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Is food supply for shellfish-eating birds in the western Wadden Sea affected by the between-species synchrony in year-to-year fluctuations of bivalve population parameters?

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Abstract

For a better understanding of functioning and stability of ecosystems, it is important to know to what extent constituent species show similarity in their long-term fluctuation patterns, i.e. whether their numbers and biomass frequently show simultaneous peaks and lows. Synchronic peaks and lows of important species would enhance variability in the functioning of the entire system and might affect its stability. When fluctuation patterns of individual species are largely independent, their peaks and lows would tend to extinguish each other's effect on overall parameters (such as total zoobenthic biomass), thus promoting system stability. A long-term (46 years) monitoring study of the macrozoobenthos in a large (50 km²) tidal-flat area revealed that the 4 most important bivalve species (3 suspension feeders: *Cerastoderma edule*, *Mytilus edulis*, *Mya arenaria* and 1 deposit/suspension feeder: *Limecola (Macoma) balthica*) frequently showed peak numbers of their recruits in the same years. The annual growth rates of the three suspension feeding species showed some synchrony as well. Annual survival rates, on the other hand, did not show any synchronization, wiping out the initial synchrony of numbers within less than 2 years. As a result, annual biomass values did not show any positive between-species correlations. Annual amounts of bivalves that are accessible as bird food rarely declined to levels below 5 g AFDW m⁻² and showed limited (5 to 10 fold difference between maximal and minimal values) variation. Oystercatchers left the area quicker in late winter and showed increased death rates at very low levels of food supply. Total bivalve bird food did not show any significant long-term trend. However, biomass of *Mya arenaria* showed an increasing trend and that of *Limecola balthica* a declining trend.

Keywords: Annual recruitment, Survival, Seasonal weight gain, Biomass, Long-term data series, Wadden Sea, *Cerastoderma edule*, *Mytilus edulis*, *Mya arenaria*, *Limecola (Macoma) balthica*

Introduction

Long-term data series on characteristics of natural populations (such as their abundance) usually show strongly fluctuating patterns. If such data series for populations of different species living in the same area frequently show their peaks and troughs in the same years, the fluctuation

patterns are more or less synchronized. Synchronization may arise whenever the processes underlying the variability are governed by a common environmental factor that fluctuates in the same way over an extensive area. Such synchrony is a frequently occurring phenomenon [1]. For example, winter character (as being governed along Atlantic coasts largely by the NAO index) is such a wide-ranging influential factor in western Europe [2], affecting not only different populations of the same species over vast areas (e.g. [3–5]), but also of different

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species over areas as large as the North Atlantic [6] or the Wadden Sea [7].

If synchrony in long-term patterns in constituent species is strong, consequences for the ecosystem may be serious if these species play a key role in the functioning of the system, e.g. by contributing high shares to total-system biomass or productivity or to food supply for birds. With strong between-species synchrony, attributes of the entire system will tend to exhibit maximal or minimal values in the same years, resulting in a system that is less stable than one with species fluctuating independently. Alternating periods of wealth and scarcity of food for birds and fishermen might be such a result [8]. In the Wash (England), [9] found that mass mortalities in oystercatchers occurred only when both cockle and mussel stocks were low. Reduced survival as a consequence of food shortage was reported in Wadden Sea populations of 2 bird species (oystercatchers and eiders) that are specialized on feeding on shellfish [10].

Fluctuations in biomass of populations of benthic animals are based on variability in both numerical abundance and growth rates [11]. Numerical abundance varies by variability in recruitment and subsequent survival. In the Wadden Sea area, severity of winters was found to positively affect subsequent summer recruitment in several bivalve species, resulting in peak recruitments in the same years over hundreds of km and in several species at the same time [7, 12]. The underlying process proved to be a positive relationship between winter temperature and spring abundance of epibenthic predators (shrimps, shore crabs), being common enemies of the tiny spat of several bivalve species which have just settled on tidal flats in spring [13–16].

So far, possible synchrony of growth rates in different species of Wadden Sea bivalves are understood less well. Changes in eutrophication state over extensive areas [17, 18], influencing concentrations of pelagic algae, might act as a common factor governing food supply and annual growth rates in the same way in several species over large areas, but there appears to be no clear evidence. Water temperatures and abundances of food competitors (and total filter feeding activity) appear to be other factors underlying observed synchronization in individual seasonal weight gains in filter-feeding bivalve species [19]. Anyhow, any between-species synchrony in annual growth rates will contribute to synchrony in their biomass values.

