

Influence of the predatory polychaete *Nephtys hombergii* on the abundance of other polychaetes

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ABSTRACT: Negative relations between abundance of the predatory polychaete *Nephtys hombergii* and values for biomass and rate of increase in 2 of its prey species, the polychaetes *Scoloplos armiger* and *Heteromastus filiformis*, are evident in long-term (18 yr) data from tidal flats in the westernmost part of the Wadden Sea. Values for prey biomass tended to decline at high *N. hombergii* biomass (above ca 0.3 g m⁻² AFDW), whereas they tended to increase at lower levels of *N. hombergii* biomass. These results corroborate Schubert & Reise's (Mar. Ecol. Prog. Ser. 34: 117–124, 1986) conclusion, based on short-term enclosure experiments, that *N. hombergii* is an important infaunal predator in the Wadden Sea.

INTRODUCTION

Both epifaunal and infaunal predators appear to affect the abundance of infaunal prey species in tidal flat sediments (Reise 1985). The role of epifaunal predators in structuring tidal flat ecosystems is well known, but the importance of infaunal predators has received little attention. Many polychaete species are potential predators of other endobenthic species (Commito & Ambrose 1985), and some North American studies suggest that predatory polychaetes such as *Nereis virens* (Ambrose 1984, Commito & Shrader 1985) and *Glycera dibranchiata* (Ambrose 1984) play a significant role in the structuring of marine sediment ecosystems. In the Wadden Sea, Schubert & Reise (1986) showed convincingly that *Nephtys hombergii* Sav. consumed substantial numbers of some other species of endobenthic polychaetes, in particular the deposit-feeders *Scoloplos armiger* (O.F.M.) and *Heteromastus filiformis* (Clap.). Frequently, the densities of *N. hombergii* on tidal flats in the Wadden Sea (Beukema 1976, Beukema et al. 1978, Dankers & Beukema 1983) should be sufficiently high to greatly reduce abundances of these prey species.

Results of the experiments by Schubert & Reise (1986) were a stimulus to closely examine an extensive set of field data from the Wadden Sea. These data were gathered during an 18 yr period of frequent sampling at 15 fixed stations on tidal flats in the westernmost part of the Wadden Sea. Abundances of *Nephtys hombergii*

fluctuated greatly in this area as a consequence of its sensitivity to low winter temperatures (Beukema 1979, 1984). Periods of high *N. hombergii* abundance alternated unpredictably with periods of scarcity (Beukema et al. 1978). If it is permissible to extrapolate the results of Schubert & Reise (1986) from small enclosures over short periods to entire tidal flats over years, then significant differences may be expected in the responses of prey populations to the observed variations in *N. hombergii* abundance. The irregular reductions in the *N. hombergii* population by severe winters thereby provided large-scale natural experiments on the predatory effects of this species.

MATERIALS AND METHODS

The 15 sampling stations are scattered over the 50 km² tidal flat area known as Balgzand (Fig. 1), which is located in the westernmost part of the Wadden Sea. Among these 15 stations, 3 are square plots of 900 m² each and 12 are transects of 1 km each. All stations are marked by permanent iron poles.

These 15 stations have been sampled in a uniform way at least annually (in late winter/early spring, mostly in March) since 1969. The 3 square plots were sampled year-round, at least 4 times per year. Sampling procedures were described in detail by Beukema (1974, 1979). In short: cores were taken and sieved in the field on 1 mm mesh screens. All samples were

