

Parallel changes of *Limecola (Macoma) balthica* populations in the Dutch Wadden Sea

J. J. Beukema*, R. Dekker, J. Drent

NIOZ Royal Netherlands Institute for Sea Research, PO Box 59, Department of Coastal Systems, and Utrecht University, 1790 AB Den Burg, Texel, The Netherlands

ABSTRACT: Long-term (>40 yr, started in the 1970s) data series of *Limecola (Macoma) balthica* dynamics in 4 distant (>100 km) areas of the Dutch Wadden Sea are described and compared, including annual recruitment, total abundance, age composition (recruits/adults) and adult survival. The aim was to determine to what extent long-term changes in *L. balthica* population attributes were synchronous in populations throughout the Dutch Wadden Sea and to identify possible underlying causes. At all 4 sites studied, changes in annual recruitment (n m⁻² of spat-sized animals in summer) was synchronous with long-term declining trends and peaks and lows occurring in the same years at all sites. Adult survival was high for the first 15 to 20 yr, but irregular after 1990 with low values for periods of varying length. In contrast to the strongly synchronized recruitment, the low-survival periods were not synchronous over the Wadden Sea. Adult density and total biomass varied in parallel over most sites and were low throughout the Dutch Wadden Sea (less than a quarter of the earlier long-term average) from 2005 onwards. The factors suggested to underlie these changes in abundance were (1) negative effects of climate warming on recruitment, which includes higher abundance of predators on young bottom stages, and (2) an unknown cause of enhanced adult mortality, possibly disease. Synchronization in recruitment, adult density and total biomass of *L. balthica* populations throughout the Dutch Wadden Sea indicates that they are part of a Wadden Sea-wide metapopulation.

KEY WORDS: Long-term data · Population dynamics · Recruitment · Survival · Synchronized changes · Climate change

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

Synchrony in fluctuations of population size at distant locations has been observed in a wide variety of species (Liebhold et al. 2004). Examples from the marine environment include rocky shore communities in Shetland (Burrows et al. 2002), invertebrate recruitment on rocky platforms in Chile (Lagos et al. 2007), recruitment in bivalves in the Wadden Sea (Beukema et al. 2001) and mussel stock size in the Wadden Sea (Folmer et al. 2014, Beukema et al. 2015).

In the present study, we compare changes in the population size of the bivalve *Limecola balthica* in

various parts of the Dutch Wadden Sea. In an earlier study of dynamics at the Balgzand site (Beukema et al. 2017), we showed that between-year variability in recruitment success and subsequent adult survival together determined year-to-year variation in the population size of this species. Therefore, in the present study, we examine how these underlying processes of recruitment and survival vary between different distant sites. In particular, we investigate to what extent these variations are in unison, causing parallel fluctuations in *L. balthica* stock size all over the Dutch Wadden Sea.

Long-term monitoring programs, executed in 4 areas in the Dutch Wadden Sea (Fig. 1), produced

*Corresponding author: jan.beukema@nioz.nl

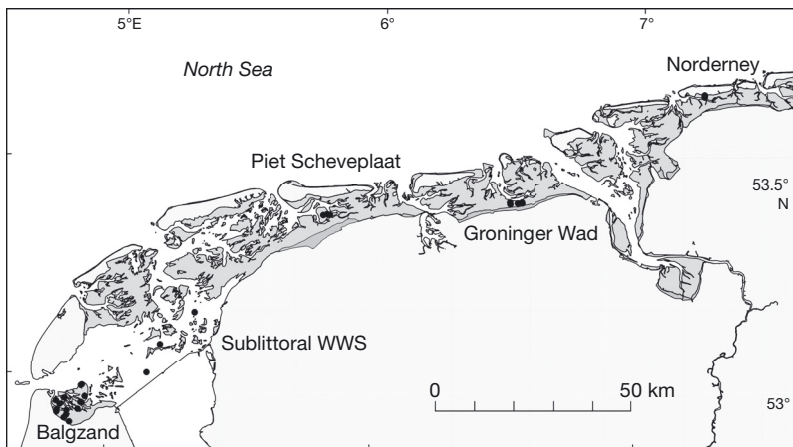


Fig. 1. The western part of the Wadden Sea, showing locations of the long-term monitoring of the macrozoobenthos (black dots). From west to east: Balgzand, sublittoral western Wadden Sea, Piet Scheveplaat and Groninger Wad

