recruitment between the two clam species (Table 1). Nine species also displayed highly significant variations in abundance between the two years (Table 1). However, interactions were numerous among these main effects, making interpretation of their overall importance difficult. Because of these strong interactions, the influence of varying clam density on macrofaunal abundance was examined separately for each clam species during each year (one-way ANOVA).

As introduced before, several functional-group hypotheses make specific predictions about the effects of both surface deposit feeders, such as *Macoma balthica*, and suspension feeders, such as *Mya arenaria*, on the abundances of species with particular trophic and mobility character-

istics (Table 2). Both *Mya arenaria* and *Macoma balthica* had qualitatively similar effects on faunal abundances during 1981 (Figure 2; Table 3). Four species exhibited a pattern of higher abundance with low densities of one or both clam species, while four other species were negatively associated with increasing clam density. *Macoma balthica* recruits were most abundant in buckets containing low densities of *Macoma balthica* and low or high densities of *Mya arenaria*. Similarly, *Heteromastus filiformis* reached highest densities with low density *Macoma balthica* treatments, and *Mya arenaria* recruits were more abundant with low densities of *Mya arenaria* adults (a similar, though non-significant, trend occurred for *Mya arenaria* recruits in low-density *M. balthica* treatments [Figure 2]). This pattern of highest densities with low clam abundance was also exhibited by a tube-dwelling spionid polychaete, *Scolecoplepides viridis*, with *Macoma balthica*. *Polydora ligni* and *Corophium lacustre* were negatively associated with increasing clam density. Both species had significantly lower densities with high densities of *Mya arenaria* and *Macoma balthica* compared to clam absence. Neither displayed a trend towards highest densities with low abundances of either clam species. Two free-burrowing species were also negatively associated with increased clam density (*Nereis succinea* with *Macoma balthica* and *Cyathura polita* with *Mya arenaria*). A ninth species, *Streblospio benedicti*, exhibited only a marginally significant response to varying *Mya arenaria* abundance.

In 1982, macrofaunal densities within the buckets were much lower than observed in 1981, reflecting lower recruitment in the Rhode River during this second year of

Table 2

Ecological attributes of principal species in the Rhode River community and predicted effects of clam abundance from functional group hypotheses. References for attributes in parentheses: 1 = BRAFIELD & NEWELL, 1961; 2 = MAURER, 1967; 3 = RHOADS & YOUNG, 1970; 4 = REINHARZ & O'CONNELL, 1981; 5 = THORSON, 1946; 6 = HINES & COMTOIS, 1985; 7 = PURCHON, 1968; 8 = CHANLEY & ANDREWS, 1971; 9 = DAUER *et al.*, 1981; 10 = FAUCHALD & JUMARS, 1979; 11 = BLAKE, 1969; 12 = GEORGE, 1966; 13 = DEAN, 1965; 14 = RASMUSSEN, 1956; 15 = BANSE, 1954; 16 = BOUSFIELD, 1973; 17 = BURBANCK, 1967; 18 = Hines, personal observations.