The strong between-species synchrony in particularly their early recruitment success [7, 16] raises the question to what extent this initial synchrony extends to older age groups and then has consequences for later biomass. The aim of the present paper is to investigate to what extent annual estimates of recruit abundance, their survival,

individual weight gain and biomass over an extended period of 4 decades were synchronized between the most important bivalve species in a Wadden Sea tidal-flat area. Particularly, we want to know to what extent the known synchronized recruitment patterns result in synchronically fluctuating biomass values and thus would affect the availability of bivalve food for birds. The bivalve species included in our study are 3 suspension-feeding species: *Cerastoderma edule*, *Mytilus edulis*, and *Mya arenaria* and 1 deposit/suspension feeding species: *Limecola (Macoma) balthica*. Together, these species constitute in most years >50% of the total biomass of the macrozoobenthos of the Wadden Sea tidal flats [20–22]. In other bivalve species living in the Balgzand area, biomass values were either invariably low (*Abra tenuis*, *Angulus tenuis*, *Mysella bidentata*, *Petricola pholadiformis*, *Scrobicularia plana*, *Spisula subtruncata*, *Crassostrea gigas*) or became high only after 2004 (*Ensis directus*: [23]).

Methods

Study area

The data on bivalves were obtained as part of a long-term program involving twice-annual sampling ever since the 1970s of the macrozoobenthic animals at 15 permanent sampling stations located on Balgzand (Fig. 1), a tidal flat area in the westernmost part of the Wadden Sea (at about 53° N and 5° E). Further details on the sampling area, the stations, and the methods can be found in [8]. For the estimates of annual recruitment, data from all 15 stations were used. For the study of growth rates, 6 stations in the central part of Balgzand (the transects numbered 4, 5, 8, 9, 10, and 11 in Fig. 1) were chosen. This part of Balgzand covered about one-third of the total Balgzand tidal-flat area of 50 km². In the part of Balgzand to the north of this area, available data on growth were scarce due to failing recruitments of the studied species in nearly all years, probably due to adverse environmental conditions (exposure to strong currents and wave action, resulting in unstable and coarse sediments). South of the selected area, growth rates were invariably lower than in the relatively homogeneous selected area, probably due to higher intertidal levels (resulting in shorter daily immersion times).

Bivalve sampling

Along each of the 1-km transects, 50 cores were taken twice-annually at equal intervals to a depth of about 25 cm. In March, when cores of nearly 0.02 m² were used, the sampled area per transect covered a total of 0.95 m². In August, using cores of nearly 0.01 m², 0.45 m² were covered per transect. Bivalves were sorted from the sieved (1-mm mesh size) samples, assigned to age classes (cohorts indicated by the year of birth),