suitable data. Unfortunately, such data were not available for German and Danish parts of the Wadden Sea. Data on the dynamics of *L. balthica* are particularly suited for studies of population biology. It is a common species in the Wadden Sea, occurring at almost all sampling sites in fair numbers of ≥ 100 ind. m^{-2} . On the tidal flats of the Dutch Wadden Sea, it ranked first for commonness (Beukema 1976). In this area, their ages can be read from annual growth marks on the shell. During the 44 yr of the study, recruits appeared almost every year in numbers exceeding $10 m^{-2}$ (Beukema & Dekker 2014). Annual survival was relatively high, but rarely catastrophic (Beukema et al. 2009). As a consequence, interruptions of series of *L. balthica* numbers by absence of data are scarce: their numbers rarely declined to levels below the detection limit of the monitoring series. Among the 4 main species of bivalves in the Wadden Sea, *L. balthica* was the one with the lowest coefficient of variation for numbers and biomass (Beukema et al. 2001).

Various studies of the possible consequences of fishery impact and of climate change indicate declining trends of Wadden Sea stocks of *L. balthica*. Sediment disturbance by cockle fishery has been suggested to reduce bivalve recruitment for prolonged periods (Piersma et al. 2001), but direct evidence for prolonged negative effects of the cockle fishery on *L. balthica* abundance appears to be lacking. The mechanical cockle fishery in the Dutch Wadden Sea was particularly intense in the 1980s and early 1990s, but ended in 2004 (as early as 1993 in some areas).

The climate in the study area is warming. The mean annual water temperatures in the Wadden Sea area show a rising trend and are now about $1.5^{\circ}C$

higher than half a century ago (van Aken 2008, Beukema et al. 2009). The Wadden Sea population of *L. balthica* lives in the warmer southern part of its distribution area (Beukema & Meehan 1985). Its reproductive output (Honkoop & van der Meer 1997, Philippart et al. 2003) and recruitment (Beukema et al. 1998, 2009) are generally higher after cold than after mild winters. Recruitment success is of overriding importance for population dynamics and production (van der Meer et al. 2001, Dekker & Beukema 2007). Rising water temperatures initiate a chain of cause–effect relationships by enhancing the pressure of epibenthic predation on tiny (< 1 mm shell length)

just-settled bivalve post-larvae, and thus reducing recruitment in several bivalve species, including *L. balthica* (Beukema & Dekker 2014). Apart from recruitment, annual survival also strongly affects *L. balthica* abundance and biomass (Beukema et al. 2010, 2017). In years with elevated temperatures, mortality rates are higher than in years with relatively low temperatures (Beukema et al. 2009). Thus, a declining trend in *L. balthica* abundance may be expected in a period with increasing temperatures, due to both reduced recruitment as well as increased adult mortality.

The aims of the present paper are:

- (1) Showing to what degree changes in the size of various *L. balthica* populations all over the Dutch Wadden Sea were in synchrony and point to the presence of a single population in this area;
- (2) Relating the changes in stock size to underlying changes in rates of recruitment and adult survival (as shown in detail for the Balgzand population by Beukema et al. 2017);
- (3) Showing how far fluctuations in recruitment and survival were in unison all over the Dutch Wadden Sea;
- (4) Trying to find underlying causes of changes in population attributes of *L. balthica*.

MATERIALS AND METHODS

Sampling areas

The 4 sampling areas were, arranged from west to east: Balgzand, Sublittoral, Piet Scheveplaat and Groninger Wad (Fig. 1). In the following, we provide

short descriptions and refer to publications for more details.

The Balgzand area of 50 km² tidal flats, with 15 sampling sites (mostly 1 km transects) at widely varying intertidal levels (between about +0.2 and -0.8 m relative to mean-tide level) and with a wide range of sediment composition, has been described in detail by Beukema & Cadée (1997). Median grain size of the sediment varies from about 90 to 250 µm and silt content from 0.1 to 30%.

The Sublittoral area is an extensive subtidal area with 3 transects of 1.5 km at depths of between 1.5 and 4.7 m below mean tide level. Median grain size of the sediment varies from about 140 to 175 µm and silt content from about 2 to 6% (Dekker 2012).

The Piet Scheveplaat area is a tidal flat of a few km² with 3 transects of 760 m at a level of +0.5 to -0.7 m relative to mean-tide level, median grain sizes of 145 to 181 µm and silt contents of 0.5 to 6.5% (Dekker 2009).

The Groninger Wad area is a 10 km² tidal flat area with 5 sampling squares of 900 m² at a level of about 0 to -0.5 m relative to mean-tide level, median grain size of 100 to 145 µm and silt contents of 1 to 10% (van der Graaf & Tydeman 2008).

