

Predatory effects of *Nephtys hombergii* on other polychaetes in tidal flat sediments

Andreas Schubert & Karsten Reise

II. Zoologisches Institut der Universität Göttingen, D-3400 Göttingen, Federal Republic of Germany
and

Biologische Anstalt Helgoland, Litoralstation, D-2282 List, Federal Republic of Germany

ABSTRACT: On tidal flats near the island of Sylt in the North Sea the endobenthic polychaete *Nephtys hombergii* (Savigny 1818) was added to enclosures. This caused a significant decline in other polychaetes, notably the deposit-feeders *Scoloplos armiger* (O. F. Müller) and *Heteromastus filiformis* (Claparede). These 2 were also the main prey components inside the guts of *N. hombergii*. Occasionally, other predatory polychaetes were eaten and the amount of nematodes ingested increased with decreasing size of *N. hombergii*. Total prey consumption is estimated to be above $1 \text{ g C m}^{-2} \text{ yr}^{-1}$ or at least one tenth of the consumption of all epibenthic predators together. Cages protecting *N. hombergii* from fish and birds caused its abundance to be elevated. The experiments suggest that *N. hombergii* is an important intermediate predator in the Wadden Sea.

INTRODUCTION

The structuring by predation of faunal assemblages in marine mud and sand is now a well-recognized phenomenon (Peterson 1979, Woodin 1983, Reise 1985a). Predator-exclusion experiments have repeatedly demonstrated strong effects of epibenthic predators on their endobenthic prey. Within the latter, however, there is additional internal predation composed of several trophic levels (Commito & Ambrose 1985a, b). In a recent study, Commito & Shrader (1985) report adding the predacious polychaete *Nereis virens* to enclosures, with the expectation of a decrease in other infaunal densities. Instead, there was a 2- to 6-fold increase. To explain this paradox, they speculated that *N. virens* preyed on an intermediate predator, the polychaete *Nephtys incisa*, thus allowing other infauna to increase.

In this study, we added *Nephtys hombergii* to field enclosures designed to evaluate its ability to reduce infaunal densities. *N. hombergii* has long been known to be a carnivore (Blegvad 1914, Clark 1962). Warwick et al. (1979), however, suspect that *N. hombergii* feeds to a considerable extent on microalgae. This may also be assumed indirectly from a study by McGrorty & Reading (1984), who found *N. hombergii* to be an abundant primary colonizer in burrow pits apparently

devoid of any other macrofauna. Here we provide evidence that adult *N. hombergii* significantly reduce the abundance of other polychaetes which serve as their principal prey. *N. hombergii* itself is susceptible to epibenthic predation.

MATERIALS AND METHODS

Study site. This investigation was conducted on tidal flats of Königshafen, a sheltered bay near the island of Sylt in the northern Wadden Sea. Physical conditions and biota are described in Wohlenberg (1937) and Reise (1985b). Tides are semidiurnal and the range is 1.8 m. Our experiments were located at 0.4 m above mean low tide level, with submersion of ca 8 h per tidal cycle. During the experiments (July to October 1984), water temperatures ranged from 13 to 20 °C, and salinity remained close to 30 ‰. Sediments are relatively coarse-grained (median 0.55 mm) with a decrease in particle size towards the low water line, and with a variable amount of shell gravel. Mussel beds were nearby and accumulated mud on their leeward sides.

The macrofauna of the more sandy sites was dominated by the orbinid polychaete *Scoloplos armiger* (hereafter referred to as *Scoloplos* assemblage), and closer to the mussel beds by the capitellid polychaete

Heteromastus filiformis (*Heteromastus* assemblage). Both *Nephtys hombergii* and *N. caeca* (Fabricius) are abundant in the area. However, the latter is almost entirely confined to the subtidal sediments, and in the following we only deal with *N. hombergii* (hereafter referred to as *Nephtys*) in the intertidal zone.

Gut content analysis and prey-choice experiments.

Nephtys were individually fixed in ethanol (70 %) within 30 min after collection. The fixation caused some specimen to evert their pharynx, though regurgitation of recently swallowed food was not observed. Body length and volume was recorded. Individuals were cut in the mid-body region and gut content was squeezed out for microscopic analysis. Prey organisms were identified by undigestible parts, such as polychaete setae, amphipod and nematode cuticles.