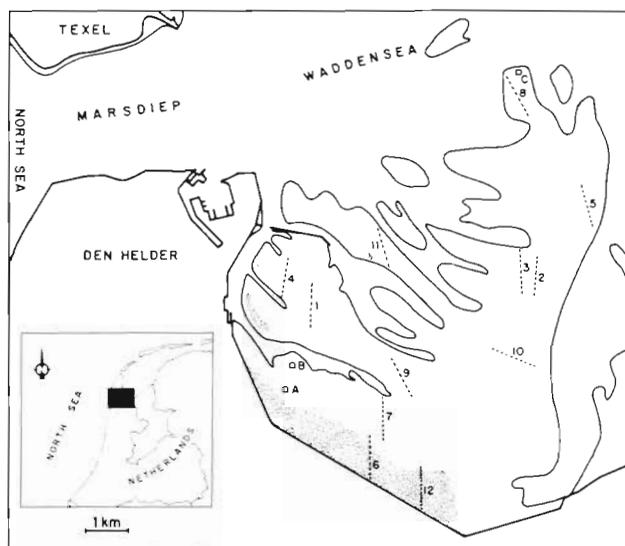


Fig. 1. Map of the Balgzand tidal flat area showing locations of sampling stations (3 square plots, 12 transects numbered 1 to 12)

sorted in the laboratory while the animals were still alive, thereby facilitating complete extraction of the worms from the sieve residues.

The total area sampled varied from 0.9 to 1.6 m² per station among the sampling events. Abundances are expressed per m², and biomass is given as g m⁻² AFDW (ash-free dry weight). In this study, biomass data are preferred over numerical abundance data for several reasons: (1) The quantities of prey consumed by *Nephtys hombergii* will be more closely related to the weights of this predator than to its numbers because the mean size of *N. hombergii* was highly variable; (2) In both predator and prey, the data on numerical abundance are less accurate than the biomass data because unknown quantities of the smallest size-classes of the worms escaped through the meshes of the sieve. These losses would have affected estimates of numerical abundance more seriously than biomass estimates because the smallest worms would contribute little to biomass but greatly to numbers; (3) Fragmented worms could be included unambiguously.

All types of tidal flats were represented among the sampling stations, from high to low water level and from soft muds to clean sands. The 3 aforementioned polychaete species are not found everywhere on these tidal flats. Each is restricted to specific ranges of intertidal levels and silt contents of the sediment (Dankers & Beukema 1983). *Nephtys hombergii* and *Scoloplos armiger* avoid the higher and siltier areas, whereas *Heteromastus filiformis* is rare in the lowest and sandiest sediments (Dankers & Beukema 1983: Fig. 23). Thus, a study of predator-prey relationships makes sense only for part of the sampled area. As criteria, firstly the

initial abundance of the prey species was used (for each individual year and sampling station, it should exceed 0.1 g m⁻² AFDW) and secondly the abundance of the predator (at each station, its biomass should exceed 0.3 g m⁻² during at least part of the years). The southwestern coastal part of Balgzand is silty and high (mostly above Mean Tide Level, MTL: the shaded parts in Fig. 1). *S. armiger* biomass values were invariably below 0.1 g m⁻² at Stns A, 4, 6, 7 and 12, and during several years also at Stns 1, 5 and 9. The exposed northeastern part of Balgzand is sandy and low with invariably low *H. filiformis* abundance at Stns C, 5 and 8, and during several years also at Stns 2, 3 and 11. None of the data from Stns 6 and 12 were used because *N. hombergii* biomass was very low during all years at these high stations. As a result, data from 10 stations could be used for each of the relations *Nephtys-Scoloplos* and *Nephtys-Heteromastus*, yielding 121 and 135 data pairs, respectively.

Mean values are shown with one standard error. By way of precaution, only non-parametric tests were used for statistical comparisons because the data were often highly variable (with variances several times higher than the means, see Beukema et al. 1983) and non-normally distributed. The following tests were used: (1) The Mann-Whitney U test (Siegel 1956) to compare the means of prey biomass values at high and low predator densities in the same season (Fig. 2 & 4) and to compare the (weighted) means of the relative changes in prey biomass after 1 yr at high and low predator densities (Table 1). (2) The Friedman 2-way analysis of variance by ranks (Siegel 1956), as modified by De Jonge (1963) to allow for unequal distances, to evaluate annual trends in the changes of prey biomass at different predator abundance (Fig. 2 & 4). (3) The Spearman rank correlation test (Siegel 1956) to measure the association between the predator abundance and the change of prey biomass (Fig. 3 & 5). All *r* values given are Spearman rank coefficients.

