Long-term observations on the dynamics of three species of polychaetes living on tidal flats of the Wadden Sea: the role of weather and predator–prey interactions

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Summary

1. On the tidal flats of the Wadden Sea, the predatory polychaete *Nephtys hombergii* (Sav.) is sensitive to low winter temperatures, whereas its main prey, the smaller polychaetes *Scoloplos armiger* (O.F.M.) and *Heteromastus filiformis* (Clap.) are not.

2. Monitoring macrofauna dynamics during the last three decades (1970–97) in two distant Wadden Sea areas revealed that *Nephtys* abundance was severely reduced in all eight coldest winters (generally to an average of < 0.1 g ash-free dry weight m^{-2}), whereas its biomass reached mean values around 1 g AFDW m^{-2} during periods with mild winters (≤ 5 days with an air temperature remaining below 0°C all day). Over-winter changes in *Nephtys* abundance were strongly related to temperature and 70% of the variability in late winter abundance of this species could be explained by temperature characteristics of the foregoing winter.

3. Biomass values of *Nephtys* observed in late winter predicted to a high degree (90%) the generally somewhat higher values in the subsequent summer. This seasonal change of predator abundance was generally not related to prey density. Only locally (in an exposed low-biomass area) and rarely (one-tenth of the years of observation) did low prey supply (if it was lower than simultaneous predator biomass) coincide with a decline, rather than the usual seasonal increase in *Nephtys* biomass.

4. A negative influence of predator abundance on prey biomass was observed in both prey species over the entire range of observed predator biomass values. The usual seasonal (winter to summer) increase of prey biomass was significantly smaller at high than at low *Nephtys* biomass and was even reduced to nil at the highest predator density observed. *Scoloplos* biomass was about four times higher after years with low (< 0.1 g m^{-2}) than after years with high (> 1.0 g m^{-2}) *Nephtys* biomass. Similar differences were observed in biomass of *Heteromastus*.

5. It is concluded that winter temperatures act as an important structuring factor in the Wadden Sea zoobenthic community by directly governing the densities of an important infaunal predator and indirectly affecting the abundance of at least two important prey species. Cold winters intervene by starting a new cycle of predator–prey interaction on average once per 3 or 4 years.

6. Predator abundance was more frequently determined by weather conditions than by food supply. Prey abundance was primarily governed by predator abundance and food supply and was only indirectly (via predator abundance) affected by the incidence of cold winters.

Key-words: biomass, *Heteromastus*, *Nephtys*, *Scoloplos*, temperatures.

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Introduction

The causes of population fluctuations within a community can be classified into two basically different groups, viz. extrinsic (environmental, abiotic) factors, such as extreme temperatures and other weather conditions, and intrinsic processes such as intra- and interspecies relations, e.g. predator–prey interactions. Generally, both kinds are at work simultaneously. Their relative importance is a fundamental question of ecological research (e.g. Andrewartha & Birch 1954) and has been a matter of long-lasting and vivid discussion with recent contributions by amongst others Leggett & Frank (1997), Leirs *et al.* (1997), Myers, Mertz & Bridson (1997) and Grenfell *et al.* (1998).

On the tidal flats of the Wadden Sea, zoobenthic communities are relatively poor in species, and rich in numbers of individuals and biomass. By core sampling at low tide, abundance parameters of infauna can be assessed relatively easily, at low costs and with high precision. Such tidal-flat areas are well suited for quantitative studies of dynamics of populations and communities.

The tidal flats of the Wadden Sea constitute a harsh environment for its faunal community. Cold winters, in particular, cause severe mortality among the populations of species that are sensitive to low temperatures. Such sensitive species are by no means rare on Wadden Sea tidal flats. In the Dutch part of the Wadden Sea, more than one-third of the 29 species that were frequently encountered in the samples of the macrozoobenthos showed unusually low values for survival (Beukema 1990: 10 species) and/or biomass (Beukema 1989: 12 species) at the end of severe winters. On the tidal flats of the Dutch Wadden Sea, these species apparently live close to the (northern and cold) edge of their area of distribution. They are generally rare or absent on tidal flats of more northern parts of the Wadden Sea (Wolff & Dankers 1983; Dekker & Beukema 1993).

Among these winter-sensitive species is an important infaunal predator, viz. the polychaetous worm *Nephtys hombergii* Sav. It is present at most of the tidal flats of the Wadden Sea (viz. at 84% of the nearly 100 transects sampled by Beukema 1976) and reaches frequently densities of several tens m^{-2} (Dankers & Beukema 1983). In the Wadden Sea, two smaller-sized worm species belong to the main prey of *Nephtys*, viz. the polychaetes *Scoloplos armiger* (O.F.M.) and *Heteromastus filiformis* (Clap.) (Schubert & Reise 1986). As the abundance of these prey species can strongly fluctuate (*Scoloplos*: Beukema 1989; *Heteromastus*: Beukema 1992), it appears worthwhile to study *Nephtys* dynamics not only in relation to winter temperatures, but to investigate also whether it is affected by the variable supply of their main prey species.

Predators frequently exert a strong influence on the dynamics of their main prey species. Ambrose (1991) and Wilson (1991) review this relationship for marine soft-bottom communities, and Estes & Duggins (1995) for the sea otter/herbivores/macro-algae three trophic-level cascade in the rocky intertidal. Reise (1985) describes several cases of predation effects in tidal-flat communities of the Wadden Sea. More specifically, Schubert & Reise (1986) observed substantial declines in the numbers of *Scoloplos* and *Heteromastus* whenever *Nephtys* was present in high densities in small enclosures in the German Wadden Sea. At a few 1000-m^2 squares in the western part of the Wadden Sea, Beukema (1987) observed higher rates of increase in the biomass of these two prey species at low than at high abundance of *Nephtys*. Thus, a significant role of this predator may be expected in governing the densities of its main prey species. So far, large-scale and long-term observations of the impact of infaunal predators on the structure of benthic communities in marine sediments appear to be scarce.

The present study is based on data gathered during long-term monitoring programmes of benthic macrofauna on tidal flats both in the western and in the eastern part of the Dutch Wadden Sea. Based on abundance data covering almost three decades, we study in detail: (i) the dynamics of the three above worm species in relation to the character of the winter; and (ii) the mutual inter-relationships between the abundance of the predator and its two most important prey. Our hypothesis is that mutual relationships will exist between the biomass values of the predator and its two main prey species. The data sets presented in the present paper may shed some light on the questions, which factors are the main structuring forces of the benthic community and what is the relative importance of the extrinsic (stochastic and highly unpredictable) and intrinsic (frequently more or less predictable) type of factors.

Materials and methods

STUDY AREA

Most data used were collected as part of a long-term monitoring programme of the macrozoobenthos at Balgzand, a 50-km^2 tidal-flat area with a tidal range of 1·4 m in the westernmost part of the Wadden Sea. Local conditions (inter-tidal level, sediment composition) at the 15 sampling stations are described in Beukema & Cadée (1997). The faunal composition is described in Beukema (1988, 1991), showing that the area is relatively poor in macrozoobenthic species (10–20 m^{-2}), but rich in numbers of individuals (hundreds or thousands m^{-2}) and biomass (mostly some tens of grams ash-free dry weight m^{-2}).

In the sheltered southern part of Balgzand ('Silt' in Fig. 1a), the tidal flats are high (above mean-tide level) and muddy. They become progressively lower and sandier towards the more exposed northern part ('Sand' in Fig. 1a). Along this gradient, the composition of the macrobenthic fauna gradually changes as individual species are usually restricted to specific ranges of inter-tidal level and sediment composition (Dankers & Beukema 1983).

