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Control of foraging behavior of individuals within an ecosystem context: the clam *Macoma balthica* and interactions between competition and siphon cropping

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Abstract *Macoma balthica* (L.) is a common clam of the estuarine seafloor, belonging to an important group of invertebrates possessing the capacity to choose between the two fundamental modes of feeding available, using its siphon to inhale either suspended food particles from the water or food particles deposited on the sediment surface. Field experiments demonstrate that intraspecific competition, effects of other competing benthic invertebrates, and complex interactions between competition and partial predation (siphon cropping by fishes) modify the foraging behavior of *Macoma.* When protected by caging from siphon nipping by fishes, *Macoma* demonstrated greater siphon regeneration at lower density, indicating the importance of competition for limited resources. In the absence of siphon croppers, these same clams also exhibited more deposit feeding at the lower density either because of improved ability to deposit-feed with longer siphons or because deposited foods become more rapidly depleted than suspended foods on local spatial scales. Addition of siphon-nipping fishes caused greater reductions in siphon size of clams at lower density, presumably because the intensity of nipping per clam was greater where clam targets were fewer and because deposit feeding, which was more intense at lower densities, confers a greater risk of cropping from greater siphon extension and activity than characterize suspension feeding. Deposit feeding by *Macoma* was reduced in the presence of siphon croppers at both high and low density of clams, but the intensity of deposit-feeding activity at low density was substantially higher than predicted by additive effects of clam density and cropping. This suggests operation of a balancing strategy in *Macoma* whereby it is accepting greater risks of partial predation when rewards of greater food harvest are larger. The surprising failure to adopt a risk-averse strategy may be explained by the non-lethal nature of partial predation, which renders siphon loss an energetic penalty replacable through regeneration. The presence of a bed of suspension-feeding *Rangia cuneata* also altered foraging behavior of *Macoma* by inducing a switch to more intense deposit feeding, in response either to the documented near-bottom depletion of suspended foods or to likely enhanced biodeposition from feces and pseudofeces. The induction of greater deposit feeding by the presence of this competing suspension feeder led to greater siphon losses during exposure to croppers because *Macoma* was practicing more risky feeding behavior. This enhanced loss of siphon tissues to croppers in the presence of the suspension-feeding *Rangia* induced an interaction between the effects of siphon croppers and *Rangia,* such that *Macoma* exhibited a larger switch away from deposit feeding in the presence of siphon croppers when *Rangia* were also present. Clearly, the foraging decisions made by individuals can only be understood in a broad holistic context of population, community, and ecosystem processes.

Key words Competition · Complex interactions
Density-dependent foraging · *Macoma balthica*
Siphon loss

Introduction

The scope of foraging theory has been greatly broadened over recent years so as to move beyond initial considerations of how to achieve maximal energetic returns from feeding (see Pyke et al. 1977) to a more comprehensive evaluation of how alternative foraging options influence the fitness of individual organisms (e.g., Stephens and Krebs 1986; Houston et al. 1988; Mangel and Clark 1988). For example, foraging decisions often imply varying risks of predation, such that selection for minimizing risk of predation can dictate adoption of a risk-averse

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foraging strategy that differs from what would be predicted on energetic grounds alone (Sih 1980; Werner et al. 1983; Schmitt and Holbrook 1985; Holbrook and Schmitt 1988; Lima and Dill 1990; Milinski 1990). Feeding behavior has also been shown to be influenced by interactions with competitors (Schoener 1971; Lawton 1987), by reproductive demands (Mangel and Clark 1986), and by chemical deterrents in prey tissues (Hay and Fenical 1988). Like other ecological processes that are influenced by multiple factors (e.g., Abrams 1987; Schmitt 1987; Peterson and Black 1988), complex interactions among these separate determinants of foraging behavior are also likely to be important (e.g., McNamara and Houston 1986).

The herbivorous invertebrates of the sedimentary seafloor do not choose prey items individually but because of their large size relative to their foods feed in bulk upon mixtures of many individual items simultaneously (Fauchald and Jumars 1979). Instead of choosing which individual prey items to pursue (Hughes 1980), these deposit and suspension feeders may vary the rate of feeding, which dictates digestive and assimilative efficiency and selectivity (Taghon 1981; Taghon and Jumars 1984; Penry and Jumars 1987). A special class of these seafloor invertebrates, the facultative suspension/deposit feeders, also possesses the ability to choose where to feed, from the water column or the sediment. This choice could be considered a form of selecting the foraging habitat, although the individual animal retains a fixed spatial position, making only changes in burial depth (Zwarts and Wanink 1989; Lin and Hines 1994). Taghon et al. (1980) showed that a spionid polychaete that possesses this ability to make facultative feeding choices between suspension and deposit feeding feeds from the water column when currents are relatively fast and from the sediments under slow flows. This foraging strategy is consistent with energetic considerations because more rapid flow implies higher advective and turbulent fluxes of suspended particles and lower potential for local depletion of the bottom boundary layers, whereas slower flows imply greater deposition of food particles on the bottom (Taghon et al. 1980; Levinton 1991).

Despite the success of energetic criteria at explaining observed foraging behaviors of facultative suspension/deposit feeders (Taghon et al. 1980; Jumars and Self 1986; Levinton 1991), the understanding of feeding behavior in this important group can be greatly enhanced by placing feeding choices in a broader context. Peterson and Skilleter (1994) showed that in a North Carolina estuary the intensity of deposit feeding in the clam *Macoma balthica*, a facultative suspension/deposit feeder, was greatly depressed in early summer in response to seasonal siphon cropping by juvenile fishes, which reduced siphon lengths and inhibited deposit feeding. Similarly intense cropping pressure has been described for several other estuarine systems (Ansell and Trevallion 1967; Trevallion et al. 1970; de Vlas 1979, 1985; Hodgson 1982; Peterson and Quammen 1982; Woodin 1982, 1984; Zwarts 1986; Zwarts and Wanink 1989; Hines et al. 1990; Coen and Heck 1991; Irlandi and Peterson 1991), so partial predation seems likely to have widespread influence on foraging behavior of benthic invertebrates.

