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ORIGINAL ARTICLE

Large-scale synchronization of annual recruitment success and stock size in Wadden Sea populations of the mussel *Mytilus edulis* L.

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Abstract Simultaneous abundance or shortage of mussels over vast areas may seriously affect fishery as well as shellfish-eating birds. We studied synchrony in annual recruit numbers and stock sizes (biomass) of mussels on the base of long-term observations in various parts of the Dutch (and German) Wadden Sea, including regular monitoring on Balgzand (a 50-km^2 tidal flat area) and published or unpublished records for other parts of the Wadden Sea. Annual records for 37 years of mussel seed abundance in the eastern and western half of the Dutch Wadden Sea proved to be mutually well correlated and were also significantly correlated with annually assessed numerical densities of mussel recruits on Balgzand. The scarce long-term series available on mussel biomass pointed to significantly positive correlations between stock sizes on Balgzand and those in the northern German Wadden Sea, at about 300 km distance. The incidence of severe winters, which occurrence is synchronized over areas in the order of thousands of km, is identified as the dominant causative factor behind Wadden Sea-wide recruitment synchrony. Severe winters are known to reduce abundance of predators on tiny bivalve spat, and this process may overrule local processes causing abundance variation in bivalves. As such extreme winters are infrequent (usually only one or two per decade), sensible studies on the phenomenon of synchronization in abundance of Wadden Sea bivalves should be based on data series of sufficient length, covering decades.

Keywords Population synchronization · Recruit density · Biomass · Monitoring · Wadden Sea

Introduction

The substantial between-year variation in stock sizes of bivalves in the Wadden Sea can largely be ascribed to variability in their annual recruitment success, as observed in three species, including the mussel *Mytilus edulis* (Beukema et al. 2010). If year-to-year fluctuations in numbers of bivalve recruits ("spat" or "seed") are synchronized over extensive areas, such as the entire Wadden Sea, biomass in these species will also tend to show their peaks and troughs in the same years over large geographic areas (with a time lag of a few years compared to recruitment). Simultaneous occurrence of minima in stock size over extensive areas will be of importance both to fisheries and to shellfish-eating birds, because no nearby alternatives for depleted stocks are then available. For example, after three successive years (1988, 1989, and 1990) with recruitment failure in both cockles and mussels over the entire Dutch Wadden Sea, only adults from the successful 1987 recruitments were present in 1990. In that year, fisheries almost completely removed the last few remaining intertidal beds of these bivalves (Beukema and Cadée 1996), aggravating serious food shortage and excessive mortality in shellfish-eating birds (Camphuysen et al. 1996).

Synchronization of recruitment success over several hundreds of kilometers (encompassing the Netherlands and

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part of the German Wadden Sea) has been shown to occur in cockles *Cerastoderma edule*, Baltic tellins *Macoma balthica*, and soft shell clams *Mya arenaria* (Beukema et al. 2001). By lack of accessible data, such large-scale synchronization has not yet been reported in mussels *M. edulis*. For two reasons, such synchronization may be expected in this species as well: (1) At the smaller scale (50 km^2) of the Balgzand area in the westernmost part of the Wadden Sea, the long-term time pattern of mussel recruitment variability significantly paralleled the patterns in the other three bivalve species (see Table 2 of Beukema and Dekker 2014) and (2) in all four bivalve species, the character of the preceding winter is an important factor that governs recruitment variation (Beukema et al. 2001; Strasser et al. 2003; Beukema and Dekker 2014) and individual winters are of similar character over areas of more than 1000 km along the coasts of Western Europe (MacKenzie and Schiedeck 2007).

In contrast to the above expectation, results of a study by Folmer et al. (2014) indicated significantly positive correlations between the areas covered by intertidal mussel beds to occur only over restricted areas, located within distances of <100 km. Their geographically highly detailed study was based on relatively short time series (1999–2010), not including any severe winter.