Prey-choice experiments were conducted in the laboratory with *Nephtys* in sieved sand and polychaete prey added to the containers. These were closed with a 0.125 mm mesh and kept for 6 d under running seawater. Subsequently, polychaetes were counted and *Nephtys* was subjected to gut analysis.

Enclosure experiments. Bottomless buckets of 30 cm diameter (0.07 m²) were pressed 25 cm into the natural sediment, flush with the ambient surface. To some buckets *Nephtys* was added while the others served as controls (see Ambrose 1984a). Buckets were arranged in a regular grid with treatments and controls alternating. Sediment from each bucket was sieved with a 1 mm mesh and the retained macrofauna was identified and counted. Abundances are compared with a non-parametric U-test after Wilcoxon & Whitney (Sachs 1984).

Enclosure Experiment 1. This experiment lasted 10 d. Twenty-one buckets were pressed into the sediment of the *Scoloplos* assemblage. Seven received 16 small *Nephtys* (<100 mm or 0.8 cm³, average 60 mm or 0.4 cm³) each, another 7 received 6 large *Nephtys* (>100 mm or 0.8 cm³, average 120 mm or 1.1 cm³) each and the remaining 7 buckets served as controls without *Nephtys* added. The numbers of added small and large *Nephtys* were chosen to give an equal amount of biomass: the weight of 2.7 small *Nephtys* corresponds to the weight of 1 large *Nephtys*. All buckets were covered with a 1 mm mesh gauze. The addition of 16 small *Nephtys* resulted in a 7-fold increase relative to control buckets. No large *Nephtys* were present in the control buckets and altogether 5 were found in the treatment with small *Nephtys*. Thus the addition of 6 large *Nephtys* per bucket constituted at least an 8-fold increase in the abundance of large *Nephtys*. At the end of the experiment, a total of 115 small and 40 large *Nephtys* were found in their respective treatments. This indicates that almost all added individuals remained inside and survived.

From each bucket 3 cores of 1 cm²/0 to 5 cm were taken. In the laboratory seawater was added, the sample agitated and the supernatant repeatedly poured through a 0.08 mm sieve. Meiofauna was identified to major taxon and counted. For comparisons all 3 samples per bucket were pooled. Three cores of 10 cm²/0 to 15 cm from each bucket were treated similarly but washed through a 0.25 mm sieve. Small macrofauna was identified and counted. The remaining sediment was sieved for large macrofauna (>1 mm).

Enclosure Experiment 2. Duration of this experiment was 43 d. Twelve buckets were pressed into the sediment of the *Scoloplos* assemblage, and 5 large *Nephtys* (as defined above) were added to each of 6 buckets. The other buckets served as controls. Buckets were covered with a 1 mm mesh. At the end of the experiment a total of 23 large *Nephtys* were found in the treatments. Thus possibly 7 individuals were lost. Abundance constituted approximately a 10-fold increase relative to natural density. Adjacent to the experimental grid, 6 samples equal in size to the buckets were taken to test for bucket artifacts.

Enclosure Experiment 3. Twenty buckets were pressed into the sediment of the *Heteromastus* assemblage and every other bucket received 1 additional large *Nephtys* (see above). The buckets remained 58 d in the sediment and were not covered with gauze. A preliminary test with such topless buckets revealed that *Nephtys* remained inside even when confined at high densities. To test whether other macrofaunal densities were a function of *Nephtys* abundance or biomass within the buckets, Spearman's rank correlation coefficients were calculated (Sachs 1984).

Exclusion of large epibenthic predators. Twelve tin frames of 50 × 50 cm were pressed 20 cm into the sediment of the *Scoloplos* assemblage, almost flush with the surface. Ten large *Nephtys* (see above) were added to each, and 6 frames were covered with chicken wire (30 mm meshes) to protect the enclosed fauna from large predators such as crabs (*Carcinus maenas* L.), flatfish and birds. After 60 d the sediment of the topless frames and of the cages was excavated and *Nephtys* were collected by hand.