Here we extend our study of how the broader ecosystem context influences feeding behavior of *M. balthica* by examining the roles of intra- and interspecific competition as well as interactions between competition and siphon cropping. Competition for food often appears to be a significant influence on growth rates of deposit feeders in marine soft sediments (e.g., Levinton and Lopez 1977; Levinton and Bianchi 1981), implying that competitors may well influence feeding behavior of deposit-feeding *Macoma* (see also Olafsson 1986; Vincent et al. 1989). Similarly, suspension feeders in soft sediments can cause depletion of suspended foods (Peterson 1979; Cloern 1982; Fréchette and Bourget 1985; Peterson and Black 1987, 1988, 1991; Fréchette et al. 1989; Monismith et al. 1990; Muschenheim and Newell 1992), again suggesting that the abundance of nearby suspension feeders is likely to play a role in dictating the foraging behavior of suspension-feeding *Macoma.* Furthermore, the effects of competitors, the risk of partial predation, and the effects of siphon nipping are likely to interact in their impact on *Macoma*'s feeding behavior. Here we present results of field tests of these hypotheses, which reveal not only the major role of competitors in dictating feeding behavior of *Macoma* but also the necessity of incorporating an appreciation of complex higher-order interactions between competition and partial predation.

Methods

Study species and sites

We chose to examine foraging behavior in *Macoma balthica* (Linné 1758), a widespread and abundant tellinid bivalve known to be a facultative suspension/deposit feeder (Brafield and Newell 1961; Reid and Reid 1969; Olafsson 1986). When deposit feeding, *Macoma* actively extends its inhalant siphon out across the substratum, by 5–6 (Brafield and Newell 1961) to as much as 10 cm (Lin and Hines 1994). As the siphon is moved across the surface, the upper layers of flocculent materials and sediment particles are sucked in (Bubnova 1972; Hulscher 1982). While suspension feeding, the inhalant siphon is held stationary with only the top 1–2 mm protruding above the surface of the sediment. Peterson and Skilleter (1994) demonstrated through laboratory trials that a measure of the inorganic sediment content in the mantle cavity, the size-adjusted ash weight of soft tissues of *Macoma,* represented a reliable index of the relative intensity of recent deposit-feeding activity and was inversely related to suspension-feeding activity. Because of the inability to observe *Macoma*'s foraging directly in the field, we used this indirect assay of feeding activity for the present study. This measure of deposit-feeding activity is quantitative and integrates over some time period less than 72 h (Peterson and Skilleter 1994).

Experiments were conducted in the field in the Neuse River estuary, North Carolina (USA) at two sites, a shallow subtidal site in the South River and in Big Creek, a small tributary of South River (see map in Peterson and Skilleter 1994). Water depth at each study site varied from 30–200 cm depending upon the level of wind-forced tide. Such mesohaline regions of estuaries in the mid-Atlantic United States are characterized by high densities of *M. balthica* as well as substantial abundances of large suspension-feeding bivalves, *Rangia cuneata* (Somersby 1831) and *Mya arenaria* (Linné 1758) (Tenore 1970; Virnstein 1977; Hines and Comtois 1985; Hines et al. 1989). In addition, large numbers of juvenile demersal fishes use these regions of the estuary as nursery grounds in spring and summer (Currin et al. 1984; Hines et al. 1990). Physical parameters of this Neuse River estuarine system are well described elsewhere (Roelofs and Bumpus 1953; Williams et al. 1973). Briefly, mean monthly water temperatures range from about 3–32° C; salinities are highly variable, although seasonal lows of 5 ppt and highs of 20 ppt are typically achieved in late winter and late summer/autumn, respectively; the system is dominated physically by wind-driven circulation and tides.

M. balthica for use in experiments were collected by suction dredge from the southern side of the Pamlico River near Indian Island. All individuals for any given experiment were collected within a week and held under identical conditions in the field until needed. Holding areas were established in shallow subtidal sediments on South River, where clams were covered by a 6x6 mm polypropylene mesh top attached to a 1-m^2 frame to protect them against predators. A small polystyrene float kept the mesh elevated off the bottom and mesh tops were replaced every 2–3 weeks to prevent their fouling.

Effects of intraspecific competition and siphon cropping

To test whether *M. balthica* varies its intensity of deposit feeding in response to changes in its own local density, the presence/absence of siphon-nipping fishes, or any interactions between intraspecific competition and cropping, we conducted a field caging experiment in November/December 1991, using two densities of clams enclosed with and without siphon-nipping fishes. Cages consisted of fences made from black plastic vexar mesh (1-cm^2 square openings), cut into strips 60-cm high and folded to form a 1×1 m square, which was then attached by plastic cable ties to 1 m-long steel corner posts as anchors and inserted 10 cm into the sediments leaving a 50-cm wall projecting above the sediment surface. Tops were made of the same mesh such that a 10-cm overhang existed on all sides. Cable ties at 10-cm intervals attached the mesh top to the walls of each cage.

The experiment employed two densities of *M. balthica*, 110 and 370 m^{-2}, and two densities of juvenile spot (the sciaenid, *Leiostomus xanthurus* Lacépède 1802), 0 and 10 fish per cage, arranged in an orthogonal design with six replicate cages for each of the six treatment combinations. To reduce the numbers of clams needed for the experiment, we constrained clams to remain inside a smaller 30×45 cm center arena by using an internal fence inserted to 9.5 cm and projecting 0.5 cm above the sediment surface. Use of this smaller experimental arena reduced the numbers of *Macoma* required to 15 and 50 for the two treatments. Cage tops were appended immediately after clams were introduced and had successfully buried, so as to prevent access by any unwanted predators or croppers. After 1 week, ten spot were added to half the cages, chosen at random. The mean standard length of fish used was 111 mm (±0.8 SE; *n*=120), which did not vary significantly among the 12 cages in one-factor ANOVA ($F_{11,108}$=1.29; *P*=0.24). The fish used in this experiment had been caught about 1 month before and maintained in field enclosures with feedings of fresh clam meat every 2–3 days. A count of fish after 2 weeks of experimentation confirmed complete survival of all fish in the experiment. After 3 weeks, the experiment was terminated by release of the fish and excavation of all clams. Of the original 24 cages, 4 were lost in this experiment because of either fish loss or crab penetration before termination. Two were "no fish/low density", one was "with fish/low density", and one was "with fish/high density". Clams were immediately preserved in 70% ethanol and returned to the laboratory, where the dry weight at 70° C of the inhalant siphon, the ash weight at 525° C of soft tissues (the index of relative intensity of deposit feeding), and the ash-free dry weight (AFDW) were determined by the methods of Peterson and Skilleter (1994).