Taxa	Adult feeding mode	Tube or burrow construction	Reproductive mode	Vertical location in sediment		Predicted effects of bivalves	
				Juvenile	Adult	<i>Macoma</i>	<i>Mya</i>
Bivalvia							
<i>Macoma balthica</i> (1, 2, 3, 4, 5, 6, 18)	Surface deposit/ facultative suspension	No	Planktonic larvae	Surface	Deep	neg. ^b	neg. ^b
<i>Macoma mitchelli</i> (1, 2, 3, 4, 6, 9, 18)	Surface deposit/ facultative suspension	No	Planktonic larvae	Surface	Subsurface	neg. ^b	neg. ^b
<i>Mya arenaria</i> (3, 4, 6, 7, 8, 18)	Suspension	Semi-permanent tube for siphon	Planktonic larvae	Surface	Deep	neg. ^{a,b,c}	neg. ^b
Polychaeta							
<i>Heteromastus filiformis</i> (4, 6, 12, 14, 18)	Subsurface deposit	Mucous-lined burrow	Brooding planktonic larvae	Deep	Deep	0	neg. ^b
<i>Eteone heteropoda</i> (6, 12, 14, 18)	Surface predator	No	Planktonic larvae	Surface	Surface	neg. ^b	neg. ^b
<i>Nereis succinea</i> (4, 6, 12, 14, 15, 18)	Surface predator	Mucous-lined burrow	Planktonic larvae	Surface	Deep	neg. ^b	neg. ^b
<i>Polydora ligni</i> (5, 6, 9, 12, 11, 18)	Surface deposit/ facultative suspension	Horizontal tube	Brooding planktonic larvae	Surface	Surface	neg. ^{b,c}	neg. ^b
<i>Scolecopides viridis</i> (5, 6, 9, 10, 12, 18)	Surface deposit	Vertical tube	Planktonic larvae	Surface	Subsurface	neg. ^{b,c}	neg. ^b
<i>Streblospio benedicti</i> (6, 9, 10, 13, 18)	Surface deposit/ facultative suspension	Horizontal tube	Brooding planktonic larvae	Surface	Surface	neg. ^{b,c}	neg. ^b
Crustacea:							
<i>Cyathura polita</i> (6, 17, 18)	Subsurface deposit	Unlined burrow	Brooding	Subsurface	Subsurface	0	0
<i>Corophium lacustre</i> (6, 16, 18)	Surface deposit/ suspension	Horizontal tube	Brooding	Surface	Surface	neg. ^{b,c}	0
<i>Leptocheirus plumulosus</i> (6, 16, 18)	Surface deposit/ scavenger	Horizontal tube	Brooding	Surface	Surface	neg. ^{b,c}	0

^a, trophic-group amensalism (RHOADS & YOUNG, 1970); ^b, adult-larval interactions (WOODIN, 1976); ^c, mobility-mode interactions (BRENCHLEY, 1981, 1982).

experiments (Figure 1; HINES *et al.*, 1987). The number of species affected by increasing clam density was also less in 1982. One species, *Corophium lacustre*, was less abundant with increasing densities of both *Mya arenaria* and *Macoma balthica*, a pattern similar to that seen for this species in 1981. Another species (*Heteromastus filiformis*) was most abundant with low *Macoma balthica* densities but exhibited only marginally significant responses to *Mya arenaria*. Three other species (*Polydora ligni*, *Scolecopides viridis*, and *Streblospio benedicti*) were significantly affected only by varying densities of *Macoma balthica*, all three having lower abundances with higher *Macoma balthica* densities relative to clam absence (Figure 3). Only one species, *Scolecopides viridis*, showed a qualitatively dif-

ferent response to clam density from 1981 to 1982. This spionid polychaete reached highest numbers with low-density *Macoma balthica* treatments in 1981, but was negatively associated with this clam in 1982. Total faunal abundances were lowest with high densities of both species during both 1981 and 1982 (Table 3; Figure 1).

DISCUSSION

Both *Mya arenaria* and *Macoma balthica* had major effects on recruitment and benthic community composition in the Rhode River. Total faunal abundances were reduced by both species during both years of experimentation, with highest clam densities having the strongest effect on faunal