At the four southernmost sampling stations, located in the 'Silt' area, biomass values of *Nephtys* were generally well below 0·1 g AFDW m^{-2}. In most years, zero values were observed at these stations. *Scoloplos* is also a rare species in this area, as is *Heteromastus* in most of it. Therefore, this area will be omitted from the present studies. The remaining 11 stations (located in the areas 'Sand' and 'Mixed' in Fig. 1a) are all well below MTL, and with more or less sandy sediments. At these stations the long-term means of annual biomass values of *Nephtys* ranged from 0·22 to 0·66 g AFDW m^{-2} (Fig. 1a).

Within the areas 'Sand' and 'Mixed', *Scoloplos* and *Heteromastus* are among the most numerous animals with numerical densities of usually hundreds m^{-2}. Their biomass values are mostly around 1 g m^{-2} AFDW in the 'Sand' area and several g m^{-2} in the 'Mixed' area. Usually, they account for > 90% of the total biomass of small worms (other small-worm species were mainly *Anaitides mucosa* (Oersted) and *Eteone longa* (Fabr.) and in the 'Sand' area also *Magelona papillicornis* O.F.M.). The relative share of each of the two main prey species differed from station to station, but groups of adjacent stations (Fig. 1b) showed similar biomass values. Where *Heteromastus* biomass was high, *Scoloplos* biomass tended to be low (most of the silty half of area 'Mixed'). *Heteromastus* biomass values were high (> 2·4 g m^{-2}) where the silt content was > 2%, whereas *Scoloplos* biomass reached maximal values where silt content was < 4% (Fig. 1b). *Scoloplos* dominated over *Heteromastus* only in the exposed northern part of Balgzand, that is at the three stations in the area 'Sand' with a silt content of 1% or lower. Because of the substantial qualitative and quantitative differences in prey supply, the two areas 'Sand' and 'Mixed' will be dealt with separately to study the influence of prey abundance on *Nephtys* dynamics.

Long-term data on the abundance of *Nephtys* and *Scoloplos* (but not of *Heteromastus*) were also regularly collected in a comparable way at five inter-tidal stations at Groninger Wad (120 km east of
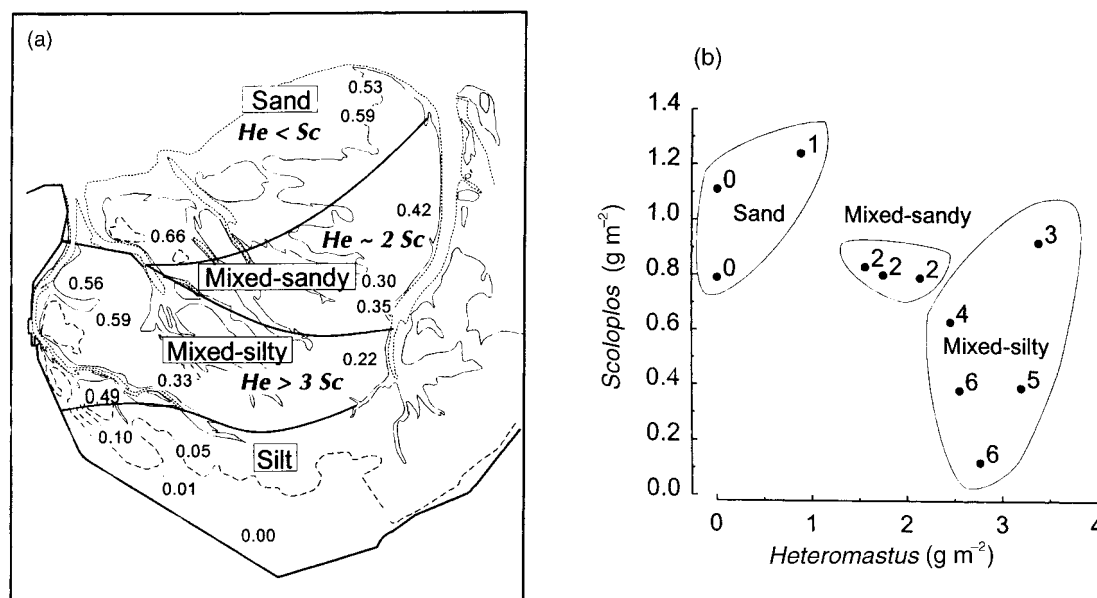

Fig. 1. (a) Map of the Balgzand tidal-flat area with location of the 15 sampling stations, indicated by the long-term (1980–97) mean values of annual biomass of *Nephtys hombergii* (in g AFDW m^{-2}, means of 36 values: 18 observed in late winter and 18 in late summer). The four zones indicated are (from north to south): (1) Sand = an exposed area with clean sands and a relatively high abundance *Scoloplos* (Sc), but not of *Heteromastus* (He); (2) Mixed-sandy = a rather sandy area with slightly (about two times) more *Heteromastus* than *Scoloplos*; (3) Mixed-silty = a more muddy area with *Heteromastus* clearly prevailing (by a factor of three or more) over *Scoloplos*; (4) Silt = a sheltered and muddy coastal area with invariably low abundance of *Nephtys* and *Scoloplos* (and at some stations also of *Heteromastus*). The thin lines indicate depths (broken line = mean tide level (MTL); full line = mean low water level; dotted line = −5 m (MTL). (b) A plot of long-term (1980–97) mean annual biomass values of *Heteromastus* and *Scoloplos* (in g AFDW m^{-2}) at the 11 stations with moderate to high abundance of *Nephtys* (the areas Sand and Mixed). The figures near the points indicate the silt contents (in percentage) of the dried sediment.

Balgzand). Data from two of these stations were omitted because they were seriously affected by waste-water discharges during part of the period of observation (Essink & Beukema 1986). The remaining three stations at Groninger Wad are located in a restricted area of about $5 \, km^2$ on a high (close to MTL) and rather muddy (silt contents around 10%) tidal flat at 1–2 km off the dyke near Noordpolderzijl (see Fig. 1 of Beukema, Essink & Michaelis 1996).

SAMPLING METHODS

The long-term sampling programme on Balgzand started in 1970 by taking annually in late winter (mostly in March) 50 samples of $0.018 \, m^2$ each equally spaced along each of twelve 1-km transects scattered over the area (Fig. 1a). Starting in 1980, these stations were also sampled in late summer, mostly in August (50 samples of $0.009 \, m^2$ each along each transect). In addition, 18–32 samples with a total area of $1–1.6 \, m^2$ were taken in each of three 1000-m^2 squares both in late winter and in late summer, starting in 1967. Data collected during the 1970–97 period were used, thus including 28 late winter and 18 late summer sampling occasions on Balgzand.

Sampling was performed in a uniform way throughout the sampling period. Sampling procedures were described earlier in detail by Beukema (1974). In short, sediment cores to a depth of about 25 cm were taken and sieved in the field on 1-mm mesh screens. All samples were sorted alive in the laboratory. The total number of samples taken per sampling occasion was between 600 and 700 with a total area of about $8 \, m^2$ in summer and $14 \, m^2$ in winter. Abundance figures are expressed in g ash-free dry weight (AFDW) m^{-2}. In studies of small worms, biomass data are preferred over numerical abundance data for three reasons:
1. biomass data are more accurate, because unknown quantities of the smallest size classes escaped through the meshes of the sieves and these losses will have affected estimates of numbers more seriously than estimates of biomass;
2. fragmented worms could be included unambiguously; and
3. the quantities of prey consumed by *Nephtys* will be more closely related to the weights of this predator than to its numbers, because the mean size of the predatory worms was highly variable.

On Groninger Wad, consistent data gathering started in 1971, but no late winter data were collected in 1981. Thus, data are available of 26 years. Details on the sampling procedure can be found in Essink (1978). Sampling was performed in a similar way as on Balgzand, yielding comparable results in the two species concerned.