The two response variables, dry weight of the inhalant siphon and the ash weight of sediments inside the clams, were each analyzed by separate three-factor ANCOVAs, with fish and clam density both fixed and cage a random factor nested within fish×clam density, and AFDW as the covariate (Winer 1971). The assumption of homoscedasticity was tested by an $F_{\max}$ test on residual sums of squares from the individual regression lines. Independence of treatments and covariate was tested by a three-factor ANOVA of the identical design as the ANCOVA but with AFDW as the dependent variable (Huitema 1980). Equality of slopes of regression lines was confirmed before any analysis of differences in intercepts (treatment effects).

Effects of interspecific interactions with suspension feeders

To test whether *M. balthica* varies its intensity of deposit feeding in response to the presence of abundant nearby suspension feeders, we conducted a field experiment in which *Macoma* was enclosed with and without the suspension-feeding bivalve *Rangia cuneata*. This experiment was initiated on 9 March 1992, at a date preceeding the seasonal development of intense siphon nipping by juvenile demersal fishes (Peterson and Skilleter 1994). We chose to add *Rangia* to form an experimental bed along the shore in an area of the South River where this clam was uncommon at the time of the experiment so that we could properly manipulate its local density. *Rangia* was planted at a density of 75 m^{-2} in a bed 2 m wide and 7 m long running parallel to shore. This density is toward the upper end of natural *Rangia* densities in this region (G. Skilleter, personal observations). Mean length of *Rangia* used was 37.5 mm (±0.3 SE; *n*=150). These clams were inserted into the sediments in normal living position with the top 1 cm exposed above the sediments: within 24 h all had completed burial leaving siphon hole connections to the water column.

M. balthica was introduced inside fenced enclosures both within and outside the experimental *Rangia* bed. Twenty *Macoma* (mean length 27 mm±0.1 SE *n*=120) were added to each of six 30×45 cm enclosures (a density of 150 m^{-2}), three inside and three outside the *Rangia* bed. The *Macoma* all buried within 1 h and remained uncovered during the experiment. The enclosures were constructed of 1-cm^2 plastic vexar mesh inserted 9 cm into the sediments to prevent clam migration, leaving 1 cm projecting above the sediment surface. The three enclosures located inside the *Rangia* bed were positioned near the shore edge of the bed where the predominant wind-driven flow ensured that water reaching the *Macoma* had passed over at least 1 m of the bed. The three control enclosures were located at separate positions about 10 m away from the bed and in slightly deeper water to ensure that water reaching them had not first passed across the *Rangia* bed. After 1 month, the *Macoma* were excavated, preserved, and processed as described above to determine the size-adjusted ash weight of inorganic sediments inside them as an index of relative intensity of deposit-feeding activity. Five 1-m^2 plots inside the *Rangia* bed were also excavated to assess the surviving density of suspension feeders in the experimental treatment.

On three occasions during the course of this experiment, we also collected and processed water samples from just shoreward of the experimental *Rangia* bed and from the nearby control area to assess whether the suspension feeders were affecting levels of suspended foods in the water column. One occasion was characterized by calm, wind-free conditions with little water movement, while on the other two sampling dates water was moving toward shore across the *Rangia* bed driven by north-west winds of 10–15 knots and south-west winds of 15–20 knots, respectively. On each sampling date, 10 1-l water samples were collected at each of two heights off the bottom (1 and 15 cm) from both the experimental and control sites. Water was collected at a rate of 0.33 l min^{-1} using a submersible pump with the inlet tube resting upon a plexiglass plate. The plate was designed to prevent contamination of samples by resuspension of particulates from the bottom during sampling. Five of each set of water samples were immediately filtered in the field through Whatman 934-AH glass microfiber filters for subsequent determination of chlorophyll a (chl *a*). Each filter paper was separately wrapped in aluminum foil and stored in the dark on ice until return to the laboratory where they were kept at –4° C until processing. Fluorometric methods of Parsons et al. (1984) were used to determine the concentrations of chl a. The other five replicate water samples were packed on ice for return to the laboratory for determination of concentration of total suspended particulates. Within 24 h each of these samples was filtered across a pre-weighed Gelman AE glass fiber filter (1-mm pore size) using a vacuum pump. Filters were dried at 60° C for 12 h and reweighed. The difference in weight was then used to calculate concentrations of total particulates.

Ash weight of inorganic sediments in soft tissues of *Macoma* inside and outside of the *Rangia* bed was analyzed by two-factor ANOVA, with treatment fixed and plots nested within treatment random. Before testing, Cochran's test at a=0.05 was used to assess equality of variances.

Effects of interaction between suspension feeders and siphon croppers

To test whether the presence and activity of siphon-nipping fishes modifies the response in feeding behavior of *M. balthica* to the presence of locally abundant suspension feeders, we conducted a caging experiment at 1 m depth in Big Creek in August 1992. We employed two densities of juvenile pinfish (the sparid, *Lagodon rhomboides* Linnaeus 1766), 0 and 6 per 1-m^2 cage, and two densities of *Rangia cuneata,* 0 and 75 m^{-2}, in an orthogonal design with five replicates of each treatment combination. Cages were again made of 1-cm^2 square black plastic mesh, but in this experiment the cages were provided mesh bottoms also. Walls rising 60 cm off the bottom were anchored by cable-tie attachment to steel corner posts. Clams were contained inside a 30×45×15 cm plastic tub, which was filled to a depth of 14 cm with sediments freshly gathered from surrounding bottom and sieved through 0.5-mm mesh. Into half of the tubs, chosen at random, we added ten *R. cuneata* (mean length 38.3 mm±0.6 SE; n=100). Into all tubs we then added 20 adult *M. balthica* (mean length 28.8 mm±0.1 SE; n=400) and allowed the clams to bury. One week later, six juvenile pinfish were added to half of the cages containing *Rangia* and to half the cages without *Rangia.* The mean standard length of pinfish of 87 mm (±1.2 SE; n=50) did not vary significantly among cages (one-factor ANOVA, $F_{9,50}$=1.2; P=0.32). The fish used for this experiment had been caught on the previous day in South River. During the 2-week experiment, one *Rangia* died in each tub containing *Rangia.* No change occurred in pinfish density.