A 17 yr data series for a part of the western Wadden Sea that was reported by Compton et al. (2016) could not be used, because the animals were not properly aged (only divided into 2 size classes).

Bivalve sampling

Most areas were sampled in a consistent way twice a year: in late winter/early spring and in late summer. Bivalves were sorted from the sieved (1 mm mesh size) samples, assigned to age classes (cohorts were indicated by the year of birth) and counted. Numerical densities were expressed in n m⁻² and presented as multi-station means. Surface areas sampled annually amounted to about 15 m² on Balgzand, 3 m² in the Sublittoral, 1.6 m² on Piet Scheveplaat and 1 to 2 m² on Groninger Wad. Core size varied from 0.01 to 0.1 m² and sampling depth from 20 to 30 cm. This variation will not have affected the estimates of *Limecola balthica* abundance.

Recruitment (numerical density of a new cohort) was assessed at a bivalve age of about 0.3 yr in late summer. At that time, the animals were still of spat size (mostly <7 mm shell length).

Annual survival of adults was expressed as the percentage of the total numbers of individuals aged ≥1.8 yr in a certain year that were still alive 1 yr later:

$$100 \times (n \text{ m}^{-2} \text{ of } 2.8^+ \text{ yr olds in year } n + 1 / n \text{ m}^{-2} \text{ of } 1.8^+ \text{ yr olds in year } n).$$

To avoid extreme variability caused by the use of too low numbers of departure, we did not use percentages that were based on numbers of 1.8⁺ yr olds of <10 m⁻².

The size of the total *L. balthica* stocks was expressed in 2 ways: in units of numerical density (n m⁻²) of adult individuals and in units of biomass (g ash-free dry mass [AFDM] m⁻²).

The statistical method used was the Pearson correlation test. Because of the extreme variability in recruitment success, recruit densities were evaluated after log₁₀ transformation.

Data sources

Balgzand data were collected by J. J. Beukema and R. Dekker and are stored in the NIOZ (Royal Netherlands Institute for Sea Research) database. Sublittoral data were collected by R. Dekker and published in a series of reports (Dekker 2012 and earlier reports in the same series). Data for years after 2010 are stored in the NIOZ data base.

Piet Scheveplaat data have been reported by Laufer (1992) for 1978 to 1990, by R. Dekker (1991 to 2008, see Dekker 2009 and earlier reports) and by some other investigators in later years (see Wanink et al. 2014 and earlier reports in the same series). Biomass data in Laufer (1992) were converted to late winter values.

Groninger Wad data were collected by K. Essink and R. Koeman and compiled by J. Drent (1976 to 2003). Part of the data were reported by van der Graaf et al. (2009) (1975 to 2006), van der Graaf & Tydeman (2008) (courtesy R. Koeman) (1998 to 2007), Wanink et al. (2014) and earlier reports in the same series (2008 to 2014).

RESULTS

Recruitment

Annual recruitment (n m⁻² of spat) of *Limecola balthica* as assessed in late summer was highly variable among years, varying over 3 orders of magnitude. Therefore, these data were plotted at a log₁₀ scale for clarity (Fig. 2). At first sight, the long-term patterns for the 4 areas shown in Fig. 2 revealed a clear resemblance, indicating that success or failure in the 4 areas took place mostly in the same years. Indeed, this synchrony proved to be statistically significant