RESULTS

Abundance and biomass of *Nephtys hombergii* and its prey

Natural density of *Nephtys* was up to 15 ind m⁻² with a corresponding biomass of 1.1 g ash-free dry weight m⁻². To estimate average abundance, 58 m² were dug up with a fork and *Nephtys* was collected by hand. A mean of 5.2 ± 4.5 m⁻² corresponding to 0.36

$\pm 0.3 \text{ g m}^{-2}$ was obtained. Length and weight of the largest individual was 190 mm and 290 mg respectively. On average, length was $64 \pm 23 \text{ mm}$ and weight was $69 \pm 47 \text{ mg}$ per individual.

To estimate macrofaunal abundance in the study area, 40 core samples of $0.07 \text{ m}^2/0$ to 25 cm were sieved through a 1 mm mesh. A mean of $1400 \pm 700 \text{ m}^{-2}$ was obtained. In the *Scoloplos* assemblage, *S. armiger* comprised 600 m^{-2} or 45 % of total macrofauna. Other abundant species were the polychaete *Lanice conchilega* (Pallas) and the amphipod *Corophium arenarium* Crawford. In the *Heteromastus* assemblage, *H. filiformis* comprised 800 m^{-2} or 43 % of the total. Other abundant species were the polychaete *Tharyx marioni* (Saint-Joseph) and the oligochaete *Tubificoides benedeni* (D'Udekem).

Less abundant species present in both assemblages were the polychaetes *Nereis virens* (Sars) and *N. diversicolor* (O. F. Müller), *Eteone longa* (Fabricius) and *Anaitides mucosa* (Oberstedt), all of which are predators on the infauna, just as *Nephtys*. This also applies to the nemertines *Lineus viridis* Johnston and *Amphiporus lactifloreus* (Johnston). The lugworm *Arenicola marina* (L.) was present with very large, deep dwelling individuals. Common bivalves found were *Mytilus edulis* (L.), *Cerastoderma edule* (L.), *Macoma balthica* (L.), *Mya arenaria* (L.) and *Ensis directus* (Conrad).

Gut contents and choices of prey

Out of 218 *Nephtys* investigated the guts of 145 (67 %) were empty, i.e. without animal prey or any other potential food particles. In the *Scoloplos* assemblage 19 % (27 individuals) contained remains of *S. armiger*, 8 % (11) of *Heteromastus filiformis* and 3 % (4) of nematodes in their guts, while 70 % (99) were empty. In one case, a *Corophium arenarium* and a proseriate plathelminth was found. In the *Heteromastus* assemblage, 23 % (18 individuals) contained remains of *H. filiformis*, 10 % (8) of nematodes, 6 % (5) of *S. armiger* and the gut was empty in 60 % (46) of the cases.

Nematodes were relatively frequent in the smallest *Nephtys* analysed, while the larger ones contained little other than remains of *Scoloplos armiger* and *Heteromastus filiformis* in their guts (Fig. 1). Because of their small size, nematodes do not seem to constitute a major prey, even in the smaller *Nephtys*. In 2 cases it appeared that nematodes were inside the intestines of a swallowed *H. filiformis*. We found also one case where *Nephtys* had swallowed the phyllodocid *Eteone longa* which in turn had swallowed the spionid *Pygospio elegans* (Claparede).

Prey-choice experiments in the laboratory revealed that *Scoloplos armiger*, *Heteromastus filiformis* and *Anaitides mucosa* were eaten by *Nephtys*. *S. armiger* often remained alive, but the tail ends were missing when kept together with *Nephtys*. This suggests tail-cropping by *Nephtys* rather than ingestion of entire prey individuals when these are fairly large. *A. mucosa* evidently was eaten; however, no setae of this species were ever found in the guts of *Nephtys*.

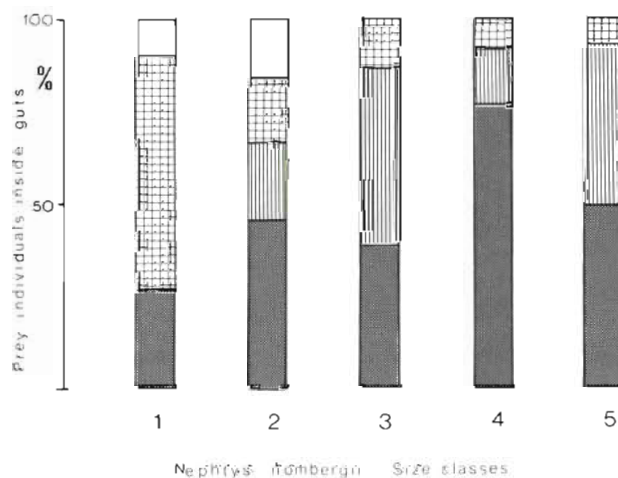


Fig. 1. *Nephtys hombergii* Percentage of prey individuals (dark: *Scoloplos armiger*, striated: *Heteromastus filiformis*, squared: nematodes; white: others) found in the guts of 73 *Nephtys* of the following size classes: 1 (<20 mg); 2 (20 to 45 mg); 3 (45 to 70 mg); 4 (70 to 95 mg) and 5 (>95 mg) in terms of ash-free dry weight

