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Infaunal predation regulates benthic recruitment: an experimental study of the influence of the predator *Nephtys hombergii* (Savigny) on recruits of *Nereis diversicolor* (O.F. Müller)

Nicolas Desroy[a,*], Christian Retière[a], Eric Thiébaut[b]

[a]*Laboratoire Maritime de Dinard, Muséum National d'Histoire Naturelle, 17, Avenue George V, B.P. 28, 35801 Dinard Cedex, France*

[b]*Université Pierre et Marie Curie–Paris VI, Laboratoire d'Océanographie Biologique et Ecologie du Plancton Marin, CNRS URA 2077, Batiment A, Case 6, 4, Place Jussieu, 75252 Paris Cedex 05, France*

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Abstract

Field and laboratory experiments were carried out to examine predatory activity effects of the infaunal polychaete *Nephtys hombergii* on the recruitment of *Nereis diversicolor*. Using *N. diversicolor* juveniles as prey, we tested the effects of (1) the temperature variations on predatory activity and (2) the predator density ($d = 114$ and 342 ind. m^{-2}) on prey mortality, on their growth and their escape behaviour. In the field, *N. diversicolor* alone ($d = 13750$ ind. m^{-2}), and *N. hombergii* ($d = 114$ and 342 ind. m^{-2}) and *N. diversicolor* juveniles together were enclosed in 15-cm dia. PVC cylinders during 12 weeks, from 7 March to 30 May 1995, in a mudflat of the Rance Estuary. In the presence of the predator, the biomass of *N. diversicolor* juveniles declined 8–12 $\times$ more than in control cylinders, whereas their individual weight was increased. Although it had little effect on the biomass of prey, predator density regulated the consumption by *N. hombergii*. Predation activity was minimal, but effective, at a temperature of 7°C, increased between 9 and 11°C, and became constant above 11°C. In the laboratory, gradual or sudden temperature variations had little effect on predatory activity of *N. hombergii*, presumably because they were already physiologically active. Reduction in the abundance of infauna may be due to prey emigration as well as predation: beyond their mortality, *N. hombergii* induced, proportional to its density, the emigration of juveniles. The experimental results suggest that infaunal predation, by regulating recruit densities, should be considered in addition to the interactions between adults as a strong force structuring soft-bottom communities.

*Corresponding author. Tel.: +33 2 99461390; fax: +33 2 99882942; e-mail: Labomar.MNHN@lmd.galeode.fr

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1. Introduction

Factors affecting recruitment rates have been shown to affect the structure and dynamics of populations of species living on hard substrata (for review see Hunt and Scheibling, 1997). Conversely, these effects on soft-bottom communities have received less attention (Woodin, 1991; Peterson and Summerson, 1992; Peterson et al., 1996; Butler and Herrnkind, 1997). From a recent review, Olafsson et al. (1994) concluded that larval supply is probably not a major determinant on the pattern of species distribution and abundance in sedimentary habitats. Factors which are known to cause mortality of recent settlers in soft-sediments, and consequently the distribution and abundance of adults, include delay of metamorphosis, physical and biological disturbances, predation, and spatial and trophic competition (Gosselin and Qian, 1997; Hunt and Scheibling, 1997). In accordance with these observations, the hypothesis that the presence of adult invertebrates in the sediments plays a significant role in affecting the recruitment success was developed a long time ago. Among the numerous biological factors considered as influencing recruitment patterns in soft sediments, predation appears as the best-documented source of early post-settlement mortality. However, most studies have focused on the effects of mobile species such as birds, shrimps, crabs, lobsters, sea stars, sea urchins or fishes (for review see Olafsson et al., 1994; Hunt and Scheibling, 1997) while very few, to our knowledge, were related to the influence of infaunal predators. As noted by Ambrose (1991), such studies are necessary because infaunal predators are permanent residents of soft-bottom communities, often mobile, long-lived and potentially capable of reaching high densities.

Field caging manipulations have shown the importance of predation in structuring soft-bottom communities (Peterson, 1979; Hall et al., 1991), but until recently this approach has been used nearly exclusively to study the effects on adult infaunal invertebrates. In recent years, there has been an increased focus on the influence of infaunal predation on recruitment sensu Connell (1985), that is settlement events and post-settlement mortalities (Wilson, 1980; Oliver et al., 1982; Peterson, 1982; Rivain, 1983; Weinberg, 1984; Elmgren et al., 1986; Crowe et al., 1987; Rönn et al., 1988; Peterson and Black, 1994; Qian and Chia, 1994; Bonsdorff et al., 1996; Gosselin and Qian, 1997). However, none of these studies addressed the effects of an abundant and mobile predatory infaunal polychaete on benthic recruitment. In this study, we use *Nephtys hombergii* (Savigny), a widely distributed predator polychaete in fine sediment communities in shallow areas, and *Nereis diversicolor* (O.F. Müller) juveniles, as a model system to examine the influence of an infaunal predator on prey recruitment. In this system, the predator may act directly on prey as consumer, inducing their mortality, or indirectly by disturbing the sediment (e.g. prey burrow destruction), thus forcing their burying and death or their emigration. This predator–prey model has been studied by Davey and George (1986) who attributed the lack of recruitment of young *N.*

diversicolor in *N. hombergii* mudflats in the Tamar estuary (England) essentially to a lack of sufficient organic resources for *N. diversicolor* to grow and thrive.