After 2 weeks, the experiment was terminated by removal of cage tops and recovery by sieving of all surviving *Macoma.* Each *Macoma* was preserved in 70% ethanol and returned to the laboratory for the standard determination of weight of inhalant siphon and of inhaled inorganic sediments, as described above. Each of these response variables was analyzed in separate three-factor ANCOVAs, with fish and *Rangia* fixed and cages nested within fish × *Rangia* a random factor. AFDW was the covariate in these analyses. Assumptions of ANCOVA were tested as described above. The nested factor cages was used as the mean square denominator for F-tests of all main effects and interactions in the ANCOVAs.

Results

Effects of intraspecific competition and siphon nipping

Inclusion of siphon-nipping spot for 3 weeks resulted in significantly smaller adjusted mean siphon sizes for *Macoma,* but the effects of fish on siphon weight also interacted significantly with clam density (Table 1). At the lower density of 110 clams m^{-2}, the presence of ten spot reduced the average weight of inhalant siphons by 53%, as compared to a reduction of only 14% at the higher density of 370 m^{-2} (Fig. 1). Each of these reductions was significant in Bryant-Paulson-Tukey (BPT) tests (Huitema 1980). BPT tests done in response to the significant interaction also revealed that average siphon weight in the absence of fish was about 30% greater for clams at the lower density (Fig. 1). Although significant heterogeneity of regression variances existed at a=0.05 (Table 1), which could not be removed by transformation, the significance level of the interaction effect (P<0.001) implies that a possible increase in the probability of type I error would not alter the qualitative inferences drawn from this experiment (Underwood 1981).

The analysis of the index of deposit-feeding activity, weight of inorganic sediments in the soft tissues, also revealed a significant effect of both fish presence and of the interaction between clam density and fish (Table 1). For clams at low density, deposit-feeding activity in the presence of fish was 15% lower than where fish had been excluded for 3 weeks, whereas for clams at high density the decrease in deposit feeding with the addition of fish was 34% (Fig. 2). This difference in the magnitude of the effect of fish with changing clam density was significant in BPT tests. Thus, despite a greater siphon loss due to fish at low clam density, the joint effects of both fish cropping and higher clam density led to larger reductions in deposit-feeding activity at higher densities of *Maco-*

Table 1 Results of ANCOVA analyses of whether siphon weight or ash weight of sediments inside of *Macoma* varied significantly in response to presence/absence of siphon-nipping fish and clam (*Macoma*) density. Data are in Figs. 1 and 2, respectively. Ash-free dry weight (AFDW) was used as the covariate. In neither analysis were slopes of regression lines significantly different (at α=0.05). ANOVA revealed no significant relationship between fish treatment, clam density, or their interaction and the covariate, AFDW. Variances were heterogeneous, even after transformation, for siphon weight (P<0.05) but not for ash weight of sediments. Significance comes from a 3-factor ANCOVA with fish treatment (F) and clam density (C) as crossed, fixed factors and cage (random) nested within F×C (*df* degrees of freedom, *MS* mean square error, *F* variance ratio tested)

Source of variation	*df*	Siphon weight			Ash weight of sediments		
		MS (×10^{-6})	F	sig	MS (×10^{-5})	*F*	sig
Fish treatment (F)	1	158	211	***	383	511	***
Clam density (C)	1	2.5	3.4	ns	1,087	1,449	***
F×C interaction	1	80	107	***	20	27	***
Cage (F×C)	16	0.8	3.3	***	0.8	0.9	ns
Residual	179	0.2			0.9		

*** P≤0.001, ns P>0.05

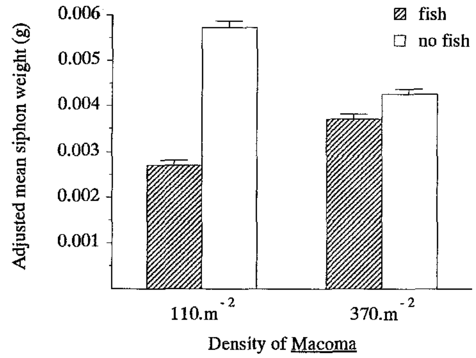

Fig. 1 Average size-adjusted weight (+SE; n=10) of the inhalant siphon of *Macoma balthica* enclosed for 3 weeks with or without 10 siphon-nipping spot *(Leiostomus xanthurus)* per 1-m^2 cage at two densities of clams. The average AFDW of soft tissues of *Macoma,* the covariate value to which size adjustment was made, was 0.057 g. This graph illustrates the nature of the significant fish×clam interaction in the 3-factor ANCOVA (Table 1)

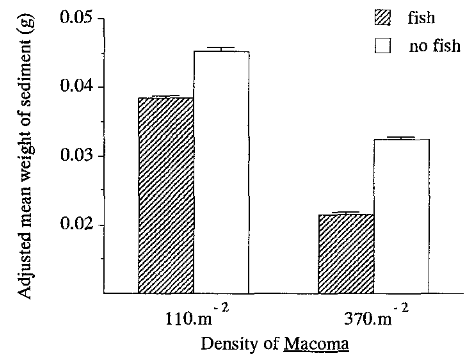

Fig. 2 Average size-adjusted ash weight (+SE; n=10) of inorganic sediments in the soft tissues of *M. balthica* after enclosure for 3 weeks with or without 10 siphon-nipping spot per 1-m^2 cage at two densities of *Macoma.* The average value of the covariate, ash-free dry weight (AFDW) to which ash weight was adjusted, was 0.057 g. This graph illustrates the nature of the significant fish×clam interaction in the 3-factor ANCOVA (Table 1)

ma. BPT tests also revealed that in the absence of fish the ash weight of inhaled sediments was significantly lower (Fig. 2) for clams at the higher density.