The present study deals with data collected over much longer periods. Long-term data on numbers and biomass were available from a monitoring program that started in the 1970s in the westernmost part of the Wadden Sea (Balgzand) and, for the entire Dutch Wadden Sea, from annual estimates (started in the 1950s) of abundance of "seed" mussels (recruits, spat, <1 year olds). The aim of the present paper is to present these (not always easily accessible) data, to include some data series from the literature from parts of the German Wadden Sea, to ascertain possible synchronization in spat abundance and biomass between distant areas, and to study relationships between annual spat abundance and subsequent stock sizes. In this way, we intend to show large-scale (Wadden Sea-wide) synchronization in mussel abundance and to discuss the process underlying synchronization in stock size: winter character-governed fluctuations in annual recruitment success.

Methods

Annual data on numerical densities (nm^{-2}) of mussel recruits and biomass (g m^{-2} of ash-free dry mass AFDM, of soft parts) of the mussel population on the 50-km^2 tidal flat area called Balgzand are available from monitoring (by sieving several hundreds of bottom cores) twice annually (in March and in August) at 15 sampling sites (12 transects of 1 km each and three squares of 900 m^2) for a 40-year period started in the mid-1970s. These data are shown in Beukema and Dekker (2007, 2014). Details on methods of mussel sampling and on the monitored area can be found in Beukema and Dekker (2007).

Though mussels were found more or less frequently at all 15 sampling stations, real mussel beds, resulting in high biomass values, were regularly encountered at only four transects (numbered 4, 5, 9, and 10 in Beukema and Dekker (2007)). Only one transect (nr 5) crossed an almost permanent bed (it was absent only for a short period from mid-1990 to mid-1991 as a consequence of intensive fishery). We present data on the total mussel population (including adults) only for this one sampling transect. It crossed the bed over a distance of mostly 50–100 m.

To quantify annual recruitment success, we used averages of recruit densities of all 15 sampling stations. Because the annual densities of these recruits covered wide ranges (from close to 0 to >500 m^{-2}) and the distribution of these numbers was far from normal, we applied a ^{10}log transformation of these numbers for regressions and statistical tests.

For the Dutch Wadden Sea at large, long data series of (rough) estimates on annual mussel seed abundance are available from two sources: Van Stralen (2002) and similar data collected by De Vlas. The latter were communicated to JJB by letter of March 20, 1992, and were partly published in Dijkema (1992). These two data series refer to estimates made both in the second half of the year of birth of the spat and in the first half of the following year (though the records were not specified as to season, only to size class of the mussels). They were largely based on the same sources: annual and monthly reports of the Ministry of Agriculture, Nature and Fishery (LNV), which were regularly published in the periodical Visserijnieuws. The series by Van Stralen (2002) was also based on reports by fishermen. Usually, neither of these reports covered each year the entire area. Details on data gathering were not consistently published with the above sources.

The two data series for the entire Dutch Wadden Sea were not based on solid data from a fixed sampling program, but on expert judgments. They were presented as annual scores on a scale of zero to four. If seed numbers were negligible (no seed fishery could be carried out), they were scored as 0.1. If seed was scarce and local (and fishery yielded insufficient seed for stocking of all culture plots), a score of one was given. If seed abundance was reasonable but not abundant, a score of two was given. Good seed numbers were scored as three and very high (superfluous) numbers as four. Though these judgments were made independently by the two investigators, they were in fact not completely independent, because they were largely based on the same sources (reports of employees of the Ministry). Therefore, we only used the averages of the two series in the present paper. The two judgments were not entirely identical: The indices by De Vlas were on average by 0.5 points higher than those by Van Stralen (1.8 vs. 1.3). The positive correlations between the two series were highly significant within each of the two parts of the Wadden Sea (with Spearman and Pearson *r* values of around 0.7 with $p < 0.001$). Spearman's correlation tests are more widely applicable than Pearson's tests and appear to be more appropriate for the present data, but in practice the correlation coefficients obtained hardly differed.