Gut content analyses have shown that *N. hombergii* is a carnivore rather than a non-selective detritus feeder (Fauchald and Jumars, 1979; Schubert and Reise, 1986; Beukema, 1987), though diatoms can represent a substantial feeding source (Warwick et al., 1979). Trophic exchanges between *N. hombergii* and various preys have been examined by Schubert and Reise (1986), who showed that the addition of *N. hombergii* in small enclosures induced a significant decline in the abundance of other polychaetes (e.g. *Scoloplos armiger* and *Heteromastus filiformis*). At a density of 5 ind. m^{-2}, total prey consumption was estimated at ≈ 1 gC m^{-2} $year^{-1}$, at least one-tenth of the consumption of all epibenthic predators. Long-term data (18 years) from tidal flats of the Wadden Sea showed that prey biomass decreased with increasing *N. hombergii* biomass (Beukema, 1987).

The purpose of the present investigation is to use both field and laboratory experiments to evaluate the effects of predatory and locomotory activities of *N. hombergii* on recruitment of *N. diversicolor*. As there is a temporal coincidence between resumption of predation by *N. hombergii* and the settlement of the first cohorts of *N. diversicolor* recruits, after the wintering growth break of *N. hombergii* observed by Retière (1979) in the Rance Estuary, we examine how temperature variations affect predation rates. Concurrently, we estimate in the field and in the laboratory the influence of predator density on recruitment, in terms of mortality, growth and emigration of prey.

2. Materials and methods

2.1. Study site

The study site is located at the mouth of the Rance basin, in the southern part of the English Channel (France), on a mudflat located 0.5 km upstream of the tidal power plant of La Rance (48°62″N; 02°02″W). This installation imposes specific tidal conditions on the waters in the basin: (1) mean water level is raised by approximately 2.5 m; (2) slack water periods are particularly long (up to 5 h); (3) emersion durations may be 2 × shorter than on the open sea; and (4) the tidal range varies between 4.0 and 5.5 m compared to 9.45 m (mean value) on the open sea, depending on the direction the turbines are operating (Retière, 1994). The study site was located at 1–4 m above low tide level. Surface seawater temperatures, daily monitored at the mouth of the estuary from 1976 to 1991, range from 6 (Feb.) to 19°C (Aug.) over the year (data Lab. Dinard).

2.2. Model species

2.2.1. Prey

In the La Rance basin, *N. diversicolor* spawns in spring, from March to May, and in autumn, from August to September (Marty, 1997). Recruits leave the parental burrow at 5–6 setigers and then settle. In this study, *N. diversicolor* was used as a model prey

species for several reasons. Its distribution overlaps with that of *N. hombergii*, and it recruits well to the *N. hombergii* muds. As its life-cycle can be manipulated in the laboratory (Marty, 1997), laboratory rearing can provide 20–28 setiger juvenile *N. diversicolor* individuals throughout the year. It is mobile, and hence we could estimate the role of predator escape responses on prey recruitment.

2.2.2. Predator

In this study, *N. hombergii* was chosen as a predator model because it is abundant in the La Rance system and mobile, thus, we evaluate the effects of the predatory activity (i.e. predation and sediment disturbance) on settled recruits. Individuals used for the experiments were directly collected from the study site. Their length varied between 78 and 110 mm (dry weight ≈ 100 mg), which correspond to 3-year-old organisms (Retière, 1979).

The unique tidal conditions described above are responsible for a large overlapping of the spatial distribution of *N. diversicolor* and *N. hombergii* on these mudflats (unpublished data). Such distribution patterns are uncommon in bays and estuaries, where *N. diversicolor* usually occupies the upper part of mudflats while *N. hombergii* colonizes the lower part. For this reason, mudflats of the La Rance basin are an appropriate place to demonstrate, from prey species such as *N. diversicolor* the life cycle of which is controlled, the importance of infaunal predatory activity on recruitment patterns of benthic species.

2.2.3. Prey and predator densities

Abundance of adults of both species on the mudflat were determined at the beginning of March as follows. Ten 0.02-m^2 cylindrical cores (dia. = 15 cm) were randomly collected on an area of 10×10 m to a depth of 0.25 m. The sediment of each sample was sieved through a 0.5-mm mesh. Organisms retained on the sieve were fixed in 4.5% formalin before counting.