In all three species, annual values of numerical density and biomass fluctuated in a synchronized way at the various Balgzand stations (see Table 1 of Beukema & Essink 1986) or on even larger scales (Beukema *et al.* 1996). Data collected at the three Groninger Wad stations showed synchronized fluctuation patterns as well (Essink & Beukema 1986). Therefore, data from different stations within the two sampling regions could be combined to reduce effects of sampling errors.

CHARACTERIZATION OF WINTERS

Data on character of the winter were taken from monthly reports of the weather station De Kooy (Royal Dutch Meteorological Institute), located at 1 km distance from Balgzand. From these reports both the numbers of cold days (i.e. days with a maximum temperature $< 0°C$) and the average air temperatures during the three coldest months (January–March, inclusive) were borrowed. For the 1970–97 period, these two parameters were strongly correlated ($r = –0.88$, $n = 28$, $P < 0.001$, Spearman rank correlation test), as was the correlation between number of cold days and the mean seawater temperature (as measured at the NIOZ pier) in the three coldest months ($r = –0.91$). Thus, either of these parameters can be used to arrange the winters in an order of severity. We chose the total number of cold days of the entire winter.

LIFE HISTORY OF THE SPECIES STUDIED

All three species studied live in the upper 10–20 cm of marine sediments, both in the inter-tidal and shallow subtidal. They are common and numerous on most of the tidal flats of the Wadden Sea (Dankers & Beukema 1983). Adults of *Nephtys* and *Scoloplos* move freely through the sediments, but *Heteromastus* adults take a vertical position (upside down) in a burrow of up to 15 cm. *Nephtys* is the bigger species with adult weights up to 200 or 300 mg AFDW. Weights of adults of the two prey species mostly range from 5 to 10 mg AFDW. Numerical densities on the Wadden Sea tidal flats usually amount to some tens m^{-2} in *Nephtys*, and to hundreds or even thousands in the two prey species (compare Table 2 of Dankers & Beukema 1983).

Nephtys spawns in spring and pelagic larvae and newly settled post-larvae occur in summer. Spawning success shows large year-to-year variation with successful reproduction occurring most frequently after mild winters and good feeding conditions (Olive *et al.* 1997). *Scoloplos* and *Heteromastus* lay eggs in cocoons in early spring at the surface of the sediment. The hatched larvae may either be transported by tidal currents or start their burrowing mode of life immediately (Wolff 1973).

Though it has been suggested that *Nephtys* is an omnivore, it appears to be a true motile predator (Fauchald & Jumars 1979) feeding on a variety of small soft-bottom organisms, in particular (parts of) small worms. In the German Wadden Sea, *Scoloplos* and *Heteromastus* were the main prey in the guts of *Nephtys*, but occasionally other worms were eaten (Schubert & Reise 1986). The two prey species appear to be true deposit feeders and it is not known whether they are selective (Fauchald & Jumars 1979).

Results

DYNAMICS OF THE THREE POLYCHAETE SPECIES

Annual late winter data series on *Nephtys* biomass are shown separately for two parts of Balgzand

(Fig. 2a: *Scoloplos*-dominated area 'Sand'; Fig. 2b: *Heteromastus*-dominated area 'Mixed') and for the Groninger Wad (Fig. 2c). In all three areas, *Nephtys* showed strongly similar fluctuation patterns with high biomass values in the mid-1970s and around 1990, and very low values everywhere in 1979, 1986, 1987, 1996 and 1997. The patterns were statistically significantly synchronized (Spearman rank tests). Spearman *r*-values amounted to $+0.72$ for the within-Balgzand comparison between *Nephtys* data included in Fig. 2a, b ($n = 28$, $P < 0.001$) and to $+0.72$ and $+0.60$ for the two comparisons between Balgzand areas and Groninger Wad (Fig. 2a vs. Fig. 2c: $n = 26$, $P < 0.001$ and Fig. 2b vs. Fig. 2c: $n = 26$, $P < 0.01$). Apparently, a common environmental factor governed the dynamics of *Nephtys* in the different areas, even if more than 100 km apart. As the minimal values of *Nephtys* biomass coincided
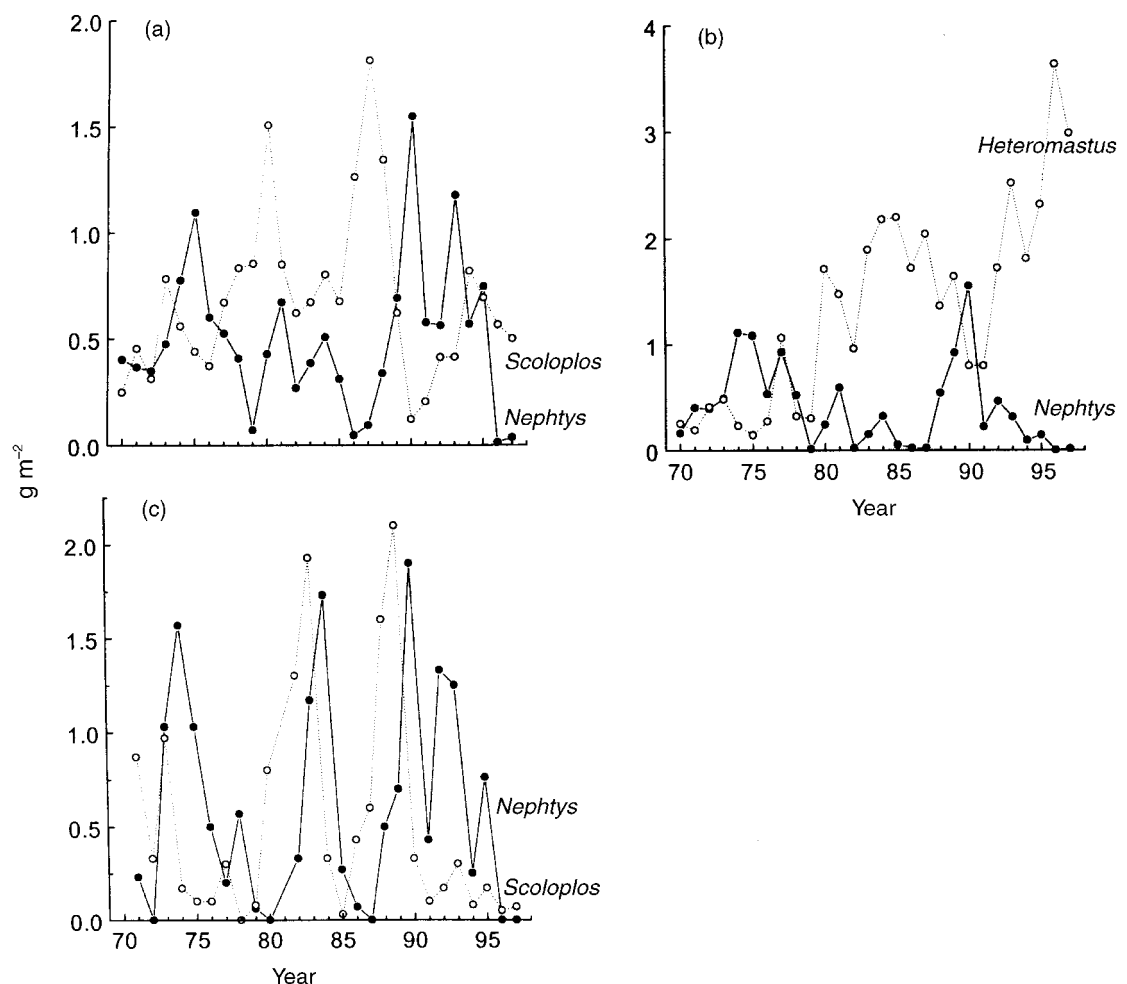

Fig. 2. Long-term changes in the abundance (g AFDW m^{-2}, annual late winter values) of the predatory worm *Nephtys hombergii* (solid points and lines in each of the graphs a, b and c) and its two main prey species (open points and broken lines) in three areas: (a) *Scoloplos armiger* in the Balgzand area 'Sand', where this species dominates over *Heteromastus* (averages of three stations; see Fig. 1a for location of the stations); (b) *Heteromastus filiformis* in the Balgzand area 'Mixed' where this species dominates over *Scoloplos* and *Nephtys* is a common species (averages of eight stations; compare Fig. 1a: 'Mixed-sandy' + 'Mixed-silty'); (c) *Scoloplos armiger* on the Groninger Wad, 120 km east of Balgzand (averages of three stations).

with the coldest winters, the possible relationship between *Nephtys* abundance and character of the winter will be explored below.