RESULTS

Response of *Heteromastus filiformis* to variation in *Nephtys hombergii* abundance

At only one of the 3 frequently sampled square plots (Stn B, Fig. 1), were both *Nephtys hombergii* and *Heteromastus filiformis* sufficiently abundant during most years to compare the changes in *H. filiformis* biomass at different levels of *N. hombergii* abundance. During each of the 18 successive years (1969 to 1986) biomass estimates were obtained for each of 4 seasons: winter, early spring, early summer and late summer. The 18 yr were divided into 2 nearly equally-sized

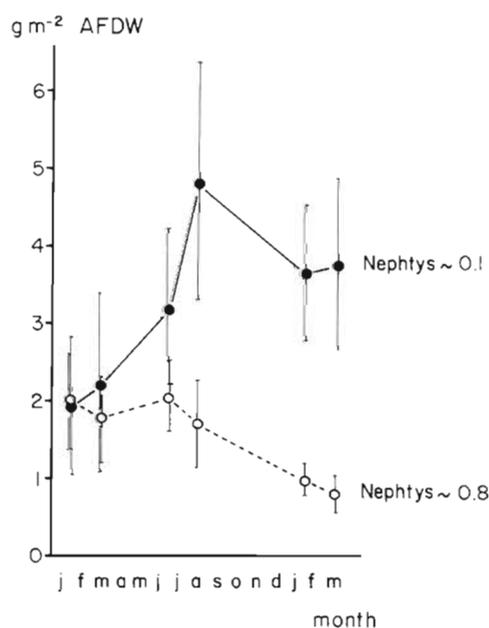


Fig. 2. *Heteromastus filiformis*. Annual course of mean biomass values (g m^{-2} AFDW, with 1 standard error) at the frequently sampled Stn B during years of low (8 yr) and high (10 yr) abundance of the predatory worm *Nephtys hombergii*

groups, with high and low predator abundance, respectively. During 10 yr *N. hombergii* biomass was judged high, i.e. between 0.4 and 1.4 g m^{-2} (mean 0.78 ± 0.10), and during the other 8 yr low: between 0 and 0.4 g m^{-2} (mean 0.14 ± 0.04). The biomass values for *H. filiformis* were averaged for these 2 groups of years separately (the values for the first few months of the next year were included to obtain the biomass change during a full year; see Fig. 2).

The *Heteromastus filiformis* biomass varied greatly from year to year, but fortunately mean values at the start of the year were nearly equal for the 2 groups of (8 and 10) years (*viz.* about 2 g m^{-2} : the 2 leftmost points in Fig. 2). However, subsequent changes in prey biomass were quite different between years with high and low *Nephtys hombergii* abundance (Fig. 2). At low predator abundance, biomass of the *H. filiformis* popu-

lations increased significantly ($p < 0.01$). *H. filiformis* populations declined at high *N. hombergii* abundance. After 1 yr of low *N. hombergii* densities, the mean abundance of *H. filiformis* nearly doubled and was significantly higher ($p < 0.05$, both for the winter and early-spring data) than the roughly halved *H. filiformis* biomass at high *N. hombergii* densities (Fig. 2: the 4 rightmost points). Mean winter and early-spring biomass values after 1 yr of low *N. hombergii* abundance were respectively 1.90 and 1.71 times higher than at the start of the year. These ratios were only 0.49 and 0.46, respectively, at high *N. hombergii* abundance. The differences between these ratios at low and high predator abundance are significant at the 0.05 level (Table 1).

Relative changes in biomass such as doubling and halving after 1 yr can also be directly related to individual values of *Nephtys hombergii* abundance in each of the 18 separate years, and evidenced by a significantly negative correlation ($r = -0.55$ for the winter data and -0.53 for the early-spring data, both $p < 0.05$). Thus, the higher the biomass of the predator was during year n , the lower the prey biomass was at the start of year $n+1$, compared to its abundance at the start of year n .