There are two main periods of recruitment on this site, from March to May and from August to October, with similar intensities (Marty, 1997). During the 1995 autumnal reproductive period, densities of recruits ($5 <$ number of setigers < 50) decreased from 25 000 (September) to 10 000 ind. m^{-2} (November) (Marty, 1997).

2.3. Field experiments

To examine the influence of the predator on prey recruitment and assess the influence of temperature on the resumption of activity by *N. hombergii*, we used 36 opaque PVC cylindrical cages (0.02 m^2 area, 30 cm high) placed partially in the sediment. They were two-thirds filled with defaunated mud and pushed in the bay substratum to a depth of ≈ 23 cm, so that sediment surfaces inside and outside enclosures were at the same level. Sediment was collected on the study site. Prior to air exposure for 1 week, the mud was passed through a 5-mm sieve to remove coarse particles and frozen for 48 h to kill alternative prey sources. Bottom and top ends of enclosures were, respectively, covered with a 0.5- and 0.2-mm single-layer nylon net inhibiting migration in and out of the

cage. On both sides, lateral windows, drilled at a level just above the sediment inside the cage and covered with a 0.2-mm nylon net, allowed seawater circulation.

The field experiment started on 7 March 1995. A homogeneous set of 275 juveniles ($\approx$22 setigers) of *N. diversicolor* (d = 13750 ind. m^{-2} corresponding to field observations) was placed on the sediment surface of each of the enclosure. *N. hombergii* individuals were added 48 h later, after the prey individuals built their burrows. The following treatments were used: 0D (no *N. hombergii* added = control treatment), 1D (two *N. hombergii* added = 114 ind. m^{-2}) and 3D (six *N. hombergii* added = 342 ind. m^{-2}), in accordance with predator densities observed in March in the field (about 100 ind. m^{-2} in the mudflat and between 300 and 400 ind. m^{-2} in subtidal communities of the Rance basin, pers. obs.). Each treatment were replicated 12×, all were regularly interspaced on an area of 40 m^2. During the experiment (84 days), experimental enclosures were brushed once every 3 days to remove algae and muddy particles. Protective stakes were set between cages and connected with ropes to exclude seabirds (*Larus argentatus*), which were able to tear up nylon tops at low tide. Throughout the experiment, surface seawater and sediment (top 4 cm) temperatures were measured every third day at low tide. Every 3 weeks during a total period of 12 weeks, three cages from each treatment were randomly collected. Samples were halved, and the upper and lower portions were, respectively, pushed through 0.2- and 0.5-mm sieves to recover *N. diversicolor* juveniles and *N. hombergii* adults. Organisms were fixed in 4.5% formalin for further analysis. Remaining dry biomass and averaged individual values of *N. diversicolor* dry weight (110°C for 24 h) were estimated for each treatment.

Dry biomass reduction (B), presumably eliminated by *N. hombergii*, in the field and laboratory experiments (Exp. 2.3 and 2.4.1) was estimated using the Allen curve method (Peer, 1970; Bougis, 1974). Biomass reduction between t_1 and t_2 is equal to the area included between the curve and the Y-axis:

$$B = \int_{n1}^{n2} W \, dn$$

Since the time period between t_1 and t_2 is short enough in our experiment (3 weeks in the field and 4 weeks at the laboratory), the integral can be approximated by the following equation:

$$B = (n_1 - n_2) \times (W_2 + W_1)/2$$

where n_1 is number of juveniles at t_1; n_2 is number of juveniles at t_2; W_1 is mean individual weight at t_1; W_2 is mean individual weight at t_2.

Only samples related to the first 9 weeks of experiment, of which the densities of remaining prey were still significant, were statistically analysed. Prior to tests for the significance of treatment effects, preliminary tests for homogeneity of variance (Cochran test) were conducted (Underwood, 1981). When this test indicated a heterogeneity of variances ($P > 0.05$), data were transformed using the logarithmic transformation $\log(x)$ and re-tested. To test the effect of predators, time and their interaction on number of surviving prey, reduction of biomass and growth of juveniles, two-way ANOVAs were conducted. Time and successively the number of surviving juveniles, the values of dry

biomass reduction per enclosure and the mean individual weight of *N. diversicolor* were, respectively, considered as factors. One-way ANOVAs followed by Tukey Kramer multiple comparison tests were performed to compare treatments for each separate date (Sokal and Rohlf, 1995). As only two densities of predator (1D and 3D) were studied, a Student *t*-test was used to compare differences between values of biomass eliminated per predator at different dates. Finally, a rank correlation test of Spearman was performed to correlate seawater and sediment temperature.