The two series cover the periods 1955–2001 (except for 1985 and 1989) and 1955–1992, respectively. The series for the western half of the Dutch Wadden Sea refer (mostly) to subtidal areas, which area does not overlap with the intertidal Balgzand. The series for the eastern half of the Dutch Wadden Sea refer almost exclusively to tidal flats. The two data series overlapped for 35 years (1955–1992, with two missing values), and their averages overlapped with the Balgzand summer monitoring for 21 years (1969–1992, with lacking August Balgzand data for 1971 and 1972).

Published long-term records of mussel biomass appear to be scarce. For Balgzand, such data are available for each year since the early 1970s (see Fig. 5b of Beukema and Dekker (2007)). For other Wadden Sea areas, we found such data in Nehls et al. (2006) and Büttger et al. (2008). Nehls et al. present monitoring data for 13 years between 1984 and 2004 on wet-weight mussel biomass in the extensive area of the northern German Wadden Sea of Schleswig-Holstein. Büttger et al. present data on ash-free dry weight for 13 years in roughly the same period on two mussel beds in a small bay on the German island of Sylt.

Results

Recruitment synchronization

Abundance of seed mussels varied strongly between years, from near-nil to superfluous. Highly abundant year classes (score of three or higher) were not frequently observed. Van Stralen (2002) gave such high scores in 16 out of 80 judgments (39 years for western half +41 for eastern half of Dutch Wadden Sea); the number of such scores by De Vlas amounted to 15 out of 74 (37 + 37). The following applies to the averages of the scores of the two judges.

In most years, the average (of the two judges) scores for mussel recruitment success were similar in the western and eastern half of the Dutch Wadden Sea (Fig. 1). As a result, the 37 annual scores that were available for each of the two halves showed a highly significant positive correlation: Spearman *r* amounting to 0.71 ($p < 0.001$).

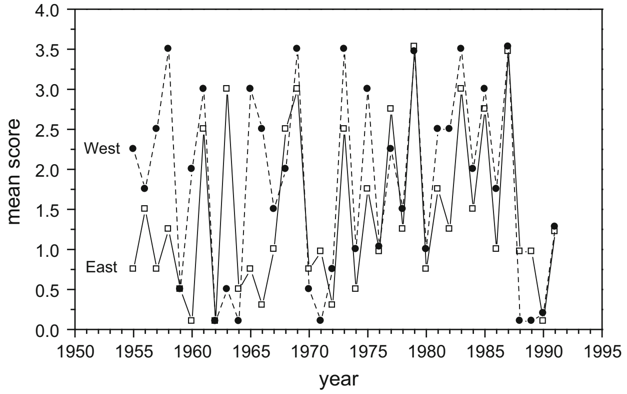

Fig. 1 Annual scores for 37 successive years (1955–1992) of mussel *Mytilus edulis* seed abundance for the two halves (*solid points* and *broken line W* = West, subtidal; *open points* and *full line E* = East, intertidal) of the Dutch Wadden Sea. Data shown are averages of the two scores given independently by two investigators: J. de Vlas (in Dijkema 1992) and M. R. van Stralen (2002)