Even higher numbers of such annual ratios of change in prey biomass are available from the transects sampled in March. Including the 18 observations from the above square-plot station, a total of 135 pairs of data could be correlated. Instead of year-round data for *Nephtys hombergii* (which would yield a true annual average for predator biomass), only one seasonal estimate is available. However, this limitation is not serious because the values for *N. hombergii* biomass in March were well correlated (r values around $+0.8$) with those in subsequent months up to, but not including, the following winter (as observed at the 2 frequently sampled square-plot stations, B and C).

The ratios of annual change of *Heteromastus filiformis* biomass (i.e. biomass in March of year $n+1$ divided by biomass in March of year n) declined with increasing values of *Nephtys hombergii* biomass in March of

Table 1. *Heteromastus filiformis* and *Scoloplos armiger*. Weighted means of relative annual changes in biomass of these prey species at high and low abundance of the predator *Nephtys hombergii*. In parentheses: no of observations (yr). * $p < 0.05$; ** $p < 0.01$

	<i>Heteromastus filiformis</i>		<i>Scoloplos armiger</i>			
	Stn B		Stn B		Stn C	
<i>Nephtys</i> biomass (g m^{-2})	High (0.78)	Low (0.14)	High (0.78)	Low (0.14)	High (0.55)	Low (0.22)
Prey changes (biomass year $n+1$ /year n)						
Winter-winter	0.49 (10)*	1.90 (8)	0.80 (10)	1.38 (8)	0.91 (9)	1.25 (9)
Spring-spring	0.46 (10)*	1.71 (8)	0.92 (10)	1.07 (8)	0.99 (9)	1.27 (9)
Combin.-combin.	0.47 (20)**	1.80 (16)	0.85 (20)**	1.19 (16)	0.97 (18)*	1.26 (18)

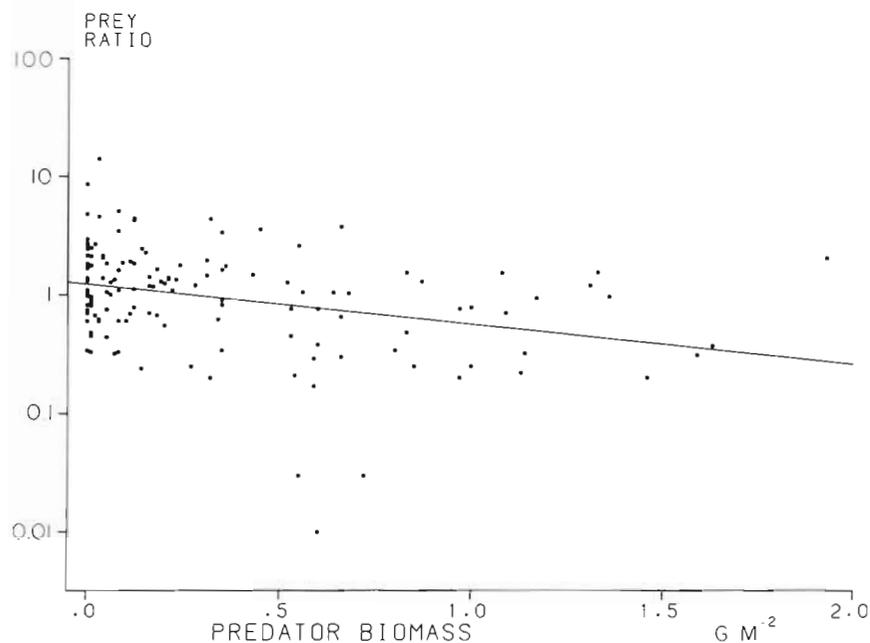


Fig. 3. Relation between abundance of the predatory worm *Nephtys hombergii* (g m^{-2} AFDW) at the start of the year and subsequent (relative) change in the biomass of its prey *Heteromastus filiformis*