2.4. Laboratory experiments

2.4.1. Influence of temperature variations on predatory activity

In order to determine how temperature variations influenced the predatory activity of *N. hombergii*, we ran another set of experiments. Three experiments were simultaneously carried out at three temperature conditions: (1) with increasing temperature (9–13°C) to simulate the change observed in the field during the experiment; (2) at 13°C corresponding to the temperature during spring recruitment of *N. diversicolor*; and (3) at 18°C, the temperature during autumnal recruitment of *N. diversicolor*. Before the start of the experiments, *N. hombergii* individuals were collected from the field, at a temperature of 9°C, and placed in thermoregulated rooms in defaunated sediment (see above): a group was subject to the field seawater temperature increase (lot A), whereas other groups were subject to (i) a gradual temperature increase of 0.5°C per day from 9 to 13°C (lot B) or 9 to 18°C (lot C); (ii) a sudden increase from 9 to 13°C (lot D) or 9 to 18°C (lot E).

For these experiments, 40 opaque PVC pots (8.5 cm dia., 10 cm high) were filled up to a height of 7.5 cm with defaunated mud and 100 μm filtered seawater. In accordance with the treatment, we placed 100 juveniles of *N. diversicolor* (≈28 setigers, $d = 20\,000$ ind. m^{-2}) reared at 10 (field temperature), 13 or 18°C as prey source. Then, for each treatment mentioned (A–E), we added one *N. hombergii* per enclosure ($d = 200$ ind. m^{-2}). Controls consisted of enclosures sowed with 100 juveniles of *N. diversicolor* reared at 10, 13 and 18°C. Temperature and day–night light regime (16/8) remained constant during experiments, except for lot A and its control for which they respectively increased from 9 to 13°C and from 14/10 to 15/9. Every treatment, with and without predator, was replicated 5×. Water was changed every 2 days to prevent excessive salinity and microalgal blooms. After 1 month of experimentation, sediment of all enclosures was sieved (0.2-mm mesh) and organisms were fixed in 4.5% formalin.

Before analysing differences between firstly mortality rates of *N. diversicolor* and secondly values of biomass reduction, the Bartlett's test was used to test for homogeneity of variances for the reasons for the difference in replicate numbers, due to the death of a *N. hombergii* (Scherrer, 1984). When the data did not conform to parametric assumptions ($P > 0.05$), a Kruskal–Wallis test followed by multiple comparison tests described by Noether (in Scherrer, 1984) were performed. Otherwise, one-way ANOVA and Tukey Kramer tests were used.

2.4.2. Influence of predator presence on the mobility of recruits

The presence of a mobile predator could cause prey migration. This hypothesis was tested in the laboratory with aquaria consisting of a PVC opaque cylinder (diam. = 16

cm; h = 30 cm) placed inside a larger opaque one (diam. = 20 cm; h = 30 cm). Both cylinders were filled with defaunated mud (see above) and put in a thermoregulated room at 13°C under a weak open seawater circulation. Test animals were added to the inner cylinder. A circular window (approx. 822 cm^2, 23 cm high) was cut out of the inner core and covered with a 1-mm mesh nylon net, allowing only *N. diversicolor* juveniles to escape and reach the protected area, because *N. hombergii* individuals were too large to pass through the net. The tops of the tubes were covered with a 0.2-mm mesh nylon net to prevent animals from escaping. All treatments had 150 *N. diversicolor* and 0D (controls) had 0 *N. hombergii*, 1D had two *N. hombergii* and 3D had six *N. hombergii*. Each treatment was replicated 3×. Recruits (≈24 setigers) and predators in 1D and 3D enclosures, respectively, corresponded to densities of 8500, 114 and 342 ind. m^{-2}). After 1 month experimental period (May to June), sediment from both tubes was sieved using 0.2-mm mesh and organisms were fixed with 4.5% formalin.

Prior to one-way ANOVA and multiple comparison tests (Tukey Kramer), data were transformed using the function arcsin $\sqrt{x}$ to assess the homogeneity of variances tested by a Cochran test.

3. Results

3.1. Field experiment

Densities of *N. diversicolor* and *N. hombergii* adults were, at the beginning of March, 55 and 85 ind. m^{-2}, respectively, on our study area. During the experiment, all predators remained alive in each treatment, except lot 3D of 9 May which contained three, four, and five individuals. A significant predator activity×time interaction affects the surviving number of juveniles (log(x) transformation), preventing a separate evaluation of the main effects (Table 1a). The one-way ANOVA indicates that, 3 weeks after the beginning of the experiment (7 March), the addition of *N. hombergii* caused a significant decrease in the number of juveniles: 80.0±36.9 (29%) and 69.7±7.8 (25%) prey were alive in 1D and 3D enclosures compared to 257.0±7.8 (93%) in controls (Table 2a). Gut content analyses revealed the presence of *N. diversicolor* setae, confirming their ingestion. Tukey Kramer tests showed that 1D and 3D treatments became significantly