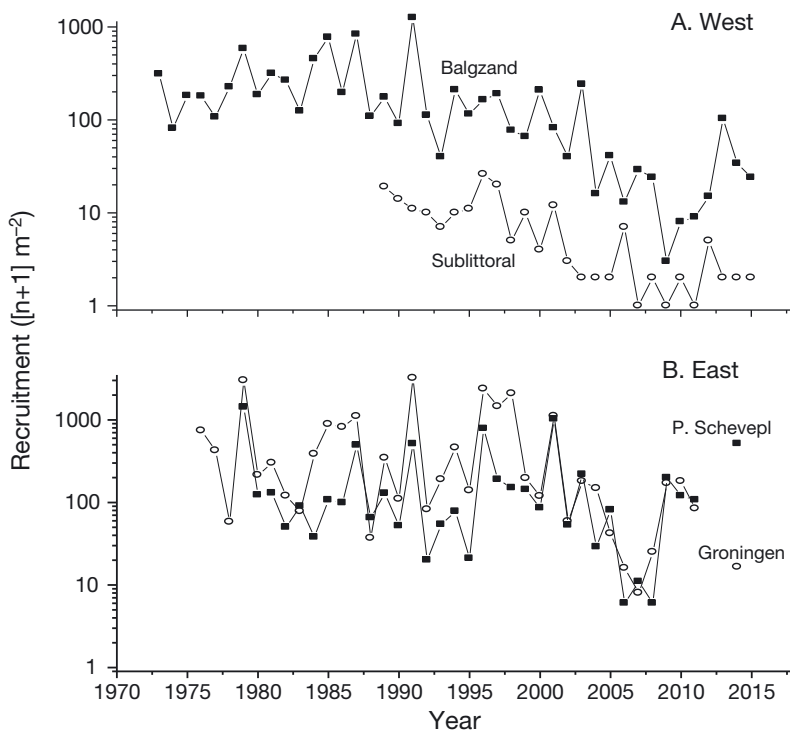


Fig. 2. Long-term data series of annual *Limecola balthica* recruitment, expressed in $n\ m^{-2}$ of spat-size individuals, assessed in late summer in 4 areas in the Dutch Wadden Sea. (A) (■) Averages of 15 sampling places scattered on tidal flats of Balgzand, in the 43 yr period from 1973 to 2015. (○) Averages of 3 transects in a sublittoral area about 25 km northeast of Balgzand in the 27 yr period from 1989 to 2015. (B) (■) Averages of 3 transects on tidal flats at Piet Scheveplaat, sampled in the 34 yr period from 1978 to 2011. (○) Averages of 5 sampling places in a tidal-flat area north of Groningen, sampled in the 37 yr period from 1975 to 2011

for 5 of the 6 possible comparisons (Table 1A). The strongest correlations ($r > 0.6$, $r^2 > 0.4$; Pearson correlation) were found in pairs of nearby places: the westernmost comparison between Balgzand and Sublittoral and the easternmost comparison between Piet Scheveplaat and Groningen.

In the years after 2000, recruitment failed ($n < 20\ m^{-2}$) several times in a more or less synchronized manner. Extremely low recruitment occurred particularly around 2007: Balgzand 2004 to 2012; Sublittoral 2007 to 2011; Piet Scheveplaat 2006 to 2008; Groningen 2005 to 2008. Significantly declining trends over the entire periods of observation were found in 3 out of the 4 studied areas. The Pearson r -values for the correlation of log recruit density with year number were: Balgzand $r = -0.70$ ($n = 43$, $p < 0.0001$), Sublittoral area $r = -0.80$ ($n = 27$, $p < 0.0001$) and Groningen Wad $r = -0.43$ ($n = 37$, $p < 0.01$). At Piet Scheveplaat, no significant negative trend was observed ($r = -0.18$, $n = 34$, $p = 0.3$).

For the first 20 to 25 yr of the period of observation, recruitment was generally successful (about 100 or more spat individuals m^{-2}) in the 3 intertidal areas (Fig. 2). During these initial periods, peaks and lows frequently occurred in the same years in the 3 areas. Peak values were found particularly after the 3 coldest winters of the period: in 1979, in 1987 and in 1996 (Wadden Sea water temperatures in winter can be found in Beukema & Dekker 2014, their Fig. 3). Indeed, in all 3 areas, recruitment in this initial period was negatively correlated with water temperature in the preceding winter: Balgzand $r = -0.74$ ($p < 0.001$), Piet Scheveplaat $r = -0.51$ ($p < 0.02$), Groningen $r = -0.59$ ($p < 0.01$).