Effects of interspecific interactions with suspension feeders

M. balthica inside the 2×7 m bed of the suspension-feeding *R. cuneata,* which had been experimentally installed at a density of 75 m^{-2}, exhibited a 27% increase in deposit-feeding activity over control *Macoma* in the absence of neighboring *Rangia* (Fig. 3: ANOVA $F_{1,4}$=18.8; P=0.01). No significant variation existed among replicate plots within *Rangia* treatments in ash weight of inhaled sediments, our index of deposit-feeding activity (ANOVA $F_{4,96}$=0.4; P=0.82).

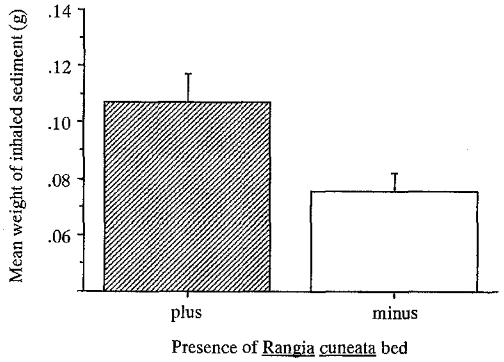

Fig. 3 Average ash weight (+SE; n=45) of inorganic sediments in the soft tissues of *M. balthica* after 1 mo in plots within and outside a 2×7 m bed of the suspension feeder *Rangia cuneata* at a density of 75 *Rangia* m^{-2}

Analysis of the seston samples revealed a significant interaction between the day of measurement and the presence/absence of *Rangia* (Table 2). On the first day when winds and water currents were negligible, total concentration of seston above the *Rangia* bed was 8% lower than in control areas outside the bed of suspension feeders (P<0.05 in SNK test: Fig. 4). On each of the other days, both characterized by more energetic wind and water current movements, the estimated reduction in seston concentrations was a non-significant 2% (Fig. 4). No effect of elevation off the bottom or of interactions between elevation and other factors was detected from this sampling (Table 2).

Analysis of chl a concentrations also revealed significant interactions among factors, in this case between elevation off the bottom and *Rangia* presence/absence and also between elevation and sampling day (Table 2). SNK tests showed that the interaction between elevation and *Rangia* was a consequence of a significant reduction, by 31% of average chl *a* concentration, by *Rangia* at 1-cm elevation but no effect at 15 cm (Fig. 5A). The difference in chl *a* concentrations between the two heights off the bottom differed among sampling days (Fig. 5B), although not in any way obviously connected to wind conditions.

Effects of interaction between suspension feeders and siphon croppers

The impact of siphon-nipping pinfish on the size (dry weight) of the inhalant siphons of *M. balthica* was significantly greater in the presence of suspension-feeding *Rangia* than in identical cages without these other clams (Table 3: ANCOVA interaction P<0.05). The reduction in siphon weight attributable to cropping by pinfish amounted to 47% in the presence of *Rangia* but only 21% in its absence (Fig. 6). Both of these effects of siphon nippers were significant in BPT tests. In cages without fish, BPT tests showed that *Macoma* siphon size did not vary in response to changing abundance of the suspension-feeding *Rangia* (Fig. 6).

The impact of siphon-nipping pinfish on the index of intensity of deposit feeding by *Macoma* varied depend-

Table 2 Results of ANOVA analyses of whether seston concentration or chlorophyll *a* concentration varied significantly in response to changing presence/absence of suspension-feeding *Rangia*, elevation off the bottom, and day of measurement. Data are in Figs. 4 and 5, respectively. Cochran's tests at α=0.05 revealed homogeneity of variances for both untransformed response variables. Significance from a 3-factor ANOVA with *Rangia* (*R*), elevation off bottom (*E*), and day (*D*) as crossed factors. Symbols as in Table 1

Source of variation	*df*	Seston			Chlorophyll *a*		
		MS ($\times 10^{-8}$)	*F*	sig	*MS* ($\times 10^{-1}$)	*F*	sig
Rangia (R)	1	304	12.4	***	0.9	5.5	*
Elevation (E)	1	6.0	0.3	ns	61	368	***
Day (D)	2	138	5.7	**	40	243	***
R×E interaction	1	1.4	0.1	ns	2.8	17	***
R×D interaction	2	102	4.2	*	0.2	1.0	ns
E×D interaction	2	13	0.5	ns	15	88	***
R×E×D interaction	2	36	1.5	ns	0.02	0.1	ns
Residual	48	24			0.2		

$^*P\leq 0.05$, $^{**}P\leq 0.01$, $^{***}P\leq 0.001$, ns $P>0.05$

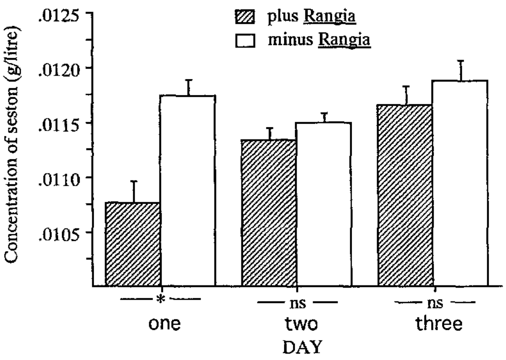

Fig. 4 Average concentrations of seston (+SE; n=10), defined as total dried particulates captured on a 1 µm filter, in the water column over a 2×7 m bed of the suspension feeder *R. cuneata* and outside the bed on each of 3 days. Significance levels ($^*P<0.05$, *ns* $P>0.05$) presented under results for each day are the outcomes of SNK tests done to explore the cause of significance of the *Rangia* × day interaction in the 3-factor ANOVA (see Table 2)

ing upon whether *Rangia* was present or not (Table 3: ANCOVA interaction $P<0.001$). In the absence of *Rangia,* the addition of pinfish resulted in a non-significant 11% reduction in ash weight of inhaled sediments by *Macoma* as compared to clams inside cages without fish (Fig. 6). In contrast, in the presence of the suspension-feeding *Rangia,* the addition of pinfish led to a significant (by BPT test) decrease of 34% in the ash weight of inhaled sediment as compared to clams maintained free of the fish (Fig. 6). Looking at this same interaction differently, *Rangia* had the effect of causing an 11% increase in deposit-feeding activity by *M. balthica* in the absence of pinfish. In the presence of pinfish, however, *Rangia* had the opposite effect of producing a 16% decrease in *Macoma*'s deposit feeding (Fig. 6).