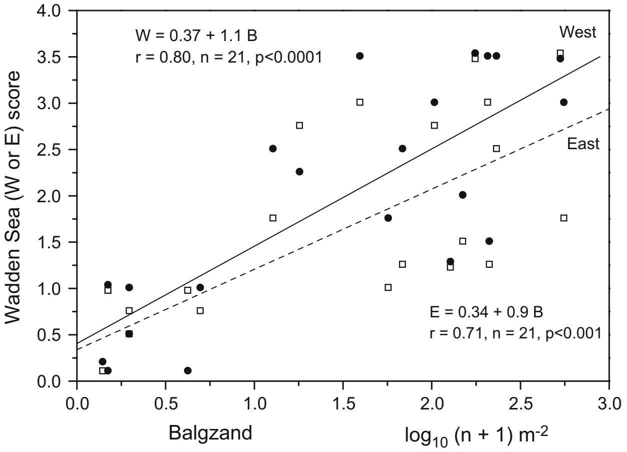

Fig. 2 Relationships between recruit densities of mussels *Mytilus edulis* assessed annually in August at Balgzand (*B*) and mean scores by two judges of mussel seed abundance, separately in the western (*W*, *solid points* and *full line*) and eastern (*E*, *open points* and *dashed line*) half of the Dutch Wadden Sea. Balgzand densities expressed in ^{10}log (n + 1) m^{-2}. Lines show best linear fits for 21 annual data (years 1969–1991, except 1971 and 1972) and show Pearson *r* values. Spearman *r* values amounted to 0.77 ($p < 0.001$) and 0.73 ($p < 0.01$), for West and East, respectively

The more exactly assessed mussel spat densities on Balgzand were positively correlated with the annual scores given for the two extensive parts of the Wadden Sea: For both the western and the eastern half of the Dutch Wadden Sea, these correlations were highly significant and hardly differed (Fig. 2). This was so both for the Balgzand spat densities as they were assessed in August (shown in Fig. 2) and for those observed half a year later in March (Table 1). This similarity was based on the strong correlation of year class strength as assessed in August or subsequent March (bottom line of Table 1). Note the similarity in all

Table 1 Correlation matrix (showing Pearson *r* values) for long-term data series of mussel seed abundance in three areas: West (western half of Dutch Wadden Sea, subtidal), East (eastern half, tidal flats), and Balgzand (westernmost part of Wadden Sea, tidal flats)

	East	Balgzand/ August	Balgzand/ March
West	0.68*** (37)	0.80*** (21)	0.78*** (23)
East		0.71*** (21)	0.73*** (23)
Balgzand/August			0.81*** (40)

For West and East, the averages of scores on a scale of 0.1 to 4 by Van Stralen (2002) and De Vlas (in letter and in Dijkema 1992) were used; for Balgzand, ^{10}log transformed numerical ($n + 1$) densities (m^{-2}) observed in August or March were used (scaling from ~0.2 to ~3). Pearson *r* values are shown with numbers of observations between brackets

*** $p < 0.001$

correlation coefficients shown in the summarizing Table 1: Neither season of observation nor part of the Wadden Sea seriously influenced magnitude of the correlation coefficients.

Recruitment and stock size

In most years, new recruitments on the most stable mussel bed on Balgzand were a failure and highly successful recruitments were exceptional events, observed only five times in 40 years (Fig. 3a). Out of these five successful recruitments, four occurred in the summers after a severe winter: 1979, 1987, 1996, and 1997. Stock size at this bed, expressed as biomass, was also highly variable (Fig. 3b). Conspicuous increases in biomass were observed in three periods: 1979–1983, 1987–1989, and 1991–1995. The first period of increase started with the successful 1979 recruitment, after which this year class dominated the stock for 6 years (solid squares in Fig. 3c). The second biomass increase started in the year of the successful recruitment of 1987, after which this year classes dominated the stock for three subsequent years (open circles in Fig. 3c). This might have lasted for more years if the mussel bed had not been removed by fishery in the summer of 1990. The increase that started in 1991 from a zero level was due to moderate recruitments in 1991 and 1992 and an exceptional one in 1994. Only the former one dominated the stock for a short period. These recruitments and those of 1996 and 1997 occurred in rather close succession, and as a consequence, none could really dominate the stock for any year (Fig. 3c). There were no successful recruitments after 1997 (Fig. 3a), and subsequent stock sizes showed a declining trend for more than a decade (Fig. 3b).

An overriding influence of degree of recruitment success on the development of subsequent stock size (Fig. 3b) was thus demonstrable in each of three periods, covering together about half of the total observation period: increasing stock sizes starting after successful recruitments (1979 and 1987) for the periods 1979–1983 and 1987–1989 (or 1990 in the months before fishery started) and consistent declines in stock sizes for the period 1998–2008, a time with only minor recruitments.

Note in Fig. 3 that during the period (1999–2010) of the study by Folmer et al. (2014), the mussel population on Balgzand was not characterized by substantial variability in recruitment or biomass and was not dominated by any single year class.