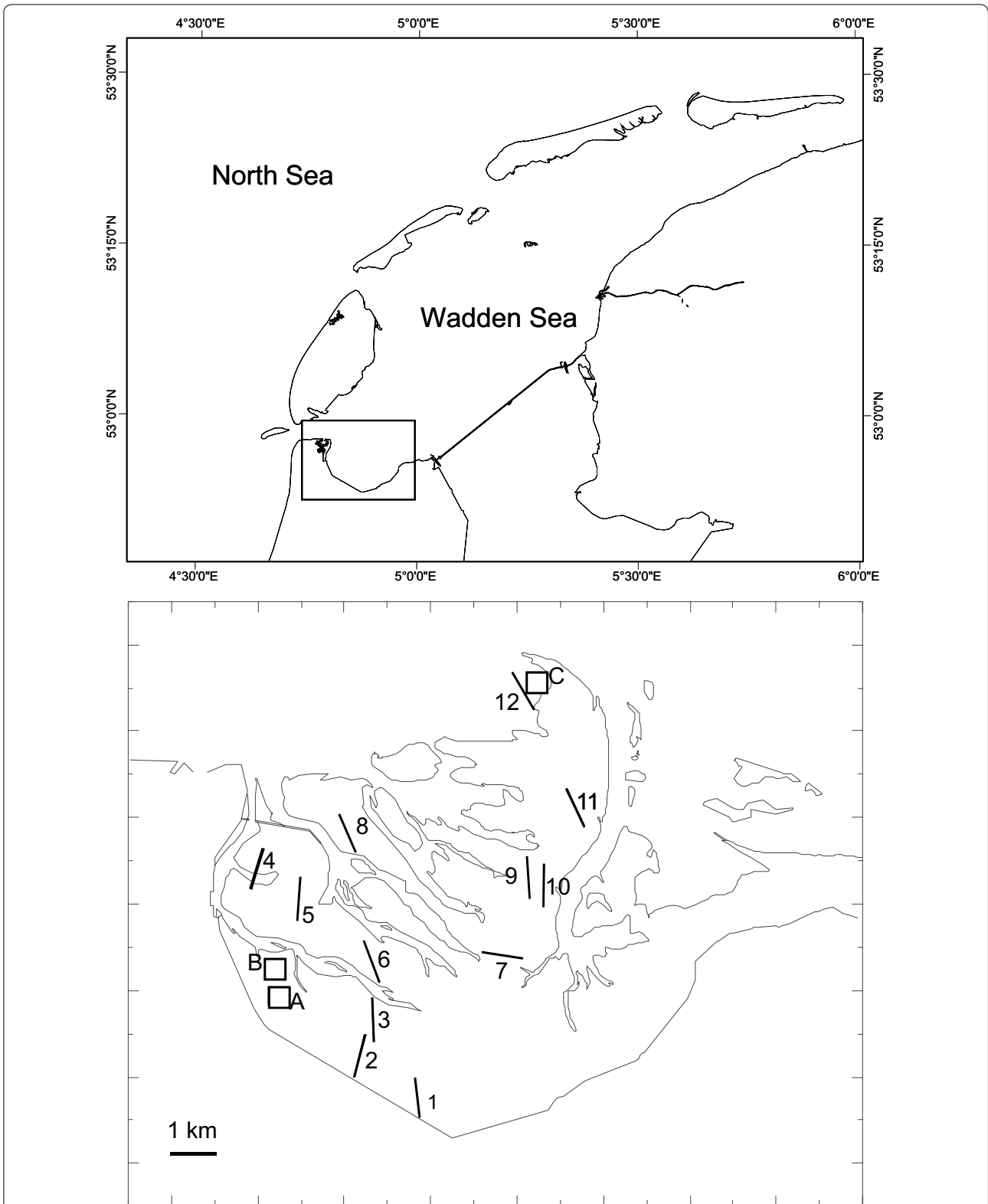


Fig. 1 Maps of (top) the westernmost part of the Wadden Sea and (bottom) the Balgzand tidal-flat area. The permanent sampling sites are indicated: 12 transects (numbered 1–12) and 3 squares (A, B, C). Bivalve growth rates were studied in detail at the 6 transects numbered 4, 5, 8, 9, 10, and 11 in the central part of Balgzand

counted (numerical density was expressed in $n\ m^{-2}$), sorted to mm shell length classes, their soft parts dried to constant weight, weighed per mm length class, incinerated and again weighed to obtain by subtraction AFDM (ash-free dry mass). Biomass was the sum of AFDM values of all individuals present of a species and was expressed in $g\ AFDM\ m^{-2}$. We show estimates observed in late winter, i.e. at the seasonal minimum [24].

Annual recruitment was estimated as a 15-station mean of densities ($n\ m^{-2}$) of 0-group (spat, summer recruits) found in late summer (mostly in August, partly in September), a few months after their settlement. The sieves retained spat of a shell length of $>1.5\ mm$. Data were available for each year of the 1973–2018 period.

Survival was expressed in a percentage: the proportion of the members of an age group still alive after a half of a full year.

Estimates of growth

Seasonal growth was defined as the mean weight increment per individual between March and August and was expressed in $g\ AFDM\ ind^{-1}$. For estimates of growth, we used data of a sampling site only if the cohort to be studied was represented with at least 3 individuals in the samples taken at the end of the growing season. For an estimate of mean growth on Balgzand in a particular year, such numbers should be available at 4 or more of the 6 selected sampling sites. During the 1976–2014 period, sufficient numbers for precise growth estimates were present in 26 years for *C. edule*, 18 for *M. edulis*, 20 for *M. arenaria* and 29 for *L. balthica*.