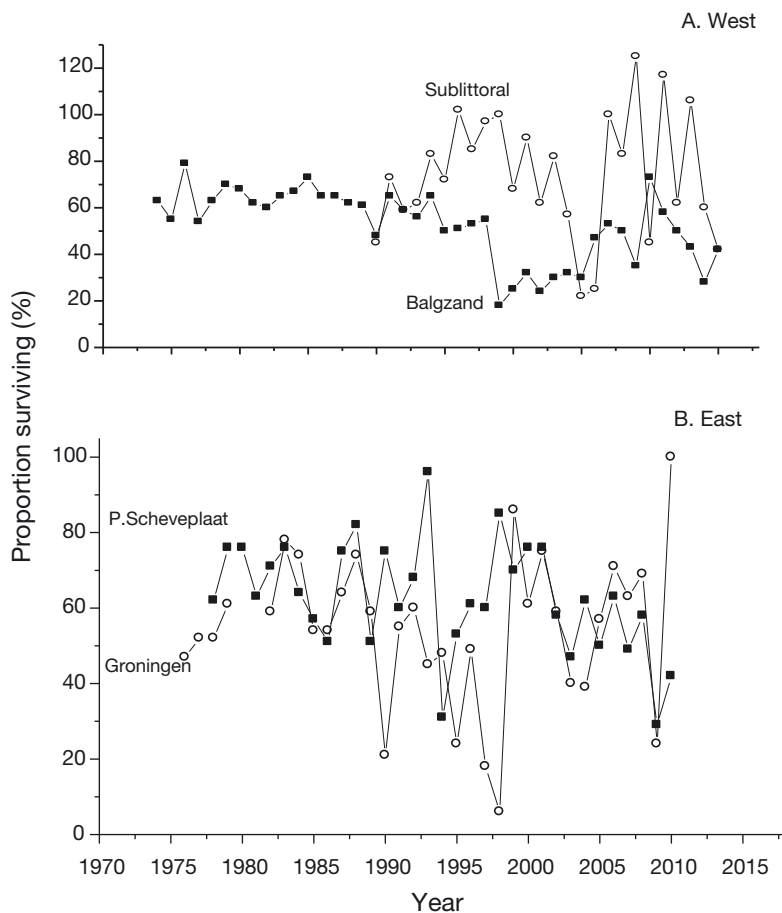
Adult survival

For prolonged initial periods, the proportions of adults that survived from one year to the next were rather constant in all areas, amounting to 60 to 80% in the 3 intertidal areas and 70 to 100% in the sublittoral area (Fig. 3). After 1989, long periods with high survival alternated with short periods with seriously reduced survival rates: single years in some locations (e.g. Groninger Wad) and periods of up to 7 yr in others (e.g. Balgzand). Generally, these short periods did not occur simultaneously in the 4 areas: Balgzand 1999 to 2005 and again 2014; Sublittoral 2005 to 2006; Piet Scheveplaat 2009 to 2010; Groningen 1990, 1995, 1997 to 1998, and 2009 (Fig. 3). As a consequence of this lack of synchronization, survival rates in the 4 areas were not significantly correlated: the 6 Pearson r -values shown in Table 1B ranged from -0.24 to $+0.09$ ($p > 0.5$ in all cases). None of the long-term trends in Fig. 3 was statistically significant.

For the 1975 to 1995 period (i.e. the period before the sudden declines in survival in most locations), we found a negative correlation between winter water temperatures and subsequent survival only at Balgzand. In the other areas, this correlation was close to 0 and non-significant. At Balgzand, survival rates were reduced by 2% for each $^{\circ}C$ rise in water temperature (for details see Beukema et al. 2017).

Table 1. Pearson r-values for correlations between time series for annual estimates of (A) recruitment, (B) survival, (C) adult numbers and (D) total biomass as observed in 4 areas in the Dutch Wadden Sea (see Fig. 1). Numbers of observations are given in brackets. * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.
AFDM: ash-free dry mass

	Sublittoral	P. Scheveplaat	Groningen
(A) Recruit densities ($\log_{10} n m^{-2}$) in late summer			
Balgzand	+0.64*** (27)	+0.35* (34)	+0.55*** (37)
Sublittoral		+0.24 (24)	+0.60** (24)
P. Scheveplaat			+0.69*** (34)
(B) Adult survival (% of initial number in late winter/early spring)			
Balgzand	+0.02 (26)	+0.06 (33)	+0.09 (33)
Sublittoral		-0.15 (21)	-0.24 (21)
P. Scheveplaat			+0.05 (31)
(C) Numerical densities ($n m^{-2}$) of adults in late winter/early spring			
Balgzand	+0.36 (27)	+0.27 (34)	+0.09 (36)
Sublittoral		+0.61** (22)	+0.50* (24)
P. Scheveplaat			+0.80*** (34)
(D) Biomass ($g AFDM m^{-2}$) in late winter/early spring			
Balgzand	+0.34 (27)	+0.30 (35)	+0.24 (37)
Sublittoral		+0.55** (22)	+0.68*** (24)
P. Scheveplaat			+0.85*** (34)



Stock size

In all 4 sampling areas, annual values of adult density (Fig. 4) and total biomass (Fig. 5) varied strongly, from close to 0 to about 3 times their long-term average. The long-term means of adult density estimates amounted to about $50 m^{-2}$ in the sampled areas in the western Dutch Wadden Sea (Fig. 4A) and substantially higher values of about 100 and $200 m^{-2}$ in the eastern half of the Dutch Wadden Sea (Fig. 4B). The long-term mean biomass values amounted to about $2 g m^{-2}$ in the 2 areas in the western part (Fig. 5A) and to higher values in the 2 areas in the eastern part (Fig. 5B; about $3 g m^{-2}$ on Piet Scheveplaat and about $6 g m^{-2}$ on Groninger Wad).