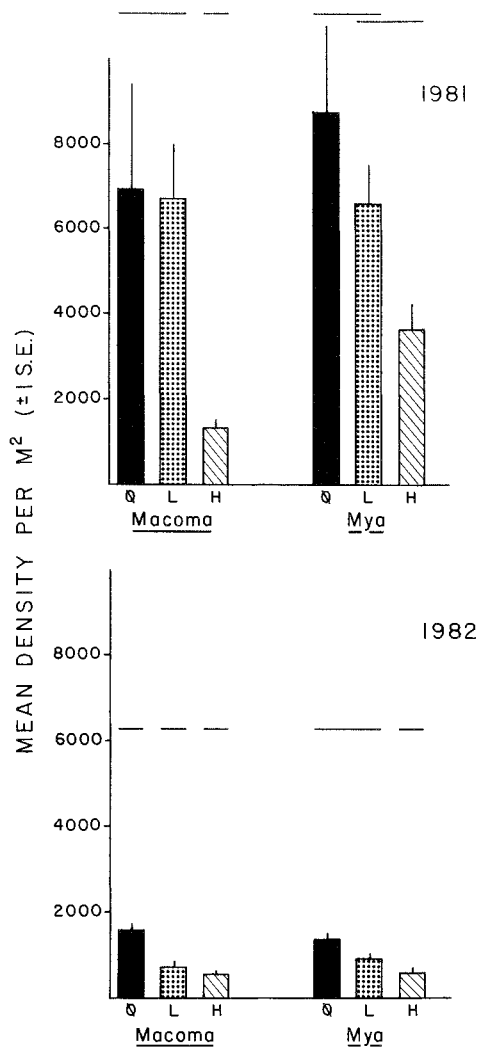


Figure 1

Influence of varying *Macoma balthica* and *Mya arenaria* densities on total macrofaunal abundances in 1981 and 1982. 0, no clams; L, 12 clams/0.06 m²; H, 50 clams/0.06 m². Means connected by lines are not significantly different (Scheffé's tests, calculated separately for both *Macoma* and *Mya*).

densities. However, the impact of these clams varied among infaunal species as well as between years. During 1981 there were two general forms of density change associated with increasing clam density: (1) a positive association of certain species with intermediate clam density, and (2) a negative association of certain other species, as well as total faunal abundance, with clam presence. Similarly, overall effects varied between years. Only about one-half of the species responding to varying clam density in 1981 were affected by either *Mya arenaria* or *Macoma balthica* in 1982. Part of this difference between years may reflect the dramatic differences in overall recruitment. Faunal densities within the buckets and in natural surrounding sediments were almost an order of magnitude lower in 1982 than in

1981. Density-dependent inhibition or enhancement of recruitment (as proposed by functional-group and competition hypotheses) may become proportionately less intense with lower juvenile abundance.

The variability between years and the variation of effects among species may also be in response to indirect effects of clam presence. The macrofauna in zero-clam treatments in 1981 were dominated by two tube-dwelling species, *Corophium lacustre* and *Polydora ligni*. Both of these species were strongly reduced in the presence of *Mya arenaria* and *Macoma balthica*. However, both *Corophium* spp. and *Polydora ligni* have been shown to aggressively exclude certain polychaetes and tube-dwelling crustaceans, including small, near-surface fauna similar to those affected in this study (LEVIN, 1982; GALLAGHER et al., 1983; WILSON, 1983). Part of the enhancement in faunal densities associated with low densities of the two clams may be in response to the reduction of these aggressive species rather than to direct enhancement by the clams. Reduction of *Polydora* and *Corophium* populations may be the result of disruption to their tube mats from bivalve feeding activities or burrow maintenance (RHOADS & YOUNG, 1970; POSEY, 1987).

Although not tested directly in this study, enhancement of macrofauna only at intermediate clam densities may occur if high densities of these bivalves have a detrimental effect that obscures indirect enhancement due to reduction of a dominant species. Such enhancement at intermediate densities of a disturber or predator has been noted in other systems with competitive dominants (PAINE, 1974; MENGE et al., 1986). The possibility that inhibition of *Corophium* and *Polydora* may benefit other fauna is supported by the general lack of macrofaunal enhancement at low clam densities in 1982, when recruitment of both *Corophium* and *Polydora* was greatly lowered. In contrast, species that were negatively associated with both high and low densities of *Macoma balthica* and *Mya arenaria* in 1981 were also negatively associated with these species in 1982. Thus, the two bivalves may affect faunal abundances both directly and indirectly. In particular, disruption of tube mats, as associated with *Polydora* and *Corophium*, may enhance abundances of species that otherwise might be inhibited by these organisms, while other species may be directly inhibited by *Macoma balthica* or *Mya arenaria* burrowing or feeding activities.

The results of this study demonstrate the importance of adult infauna in regulating recruitment into a benthic community; however, they fail to support functional approaches to understanding these interactions. At least during the first year of experiments, *Mya arenaria* and *Macoma balthica* had generally similar effects on the abundances of other fauna. This similarity occurred despite the different feeding modes of the species and the different effects of these two species that are predicted from various functional-group hypotheses. For example, the suspension-feeding *Mya arenaria* is predicted to affect negatively species that have planktonic larvae but to have less of an effect on species that brood their young (adult-larval interaction