Enclosure experiments

The enclosure of small and large *Nephtys* in the *Scoloplos* assemblage over a period of 10 d caused a significant decline in the densities of *S. armiger* and *Anaitides mucosa* (Fig. 2). A decrease in total macrofauna abundance was significant only with small *Nephtys* added to the enclosures. However, the relative composition of the macrofauna was changed markedly, regardless of whether small or large *Nephtys* were added. No significant effects of the *Nephtys* addition could be found for the small macrofauna (<0.25 mm) which was dominated by the 0-groups of cockles and *S. armiger*. Neither were there any significant treatment effects detectable on meiofauna (<0.08 mm) which was entirely dominated by nematodes (75 % of abundance).

The second enclosure experiment in the *Scoloplos* assemblage lasted considerably longer (43 d), and only large *Nephtys* were added. Compared to control buckets macrofaunal density declined significantly in the presence of *Nephtys* (Table 1). This time, *S.*

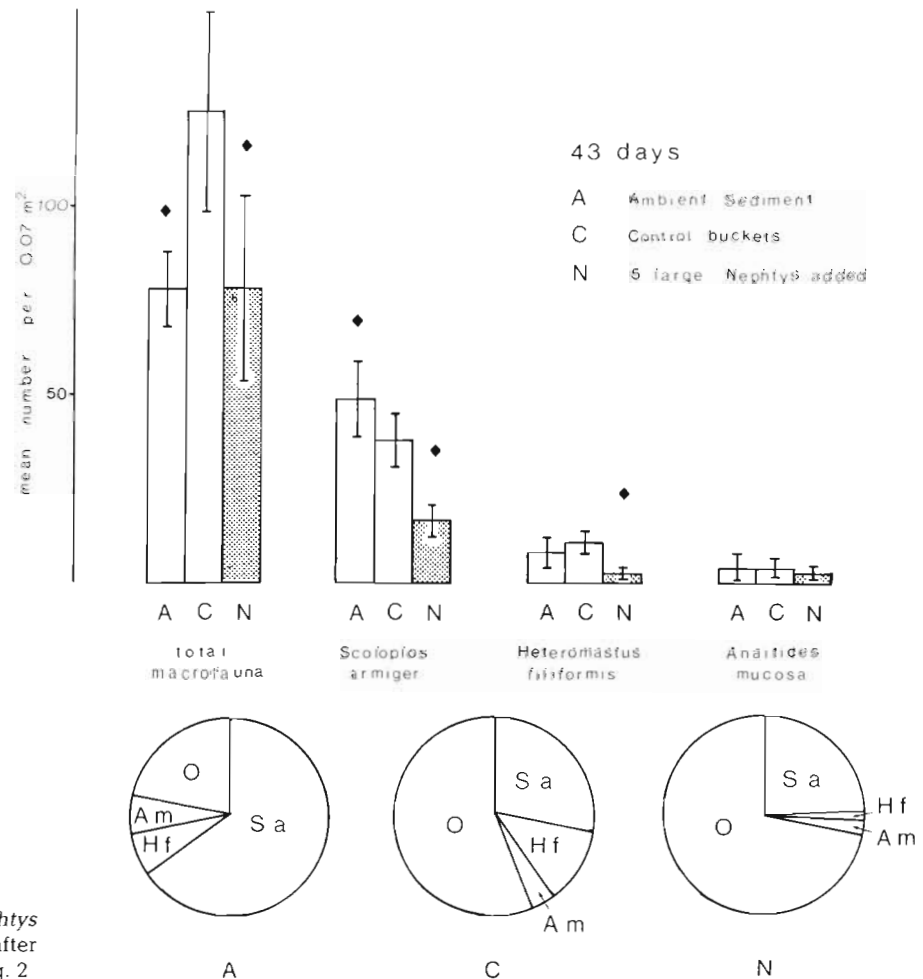


Fig. 3. Effects of enclosed large *Nephtys hombergii* on other macrofauna after 43 d. For further explanation see Fig. 2