Table 1
Results of two-way ANOVA used to test for time and density treatment effects on (a) the number of surviving *N. diversicolor* juveniles (log(x) transformation), (b) the reduction of dry biomass per enclosure and (c) the individual weight of *N. diversicolor*

Source of variation	(a)			(b)			(c)		
	df	MS	F value	df	MS	F value	df	MS	F value
Total	26	1.728		26	7833.60		26		
Predator	2	13.475	114.195***	2	33230.19	167.485***	2	0.408	33.719***
Time	2	5.073	42.991***	2	47100.22	237.392***	2	3.042	251.405***
Predator×time	4	1.429	12.110***	4	9860.38	49.698***	4	0.294	24.298***
Error	18	0.118		18	198.41		18	0.012	

Significance levels are indicated (ns, $P \geq 0.05$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

Table 2
Effect of the predator abundance on (a) the number of surviving juveniles (log(x) transformation), (b) the dry biomass reduction per enclosure and (c) the mean individual weight of *N. diversicolor*

Treatment	Mean±SD	*N*	Statistical comparison			ANOVA (df)
(a) Number of juveniles						
28 March						
0D	257.00±7.789	3	0D	1D	3D	$F=10.767$ (2, 6)
1D	80.00±36.851	3				$P=0.0103$*
3D	69.67±7.760	3				
18 April						
0D	243.33±4.03	3	0D	3D	1D	$F=60.555$ (2, 6)
1D	34.33±5.91	3				$P=0.000105$***
3D	49.67±12.47	3				
09 May						
0D	215.67±9.53	3	0D	1D	3D	$F=81.219$ (2, 6)
1D	17.00±7.79	3				$P=0.000045$***
3D	5.00±0.82	3				
(b) Dry biomass reduction						
28 March						
0D	2.507±0.903	3	0D	3D	1D	$F=29.533$ (2, 6)
1D	27.183±5.928	3				$P=0.000784$***
3D	25.450±1.606	3				
18 April						
0D	9.600±1.993	3	0D	3D	1D	$F=45.182$ (2, 6)
1D	110.027±5.985	3				$P=0.00024$***
3D	82.357±17.819	3				
09 May						
0D	24.540±4.416	3	0D	1D	3D	$F=111.527$ (2, 6)
1D	199.693±20.060	3				$P=0.000018$***
3D	258.063±19.305	3				
(c) Individual weight						
28 March						
0D	0.234±0.054		0D	3D	1D	
1D	0.222±0.052					$F=0.780$ (2, 6)
3D	0.191±0.010					
18 April						
0D	0.543±0.054	3	0D	3D	1D	$F=8.784$ (2, 6)
1D	0.857±0.027	3				$P=0.0165$*
3D	0.668±0.116	3				
09 May						
0D	0.768±0.016	3	0D	1D	3D	$F=35.501$ (2, 6)
1D	1.494±0.176	3				$P=0.0005$***
3D	1.855±0.144	3				

Significance levels of ANOVAs are indicated (ns, $P\geq0.05$; *$P<0.05$; **$P<0.01$; ***$P<0.001$). Horizontal lines link treatment groups that are statistically equivalent using the Tukey Kramer multiple comparisons test ($\alpha=0.05$). N = number of observations.

Table 3
Dry biomass reduction per *N. hombergii* at different predator density (1D, 3D) and comparison with Student's *t*-test

Date	1D	3D	t_c value	Level of significance
28 March	13.593±3.631	4.243±0.326	4.442	$P=0.011$*
18 April	55.013±3.661	13.727±3.636	13.861	$P=0.000079$***
09 May	99.847±12.284	64.500±12.156	3.347	$P=0.029$*

Levels of significance are indicated (ns, $P\geq0.05$; *$P<0.05$; **$P<0.01$; ***$P<0.001$).

different between each other after 9 weeks of experiments (Table 2a). As above, the effect of the interaction predatory activity×time was significant on dry weight reduction of prey (Table 1b). From 28 March to the 9 May, in the presence of predators, values of dry biomass eliminated per enclosure were 8–12× greater than those observed in controls (Table 2b). Biomass reductions observed in 1D and 3D enclosures remained similar at 3 and 6 weeks, and became different after 9 weeks. Values of prey dry weight, calculated on final numbers of *N. hombergii*, show that each predator of the 1D enclosures eliminated between 1.5 and 4× more prey than did individual predators in 3D enclosures (Table 3).