Statistics

For evaluations of statistical significance of correlations, we used the Spearman rank correlation test. This is a simple test, making no demands as to a (normal) distribution of the data used. Note that if several statistical tests are being performed simultaneously (as is the case in most of our Tables), a Bonferroni correction should be applied: the alpha level of statistical significance should be lowered. In the present paper, this means that a correlation should be considered as statistically significant only if $p < 0.01$ instead of $p < 0.05$.

Results

Between-year variation in recruitment

Patterns of between-year variation in numbers of recruits showed high similarity between the 3 most important suspension-feeding bivalve species *C. edule*, *M. edulis*

and *M. arenaria*: peaks and lows of their recruitment success often occurred in the summers of the same years. As a consequence, correlation coefficients between recruit numbers in these 3 species at an age of about 0.3 year were high (around +0.6) and statistically highly significant, even if a Bonferroni correction is applied (first column of Table 1). Correlations of recruit numbers of these 3 species with those of *L. balthica* were lower (around +0.4) and only just significant.

In late winter (about 10 months, 0.8 year, after the reproduction period) all correlations between the recruit numbers of the various species were lower and significant only for the pairs *C. edule*/*M. edulis* and *C. edule*/*M. arenaria* (second column of Table 1). One year later (age 1.8 year), all correlations had become low and generally non-significant (third column of Table 1). Thus, the initial strong synchrony in recruit numbers at an age of 0.3 year rapidly faded away with age, apparently by between-species differences in recruit survival.

The 4-species sums of the recruit densities varied strongly from year to year, but without a clear trend (Fig. 2). Maximal values were around 50 times higher than minimal values, both in summer (at age 0.3 year) and in winter (at age 0.8 year).

Between-year variation in survival

None of the 6 species pairs showed a significant correlation between (half-)yearly survival rates (Table 2). High correlation values (r values of >0.5) only occurred in pairs with very low numbers (<10) of available observations. Such high correlations were non-significant and will have arisen by chance. Thus, survival rates of the various species fluctuated in their own, non-synchronized, species-specific ways.

Table 1 Coefficients of between-species Spearman correlation estimates of population densities ($n\ m^{-2}$) of year classes in 4 bivalve species (*Cerastoderma edule*, *Mytilus edulis*, *Mya arenaria* and *Limecola balthica*) as assessed at an age of 0.3 year (in August of their first summer), 0.8 year (in February/March at the end of their first winter), and 1.8 year (at the end of their second winter) for the 1973–2016 period ($n=44$)

Age (years)	0.3	0.8	1.8
<i>Cerastoderma</i> — <i>Mytilus</i>	0.64***	0.48**	0.30*
<i>Cerastoderma</i> — <i>Mya</i>	0.63***	0.52***	0.28
<i>Mytilus</i> — <i>Mya</i>	0.55***	0.27	0.05
<i>Cerastoderma</i> — <i>Limecola</i>	0.43**	0.34*	0.21
<i>Mytilus</i> — <i>Limecola</i>	0.36*	0.29	0.27
<i>Mya</i> — <i>Limecola</i>	0.35*	0.12	0.24

Statistical significance indicated without Bonferroni correction: *($p < 0.05$), **($p < 0.01$) or ***($p < 0.001$). With this correction ($n=6$: the number of calculations within a column) one * should be omitted

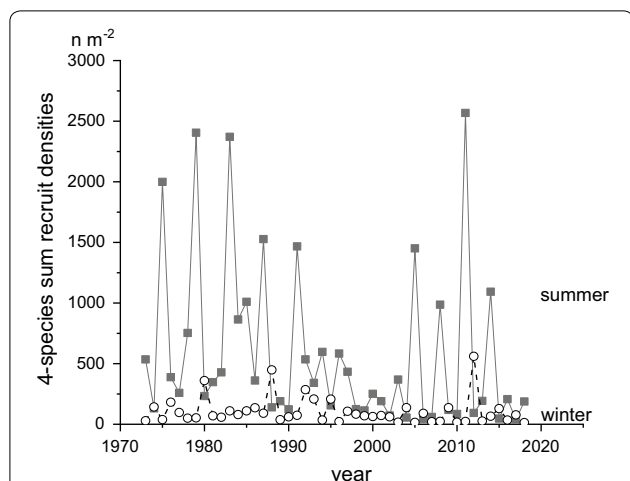


Fig. 2 Long-term (the 46 years 1973–2018) data series of annual abundance (sums of 4 species, in $n\ m^{-2}$) of 0-group individuals observed on Balgzand (means of 15 fixed sampling sites) in late summer (solid points) and subsequent late winter (open points)