year n (Fig. 3: $r = -0.32$, $p < 0.001$). The data in Fig. 3 are plotted on a semi-logarithmic scale to show equal distances from equality for both doubling and halving of prey abundance. The best-fitting straight line is described by: $\log(\text{ratio of annual change of } Heteromastus) = 0.10 - 0.37(Nephtys \text{ biomass})$. This formula indicates that: (1) in the absence of *N. hombergii*, *H. filiformis* increases an average of about 25% per year (as 0.10 equals $\log 1.25$); (2) *H. filiformis* remains (on average) stable at an *N. hombergii* biomass of about 0.3 g m^{-2} (as 0.10 divided by 0.37 equals about 0.3); (3) *H. filiformis* decreases (on average) at any biomass of *N. hombergii* higher than about 0.3 g m^{-2} , and decreases faster at greater *N. hombergii* biomass. For instance, *H. filiformis* biomass roughly halves each year at 1 g m^{-2} of *N. hombergii* (as -0.27 equals $\log 0.54$).

Response of *Scoloplos armiger* to variation in *Nephtys hombergii* abundance

Changes in *Scoloplos armiger* biomass were analysed in a similar manner to those shown above for *Heteromastus filiformis*. Because the distributions of *Nephtys hombergii* and *S. armiger* overlap to a greater extent than those of *N. hombergii* and *H. filiformis* (Dankers & Beukema 1983: Fig. 23), the available data allowed a detailed study on the relations between *N. hombergii* and *S. armiger* at 2 of the frequently sampled square-plot stations (B and C). For Stn B, the same division in years with high and low predator abundance was made as mentioned above for the *Nephtys-Heteromastus* relation. Stn C was located at a low intertidal level where *N. hombergii* abundance varied little (for reasons explained in Beukema 1984), its mean

biomass during the group of 9 yr with relatively high densities was $0.55 \pm 0.05 \text{ g m}^{-2}$, and its mean biomass during the 9 yr of low densities $0.22 \pm 0.03 \text{ g m}^{-2}$.

The annual courses of *Scoloplos armiger* biomass were similar at the 2 stations (Fig. 4a, b). Beginning with roughly the same biomass in winter and early spring, the biomass values for *S. armiger* appear to reach higher mean values during the months subsequent to low *N. hombergii* biomass than during the months subsequent to high *N. hombergii* biomass. Because of high year-to-year variability (already present at the start of the year), the differences are, however, statistically nonsignificant.

After 1 yr of low *Nephtys hombergii* biomass, *Scoloplos armiger* biomass increased by a mean of about 20%, whereas it declined by a similar mean percentage at high *N. hombergii* biomass (Table 1). At each of the 2 stations, the differences between these ratios are statistically significant only for the combined January and March data (Table 1).

Direct correlations of the individual annual ratios of change in *Scoloplos armiger* biomass at the 2 square-plot stations with mean annual *Nephtys hombergii* biomass yielded negative correlations in all 4 cases (2 stations \times 2 months). Values of r varied from -0.20 to -0.60 , but only one of those correlations was significant at $p < 0.05$ (the one for January data at Stn B).

By including the transect data, 121 pairs of data on *Nephtys hombergii* abundance versus ratio of annual change in *Scoloplos armiger* abundance were available. The resulting relation was again negative (Fig. 5: $r = -0.21$, $p < 0.02$) with a best-fitting straight line described by: $\log(\text{ratio of annual change of } Scoloplos) = 0.11 - 0.38(Nephtys \text{ biomass})$. This formula strongly