On the mudflat, top sediment (4 cm) and surface seawater temperatures, which varied, respectively, from February to May, between 6.3 and 17.2°C, and between 5.5 and 16.0°C, were strongly correlated ($r_s=0.9041$). Thus, we used the seawater temperature to evaluate resumption of predation by *N. hombergii*. Reduction of prey dry weight due to predatory activity varied with temperature (Fig. 1). At a density of 114 ind. m^{-2} (1D) at temperatures from 6 to 9°C (between 7 and 28 March), one *N. hombergii* eliminated a biomass of 13.6 mg of juvenile dry weight. From 28 March to 18 April, the temperature increase did not exceed 2°C, but this value was for 41.3 mg. Finally, after 18 April, in spite of a temperature increase of 5°C, biomass reduction remained steady at around 45.0

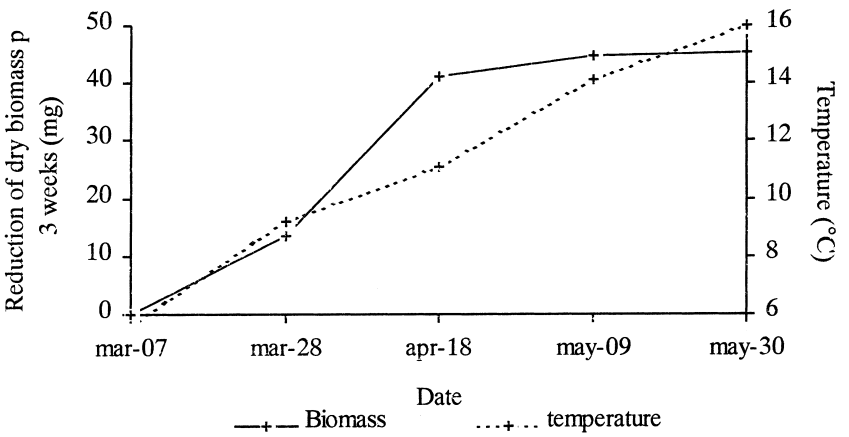

Fig. 1. Mean values of dry biomass of *N. diversicolor* juveniles eliminated per 3 weeks, in 1D enclosures (114 ind. m^{-2}), in relation to the spring rise in seawater temperature.

mg. All these results suggest that predation intensity clearly increases at seawater temperatures ranging from 9 to 11°C. These estimations, although confounded by the changing prey densities during the experiment, take into account the growth of recruits. From this point of view, there were significant predatory activity×time interaction effects on juvenile individual dry weight values (Table 1c). One-way ANOVAs demonstrated significant differences between control and predator inclusion treatments (Table 2c). Although effects of predatory activity became significantly more pronounced with time, they remained significantly independent of predator densities.

3.2. Laboratory experiments

3.2.1. Influence of temperature variations on predatory activity

During the experiment, only one *N. hombergii* from lot E died. Juvenile mortality and dry biomass reduction values were significantly different in *N. hombergii* addition treatments compared with control treatments (Tables 4 and 5). In terms of mortality rates, the effects induced by predators exposed to a gradual increase in temperature were not significantly different from those observed with individuals exposed to a thermal shock, at both temperatures (lots B and D not significantly different, lots C and E not significantly different, Table 4). In spite of an abnormally high mortality rate of juveniles in 18°C control enclosures, no major difference between A, B, D, C and E treatments was observed. In terms of biomass reduction, multiple comparison tests, which individualized three groups of significantly different treatments: C_{field}–C_{13}, A–D–C_{18}–B and C–E, suggest that temperature increase mode did not influence the

Table 4
Effects of temperature changes on the mortality rate of *N. diversicolor* juveniles

Treatment	Mortality rate±SD	*N*
Field temperature		
Control	0.150±0.040	5
Field (A)	0.658±0.094	5
13°C		
Control	0.158±0.078	5
Gradual increase (B)	0.864±0.039	5
Rapid increase (D)	0.726±0.150	5
18°C		
Control	0.464±0.063	5
Gradual increase (C)	0.918±0.007	5
Rapid increase (E)	0.885±0.062	4
Statistical comparison		Kruskall–Wallis
	$\underline{C_{field}\ C_{13}\ C_{18}\ A\ D\ B\ E\ C}$	$H_c = 41.982 P < 10^{-6}$***

Horizontal lines link treatment groups that are statistically equivalent using the Tukey Kramer multiple comparisons test ($\alpha = 0.05$). Control field (C_{field}), field increase in temperature. Control 13°C (C_{13}), constant temperature of 13°C. Control 18°C (C_{18}), constant temperature of 18°C. Lot A, field increase in temperature. Lot B, gradual increase in temperature from 9 to 13°C. Lot C, gradual increase in temperature from 9 to 18°C. Lot D, thermal shock from 9 to 13°C. Lot E, thermal shock from 9 to 18°C. *N* = number of observations.