The course of the annual biomass values of the two prey species (Fig. 2a, c: *Scoloplos*; Fig. 2b: *Heteromastus*) differed distinctly from the common pattern observed in *Nephtys*. However, the fluctuation patterns of the three species appear to be related in some ways. In the first place, there are several instances of dips of predator abundance followed by peaks of prey abundance about one year later, e.g. maximal values of *Scoloplos* abundance at Balgzand in 1980 and 1987 occurred 1 year later than minimal *Nephtys* values in 1979 and 1986, respectively (Fig. 2a), and the *Scoloplos* peaks at Groninger Wad in 1988 and 1989, 1 or 2 years after the 1987 dip in *Nephtys* (Fig. 2c). On the other hand, low values of *Scoloplos* biomass were observed at Balgzand in 1990 and 1991, 1 year after the high values of *Nephtys* in 1989 and 1990 (Fig. 2a). At Groninger Wad, low *Scoloplos* values were observed in 1975, 1985 and 1991, invariably 1 year after a high value of *Nephtys* biomass (Fig. 2c). Correlation coefficients between *Nephtys* and *Scoloplos* biomass values calculated with different time-lags (from +4 to –4 years) yielded in both data sets (Balgzand and Groninger Wad) minimal r-values (–0·52 and –0·42, respectively) for a time-lag of 1 year (*Nephtys* in year n and *Scoloplos* in year $n + 1$). The underlying process will be dealt with below under the heading '*Nephtys* abundance and subsequent prey dynamics'.

In the case of *Heteromastus,* similar relationships can be noted in Fig. 2b. However, in this species a consistent and dramatic increase during the period of observation was the prevailing change, making time-lag correlation with *Nephtys* meaningless.

In the following, fluctuation patterns shown in Fig. 2a–c will be related successively to winter temperatures, prey abundance and predator abundance.

CHARACTER OF THE WINTER AND *NEPHTYS* DYNAMICS

At the end of winter, the abundance of *Nephtys* was found to be highly dependent on the temperatures experienced during the foregoing winter months. The colder the winter was, the lower was the *Nephtys* biomass at the end of the winter (Fig. 3a). This correlation was significantly ($P < 0·001$) negative both at Balgzand and at Groninger Wad. The cause of this relationship between *Nephtys* abundance and character of the foregoing winter will have been the lower survival during cold than during mild winters. The proportion of *Nephtys* biomass in late summer that was still alive at the subsequent late winter sampling declined with the number of cold days experienced (Fig. 3b). This cor-
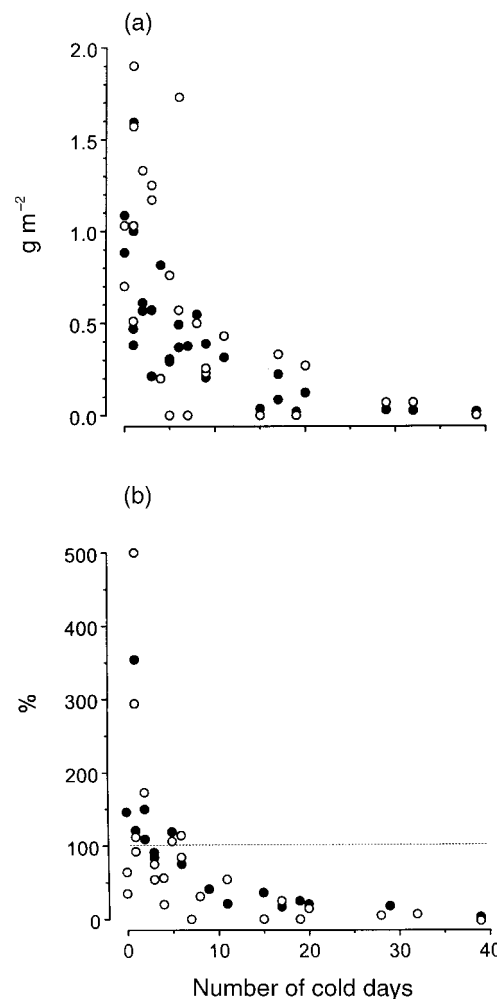
Fig. 3. The relationships between character of the winter (expressed in the number of days with a maximum air temperature < 0°C in the Balgzand area) and the fate of *Nephtys hombergii* on the tidal flats of Balgzand (closed points, means of the 11 *Nephtys*-rich stations) and Groninger Wad (open points, means of three stations), expressed in: (a) mean biomass in the subsequent late winter/early spring period (in g AFDW m^{-2}), and (b) the proportion (in percentage) left in this period of the biomass observed in the preceding sampling period in late summer. Spearman correlation coefficients in (a) Balgzand: $r = -0·87$, $P < 0·001$, $n = 28$, Groningen: $r = -0·70$, $P < 0·001$, $n = 26$, and in (b) Balgzand: $r = -0·94$, $P < 0·001$, $n = 17$, Groningen: $r = -0·73$, $P < 0·001$, $n = 24$.

relation was significant ($P < 0·001$) both at Balgzand and at Groninger Wad. As a consequence of this close relationship, most of the variability (about 70% at Balgzand) in late winter biomass was explained by the parameters (number of cold days, average temperature of the coldest months) of winter. After all winters with more than about 10 cold days (with a maximum temperature not exceeding 0°C, compare Fig. 3), < 50% of the late summer biomass was still present in late winter. On average,

this proportion was < 25% (closed points in Fig. 4a, c). On the other hand, after mild or close-to-average winters *Nephtys* biomass had hardly changed during the winter half-year (open points in Fig. 4a, c).

During the 28 years of the 1970–97 period of observation, eight of such cold winters (with > 10 cold days) occurred (viz. in early 1970, 1979, 1982, 1985, 1986, 1987, 1991 and 1996). Thus, on average once every 3 or 4 years, the stock of *Nephtys* was severely reduced. Such cold winters occurred more or less randomly over the period of observation. The length of the periods with undisturbed development of the *Nephtys* population ranged from 1 (viz. 1985–86 and 1986–87) to 9 (viz. 1970–79) years.