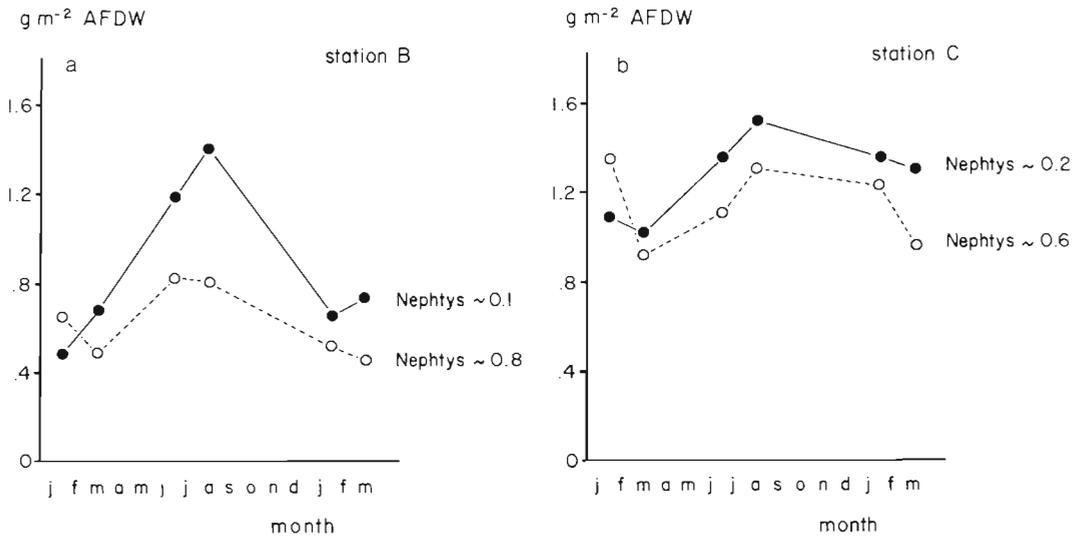


Fig. 4. *Scoloplos armiger*. Annual courses of mean biomass values (g m^{-2} AFDW) at 2 frequently sampled stations during years of low and high abundance of the predatory worm *Nephtys hombergii*. (a) Stn B; (b) Stn C

resembles the one obtained for *Heteromastus filiformis* (see above) and is interpreted similarly.

DISCUSSION

From an analysis of gut contents of *Nephtys hombergii* collected at tidal flats near Sylt in the Wadden Sea, Schubert & Reise (1986) concluded that the worms *Scoloplos armiger* and *Heteromastis filiformis* are major prey of this predatory polychaete. Some other worm species were also observed in the guts of *N. hombergii*, but only in small numbers. In enclosure experiments in the same area, they found consistent,

substantial declines in the numbers of both *S. armiger* and *H. filiformis* in the presence of high densities of *N. hombergii*, while densities of other endozoobenthic species were not consistently affected. Though the predator densities in these enclosure experiments were unrealistically high (about 10 g AFDW m^{-2} , or about 10 times a high natural density of *N. hombergii* on tidal flats of the Wadden Sea), a rough estimate could be made of predation rates at natural densities for entire years. Schubert & Reise estimated an annual consumption per medium-sized *N. hombergii* (about 70 mg AFDW) of 300 to 700 mg of worms (or roughly 4 to 10 times their own weight).

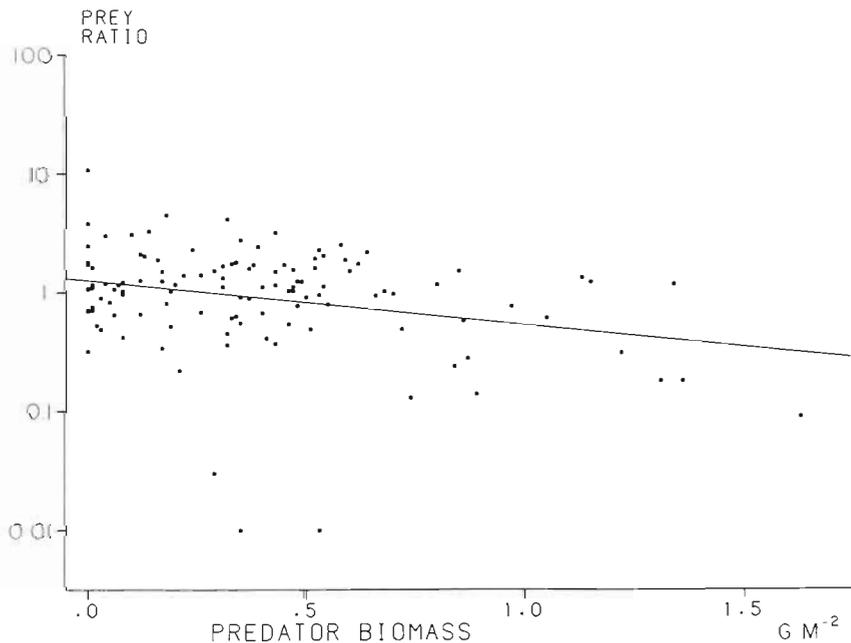


Fig. 5. Relation between abundance of the predatory worm *Nephtys hombergii* (g m^{-2} AFDW) at the start of the year and subsequent (relative) change in the biomass of *Scoloplos armiger*