Table 5
Effect of temperature changes on the dry biomass reduction of *N. diversicolor* juveniles

Treatment	Mean biomass reduction±SD	*N*
Field temperature		
Control	3.922±0.832	5
Field (A)	13.344±1.770	5
13°C		
Control	4.078±1.906	5
Gradual increase (B)	15.560±1.119	5
Rapid increase (D)	13.606±1.710	5
18°C		
Control	13.744±2.135	5
Gradual increase (C)	19.954±1.927	5
Rapid increase (E)	20.022±1.967	4
Statistical comparison		ANOVA (df)
	$\underline{C_{field}\ C_{13}\ A\ D\ C_{18}\ B\ C\ E}$	$F=49.526$ (7, 31)
		$P<10^{-6}$***

Horizontal lines link treatment groups that are statistically equivalent using the Tukey Kramer multiple comparisons test ($\alpha=0.05$). Control field (C_{field}), field increase in temperature. Control 13°C (C_{13}), constant temperature of 13°C. Control 18°C (C_{18}), constant temperature of 18°C. Lot A, field increase in temperature. Lot B, gradual increase in temperature from 9 to 13°C. Lot C, gradual increase in temperature from 9 to 18°C. Lot D, thermal shock from 9 to 13°C. Lot E, thermal shock from 9 to 18°C. *N*=number of observations.

predatory activity (Table 5). Linkage between 18°C control and A, D, and B treatments seems artificial and only due to the high 'natural' mortality of juveniles observed at 18°C. Thus, if we substract values of 13 and 18°C controls from those observed in, respectively, B, D and C, E treatments, it appears that dry juvenile biomass eliminated by *N. hombergii* varied between 9.5 and 11.4 mg at 13°C and between 6.2 and 6.3 mg at 18°C.

3.2.2. Influence of predator presence on the mobility of recruits

Emigration was significantly increased in the presence of predators (Table 6): 10.4, 18.0 and 26.5% of recruits left the central enclosures when none, two, and six *N. hombergii* were added, respectively. We could not assess whether emigration occurred by crawling at the surface within the sediment, or by swimming in the water column.

Table 6
Effect of the predator on the emigration rate of *N. diversicolor* juveniles

Treatment	Mean emigration rate±SD	*N*	Statistical comparison			ANOVA (df)
0D	0.104±0.011	3				$F=114.263$ (2, 6)
1D	0.180±0.014	3	0D	1D	3D	$P=0.000017$***
3D	0.265±0.014	3				

Horizontal lines link treatment groups that are statistically equivalent using the Tukey Kramer multiple comparisons test. *N*=number of observations.

4. Discussion

Infaunal predators often act as an intermediate link between higher epibenthic predators (avifauna, piscifauna and mobile epifauna) and the nonpredatory infauna (Commito, 1982; Ambrose, 1984c) or meiofauna (Clavier, 1981). They may also become main predators or cause significant perturbations when other forms of biotic control are rare or absent (Ambrose, 1984a,b; Commito and Ambrose, 1985).

Our experimental results support the hypothesis that infaunal predation is a structuring force in soft-bottom communities and can regulate populations of recruits. In our field experiments, the addition of *N. hombergii* caused the mortality of almost all *N. diversicolor* juveniles during the first 9 weeks. The use of inclusion cages to study predatory–prey interactions is a crude method. The technique used to treat the sediment would cause a major change of its characteristics and influence the animal responses (Hulberg and Oliver, 1980): the defaunation restricts the dietary choices of the implanted *N. hombergii* depriving them of the normal range of prey items as well as any effect of changes to the organic carbon content of the sediments. However, this device remains one of the well-adapted techniques for studying interactions between a few number of species in the field.

At our study site, the predatory activity was minimal but measurable at a temperature of 7°C, increased at temperatures between 9 and 11°C, and then became constant. Predation by *N. hombergii* resumes at temperatures close to 10°C. More generally, *N. hombergii* is physiologically active in spring and summer, when almost all macrobenthic species recruit to the bottom. According to our experiment, *N. hombergii* eliminated biomass values significantly more highly at 18 than at 13°C, thus independently of the mode of temperature increase. However, despite an abnormally high mortality of prey in 18°C control enclosures, mortality rates observed in predator addition treatments at 13 and 18°C remained similar. Such a result means that *N. hombergii* eliminated fewer prey at 18°C. As shown by Scaps et al. (1993), such a high mortality rate in our 18°C treatments could be the consequence of a stress suffered by these sets of juveniles during their rearing stage. These authors and Marty (1997) also showed that growth of juveniles of *N. diversicolor* was more important at 18 than at 13°C. Consequently, the fact that juveniles killed by predators in 18°C treatments were larger than at 13°C was responsible for differences of comparison test results concerning mortality rates or biomass reduction values. Although the reduced predation efficiency at 18°C could also be attributable to the low number of available prey, our correction calculations of biomass indicate that the influence of temperature fluctuations, in the range of 11 to 18°C, on the predatory activity would be minimal.