armiger and *Heteromastus filiformis* showed significant treatment effects while *Anaitides mucosa* did not (Fig. 3). The comparison with ambient sediment revealed bucket artifacts. Macrofauna was significantly more abundant inside control buckets, mainly because of high immigration rates by early settling stages of *Nereis diversicolor* and the crab *Carcinus maenas*. Both were also highly abundant in the *Nephtys* treatment. *Nephtys* obviously did not prey on these juveniles. Another bucket artifact is a significantly decreased density of *S. armiger*, possibly caused by altered sediment properties.

The third enclosure experiment was done in the *Heteromastus* assemblage. One large *Nephtys* was added to each of 10 buckets out of 20. This time artifacts were avoided because the buckets were not covered with gauze. This addition treatment remained within the natural variability of *Nephtys* abundance. After 58 d a range of 0 to 4 *Nephtys* were found per bucket, and the addition treatment did not result in a consistently elevated density. Assuming that the abundance of *Nephtys* within buckets at the end of

experiment corresponds with predation pressure inside these buckets, a correlation analysis was conducted. Spearman rank correlations indicate negative

Table 2. Linear regressions and Spearman's rank correlation coefficients (r_s) for *Nephtys* abundance (NA) and biomass (NB) and macrofaunal prey abundance (y), calculated from buckets in the *Heteromastus* assemblage, 10 of which had received 1 additional large *Nephtys* 58 d before. $y = a + bx$ where $x = NA$ or NB ; $a, b =$ coefficients. * $p < 0.05$; ** $p < 0.01$ for r_s

x ; y	a	b	r_s
NA ; total macrofauna	124.8	-15.1	-0.470*
NB ; total macrofauna	120.5	-0.95	-0.405*
NA ; <i>Scoloplos</i>	33.8	-3.50	-0.249
NB ; <i>Scoloplos</i>	36.7	-0.39	-0.517*
NA ; <i>Scoloplos</i> biomass	0.3	-2.81	-0.112
NB ; <i>Scoloplos</i> biomass	0.42	-0.56	-0.494*
NA ; <i>Heteromastus</i>	52.8	-10.7	-0.425*
NB ; <i>Heteromastus</i>	51.9	-0.76	-0.523**
NA ; <i>Scoloplos</i> & <i>Heteromastus</i>	86.6	-14.2	-0.564**
NB ; <i>Scoloplos</i> & <i>Heteromastus</i>	88.6	-1.15	-0.582**
NA ; other macrofauna	38.2	-0.87	-0.102
NB ; other macrofauna	31.9	0.20	0.143

effects of *Nephtys* abundance and *Nephtys* biomass on the densities of *Scoloplos armiger* and *H. filiformis* but not on other macrofauna (Table 2).

Epibenthic predation on *Nephtys*

Cages covered with 30 mm chicken wire retained significantly more individuals of *Nephtys* than the topless cages (8.5 ± 1.5 versus 5.7 ± 1.3 ; U-Test: $p < 0.05$). This corresponds to a decrease of 33 % in *Nephtys* abundance within 60 d, attributable to large epibenthic predators. The decrease in biomass was in the same range, but not significant (0.8 ± 0.2 versus 0.5 ± 0.2 g).

DISCUSSION

Our field experiments demonstrate that the endobenthic *Nephtys hombergii* does affect the density of other endobenthic macrofauna, while it is itself prey to large epibenthic predators. Gut content analysis confirmed that the investigated *Nephtys* are carnivores that prey mainly on other polychaetes.

Artifacts of field experiments

Our field experiments were not free of artifacts. Pressing buckets into the sediment injures or kills infauna. This attracts *Anaitides mucosa* which is a carnivorous scavenger (see also Reise 1979a, b). In the first experiment, with a duration of only 10 d, *A. mucosa* was 6 times more abundant in control buckets ($25 [9]$ ind 0.07 m^{-2}) than in the ambient sediment ($4 [2]$ ind 0.07 m^{-2}). In the buckets with *Nephtys* added, *A. mucosa* was either eaten or scared away. This disturbance effect does not last very long, however, because all carrion is consumed or has decayed (after 3 to 4 wk according to M. Hüttel unpubl.). Therefore, no elevated density of *A. mucosa* was observable at the end of the second experiment which lasted 43 d.