The data gathered on Balgzand (a tidal flat area with a very similar ecosystem) and presented above offered an opportunity to test the foregoing extrapolations from small-scale, short-term experiments. In the case of the square-plot sampling station, B (Fig. 2 & 4a), the difference between mean *Nephtys hombergii* biomass during years with high and low abundance amounted to $0.78 - 0.14 = 0.64 \text{ g m}^{-2}$. By the calculations of Schubert & Reise (1986), such an amount of extra *N. hombergii* biomass would consume annually between 2.7 and 6.4 g m^{-2} of prey worms (i.e. 4 to 10 times their own weight). The actual mean difference in biomass of prey worms observed at the end of the year at Stn B was 2.7 g m^{-2} of *Heteromastus filiformis* + 0.1 g m^{-2} of *Scoloplos armiger* = 2.8 g m^{-2} for the January data and $3.0 + 0.3 = 3.3 \text{ g m}^{-2}$ of prey worms for the March data. Due almost exclusively to the strong reduction in the biomass of *H. filiformis* (Fig. 2), these figures are within the lower end of the range expected based on estimates by Schubert & Reise.

At Stn C (Fig. 4b), the difference in *Nephtys hombergii* biomass between the groups of years with high and low predator abundance was $0.55 - 0.22 = 0.33 \text{ g m}^{-2}$, with an expected consumption of between 1.4 and 3.3 g m^{-2} . Almost no *Heteromastus filiformis* occurred at this sandy station. The reduction in *Scoloplos armiger* biomass (Fig. 4b) amounted to only about one tenth of the foregoing estimate of *N. hombergii* consumption.

Thus, at both stations *Scoloplos armiger* appears to be reduced to a much lesser extent than would be expected from the Schubert & Reise estimates, whereas *Heteromastus filiformis* did show the expected reduction in biomass. This difference in response between the prey species could easily arise from the different ways in which *Nephtys hombergii* attacks these species. In a laboratory feeding experiment, Schubert & Reise (1986) observed that *N. hombergii* swallowed *H. filiformis* whole, but ate only tail ends of *S. armiger*. The latter thus remained alive and regenerated their tail ends. Cropping regenerating tail ends would only slightly reduce biomass compared with the destruction of entire worms. As in the case of tails of lugworms cropped by plaice (Beukema & de Vlas 1979, de Vlas 1979), production by such prey populations is actually much higher than estimates from dynamics of numbers would suggest. Thus, *N. hombergii* might have consumed much higher amounts of *S. armiger* than the reduction in biomass in this prey would suggest.

The second set of data presented (mainly transect data) indicates that *Nephtys hombergii* effectively regulates abundances of the 2 prey species (Figs. 3 & 5). The prey populations tend to decline at high predator abundance (i.e. above 0.3 g m^{-2}) and tend to increase at lower predator densities. This crucial density of 0.3 g m^{-2} of *N. hombergii* equals the mean density observed

during a separate large-scale survey (99 transects) of tidal flat fauna from the Dutch Wadden Sea (Beukema 1976).

Fig. 3 & 5 show a high scatter of individual data. Thus, no conclusion can be drawn about the possible shape of a best-fitting curve and no special meaning should be attached to the straight lines drawn. The only conclusion in this matter that appears to be warranted is that the relations between predator abundance and rate of change of prey biomass are negative for both prey species. The high scatter indicates that other environmental factors also affect abundances of *Heteromastus filiformis* and *Scoloplos armiger*. However, *Nephtys hombergii* appears to be an important predator that controls, in part, abundances of 2 infaunal polychaetes on tidal flats in the Wadden Sea.

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