Late winter values of *Nephtys* biomass were thus highly variable from year to year. They predicted, to a large extent, the biomass values during the remainder of the year (Fig. 4b,d). At Balgzand, the variability in summer biomass was explained for almost 90% by the preceding late winter biomass value (Fig. 4b). On average (11 stations, 18 years), late winter and late summer biomass values of *Nephtys* at Balgzand amounted to 0.37 ± 0.09 and 0.48 ± 0.09 g AFDW m^{-2}, respectively (means and SE). At Groninger Wad these figures amounted to 0·61 and 1·06 g m^{-2}, respectively. Seasonal increments between winter and summer were more frequent than declines (15 out of the 18 years at
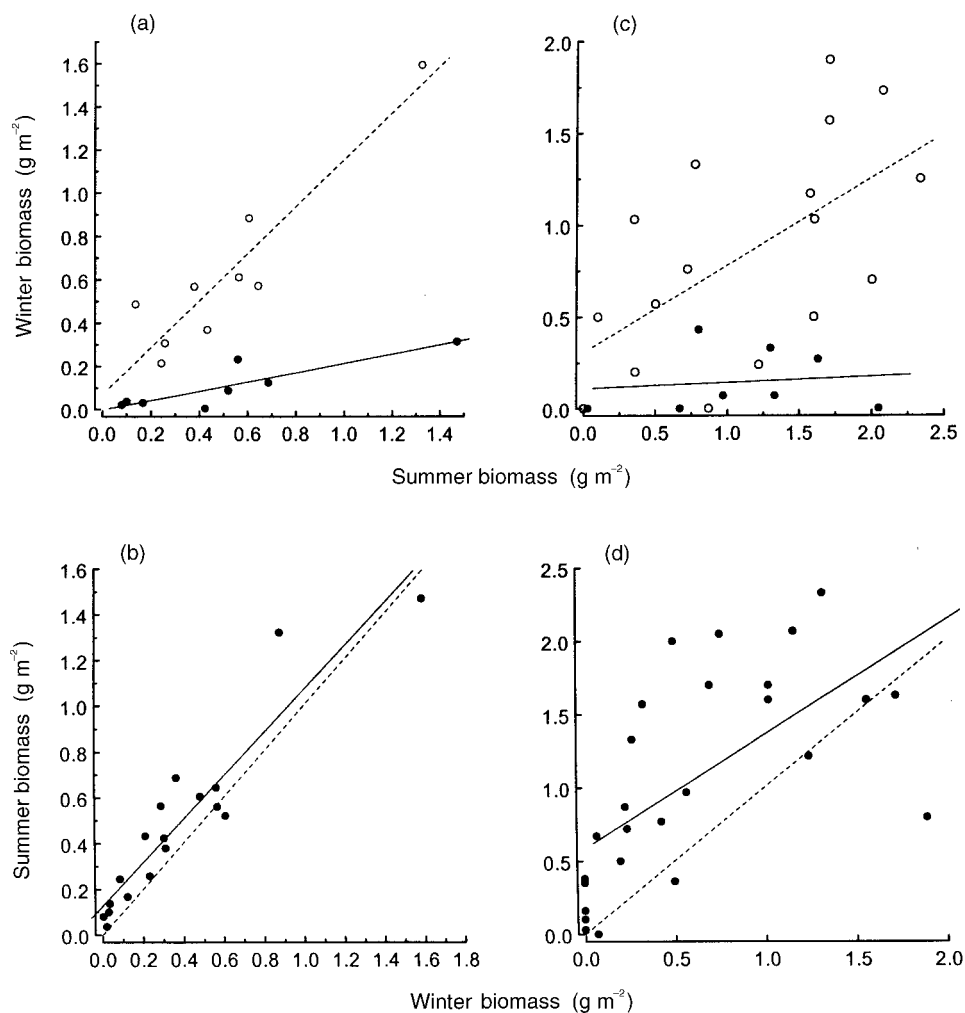

Fig. 4. The dependence of *Nephtys hombergii* biomass (in g AFDW m^{-2}) on the biomass value observed 6 months earlier in two areas: (a, b) Balgzand (means of 11 *Nephtys*-rich stations) and (c, d) Groninger Wad (means of three stations). (a, c) Dependence of late winter biomass (WB) on that of the foregoing late summer (SB) in two groups of years (open points and broken line = including a mild winter; closed points and full line = including a cold winter). (b, d) Dependence of late summer biomass (SB) on that of the foregoing late winter (WB), showing also the (broken) line SB = WB. Regression lines: (a, ○) WB = + 0·07 + 1·09 SB ($r^2 = 0.85$, $n = 9$, $P < 0.001$), (a, ●) WB = –0·00 + 0·22 SB ($r^2 = 0.76$, $n = 8$, $P < 0.01$), (c, ○) WB = + 0·31 + 0·48 SB ($r^2 = 0.60$, $n = 17$, $P < 0.05$), (c, ●) WB = + 0·11 + 0·03 SB ($r^2 = 0.12$, $n = 8$, $P > 0.05$), (b) SB = + 0·10 + 0·93 WB ($r^2 = 0.88$, $n = 18$, $P < 0.01$), (d) SB = + 0·58 + 0·78 WB ($r^2 = 0.64$, $n = 26$, $P < 0.01$).

Balgzand, and 21 out of 26 years at Groninger Wad; in both areas $P < 0.01$, ranked sign test). At Balgzand, the few winter-to-summer declines were relatively small (Fig. 4b). The Groninger Wad data set (Fig. 4d) showed similar patterns, but with higher scatter, probably due to the lower number of stations sampled (3 vs. 11 at Balgzand).

PREY SUPPLY AND *NEPHTYS* DYNAMICS

The influence of prey abundance on *Nephtys* dynamics will be studied only for the spring/summer season, because changes in *Nephtys* abundance in winter were dominated by temperature effects (Fig. 3). Our hypothesis is that seasonal increase in *Nephtys* biomass will be greater in years with a high than in years with a low prey biomass. For obvious reasons, this study will be made separately for the parts of Balgzand where each of the two prey types dominates (compare Fig. 1). We refrain from studying his relationship for the Groninger Wad data set, because no data are available on *Heteromastus* and this prey will have been the main one there (as judged from the rather high silt contents of the local sediments).

Influence of Scoloplos *abundance in the 'Sand' area of Balgzand*

The Balgzand area 'Sand' with relatively high *Scoloplos* and low *Heteromastus* abundance is characterized by a uniformly high *Nephtys* abundance of about 0·6 g AFDW m^{-2} (Fig. 1a: the three stations in the northernmost part of Balgzand). Prey abundance, on the other hand, was generally low in this area with a long-term mean late winter biomass of small-worm species of only 0·9 g AFDW m^{-2} (including 0·7 g of *Scoloplos*). In this area, *Nephtys* biomass usually increased between late winter and late summer (Fig. 5a). The exceptional 3 years that showed a decline were among the 4 years that started with the lowest values for *Scoloplos* biomass (Fig. 5a). As the biomass of *Heteromastus* and other small worms was always low in this area, 2 of these 3 years also started with the lowest values for the sum of the biomass values of all small worm species together. Other small worms did not add more than 0·1 g m^{-2} to potential prey biomass in these 2 years. Total prey biomass in the 'Sand' area was always substantially lower than in the 'Mixed' area of Balgzand. Thus, if anywhere prey supply might limit seasonal *Nephtys* increases, it would be in the poor 'Sand' area. Though the correlation shown in Fig. 5a was statistically non-significant (Spearman $r = +0.14$, $n = 18$), it will, nevertheless, be meaningful that the *Nephtys* population consistently showed a decline, rather than its usual seasonal increase if the biomass of its main prey and of all potential worm prey were < 0.3 g AFDW m^{-2} in
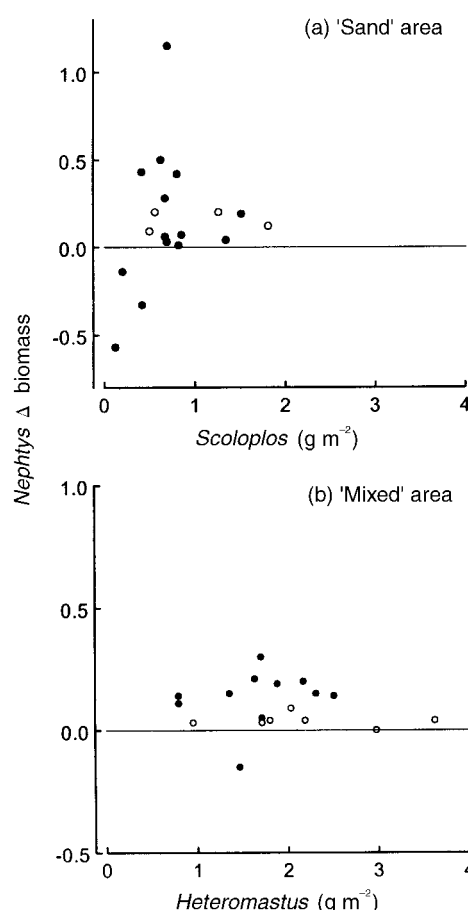
Fig. 5. The relationships between prey abundance (g AFDW m^{-2}) of either *Scoloplos armiger* (a) or *Heteromastus filiformis* (b) in late winter and biomass change in *Nephtys* during the subsequent 6-month period in two areas: (a) the northern part 'Sand' of Balgzand (where *Scoloplos* is by far the most important prey type), and (b) the 'Mixed' part of Balgzand (where *Heteromastus* is the most important prey type). One point for each year. The open points refer to the years starting with a very low *Nephtys* biomass.