Discussion

Peterson and Skilleter (1994) showed that, while an understanding of food fluxes as determined by variation in

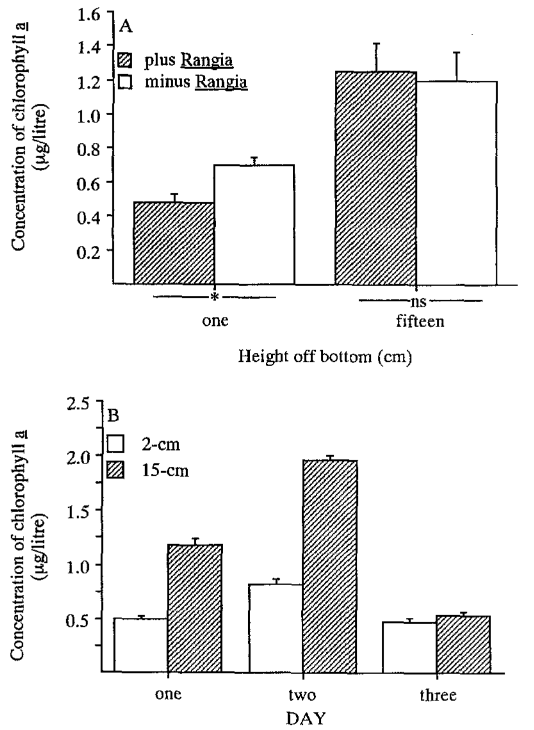

Fig. 5 A Average concentrations of particulate chorophyll *a* (+SE; n=15), as extracted from Whatman 934-AH filters, in the water column at two different elevations off the bottom over a 2×7 m bed of the suspension feeder *R. cuneata* at a density of 75 m^{-2} and outside the *Rangia* bed. Significance levels (* $P<0.05$, *ns* $P>0.05$) presented under the bars are the outcomes of SNK tests done to explore the cause of significance of the *Rangia* × elevation interaction in the 3-factor ANOVA (see Table 2). **B** Average concentrations of chlorophyll *a* (+SE; n=10) in the water column at two different elevations above the bottom on each of 3 days. This graph illustrates the nature of the significant elevation × day interaction in the 3-factor ANOVA (Table 2)

flow regimes indeed helps explain feeding choices and switches in feeding behavior of facultative suspension/deposit feeders in a natural field environment (predictable from the earlier work of Taghon et al. 1980; Jumars and Self 1986; Levinton 1991), the direct effects

Table 3 Results of ANCOVA analyses of whether siphon weight or ash weight of sediments inside of *Macoma* varied significantly in response to presence/absence of siphon-nipping fish and presence/absence of suspension-feeding *Rangia*. Data are in Fig. 6. AFDW was used as the covariate. In neither analysis were slopes of regression lines significantly different (at α=0.05). ANOVA revealed no significant relationship between fish treatment, *Rangia* treatment, or their interaction and the covariate, AFDW. Variances were homogeneous in both cases at α=0.05. Significance comes from 3-factor ANCOVA with fish treatment (*F*) and *Rangia* treatment (*R*) as crossed, fixed factors and cage (random) nested within F×R. Symbols as in Tables and 2

Source of variation	*df*	Siphon weight			Ash weight of sediments		
		MS ($\times10^{-6}$)	F	sig	MS ($\times10^{-5}$)	*F*	sig
Fish treatment (F)	1	132	40	***	1500	36	***
Rangia treatment (R)	1	47	14	***	0.07	0.02	ns
F×R interaction	1	16	4.8	*	126	10	**
Cage (F×R)	16	3.3	1.2	ns	41	0.5	ns
Residual	159	2.8			78		

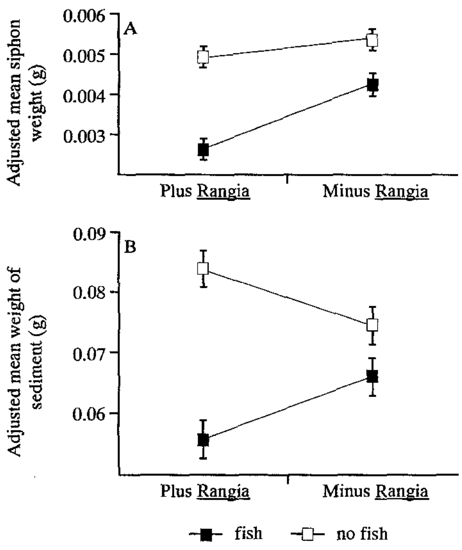

Fig. 6 A Average size-adjusted weight (±SE; n=15) of the inhalant siphon (*top*) and **B** average size-adjusted ash weight of inorganic sediments in soft tissues of 20 *M. balthica* caged for 2 weeks with and without 6 pinfish *(Lagodon rhomboides)* in the presence and absence of 10 suspension-feeding *R. cuneata.* The average value of AFDW, the covariate to which size adjustment was made, was 0.142 g. These graphs depict the nature of the significant fish × *Rangia* interactions demonstrated in 3-factor ANCOVAs (Table 3)

of siphon croppers must also be included to more fully explain foraging behavior of these seafloor invertebrates. Just as foraging theory has evolved beyond its initial restricted focus on purely energetic consequences of foraging alternatives (see Pyke et al. 1977; Hughes 1980; Stephens and Krebs 1986) to include dynamic modeling of how multiple selective forces contribute to the adoption of certain foraging behaviors (e.g., Houston et al. 1988; Mangel and Clark 1988), so must our understanding of the processes that dictate feeding behavior in marine invertebrates be expanded.