An immigration of 0-group *Nereis diversicolor* and *Carcinus maenas* occurred in treatments and controls alike. This event did not affect the experiment because neither was prey for *Nephtys*. In the 10 d experiment, almost all *Nephtys* survived. Enclosure over 43 d caused a loss of about 20 %.

Diet of *Nephtys*

Enclosure experiments and gut content analysis revealed that *Nephtys* preyed on the polychaetes *Scoloplos armiger*, *Heteromastus filiformis*, *Anaitides mucosa*, *Eteone longa*, on nematodes, a plathelminth

and the amphipod *Corophium arenarium*. Ivlev-indices of prey selectivity are all positive for the polychaetes, both when gut content is compared to abundance in the sediment and when the difference between *Nephtys* enclosures and control buckets is considered. In a laboratory feeding experiment, *Nephtys* swallowed *H. filiformis* whole, while the larger *S. armiger* mainly sacrificed their tail ends (in one case the front end) to the predator. Gibbs (1968) observed that female *S. armiger*, regenerating a major portion of their body, contained only small immature oocytes just before the breeding season. Thus, tail-cropping will not only affect body-size but also fecundity in the prey population.

Small macrofauna and meiofauna do not seem to constitute a major component in the diet of adult *Nephtys* at Sylt (see also Reise 1979b). Only the smallest *Nephtys* investigated contained a high proportion of nematodes in their guts. A carnivorous habit of *Nephtys* is also suggested by the fact that most guts were empty.

Fauchald & Jumars (1979) reviewed the feeding habits of nephtyids and consider the genus *Nephtys* to be composed primarily of predators. Polychaetes are frequently mentioned as prey for *N. hombergii*; however, small bivalves, crustaceans and forams have also been found in the guts (Blegvad 1914, Clark 1962, Ockelmann & Muus 1978). Warwick & Price (1975) found nematodes, ostracods, a small crab and diatoms within the guts of a population dwelling in the mud of the Lynher estuary (England). In a simulation model for the energy flow through this estuarine benthos, Warwick et al. (1979) discovered that there was not enough meiofaunal and macrofaunal prey to maintain this *Nephtys* population. As a solution, they suggested that *N. hombergii* feeds primarily on phytobenthos.

The population density on the Lynher mud flat was much higher (855 m^{-2}) than the one on the Sylt sandy flat (5 m^{-2}). This difference is not limited to a stronger 0-group (82 % in the Lynher versus 44 % at Sylt), which may to some extent originate from different methods (sieving versus collection by hand), but also the 1+ groups are at least 10 times more abundant on the Lynher mud flat compared to the sand flat near Sylt. Apparently, these *Nephtys hombergii* seem to behave quite differently. Either this species switches to omnivory in certain habitats and when population density becomes high, or *Nephtys hombergii* in fact comprises more than one species.

Estimates of consumption

Consumption rates were not measured directly. However, a very rough estimate may be obtained from the enclosure experiments. Assuming that *Nephtys*

prey on other macrofauna during 9 mo of the year (winter excluded) and that feeding rates of *Nephtys* within enclosures approximate natural rates, then 60 to 80 prey individuals are consumed annually by a medium sized *Nephtys* (Table 3). In other words, every 3 to 4 d one prey individual in the macrofaunal size range is eaten.

Table 3. *Nephtys hombergii*. Amount of prey consumed by 1 *Nephtys* over 9 mo, calculated from differences between control buckets and the *Nephtys* treatments (Experiment 1 and 2) and the slope of regression lines (Experiment 3). n: small; N: large *Nephtys* added

Prey components	Experiment			
	1n	1N	2N	3N
Total macrofauna (ind)	61	81	64	68
<i>Scoloplos armiger</i> (ind)	26	58	29	16
<i>Scoloplos armiger</i> (mg)	320	730	300	240
<i>Heteromastus filiformis</i> (ind)	—	—	—	49
<i>Heteromastus filiformis</i> (mg)	—	—	—	240

In the *Scoloplos* assemblage *S. armiger* was the dominant prey and consumption rate is estimated at 38 prey individuals annually, corresponding to an ash-free dry weight of 400 mg yr⁻¹. This will be an underestimate, because tail-cropping is not included. On the other hand, potential prey individuals may have escaped from the buckets before *Nephtys* could get them (see Ambrose 1984d). This is likely to be the case with the surface-mobile *Anaitides mucosa* but not with the subsurface-feeding *S. armiger* and *Heteromastus filiformis*. *S. armiger* comprised about 60 % of all macrofaunal prey, thus the total biomass consumed is probably about 700 mg yr⁻¹.