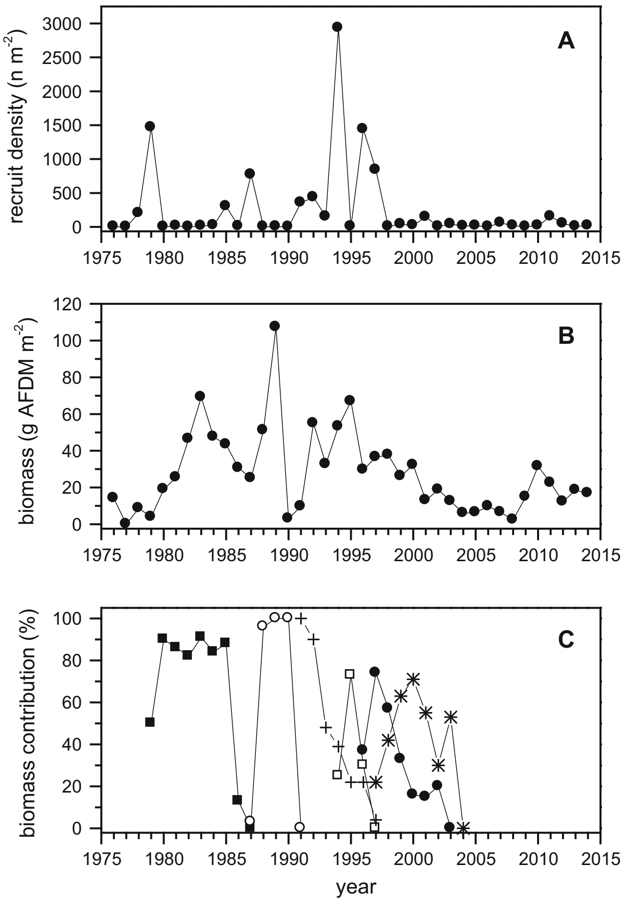

Fig. 3 Time series (1975–2014) of data collected annually in August along a transect on Balgzand that crossed a large and nearly permanent mussel bed. All data refer to the entire transect; abundance figures for the part of the transect within the bed were roughly an order of magnitude higher. **a** Numerical densities (nm^{-2}) of young-of-the-year mussels; **b** biomass of all mussels present (in g AFDM m^{-2}); **c** share (in %) to total mussel biomass of the five strongest cohorts: (*solid squares*) born in 1979, (*open circles*) born in 1987, (*open squares*) born in 1994, (*solid circles*) born in 1996, and (*stars*) born in 1997. Shares of one smaller cohort (*crosses* born in 1991) were also added, because this cohort dominated mussel biomass in 2 years (1991 and 1992) following the total removal of the bed in the second half of 1990 by fishery

Biomass synchronization

From the above conclusions about the existence of (1) synchronization in recruitment success over vast areas and (2) significant influence of recruitment success on subsequent stock size, some synchronization may be expected in mussel biomass over extensive areas. For the 50-km^2 Balgzand area, annual estimates of mussel biomass are available for the last four decades (shown in Fig. 5b of Beukema and Dekker (2007)). Unfortunately, only few long-term data series appear to be available on estimates of mussel biomass in other Wadden Sea areas. Data for 13 years were published for areas in the northern part of the German Wadden Sea (Nehls et al. 2006; Büttger et al. 2008, 2014), about 300 km NE of Balgzand. The estimates by Nehls et al. (2006) were 13 annual averages (from the 1988–2004 period) over a vast area (about 70 × 20 km) that included the small area (two mussel beds) studied by Büttger et al. (2008) for 13 years (within the 1988–2004 period).

The positive correlations between annual mussel biomass values in the two distant areas (Balgzand and northern part of German Wadden Sea) were not very strong (r^2 values of about 0.3), but proved to be (just) significant (Fig. 4a, b). Some synchronization appeared to be present in the years when mussel biomass was high or low, respectively, in areas that were around 300 km apart.