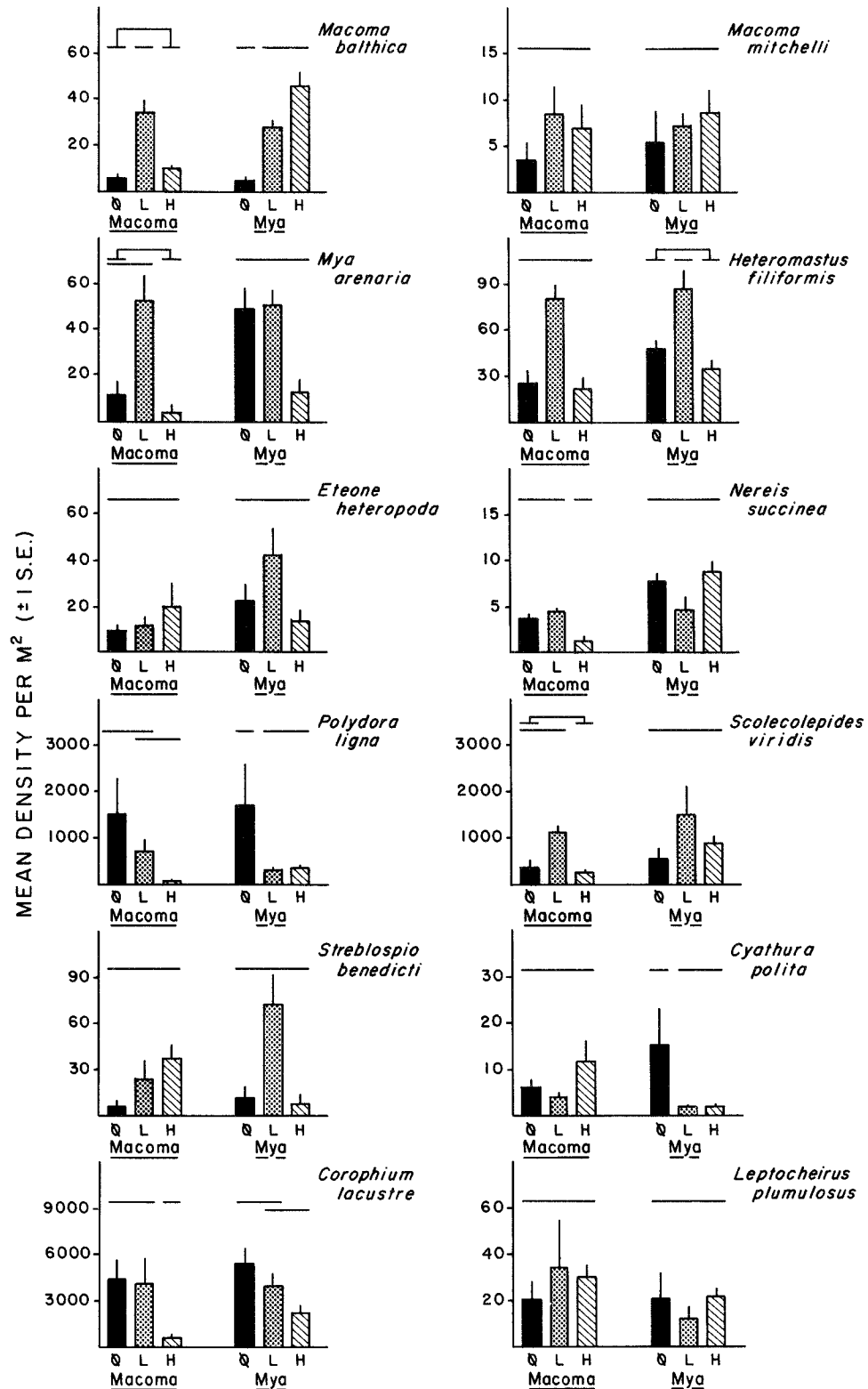


Figure 2

Influence of varying *Macoma balthica* and *Mya arenaria* densities on common macrofauna during 1981. 0, no clams; L, 12 clams/0.06 m²; H, 50 clams/0.06 m². Means connected by lines are not significantly different (Scheffé's tests, calculated separately for both *Macoma* and *Mya*).