late winter. These prey biomass values were less than half of the *Nephtys* biomass at that time. Exclusively in the 3 years that showed the exceptional decline of *Nephtys* biomass between late winter and late summer, biomass of the predator was larger than that of the potential prey at the start of the growing season in late winter. In the other 15 years that showed the usual seasonal increase of *Nephtys* biomass, prey biomass exceeded predator biomass in late winter.

Because, initially, low biomass values of *Nephtys* (as occurred in years starting with a severe winter) might have limited the potential to increase in such years, these years were marked (open points) in Fig. 5. Increases were, indeed, rather low in these years, but omission of these points from Fig. 5 did not substantially change the relationships and correlation coefficients.

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Influence of Heteromastus *abundance in the 'Mixed' area of Balgzand*

No clear relationships were observed between late winter prey biomass values and changes in *Nephtys* biomass during subsequent spring/summer periods in the area 'Mixed'. As the biomass values for *Heteromastus* generally exceeded those for *Scoloplos* by far, the relationship is shown for the former prey species only (Fig. 5b). Spearman rank tests, however, were applied for *Scoloplos* and *Heteromastus* biomass separately as well as for their sums in each of these two areas. The observed Spearman *r*-values ranged from -0.17 to $+0.17$, all of them being far from statistically significant ($n = 18$ in each case). Moreover, the rare declines of *Nephtys* biomass values between winter and summer did not occur specifically in years with low prey supply.

It will be meaningful that late winter values of total biomass of small-worm species in the area 'Mixed' were never below about $1.0\,\mathrm{g}\;\mathrm{m}^{-2}$. Thus, prey supply values as low as observed in some years in the *Scoloplos*-dominated area 'Sand' (Fig. 5a) were never found in the part of Balgzand where *Heteromastus* was the most important prey type. Apparently, prey supply in the *Heteromastus*-dominated Balgzand areas was never a limiting factor for *Nephtys* increase.

CHARACTER OF THE WINTER AND PREY ABUNDANCE

Neither in *Scoloplos* nor in *Heteromastus* were late winter biomass values significantly related to the character of the preceding winter months. Correlation coefficients with the numbers of cold days ranged between -0.12 and -0.18 for these two species at Balgzand (both species tested) and Groninger Wad (*Scoloplos* only). At $n = 26$–28, these figures were far from statistically significant.

The biomass values of the two prey species, however, tended to be higher if the winter of one full year earlier had been cold than when it had been mild or close to average. Spearman *r*-values for the relationships with the numbers of cold days 1 year earlier amounted to $+0.42$ (Balgzand) and $+0.23$ (Groninger Wad) in *Scoloplos* and to $+0.26$ in *Heteromastus* (Balgzand). At $n = 26$ or 27 only the correlation coefficient in *Scoloplos* on Balgzand was significant ($P < 0.05$). As a cold winter was invariably followed by a full year characterized by a low *Nephtys* abundance (Figs 3a and 4b), this low predator abundance may have been the cause of the relatively high prey abundance a full year after a cold winter. This will be explored below.

NEPHTYS ABUNDANCE AND SUBSEQUENT PREY DYNAMICS

Our hypothesis is that prey biomass will decrease more (or increase less) during periods with high than during periods with low *Nephtys* abundance, resulting in lower prey biomass values after years with high than after years with low *Nephtys* abundance. Thus, we studied both the absolute values of prey biomass (in late winter) after years with different predator abundance and the changes in prey biomass from late winter to late summer at different predator abundance. For predator abundance, we used the late winter values at the start of the year, because late summer biomass values of *Nephtys* were well correlated with (and at Balgzand also close to) the preceding late winter figures (Fig. 4b,d). Thus, the observed late winter values were representative for (almost) the full year following. The two prey species will be dealt with separately, but at Groninger Wad only *Scoloplos* could be studied.

Influence of Nephtys *on* Scoloplos

At Balgzand, *Scoloplos* biomass values in late winter were generally higher after years with low *Nephtys* biomass than after years with high predator biomass (Fig. 6a). The Spearman rank correlation coefficient r amounted to -0.57 ($n = 27$, $P < 0.01$) for the relationship between S*coloplos* biomass in late winter of year $n + 1$ and *Nephtys* biomass in late winter of year *n*. At Groninger Wad, a similar relationship was observed (Fig. 6b) with a Spearman $r = -0.44$ ($n = 24$, $P < 0.05$).

Generally, the abundance of *Scoloplos* increases strongly during the spring/summer half year. At Balgzand, in half of the 18 years 1980–97, the late summer biomass amounted to even more than twice the preceding late winter value, whereas it was lower in only 2 years. The seasonal biomass increase in this prey was larger as the abundance of the predator was lower ($r = -0.46$ for ratio summer/winter and -0.44 for difference summer $-$ winter; both $P < 0.05$, one-sided, $n = 18$). At Groninger Wad, similar relationships were found with *r*-values of -0.51 and -0.54, respectively. At $n = 26$, these correlation's were statistically significant at the 0.02 level.

Influence of Nephtys *on* Heteromastus

As in *Scoloplos,* biomass values in *Heteromastus* were generally lower after years with high predator biomass than after years with low *Nephtys* biomass (Fig. 6c). The Spearman *r*-value amounted to -0.54 ($n = 27$, $P < 0.01$). In this prey species, the biomass values were less homogeneous than in *Scoloplos* (compare the degree of overlap of the various types of points in each of Fig. 6a,c). Biomass values of
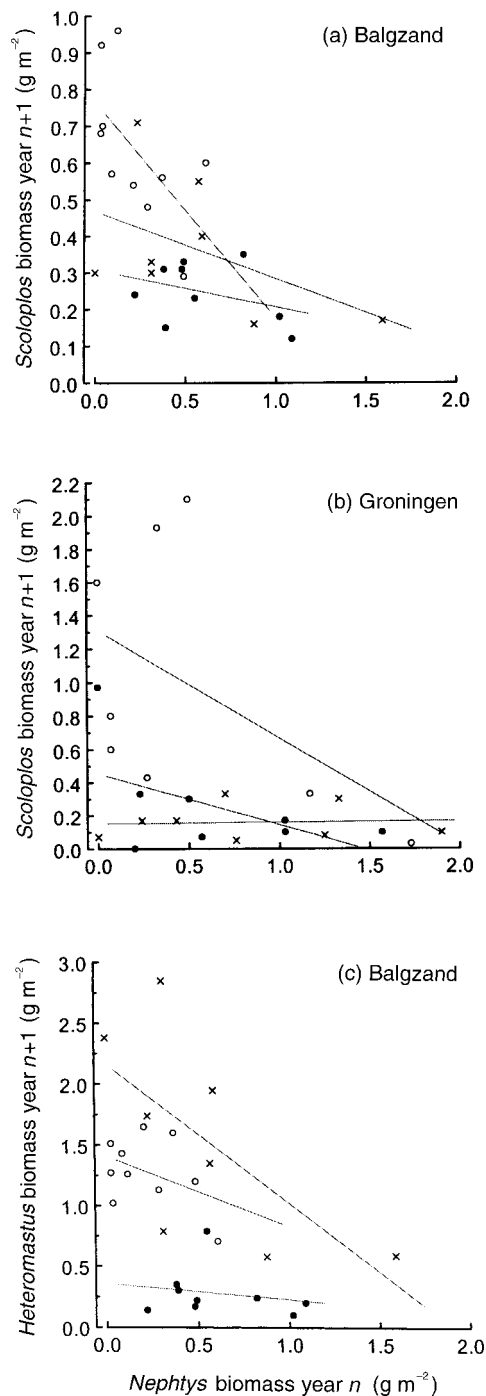
Fig. 6. The relationship between *Nephtys* biomass (g AFDW m^{-2}) in late winter of year *n* and the biomass values of the two main prey species 1 year later. (a) *Scoloplos* on Balgzand, averages of data of 11 stations in the areas 'Sand' and 'Mixed' with frequently high *Nephtys* abundance; (b) *Scoloplos* on Groninger Wad, averages of three stations; (c) *Heteromastus* on Balgzand, averages of the same 11 stations as used in (a). The 27 points of Balgzand and 24 points for Groninger Wad have been divided into three groups:● for values observed in the 1970s, cir; for those in the 1980s, and × for those in the 1990s.