Table 2 Coefficients of between-species Spearman correlations in various years of the 1979–2013 period for the survival (at age of 0.3 to 0.8, 0.8 to 1.8, and over 1.8 year)

Age (years)	0.3–0.8	0.8–1.8	1.8+
<i>Cerastoderma</i> — <i>Mytilus</i>	+0.21 (25)	−0.05 (9)	−0.29 (8)
<i>Cerastoderma</i> — <i>Mya</i>	+0.34 (30)	−0.10 (9)	−0.10 (8)
<i>Cerastoderma</i> — <i>Limecola</i>	+0.15 (37)	+0.22 (21)	+0.14 (16)
<i>Mytilus</i> — <i>Mya</i>	+0.36 (19)	−0.54 (6)	−0.62 (5)
<i>Mytilus</i> — <i>Limecola</i>	−0.21 (22)	−0.44 (11)	−0.13 (15)
<i>Mya</i> — <i>Limecola</i>	+0.20 (29)	+0.18 (10)	0.08 (15)

The numbers of years (n) in each comparison is indicated between brackets, being the number of years in which the 2 species involved were sufficiently numerous ($> 5\ m^{-2}$ at the start of the period). There were no significant correlations

Between-year variation in growth rates

Growth rates in the 3 suspension-feeding species (*C. edule*, *M. edulis* and *M. arenaria*) were well synchronized. Table 3 shows the highly significant correlation coefficients of around +0.7. Correlations of these species with *L. balthica* were close to 0 and far from significant (last column of Table 3).

Maximal growth values were 5 to 10 times higher than minimal values in the various species. Growth rates were particularly high in the 1990s. Lower than average growth rates were observed in all 3 suspension-feeding species in 1988 and particularly in 2012. These 2 years were characterized by the highest recruit densities at the start of the growing season of the entire 42-year period of observation (Fig. 2).

Table 3 Coefficients of between-species Spearman correlations in various years of the 1979–2015 period for their seasonal weight gains between March and August (in $g\ AFDM\ ind^{-1}$)

	<i>Mytilus edulis</i>	<i>Mya arenaria</i>	<i>Limecola balthica</i>
<i>Cerastoderma edule</i>	+0.68** (16)	+0.66** (15)	−0.09 (20)
<i>Mytilus edulis</i>		+0.69** (12)	+0.05 (16)
<i>Mya arenaria</i>			−0.22 (17)

The numbers of years (n) in each comparison is indicated between brackets, being the number of years in which the 2 species involved were sufficiently numerous at 4 or more out of the 6 sampling stations. Statistical significance indicated by ** ($p < 0.02$)

Between-year variation in biomass

Fluctuations in biomass values were rather strong (Fig. 3) and showed hardly any correlations between the 4 species: Spearman-r values were generally close to 0 (Table 4). Only the negative correlation between *M. arenaria* (including big individuals) and *L. balthica* was statistically significant ($p < 0.05$), but became non-significant after Bonferroni correction.

C. edule and *M. arenaria* contributed most to total-bivalve biomass (Figs. 3a and b) and fluctuated strongly. The 2 other species (*M. edulis* and *L. balthica*) contributed minor amounts in most years.

Long-term (1973–2018) trends in biomass values for the separate species (last column of Table 5) were non-significant in *C. edule* and in *M. edulis*, but positive in *M. arenaria* (both for all individuals and for those of $< 5\ cm$ shell length) and negative in *L. balthica*. The observed declining trends in recruitment and in survival at higher ages may explain the decline of *L. balthica* biomass (Table 5). The increase in *M. arenaria* biomass may be explained by increasing survival at higher ages (Table 5). In *M. edulis*, all long-term trends in population parameters were non-significant. In *C. edule*, a declining trend in summer recruitment was compensated by increasing trends in survival, resulting in an absence of trend in biomass (Table 5).