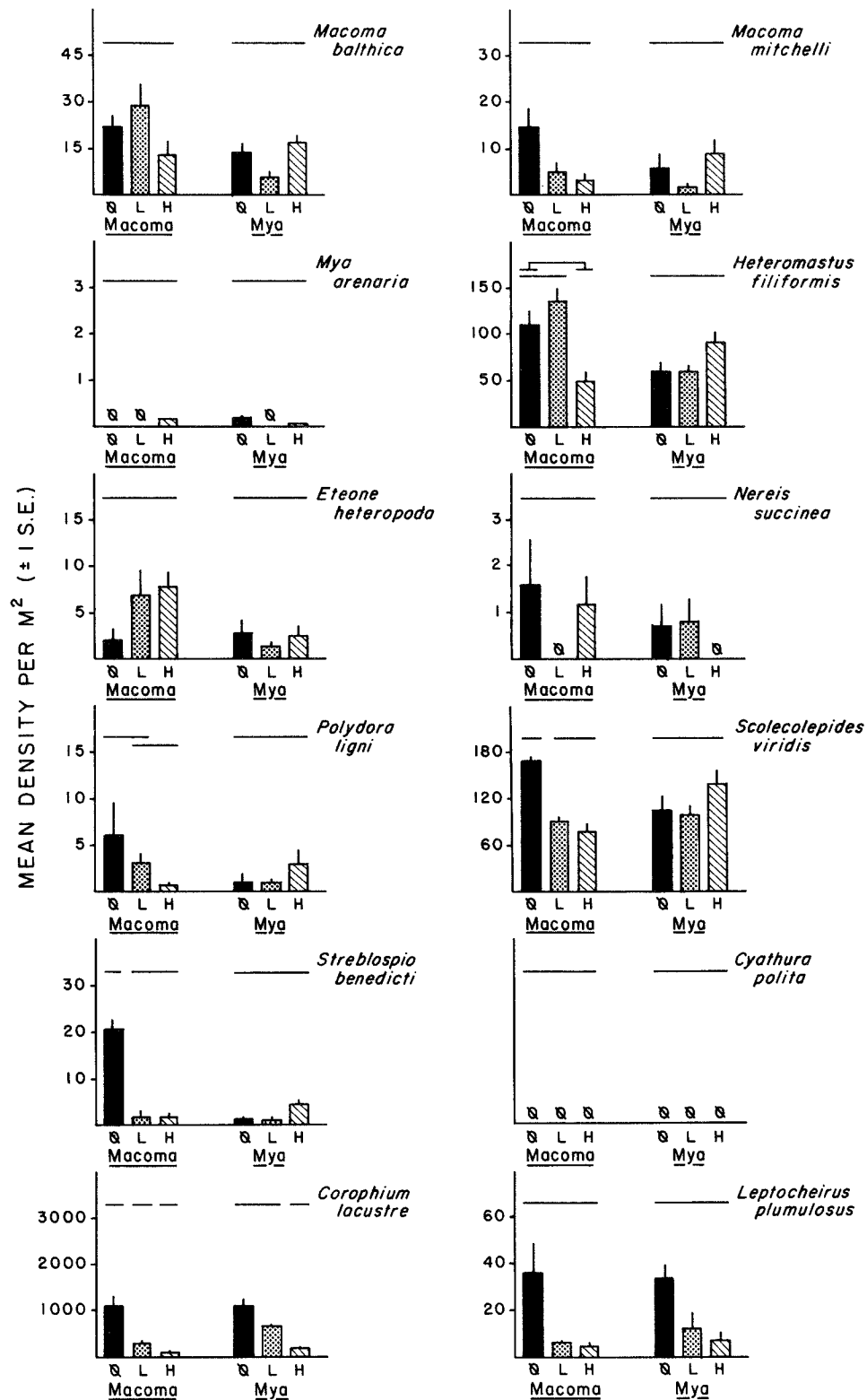


Figure 3

Influence of varying *Macoma balthica* and *Mya arenaria* densities on common macrofauna during 1982. 0, no clams; L, 12 clams/0.06 m²; H, 50 clams/0.06 m². Means connected by lines are not significantly different (Scheffé's tests, calculated separately for both *Macoma* and *Mya*).

Table 3

Influence of varying densities of *Macoma balthica* and *Mya arenaria* on the abundances of common macrofauna. Values are *F*-ratios from a one-way analysis of variance.