Stock changes from one year to the next were generally only moderate: the observed fluctuations (Figs. 4 & 5) were characterized by prolonged periods with either continually increasing or continually declining trends. In the 2 sampling areas in the eastern Dutch Wadden Sea, patterns of fluctuations in numbers and biomass resembled each other rather closely and the correlations of their annual values were highly significant (Table 1C,D; Pearson $r = +0.80$ and $+0.85$, $n = 34$, $p < 0.001$, for adult numbers and total biomass, respectively). The pattern found in the sublittoral of the west-

Fig. 3. Long-term data series of annual *Limecola balthica* survival, expressed as a percentage of individuals >1.8 yr old that were still alive 1 yr later. Numbers assessed in late winter/early spring in 4 areas in the Dutch Wadden Sea. (A) (■) Averages of 15 sampling places scattered on tidal flats of Balgzand in the 44 yr period from 1973 to 2016. (○) Averages of 3 transects in a sublittoral area about 25 km northeast of Balgzand in the 26 yr period from 1990 to 2015. (B) (■) Averages of 3 transects on tidal flats at Piet Scheveplaat, sampled in the 33 yr period from 1978 to 2010. (○) Averages of 5 sampling places in a tidal-flat area north of Groningen, sampled in 33 yr within the period from 1976 to 2010

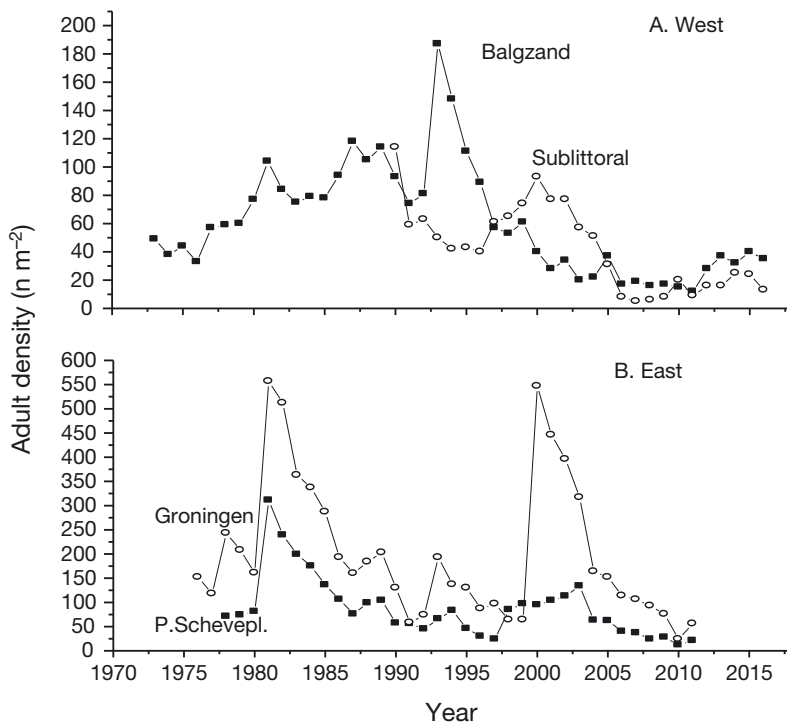


Fig. 4. Long-term data series of annual estimates of numerical density of adult (aged 1.8 yr or more) *Limecola balthica* in late winter/early spring, in 4 areas in the Dutch Wadden Sea. (A) (■) Averages of 15 sampling places scattered on tidal flats of Balgzand, sampled in the 44 yr period from 1973 to 2016. (○) Averages of 3 transects in a sublittoral area about 25 km northeast of Balgzand, sampled in the 27 yr period from 1990 to 2016. (B) (■) Averages of 3 transects on tidal flats at Piet Scheveplaat, sampled in the 34 yr period from 1978 to 2011. (○) Averages of 5 sampling places in a tidal-flat area north of Groningen, sampled in the 36 yr period from 1976 to 2011

ern Dutch Wadden Sea showed some resemblance with the 2 patterns found in the eastern Dutch Wadden Sea with statistically significant (mostly $p < 0.01$) r -values of around +0.6 (Table 1C,D). Only the Balgzand patterns for both adult densities as well as biomass clearly differed from the 3 other areas, with non-significant r -values mostly of around 0.3 for all 6 correlations with the other areas. Unique characteristics at Balgzand were peaks around 1987 and 1993, and a lack of the peaks that occurred in the 3 other areas around 2002.