In the field, high densities of predators significantly reduced their individual effects on *N. diversicolor* mortality. At a density of 342 ind. m^{-2}, one *N. hombergii* eliminated 1.5–4× fewer *N. diversicolor* recruits than at a density of 114 ind. m^{-2}. The reason for this decrease in predation rates may be related to the randomness of their movement which may result in interference with conspecifics and even mortality. Beyond the global biomass of prey decrease, predation, by limiting intra-specific relationships, could allow the increase of the individual dry weight of *N. diversicolor* juveniles. Such a hypothesis is confirmed by the results of Marty (1997) which show, in the laboratory, that growth of *N. diversicolor* juveniles was in inverse proportion to their density.

We observed in narrow aquaria, that *N. hombergii* essentially moves in the surface layers of the sediment, where young *N. diversicolor* and, more generally, newly settled recruits are present. Indeed, populations of *N. hombergii* are mainly distributed within the top 5 cm of sediment (Clavier, 1981). From this point of view, the information on the effects of bioturbation is often contradictory. Some species (e.g. *Macoma balthica* (L.) post-larvae) needed to be buried up to 8–10 days before increased mortality became evident (Elmgren et al., 1986), thus suggesting that effects of bioturbation in our study were minor compared to those of direct predation. Crowe et al. (1987) reported that disturbance caused by *Amphiura filiformis* (O.F. Müller) had a little negative effect and that the inhibition of the recruitment of most taxa was due to the ingestion of settlers and newly settled juveniles. On the contrary, Brenchley (1981) and Wilson (1981) considered it as an important factor inhibiting survival of recruits; these effects are, however, often difficult to separate from those induced by predation (Rhoads and Young, 1970; Wiltse, 1980; Ambrose, 1984d; Le Calvez, 1986; Posey, 1987; Rönn et al., 1988). Recently, Watzin (1986) demonstrated that permanent meiofaunal predators and disturbers (notably Turbellarians) were also a significant source of mortality for newly settled macrofaunal juveniles.

Our experiments suggest that the destruction of prey burrows induced by the movements of predators may have caused both mortality and emigration of prey recruits: young *N. diversicolor* actively moved away from disturbed areas. They clearly show a positive relationship between the intensity of the escape behaviour and the predation risk, as measured by predator density. However, we probably underestimate potential emigration rates because of the gradual reduction of the prey abundance, and in turn the number of inter-individual interactions, in the test cylinders during the experiment. The route used by the recruits leaving the area exposed to predation (within the sediment, or crawling at the sediment/water interface, or swimming) remains undetermined. The response observed for the recruits differs from that commonly observed for adults of *N. diversicolor*, which reacted by withdrawing into their burrows in the presence of predators (Esselink and Swarts, 1989). Thiel and Reise (1993) described a similar response for adults which are able, during periods of migration to new sites, to prolong their swimming time to avoid tidal flats where large numbers of nemertines (*Lineus viridis*) live. By quantifying the importance of prey emigration in predator/prey interactions in relation to predation risk, our results support the hypothesis of Ambrose (1984c) that the reduction of infauna in predation inclusion experiments may be due to prey emigration as well as direct predation. In a macrotidal regime, a local process such as predation could induce emigration over relatively large distances. Conversely, the settling of drifters could potentially have an effect on predator/prey interaction.

According to Warwick and Price (1975), Price and Warwick (1980) and Oyenekan (1986), *N. hombergii* is the main secondary producer of the *M. balthica* community of British estuaries. From field experiments on tidal flats of Königsafen (Wadden Sea), Schubert and Reise (1986) showed that *N. hombergii* caused a significant decline in polychaetes, notably *S. armiger* and *H. filiformis*. Annual consumption per medium-size *N. hombergii* varied from 300 to 700 mg AFDW. Without neglecting, firstly, that the lack of prey choice in our experiment can induce an over-estimation and, secondly, that field experimental densities of predator (114 and 342 ind. m^{-2}) employed were both higher than the natural field density (85 ind. m^{-2}), our field results indicated that one *N.*

hombergii individual (density of 114 ind. m^{-2}) reduced the biomass value by 100 mg dry weight of *N. diversicolor* juveniles (roughly its own weight) in 9 weeks, 8–12× more than in predator removal treatment. This underlines the impact of infaunal predation on populations of recruits. Since seawater temperature is above 9°C from March to December, the biomass reduction per year and adult of *N. hombergii* would be roughly in the order of 500 mg of dry weight.

Our study confirms results of previous works on the effects of predatory infauna on recruitment. Considering that early post-settlement mortality influences the distribution and abundance of adults, infaunal predators could contribute significantly to the structuring of infaunal communities. These considerations underline the necessity of considering the early post-larvae and juvenile survival in elaboration of life history models.

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