Taxa	1981		1982	
	<i>Macoma</i>	<i>Mya</i>	<i>Macoma</i>	<i>Mya</i>
Bivalvia				
<i>Macoma balthica</i>	18.30***	11.73**	1.44 ^{ns}	2.63 ^{ns}
<i>Macoma mitchelli</i>	0.67 ^{ns}	0.27 ^{ns}	2.68 ^{ns}	2.65 ^{ns}
<i>Mya arenaria</i>	6.29*	4.90*	0.73 ^{ns}	0.91 ^{ns}
Polychaeta				
<i>Heteromastus filiformis</i>	4.48*	14.95***	6.07**	3.85*
<i>Eteone heteropoda</i>	0.59 ^{ns}	1.70 ^{ns}	1.86 ^{ns}	0.28 ^{ns}
<i>Nereis succinea</i>	9.36**	1.40 ^{ns}	2.14 ^{ns}	1.58 ^{ns}
<i>Polydora ligni</i>	6.11*	4.26*	4.40*	2.01 ^{ns}
<i>Scolecopides viridis</i>	5.37*	2.49 ^{ns}	5.30*	2.81 ^{ns}
<i>Streblospio benedicti</i>	2.06 ^{ns}	4.30*	7.01**	1.63 ^{ns}
Crustacea				
<i>Cyathura polita</i>	1.73 ^{ns}	7.31**	— ^a	— ^a
<i>Corophium lacustre</i>	9.58**	5.58*	17.77****	11.86***
<i>Leptocheirus plumulosus</i>	0.17 ^{ns}	0.45 ^{ns}	3.26 ^{ns}	2.06 ^{ns}
Total macrofauna	11.35**	5.82*	29.59****	11.25***

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ****, $P < 0.0001$; ^a, absent.

hypothesis; WOODIN, 1976). In this study, *Mya arenaria* at low densities enhanced the densities of certain species with planktonic larvae (e.g., *Macoma balthica* and *Heteromastus filiformis*) while high densities of this bivalve negatively affected organisms that brood their young (e.g., *Corophium lacustre*). *Macoma balthica* is predicted to affect negatively suspension-feeding species (trophic-group amensalism; RHOADS & YOUNG, 1970), species with non-burrowing larvae (adult-larval interaction hypothesis; WOODIN, 1976), and sedentary species (mobility-mode hypothesis; BRENCHLEY, 1981, 1982). Some members of all three groups were enhanced at low densities of *Macoma balthica* while others were negatively associated with this clam. Both clams appeared to have a variety of effects on functionally similar species. For example, both species negatively affected certain tube builders, such as *Corophium lacustre* and *Polydora ligni*, but were positively associated with other tube dwellers, such as *Streblospio benedicti*. Thus, predictions based solely on a species trophic type or mobility mode do not explain adequately the effects of these bivalves on recruitment.

These results join a growing literature emphasizing caution in the use of functional approaches to benthic communities. Several studies have shown that functional-group interactions may be important under certain circumstances, usually involving large, active, burrowing species (ALLER & DODGE, 1974; RONAN, 1975; PETERSON, 1977, 1984; BIRD, 1982; POSEY, 1986, 1987). However, the importance of these density-dependent group effects may vary depending upon the relative sizes of the interacting species (WILSON, 1981; PETERSON, 1984; DEWITT & LEVINTON, 1985), activity rates (WILSON, 1984; POSEY, 1987), or life-

history characteristics (WEINBERG & WHITLATCH, 1983). In this study, *Mya arenaria* and *Macoma balthica* were predicted to have specific effects on other macrofauna. In actuality, their effects varied, some consistent with functional-group hypotheses and some not. Many of these inconsistencies may be related to the relative sizes or activity of the species involved as well as to indirect effects resulting from the reduction of aggressive or dominant species. This study emphasizes the growing consensus that functional-group approaches must be viewed with caution and may apply primarily under restricted conditions involving large or functionally dominant organisms.

ACKNOWLEDGMENTS

We thank R. N. Lipcius, W. H. Wilson, Jr., and two anonymous reviewers for comments on earlier drafts of this manuscript. We are grateful for K. L. Paige for field assistance. This research was supported in part by the Smithsonian Environmental Sciences Program.

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