Heteromastus were generally lower in the 1970s (solid points in Fig. 6c) than in both the 1980s and the 1990s if compared at the same *Nephtys* abundance (Fig. 6c). In *Scoloplos* a similar difference between the decades was observed at Balgzand (Fig. 6a), though less markedly, whereas these differences were inconsistent at Groninger Wad (Fig. 6b). Compare also Fig. 2b with Fig. 2a, c: the upward trend with time was much stronger in *Heteromastus* than in *Scoloplos*.

In *Heteromastus*, biomass also increased significantly in the spring/summer half year in nearly all years. Again, this seasonal increase was larger as *Nephtys* biomass was lower: $r = -0.40$ for the ratio summer/winter and $r = -0.54$ for the difference summer – winter (both $P < 0.05$).

Influence of Nephtys *on* Anaitides

Because Schubert & Reise (1986) found that the polychaete *Anaitides mucosa* was eaten by *Nephtys* in the laboratory and showed reduced abundance in part of their enclosure experiments, we studied also the relationship between the annual biomass of this species and *Nephtys* abundance in the foregoing year at Balgzand. The correlation proved to be weak and was far from significant ($r = -0.05$, $n = 27$, $P > 0.1$).

Influence of Nephtys *on total prey abundance*

From the foregoing, it will be clear that total prey abundance (*Scoloplos* + *Heteromastus*) increased more in years with low than in years with high predator abundance. The summer/winter ratio of prey biomass was, indeed, higher as *Nephtys* biomass had been lower (Fig. 7a: $r = -0.53$, $n = 18$, $P < 0.05$) as was the difference summer minus winter prey biomass (Fig. 7b: $r = -0.63$, $n = 18$, $P < 0.01$). Only in the one year with the highest *Nephtys* abundance ever observed was the seasonal increase in prey biomass reduced to nil. In all other years, prey biomass showed its usual increase between late winter and late summer, though this increase was stronger at low than at high predator abundance. A 1-g m^{-2} higher *Nephtys* biomass reduced prey biomass by almost 2 g m^{-2} (Fig. 7b).

Discussion

The availability of long-term and homogeneous data series on population sizes of different species within the same community opens excellent opportunities to evaluate the relative importance of different types of factors affecting dynamics of populations. Such a long-term approach is followed in an increasing number of publications reporting simultaneously on the influences of both abiotic and biotic factors in

Table 1. Some examples of recent long-term studies showing involvement of both abiotic and biotic factors in the determination of population dynamics of (groups of) species. n = number of years of observation period

Species	n	Kind of factor involved Abiotic	Biotic	Reference
Moose	18	Winter weather	Predators	Post & Stenseth (1998)
White-tailed deer	11	Winter weather	Predators	Post & Stenseth (1998)
Red deer	30	Winter weather	Competition	Forchhammer *et al.* (1998)
Oystercatcher	21	Winter temperatures	Food	Camphuysen *et al.* (1996)
Sablefish	23	Currents	Food	McFarlane & Beamish (1992)
Cod	30	Salinity	Parents stock	Myers *et al.* (1993)
Copepods	25	Weather	Food/predators	Frid & Huliselan (1996)
Zooplankton	29	Upwelling (wind)	Predators	Verheye & Richardson (1998)
Baltic clam	24	Winter temperatures	Predation	Beukema *et al.* (1998)
Zoobenthos	15	Winter temperatures	Food	Buchanan & Moore (1986)
Worms	28	Winter temperatures	Predation/food	Present paper

natural ecosystems. Table 1 enumerates some recent examples of such studies, including mammals, birds, fishes and various invertebrates.

In the marine benthic realm, decades-long data series appear to be rather rare and are often of an intermittent nature (Pearson & Barnett 1987), and most of these appear to be terminated (Duarte 1992). One of the features of the present three-decade long series on bottom animals living on tidal flats of the Wadden Sea is the repeated incidence of an (almost) complete and sudden disappearance of an important predator from the system as a consequence of the extreme environmental conditions during a severe winters (Fig. 3). In other areas, oxygen depletion has been observed as another cause of similar sudden declines in *Nephtys* (Weigelt 1991). Such declines of a species over extensive geographical areas offer unique opportunities study population dynamics on a large spatial scale in both the directly affected species and its predators, prey or competitors. Strongly reduced *Nephtys* densities after cold winters were not only observed at the present study sites, but were found to occur over vast geographical areas (hundreds of km), including the inter-tidal flats over the entire Wadden Sea (see Fig. 2b and Table 1 of Beukema *et al.* 1996) and also nearby subtidal areas (Beukema, Dörjes & Essink 1988). Such synchronized reductions over extensive areas point to a large-scale environmental influence as a common cause. The character of the winter is each year similar over vast areas in western Europe (Beukema *et al.* 1996). The observed correlation of (changes in) *Nephtys* abundance with numbers of cold days (and mean temperatures in winter), therefore, will indicate a common cause, viz. the character of the winter.

Irrespective of current prey densities, the densities of the predator are suddenly and strongly reduced in a severe winter, and a new cycle of interactions can start. In this way, Nature offers the conditions for a large-scale experiment every 1–10 years or so.

At the low levels of predator abundance after a cold winter, biomass values of the two prey species increased much faster than at high *Nephtys* biomass. This was so both for relative (Fig. 7a) and absolute (Fig. 7b) prey abundance, resulting in a negative relationship between predator abundance and prey densities 1 year later (Fig. 6). The hypothesis of a negative influence of predator abundance on changes in prey biomass was thus born out. Again, the observed correlative relationships will point to underlying causative processes, as they corroborate results of enclosure experiments by Schubert & Reise (1986) and of detailed small-scale field observations by Beukema (1987). We are not aware of any evidence for alternative hypotheses, such as possibly higher food availability for the prey populations after cold than after mild winters (their own abundance was similar after mild and cold winters).