More or less consistently declining long-term trends were observed on Balgzand starting from 1993 to 1996, in the Sublittoral from 2000 to 2002, on Piet Scheveplaat from 2001 to 2003 and on Groninger Wad from 2000 to 2002. The synchronized declines in the latter 3 areas which started in 2001 were all statistically significant ($p < 0.02$), with Pearson r -values for correlations with year number of around -0.7 .

DISCUSSION

Synchronized recruitment

Years of successful and failing recruitments alternated in largely similar ways in the 4 sampling areas. Moreover, the areas had a downward long-term trend in common. Such synchronization points to a common controlling mechanism that is effective all over the Wadden Sea. The warming climate could be such a cause: water temperatures increased between 1970 and 2010 all over the Dutch Wadden Sea and fluctuated in harmony (Tulp et al. 2012). Recruitment was indeed high everywhere after the 3 coldest winters (1979, 1987 and 1996) of the study period and we found negative correlations between winter temperatures and subsequent recruitment for the first half of the period of observation when recruitment was still at a high level. Cold winters cause low abundance of the main predators (shrimps and shore crabs) of tiny, just-settled, bivalve spat (Strasser 2002, Strasser et al. 2003, Beukema & Dekker 2005, 2014). As a consequence, high proportions of the spat survive. Shore crab abundance strongly increased (about 5-fold) all

over the Dutch Wadden Sea between 1994 and 2010 (Tulp et al. 2012). Shrimp abundance strongly increased during the last 4 decades in the western half of the Dutch Wadden Sea, remained at roughly the same level in the area around Piet Scheveplaat and halved in the area around Groninger Wad (Campos et al. 2010, Tulp et al. 2012). The increases in total (crab + shrimp) epibenthic predation pressure might largely explain the observed declining trends in recruitment success in *Limecola balthica* all over the Dutch Wadden Sea, but probably not the sudden and dramatic declines between 2005 and 2010.

Synchronization in *L. balthica* recruit abundance appears not to be restricted to the Dutch Wadden Sea. For the 1976 to 1999 period, recruitment at the German island of Norderney was reported to be significantly positively correlated with that in Groningen and Balgzand (Beukema et al. 2001). The peaks observed on Balgzand in 1979 and 1987 were also found at Norderney (Strasser et al. 2003).

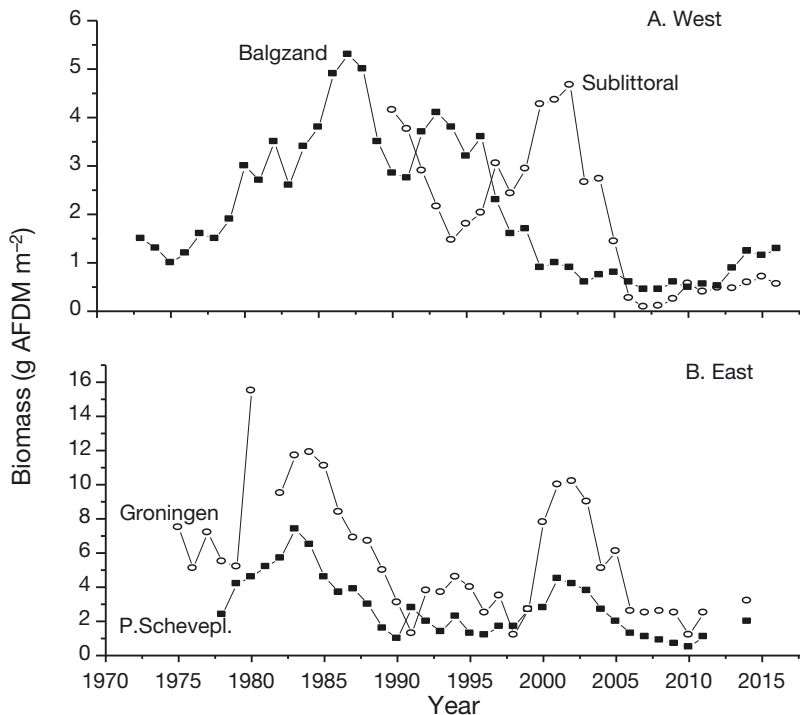


Fig. 5. Long-term data series of annual total *Limecola balthica* biomass in late winter/early spring, in 4 areas in the Dutch Wadden Sea, as detailed in the legend of Fig. 4, with the addition of some estimates for years that lack age distributions. AFDM: ash-free dry mass