Total bivalve biomass values (Fig. 3c) showed a significant long-term trend ($r = +0.35$, $n = 46$, $p < 0.05$). Not all of the bivalve biomass is available as bird food. Nearly all *M. arenaria* of $> 5\ cm$ shell length live too deeply buried ($> 15\ cm$ below the surface) to be within the reach of any bird [25]. Therefore, we show in Fig. 3c in addition to summed biomass values of all bivalves also those of the smaller ones (by excluding biomass of *M. arenaria* of $> 5\ cm$). The annual biomass values of these smaller bivalves showed no significant long-term trend ($r = 0.04$, $n = 46$, $p = 0.8$). Year-to-year variation amounted to a factor of 6 between maximal and minimal values in total biomass and a factor of 10 for the “small” group of accessible bivalves.

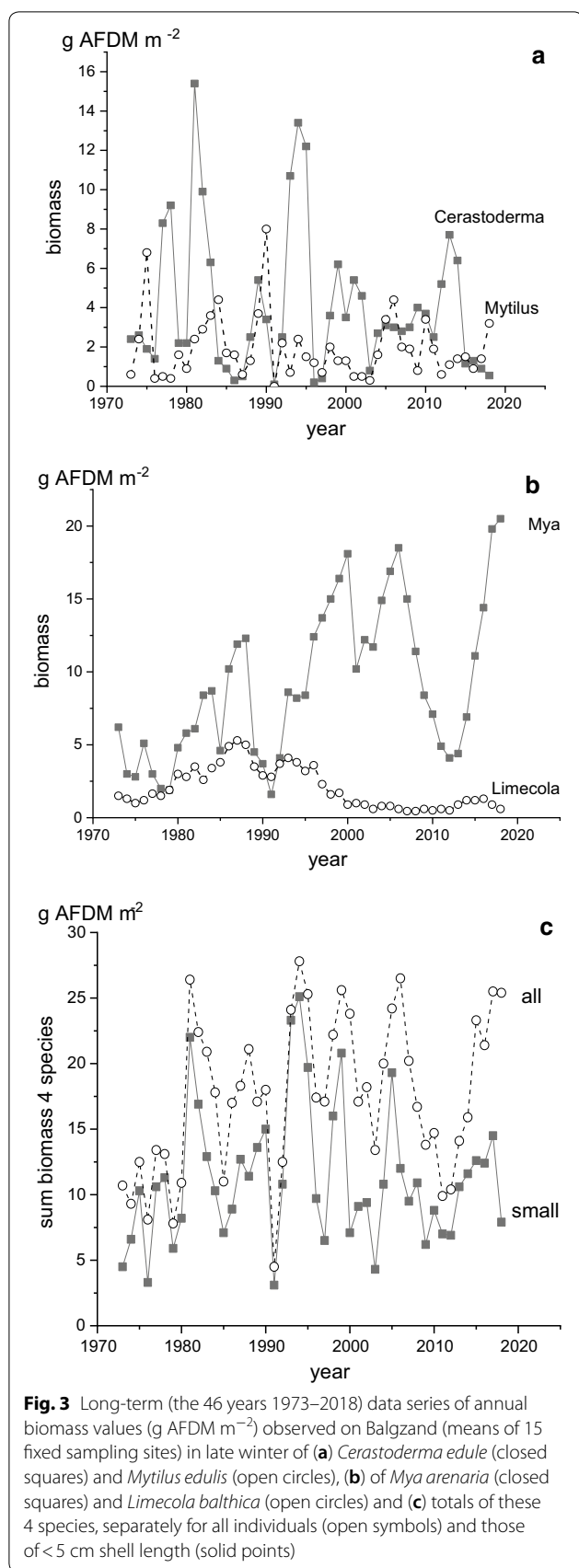


Table 4 Coefficients of between-species Spearman correlations in various years of the 1970–2017 period (n=48) for their total biomass (in g AFDM m⁻²) in late winter