Thus, prey densities were affected directly by predator abundance in the preceding year. As predator abundance was strongly affected by foregoing winter temperatures, prey densities, in turn, showed a (relatively weak) relationship with winter temperatures 1 year earlier: the colder a winter was, the more abundant were the prey at the sampling occasion slightly over 1 year later. It should be added that winter temperature-governed changes in the abundance of *Nephtys* could not fully explain the observed dynamics of *Scoloplos* and *Heteromastus*. Both prey species showed also a long-term increasing trend that was particularly outspoken in *Heteromastus* (Fig. 2b), but was simultaneously observed also in several other worm species (Beukema 1991) and was not accompanied by any clear declining long-term trend in the abundance of the predator. Therefore, the long-term upward trends in these prey of *Nephtys* will not have been caused primarily by changes in *Nephtys* abundance, but probably originated in the first place from an increased food supply for benthic deposit feeders as a consequence of eutrophication (Beukema 1991; Beukema & Cadée
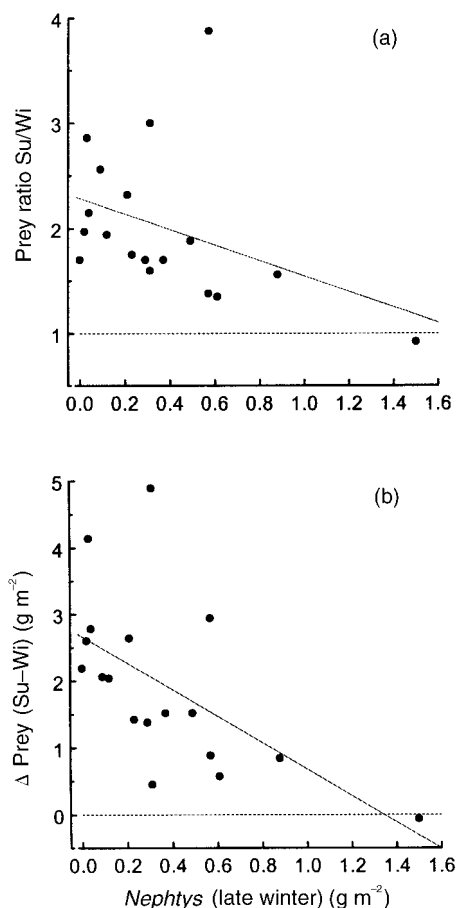
Fig. 7. The relationships between *Nephtys* biomass in late winter (in g AFDW m^{-2}) and changes in total prey (*Scoloplos* plus *Heteromastus*) biomass during the subsequent half year, expressed as: (a) the ratio of late summer to preceding late winter biomass, and (b) the absolute difference between late summer and preceding late winter biomass (in g AFDW m^{-2}). Both graphs refer to the same averages of 11 *Nephtys*-rich sampling stations on Balgzand (those in the areas Sand and Mixed, cf. Fig. 1) and show one point for each of the 18 years of the 1980–97 period. Best linear fits were: (a) prey ratio = 2·28–0·74 × predator biomass, and (b) prey difference = 2·66–1·98 × predator biomass.

1997). In *Heteromastus* populations, long-term increases in abundance without concomitant declining trends in their predators have also been observed in other areas (e.g. Buchanan & Moore 1986). In conclusion, top-down as well as bottom-up processes played major roles in the dynamics of the two prey species, whereas the influence of winter temperatures was weak and indirect.

As to the reverse relationship, a clear influence of prey abundance on predator dynamics appeared to be generally absent over the usual ranges of prey supply (Fig. 5). Only at extremely low prey densities (prey biomass values < 0·5 g m^{-2}) that were even lower than simultaneous predator biomass values and occurred only rarely in a small and exposed

area with an invariably impoverished benthic fauna (Beukema & Cadée 1997), the usual seasonal increase in predator biomass changed to a decline. So only limited evidence was found to corroborate the hypothesis that prey abundance would affect predator density, leaving winter temperatures as the main factor determining predator abundance.

The full cycle of predator–prey interactions, as predicted by simple models of the Lotka–Volterra type, started in the species studied in the usual way, that is prey density increased at low predator abundance (as occurred repeatedly after a cold winter). More or less at the same time, predator abundance started to increase too and reached, after a time-lag of 1 or 2 years, a sufficiently high level to cause substantial declines in prey abundance. However, the final piece of the cycle (i.e. declining predator densities caused by low prey supply) was hardly observed. Instead, sudden drops in predator biomass were encountered at a broad range of prey densities and always in cold winters (the heavy lines in Fig. 8). Usually, interruptions by cold winters ended cycles that were still far from complete. The only long period without a severe winter interruption was 1970–79. During this period, the *Nephtys–Scoloplos* interaction showed the predicted counter-clockwise cycle rather neatly (Fig. 8). This cycle was completed between 1977 and 1978, and thus lasted between 7 and 8 years. With such cycle lengths, all other started cycles were bound to be interrupted in a more or less early stage by a cold winter (1982, 1985, 1986, 1987, 1991 and 1996), long before the full cycle was completed by predator reductions as a consequence of low prey supply.

Summarizing the results of the present study: both extrinsic (low temperatures in winter) and intrinsic factors (interrelationships between species) played a clear role in governing fluctuations within the tidal-flat benthic community. Predator abundance was reduced to very low levels in more than 25% of the years by cold winters (Fig. 3). Such low *Nephtys* abundance persisted through the remainder of the year (Fig. 4b,d). A clear limitation of predator abundance by prey supply was less frequent and limited to a small and poorly populated part of the study area (compare Fig. 5a with Fig. 5b). The two prey species, on the other hand, were not directly affected by winter temperatures and their fluctuations were clearly related to predator abundance (Figs 6 and 7). Cold winters, however, could exert an influence on prey biomass in an indirect way and with a time lag, viz. via predator abundance. Thus, for an explanation of the fluctuation patterns observed in three tidal-flat polychaete species, weather effects were at least as important as interrelationships between the studied species. Cold winters
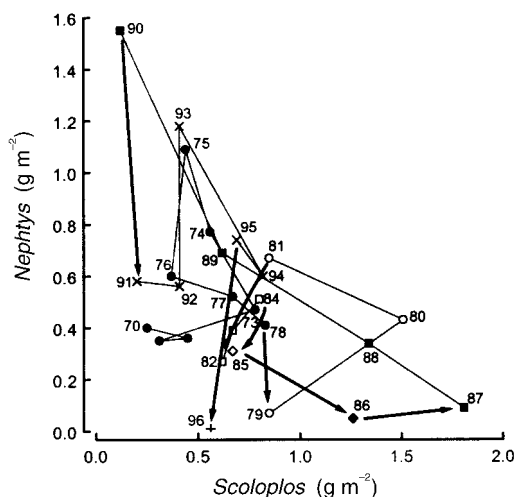
Fig. 8. Plots of simultaneously observed annual biomass values of prey (*Scoloplos*, horizontal axis) and predator (*Nephtys*, vertical axis), showing counter-clockwise rotation of time trajectories (directions denoted by year numbers and arrows). Data shown are values observed in the 'Sand' area of Balgzand (the same as in Fig. 2a). The heavy arrows represent changes occurring in years including a cold winter (> 10 cold days).

frequently broke running cycles and started new cycles of predator–prey interactions (Fig. 8).

By using part of the present data set (viz. the data on *Nephtys* and *Scoloplos* collected on Balgzand), Van der Meer, Beukema & Dekker (1999) reached similar conclusions. In addition, they found that the relative changes of the predator and prey populations were density dependent.

Results of other recent long-term studies (Table 1) indicate that dynamics in several species are affected simultaneously by both abiotic and biotic factors, the latter including either or both bottom-up (feeding) and top-down (predation) processes. Frequently, such different types of factors will not act in an independent way. In the above case, prey abundance was influenced by winter weather via predation pressure. In several cases mentioned in Table 1, physical factors affected the size of populations both directly, and via quantity and/or quality of their food supply. A simple correlative approach is then bound to fail in pointing to the exact causative process. Experiments and modelling will be indispensable complements to reach a full and sound understanding of the causation of variation in abundance. Consistent collection of long-term data series, however, will have to provide the essential facts to judge to what extent various processes are effective in control of population size of species in their natural environment.

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