In this study, we do extend our appreciation of the factors that control foraging in facultative suspension/deposit feeders by demonstrating the need to consider the effects of both intra- and interspecific competition and their interactions with partial predation. When protected from the influence of siphon-cropping fishes by caging, *M. balthica* achieved greater siphon regeneration when at low than at high density (Fig. 1). This inversely density-dependent regeneration implies intraspecific competition among the clams, probably for limited food resources, judging from previous knowledge of deposit feeders (e.g., Levinton and Bianchi 1981) and of *M. balthica* itself (Hummel 1985; Olafsson 1986; Thompson and Nichols 1988; Vincent et al. 1989; Kammermans et al. 1992). After exclusion of siphon-cropping fish, these same clams exhibited more deposit feeding at low than at high density (Fig. 2). This response may follow solely from the density-dependent difference in size of the inhalant siphon and its influence on efficiency of deposit feeding. Alternatively, the reduction in deposit feeding at high intraspecific density in the absence of siphon nippers may be explained by an hypothesis of Peterson (1982) and Hunt et al. (1987). Those papers argued that for a given feeding rate deposit feeders should deplete foods locally more than suspension feeders, whose effects extend quickly over large spatial scales consistent with the excursion of the water mass passing over them. As crowding increases, a population of facultative suspension/deposit feeders would thus be expected to exhibit some degree of switching away from deposit feeding and towards suspension feeding because of this asymmetry in the rates of intraspecific depression of food concentrations between suspension and deposit feeding.

Intraspecific density of *M. balthica* also plays a large role in determining the impact of siphon-cropping fishes on feeding behavior of the clams. At the lower clam density, siphon-nipping spot reduced the size of *Macoma*'s siphon by a much larger degree than observed at the higher clam density (Fig. 1). This response presumably is the joint consequence of a greater ratio of fish to target siphons at low clam density, such that intensity of fish interactions per clam is greater, and of the greater intensity of deposit feeding, the more risky feeding behavior, at the lower clam density. Despite the more intense cropping of siphons and shorter average siphon sizes of *Macoma* at low clam density, the reduction in deposit-feeding activity caused by the presence of siphon-cropping fish was substantially greater at high *Macoma* density (Fig. 2). Thus, not only does intraspecific density of *Macoma* influence its foraging behavior but also intraspecific density interacts with siphon nipping to further alter *Macoma*'s observed feeding behavior. More importantly, the greater reduction in deposit feeding caused by the presence of fish at high than at low clam density cannot be explained by direct effects of reduced efficiency of smaller siphons because the effect of fish on siphon size was actually much greater at the lower density. The failure of fish effects on siphon size to explain the degree to which *Macoma* reduced its deposit-feeding activity in the presence of croppers implies that the clams are detecting and responding behaviorally to fish presence by adjusting their practice of risky behavior.

Foraging theory may help explain why the level of deposit feeding in *M. balthica* when at low density and in the presence of siphon-cropping fish is substantially greater than would be expected from the additive direct effects of clam density and fish presence and why siphon size in this case fails to predict differences in deposit-feeding activity. This response may represent evidence of a balancing foraging strategy (*sensu* Cerri and Fraser 1983) by *M. balthica*, in which it is accepting greater risks of siphon cropping when there are greater potential rewards of more food, namely under reduced intraspecific competition. Our data on the slower rate of siphon regeneration at higher intraspecific density and the demonstrations by Olafsson (1986) and Vincent et al. (1989) of reduced growth of deposit-feeding *M. balthica* at higher densities reveal that feeding is more rewarding at low than at high density for *Macoma.* It is also clear from all our experiments manipulating access by croppers that *Macoma* is subjected to tissue loss during exposure to these siphon croppers. We thus placed *Macoma* in our experiment in a conflict situation (Mittelbach 1978; Sih 1980; Werner et al. 1983; Lima 1985), where the clams were forced in the presence of siphon croppers to choose between conducting the more rewarding deposit feeding at greater risk of siphon cropping or conducting the less rewarding but less risky suspension feeding as an alternative. These experiments revealed significant effects of clam density (a surrogate for food availability) and croppers, as well as an interaction between these two variables. Those are the three necessary conditions to demonstrate existence of a balancing strategy (Cerri and Fraser 1983). Our design has the effect of varying the level of partial predation along with food availability in that with constant numbers of croppers but changing densities of clams the ratio of croppers to clam targets was greater at low clam density. Nevertheless, this design actually proves to provide a stronger test of the existence of a balancing strategy in *Macoma* than an alternative holding the cropper-to-clam ratio constant across density treatments because, despite the more intense risk of cropping per individual clam at lower clam density, *Macoma* still chose to practice more of the risky deposit-feeding behavior at low clam density than predicted by the separate effects of clam density and cropper presence.

These results provide a stark contrast to the results of other foraging studies, which have shown consumers forgoing the prospects of greater food harvest so as to minimize risk from predation (e.g., Milinski and Heller 1978; Sih 1980; Werner et al. 1983; Holbrook and Schmitt 1988). Here *M. balthica* appears to accept the higher risk of cropping in return for the greater expected gains in food harvest at low density. This strategy may be optimal because cropping in this system (and most others: see Peterson and Quammen 1982) is not lethal; siphon cropping is equivalent to a growth penalty because, through subsequent feeding, the siphonal tissues are regenerated. We do not possess the comparative data on the differential growth rates and fecundities that are achieved under these alternative foraging strategies to assess optimality. Yet this intriguing result implies the operation of some foraging rule in *M. balthica* in response to the interaction between intraspecific competition and risk of partial predation. The growth penalty that croppers exact from *Macoma* in our system is analogous to the penalty experienced by plants during most types of herbivory and by clonal animals during cropping by predators. In both of those cases, death of the prey is not the consequence of feeding by the consumer. Thus, it is possible that the results of this study showing *Macoma* willing to take higher risks of siphon losses under conditions of greater feeding reward may prove to be more generally applicable to plant-herbivore and clonal animal-grazer interactions than the previously available results of experiments manipulating risk of true predation (reviewed in Sih 1987).