Nehls et al. (2006) presented simultaneous annual estimates on both mussel biomass and mussel bed area in the northern part of the German Wadden Sea. These two estimates on mussel abundance proved to be strongly correlated ($r = +0.90$, $n = 13$, $p < 0.0001$). In the above, we chose for the biomass estimate, because no data were available on mussel bed area on Balgzand.

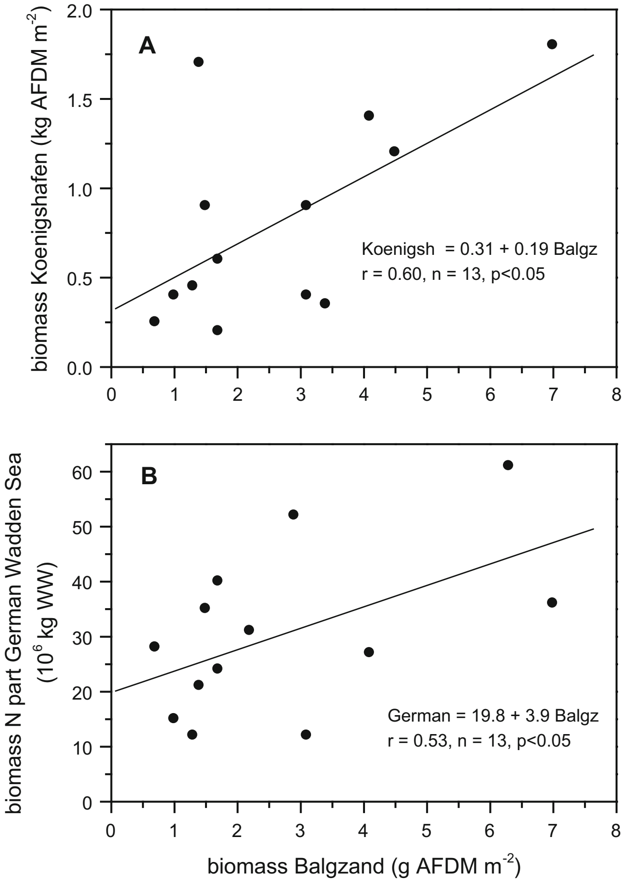

Fig. 4 Relationships between biomass of mussels *Mytilus edulis* assessed annually on Balgzand (in g AFDM m^{-2}, means of March and August data at 15 sampling stations) and mussel biomass recorded in two other Wadden Sea areas: **a** means of two mussel beds in Königshafen in 13 years between 1984 and 2005, in kg AFDM m^{-2} (from Fig. 2a of Büttger et al. 2008), **b** total mussel biomass in an extensive area in the northern German Wadden Sea (Schleswig-Holstein) in 13 years between 1988 and 2004, in 10^6 kg wet weight (from Fig. 2b of Nehls et al. 2006)

Discussion

The main result reported in the present paper is that annual mussel recruitments in mussels *M. edulis* tended to be similar all over the Dutch Wadden Sea (Figs. 1, 2). For an explanation of this large-sale synchronization, it should be noted that in several bivalve species, including *M. edulis*, recruitments tend to be successful in particular (though not exclusively) after cold winters (Beukema et al. 2001; Strasser et al. 2003; Beukema and Dekker 2005, 2014). Winters are of a similar character over extensive geographic areas (MacKenzie and Schiedeck 2007). The process by which winter temperatures govern subsequent bivalve recruitment appears to be the positive influence of winter temperature on spring abundance of epibenthic predators (shrimps and shore crabs) on the tiny, just-settled, post-larvae of bivalves. The colder the winter is, the lower is the predation pressure on early bivalve spat and the more of them are surviving to larger recruits in summer (Beukema and Dekker 2014). Thus, a background process that might explain the large-scale synchronization of bivalve recruitment success appears to be available. This is not to say that the variability in mussel recruitment success is fully explained by preceding winter temperatures. According to Beukema and Dekker (2014: their Fig. 5c), winter temperatures explain about 40 % of the year-to-year variation in mussel recruitment, leaving ample room for other recruitment-influencing environmental factors. In particular during prolonged periods without severe winters, such other factors might become prominent and these factors might be of a more local nature.