With a population density of 5 *Nephtys* m⁻², total macrofauna consumed is in the order of 300 to 400 prey individuals m⁻² yr⁻¹. This is approximately 2.5 to 4.0 g m⁻² yr⁻¹ in terms of ash-free dry weight or 1.0 to 1.6 g C m⁻² yr⁻¹. Starting with another set of assumptions for the *Nephtys* population (Warwick & Price 1975, Beukema 1981), a P/B-ratio of 2 and an ecological efficiency of 20 %, the *Nephtys* biomass of 0.14 g C m⁻² is expected to consume 1.4 g C m⁻² yr⁻¹.

These estimates may be compared to those published for epibenthic predators in the intertidal Wadden Sea (g C m⁻² yr⁻¹): *Carcinus maenas* 2.0 (Scherer & Reise 1981), *Crangon crangon* 2.7 (Kuipers & Dapper 1981), fish 3 and birds 2 (Beukema 1981, Kuipers et al. 1981); about 10 altogether. Thus, in terms of biomass, the population of the endobenthic *Nephtys hombergii* consumes at least one tenth of all epibenthic predation combined.

Predatory role of *Nephtys*

Nephtyids are mostly vagile carnivores and have a very large eversible pharynx with a pair of small jaws (Fauchald & Jumars 1979). They are capable of very fast burrowing and good swimming (Mettam 1967, Trevor 1976, Gibbs & Bryan 1984). We have seen them rarely on the sediment surface, which suggests that hunting of prey occurs within the sediment. This mode of feeding excludes most surface-dwelling fauna and tube-building polychaetes (like *Lanice conchilega*) from their prey spectra.

Other field experiments with carnivorous or omnivorous polychaetes (Commito 1982, Ambrose 1984a, b, Commito & Shrader 1985) disclosed much trophic complexity lurking below the sediment surface. This makes it difficult to differentiate between direct and indirect effects of predator additions and removals. In the case of adult *Nephtys hombergii* on the sand flat near Sylt, the realized prey spectrum is rather narrow, and affected are primarily the established adult populations of 2 deposit-feeders. *Scoloplos armiger* and *Heteromastus filiformis* are more or less sedentary, feed below the surface and do not build solid tubes. In the *Scoloplos* assemblage we roughly estimate an annual consumption of 130 to 290 *S. armiger* individuals m⁻² which is 20 to 50 % of its standing stock. In the *Heteromastus* assemblage, we estimate 245 m⁻² *H. filiformis* individuals or about 30 % of the standing stock are eaten annually. These estimates neglect the respective juvenile populations, as *Nephtys* seems to prey preferentially on adult individuals.

Nephtys hombergii also preys to some extent on other endobenthic predators, such as *Anaitides mucosa* and *Eteone longa*. These 2 and *N. hombergii* overlap in their prey spectra, with *Nephtys* being the top-predator relative to the others (M. Hüttel unpubl., authors' own data). It may be that these predators preyed more effectively in the control buckets than in the presence of *Nephtys*. This might mask some direct effects of *Nephtys*, and then our estimates on the amount of prey individuals eaten are too low. *Nephtys* is not the ultimate top-predator within this sediment. The nemertine *Lineus viridis*, also common on this sandy flat, has been observed to swallow *Nephtys* (W. Nordhausen unpubl.).

The above estimates imply that *Nephtys hombergii* deprives crabs, fish and birds of a substantial amount of their polychaete prey. On the other hand, nephtyids are known to be prey of crabs, fish and birds (Blegvad 1914, Bryant 1979, de Vlas 1979). This is substantiated by our caging experiments and documents the role of *Nephtys* as an intermediate predator (*sensu* Ambrose 1984c) in the food chain of tidal flats.

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