	<i>Mytilus edulis</i>	<i>Mya arenaria</i>	<i>Limecola balthica</i>
<i>Cerastoderma edule</i>	+0.14	-0.06 (-0.02)	-0.10
<i>Mytilus edulis</i>		-0.05 (+0.06)	+0.07
<i>Mya arenaria</i>			-0.33 (-0.22)*

Statistical significance indicated by * (p < 0.05). Data for *M. arenaria* of < 5 cm between brackets

Total accessible bivalve biomass was strongly related with preceding recruitment success of the bivalves (Fig. 4). For this relationship, we summed the recruit densities found in late winter, but multiplied those of *L. balthica* by 0.1, because individual weights in subsequent years are in this species only one tenth of those in the other 3 species [11]. Up to about 300 recruits m⁻², biomass values were found to increase linearly with recruit densities (by 0.05 g per recruit). The 4 points at recruit densities of > 300 m⁻² showed much lower biomass values than expected from this linear relationship. These high densities were due to very high recruit numbers in summer 1987/winter 1988 (in all 4 species) and particularly in summer 2011/winter 2012 (exceptionally high recruitments in *C. edule* and in *M. arenaria*). In the subsequent growing seasons of 1988 and 2012, growth rates were below the long-term average in all species, particularly at the highest densities in 2012 [19]. As a result, individual weights in the subsequent years were low, causing relatively low biomass values at the start of the 4 years 1989, 1990, 2013, and 2014. Consequently, the relationship between recruitment and subsequent biomass was dome-shaped (Fig. 4).

Discussion

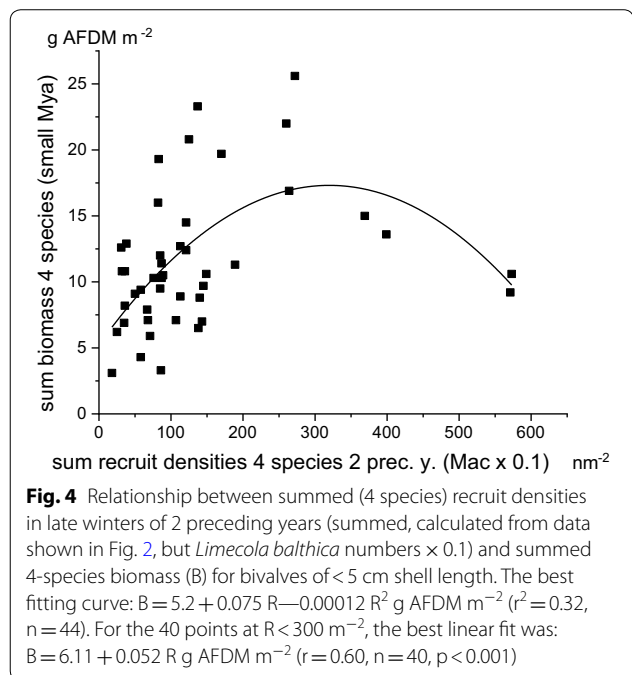
The main result of the present paper is the observation that the annual biomass values turned out to be uncorrelated between the 4 species, despite the strong between-species correlations in both their annual abundance at recruitment (i.e. at spat size, at an age of 0.3 or 0.8 y) as well as in their growth rates (in 3 species). Between-species synchronization of recruitment was reported earlier in [16] and in [7], synchronization in growth rates in [19]. These papers described the correlations in much more detail than in the present paper, but for shorter data series and without considering consequences for availability of bird food.

The highly variable and species-specific annual survival rates soon wiped out the between-species correlations in numbers of young animals, namely before their weights had become high enough to seriously contribute to biomass values. Year-to-year variability in annual biomass

Table 5 Long-term trends in (1) annual recruitment ($n\ m^{-2}$ at an age of 0.3, 0.8, and 1.8 year) for the 1973–2015 period ($n=43$), (2) survival (% still present half a year after the age of 0.3 year, 1 year after an age of 0.8 year, and 1 year after an age of 1.8 year or more) for 15 to 40 years of the 1973–2015 period (calculated only if at least $10\ m^{-2}$ were present at the start of the period), (3) growth rate ($g\ AFDM\ ind^{-1}$) for the 1976–2014 period ($n=18$ to 29), and (4) late-winter biomass ($g\ AFDM\ m^{-2}$) for the 1973–2018 period ($n=46$)