Our experiments demonstrated that intraspecific interactions with other potentially competing benthic invertebrates also play important roles in dictating foraging behavior in *M. balthica*, acting both independently and also through interactions with siphon croppers. In the absence of siphon nippers, *R. cuneata* caused a substantial increase in the intensity of deposit feeding by *M. balthica* (Fig. 3). This increase in deposit feeding presumably reflects a quantitative reallocation of feeding effort away from suspension feeding and toward deposit feeding (as described by Brafield and Newell 1961; Hughes 1969; Reid and Reid 1969; Levinton 1971; Olafsson 1986; Lin and Hines 1994). The influence of the suspension-feeding *Rangia* is presumably indirect, operating through changes in food concentrations. Consistent with other demonstrations of the influence of beds of suspension feeders (Fréchette and Bourget 1985; Peterson and Black 1987, 1991; Fréchette et al. 1989; Muschenheim and Newell 1992), our observations reveal that a bed of *R. cuneata* is able to cause depletion of seston in the water column (Fig. 4) and its feeding can reduce chl *a* concentrations near the bottom (Fig. 5) where suspension-feeding *Macoma* would also be feeding. The switch in feeding by *Macoma* away from suspension feeding and toward deposit feeding in the presence of the bed of suspension-feeding *Rangia* is a predictable effect of interspecific competition with *Rangia.* Although we did not also measure their contribution to surface organics, *Rangia* may also have augmented the profitability of surface deposit feeding through biodeposition of feces and pseudofeces.

The suspension-feeding *Rangia* also affected the foraging behavior of *M. balthica* indirectly by greatly enhancing the influence of siphon-nipping fishes. In the presence of dense *Rangia* but in the seasonal absence of siphon-nipping fish, *Macoma* exhibited a switch in feeding towards more intense deposit feeding (Fig. 3). This identical response was induced by manipulating *Rangia* presence/absence under conditions of experimental exlusion of fish (Fig. 6). The interaction between the presence of *Rangia* and siphon croppers on deposit-feeding activity by *Macoma* can be best be interpreted by assuming a temporal sequence of events. The loss of siphon tissues to pinfish was much greater for those *Macoma* that were simultaneously exposed to the presence of *Rangia* than for those *Macoma* in the absence of the competitor/biodepositer (Fig. 6), presumably because the enhanced deposit-feeding activity in the presence of *Rangia* had exposed *Macoma* siphons to greater risk of cropping. As a consequence of greater siphon losses to croppers in the presence of *Rangia, Macoma*'s deposit-feeding behavior was then subsequently depressed more by croppers when the competing *Rangia* were also present (Fig. 6). An alternative explanation for this interaction, that *Macoma* was practicing risk-averse behavior in reducing deposit feeding in the presence of both *Rangia* and fish, does not adequately explain why siphon nipping was more intense when *Rangia* was present.

An understanding of the factors that control foraging behavior in facultative suspension/deposit feeders clearly requires knowledge of the role of complex indirect interactions among competitors and partial predators. Interestingly, the impact of siphon impairment by pinfish and other croppers has the implication of forcing more intense competition between *Macoma* and various suspension feeders because of an induced switch away from deposit feeding and towards more suspension feeding than would otherwise be conducted. Unlike the role of predation in reducing the intensity of competition (Paine 1966), the role of partial predators in this system induces more intense intraspecific competition among individual facultative suspension/deposit feeders as it forces a narrowing in the actual use of available food resources. Interestingly, this reduction in deposit-feeding activity induced by croppers will simultaneously reduce the intensity of competition for deposited food resources. Thus, the direct effects of croppers like the indirect effects of predators acting through induction of risk-averse foraging behaviors imply important but mixed consequences for competition within the broader community (e.g., Werner et al. 1983; Abrams 1987; Sih 1987).

Although experiments conducted in this study were restricted to assessments of factors influencing foraging behavior of a facultative suspension/deposit feeder, the impacts of croppers and of the choice between suspension and deposit feeding in this group of organisms can have profound indirect effects on their susceptibility to predation and thus on community organization. Either loss of siphon tips to croppers or the choice to deposit feed on the sediment surface forces *Macoma* and other buried invertebrates to live closer to the surface of the sediment (Zwarts and Wanink 1989; Lin and Hines 1994). This increases their risk of predation from crabs, birds, and other digging predators (Reading and McGrorty 1978; Blundon and Kennedy 1982; Zwarts 1986; Zwarts et al. 1992). The blue crab, *Callinectes sapidus,* is extremely abundant in the mesohaline regions of mid-Atlantic estuaries and its predation on thin-shelled bivalves such as *Macoma* can be intense (Hines et al. 1990). Furthermore, *Macoma* is a principal food source for overwintering ducks in the Pamlico Sound system (Lovvorn 1987). The inability of a *Macoma* with a cropped siphon to occupy a refuge from these excavating predators at depth in the sediments may lead to an important indirect effect of cropping on predation, especially by blue crabs because they are active during the same season as the siphon-cropping juvenile fishes. The influence of such indirect interactions on predation rate in natural ecosystems may be more the rule than the exception (e.g., Abrams 1987; Schmitt 1987; Martin et al. 1989). To the degree that those *M. balthica* in our Neuse River estuarine system experience enhanced risks of predation after loss of siphonal tissue, the acceptance of the more risky deposit-feeding behavior confers more than just an energetic cost. We do not, however, possess any quantitative assessment of the increase in risk of predation that accompanies the adoption of deposit feeding by *Macoma* in our study system.

The clear implication of this study is that complex interactions between competition and cropping can modify foraging behavior in major ways. Peterson and Skilleter (1994) showed that knowledge of the flow conditions and energetics of the habitat are insufficient to explain observed feeding behaviors of *M. balthica* and that the cropping of its feeding organ by juvenile demersal fishes must also be considered. Here, we demonstrate that intra- and interspecific competition and the complex interactions between competition and cropping also influence the foraging behavior of this species. Consequently, as argued persuasively by Stephens and Krebs (1986) and Mangel and Clark (1988), foraging behavior must be understood in a broad synthetic context of the multitude of processes that affect the fitness and performance of the individual organism. For marine benthic ecology, this principle demands an integration of three previously separate areas of investigation, on the influence of physical boundary-layer processes on feeding biology, on partial predation by croppers and predation risk, and on competition for suspended and deposited food resources. Thus foraging decisions and feeding behaviors of an individual organism can be fully understood only within a context of the entire ecosystem in which they are expressed. Study across ecological levels of organization from the individual organism to the population, the community of interacting populations, and to the ecosystem is required.

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