Synchronization of recruitment success in distant parts of the Wadden Sea will promote synchronization of mussel stock size, as strong year classes can dominate mussel beds for prolonged periods (Fig. 3c). A comparison of long-term patterns of mussel biomass in distant parts (300 km apart) of the Wadden Sea corroborated this expectation (Fig. 4), though data of only rather few (13) years were available for comparison and the statistical significance of the observed positive correlations was not high.

Mussel biomass is strongly correlated with bed size (Nehls et al. 2006). Therefore, we would expect synchronization of mussel bed size over extensive areas as well. Büttger et al. (2014) showed strong correlations of the size of areas covered by mussels in a 14-year period in three subareas within the North Frisian Wadden Sea that were up to about 60 km apart. The study by Folmer et al. (2014) covered the entire Wadden Sea and referred to a period of 12 years (1999–2010) and no less than 36 subareas. It revealed synchrony in variation of bed size (“coverage” in terms of these authors) to be almost restricted to adjacent or nearby subareas. However, subareas further apart than about 100 km tended to show negative rather than positive correlations (see Fig. 4 of Folmer et al. 2014). For instance, they found strong positive correlations within the western as well as within the eastern half of the Dutch Wadden Sea. The correlations between these two parts of the Dutch Wadden Sea were at most weak, but often absent and sometimes even negative. Unbroken parts of the Wadden Sea with positive correlations of coverage had a restricted size with diameters of between 60 and 90 km. Usually, neighboring areas that were characterized by an own variation pattern in mussel bed size were separated by major tidal streams, such as river mouths.

The results reported by Folmer et al. (2014) differ from ours in the size of the area showing more or less similar fluctuation patterns in stock size (assessed either by biomass or by bed size). One of the causes of this difference may be the difference in length of the time series used: 12 years in the Folmer study versus 37 in the present one. In addition, it should be noticed that the 12 years (1999–2010) studied by Folmer et al. (2014) did not include any really severe winter. In the western Wadden Sea, mean water temperatures for the two coldest months (January + February) varied between +1.6 and +4.6 °C for these 12 years and covered the wider range of −1.7 to +6.2 °C for the 37 years of the 1955–1992 period (for which data were included in Fig. 1). Within the latter period, six winters were severe, with January/February temperatures of well below +1.6 °C (Van Aken 2008). A lack of really cold winters in the period studied by Folmer et al. (2014) means that mussel populations were not exposed to Wadden Sea-wide extreme forces within that period. This may explain the prevalence of more local conditions affecting mussel bed size as observed by Folmer et al. (2014). In most (almost 30) of the 36 subareas they studied, fluctuations of mussel stock sizes were minor during the 1999–2010 period (see their Fig. 3), pointing to an overall lack of drastic incidents causing sudden changes in mussel abundance (such as violent gales and ice winters). It is conceivable that local effects will be predominant causes of changes in mussel stock size during periods that lack wide-scale drastic incidents such as severe winters. With continuing climate warming, the occurrence of severe winters will become less frequent. This may lead to a rare occurrence of highly successful mussel recruitments over vast areas, resulting in lower variability and less synchronization in mussel stock sizes.

Summarizing conclusion: Long-term data series of changes in mussel population sizes and mussel recruitment success revealed synchronization of peaks and low points over vast areas of several hundreds of kilometers. One of the main processes leading to synchronized fluctuations in mussel stock size was the synchronized nature of annual recruitment as governed by the relationship between winter character and subsequent recruitment success in summer. Because of the erratic and infrequent occurrence of severe winters in the studied area, long-term time series are needed to demonstrate large-scale synchronization in mussel stock size. Shorter studies for periods lacking severe winters, such as the one by Folmer et al. (2014), are appropriate to reveal synchronizing effects of other environmental factors which appear to act at a smaller scale of tens rather than hundreds of kilometers.

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