Age (years)	Recruitment			Survival			Growth	Biomass
	0.3	0.8	1.8	0.3–0.8	0.8–1.8	1.8+		
<i>Cerastoderma edule</i>	-0.44**	-0.09	+0.20	+0.25	+0.35	+0.14	-0.23	-0.15
<i>Mytilus edulis</i>	-0.26	-0.09	-0.05	+0.18	-0.16	-0.44	+0.11	-0.11
<i>Mya arenaria</i>	-0.09	+0.12	+0.34*	+0.33	-0.17	-0.03	+0.12	+0.57***(+0.31*)
<i>Limecola balthica</i>	-0.68***	-0.49**	-0.41**	+0.55**	+0.29	-0.66***	-0.02	-0.51***

Significance indicated by * ($p < 0.05$), ** (< 0.01) or *** (< 0.001); Spearman rank test. Biomass data for *Mya arenaria* separately for all individuals and (between brackets) for those of $< 5\ cm$ shell length



values was then much lower than in annual recruitment, a factor 5 to 10 as compared to about 50 between maximal and minimal annual values in biomass and recruitment, respectively. Coefficients of variation were higher for recruitment than for biomass in each of the 3 species studied in [11], those for growth and mortality being even lower. The strong between-species synchronization and high variability in annual recruitment were not reflected in the moderate and non-synchronized variability in annual biomass. Judged from annual biomass estimates, the system was thus much more stable than judged from annual recruitments. Birds feeding on bivalves were less hard hit by the high variability in recruitment than in the case recruitment variability was passed on to biomass.

We found a positive long-term trend in total bivalve biomass. However, this trend was due to the strong increasing trend in big *Mya arenaria* which are of little significance as food for birds. The corrected total-biomass values (by omitting big *M. arenaria*) did not show any long-term trend. The hardly significant increase in biomass of small *M. arenaria* was compensated by the highly significant long-term decline in *Limecola balthica* biomass (Table 5). The increase or lack of a long-term trend in bivalve biomass is remarkable in view of the significantly declining eutrophication state of the Dutch Wadden Sea, showing chlorophyll concentrations in the main tidal stream decreasing from 15 to $20\ mg\ m^{-3}$ in the 1970s, 1980s and 1990s to about $10\ mg\ m^{-3}$ in the 2010s [19].

The lowest values for total biomass (both for the group of small bivalves and that of all bivalves) were observed in early 1991 (Fig. 3c) and had a known cause: in the summer of 1990 the area was fished intensively for cockles and particularly for mussels. The resulting densities of these food species were extremely low and apparently forced the bivalve-eating birds to switch to other species, resulting in low survival and ultimately low biomass of *L. balthica* as well as small *M. arenaria* [26, 27]. Consequently, total bivalve biomass reached the lowest value of the 46-year period of observations. In 1991, oystercatcher numbers in the area declined unusually rapidly after February [26]. The second lowest value for biomass of small bivalves was found in 1976 (Fig. 3c). Exactly in 1991 and 1976, numbers of dead oystercatchers found in February along the coast were the highest of the studied 1975–1996 period [10]. This shows the relevance of the results of the present study for bird food supply and bird mortality.

As shown earlier by a less direct method in [11], we found annual recruitment success to determine to a considerable extent biomass in the years after

recruitment (Fig. 4). Biomass in subsequent years increased linearly with an increase of preceding recruit numbers up to some 300 recruits m^{-2} in late winter. Biomass in years after exceptionally high recruitments (occurring only twice in the 40-year period of observation, in 1987 and in 2012) did no longer follow the above linear relationship, but showed reduced biomass values for 2 subsequent years as a consequence of lower growth rates at very high densities (as reported in [28] and in [19]). The resulting curve in Fig. 4 shows a dome-shaped relationship between recruitment and subsequent biomass. Maximal biomass values were found after recruitments of above-average, but not maximal, recruitment success.

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Authors' contributions

JJB did most of the writing, RD most of the data collection. Both authors read and approved the manuscript.

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Availability of data and materials

Data are stored in the data base at NIOZ, P.O. Box 59, 1790AB Den Burg Texel, The Netherlands.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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