Non-synchronized survival

For a long initial period (before 1989), survival rates were invariably high, around $60\% \text{ yr}^{-1}$ or higher. Starting from 1990, however, years or groups of years were observed at all locations with substantially lower survival. These years were not synchronized, pointing to local causes, which are as yet unknown. A detailed study on Balgzand revealed a shifting geographic pattern of survival rates, suggesting the expansion of a contagious disease, taking about 5 yr to reach all sampling sites within the 50 km^2 area (Beukema et al. 2017). However, the exact cause of the catastrophic mortalities is still an object of investigation. So far, the earlier stable situation has not yet been restored anywhere: years with low survival still occasionally occur in all sampling areas.

Partly synchronized stock sizes

At any moment, stocks of *L. balthica* are made up of several year classes. As a consequence, between-year changes in stock size were relatively small (by

the autocorrelation of data of successive years). Generally, dramatic changes only occurred over periods of several years. Gradual changes were also promoted by the non-simultaneous occurrence of incidences of reduced survival at nearby sampling places (as shown within the Balgzand area by Beukema et al. 2017). The monitored tidal-flat areas were relatively rich in *L. balthica*; Dutch Wadden Sea-wide mean biomass values of this species on tidal flats were 2.2 and $1.3 \text{ g AFDM m}^{-2}$ in the 1970s (Beukema 1976) and 2000s (Compton et al. 2013), respectively.

The long-term patterns for adult densities and total biomass were clearly similar between the 2 easternmost sites with peaks in the early 1980s and again around 2000. For the 1990 to 2007 period, observations made by De Mesel et al. (2011) revealed a similar pattern, not only in the entire eastern half of the Dutch Wadden Sea, but also in the nearby coastal zone of the North Sea. A similar pattern for biomass was also observed about 60 km east of Groninger Wad, at the German island of Norderney (Beukema et al. 1996).

On Balgzand, however, a unique pattern was found, with a strong abundance peak in 1992 to 1993 (due to an extraordinarily successful recruitment in 1991), followed by a prolonged decline for a long period that was characterized by declining recruitments and adult survival rates. Recruitment was only found to increase again to levels close to those observed earlier during the most recent years. For the last 2 decades, such patterns were also observed in part of the western half of the Dutch Wadden Sea (Compton et al. 2016, De Mesel et al. 2011) and also in the coastal zone of the mainland south of the Wadden Sea (De Mesel et al. 2011). Even farther south, in the south-westernmost part of The Netherlands, different patterns were found. Thus, the Balgzand patterns of adult densities and recruitment were representative for a wider area, including the westernmost part of the Dutch Wadden Sea and the mainland coast south of it (almost 200 km).

In all Wadden Sea areas outside Balgzand, consistent declines in adult abundance and biomass started several years later than on Balgzand: around 2003. In these areas, recruitment success remained high until

this time. Everywhere in the Dutch Wadden Sea, adult numbers and biomass were low after 2005 and recruitment was low for these years, whereas years with low adult survival were still frequent. Both recruitment and survival (mortality) are known to seriously affect biomass in *L. balthica* and other bivalves (van der Meer et al. 2001, Beukema et al. 2010, Magelhães et al. 2016).

CONCLUSIONS

In the 4 sampling areas scattered over the Dutch Wadden Sea, we found several similarities in the long-term patterns of recruitment success and total abundance. Low values were observed everywhere in the Dutch Wadden Sea for the most recent decade, when recruitment was low and years of low survival were frequent. Such similarities point to the existence of 1 single population of *Limecola balthica* in the Dutch Wadden Sea (extending to the near-coastal areas of the North Sea along the Dutch mainland coast and the Dutch Frisian Islands). This population was struck by incidences of sudden marked reductions in survival that occurred everywhere in the Dutch Wadden Sea after 1990, but at different times and lasting for 1 to 7 yr. In addition to the reduced recruitment, which has been occurring everywhere in the Dutch Wadden Sea since 2000, adult stocks have also declined during the same period. It is difficult to tease apart the influences of recruitment and survival. An attempt with the Balgzand data (Beukema et al. 2017) indicated a decisive influence of reduced survival, affecting recruitment via adult stock size, the latter becoming too small to produce sufficient offspring.

Negative fishery effects cannot explain the ubiquitous decline of stocks around 2000, as fishery for cockles and mussels on tidal flats ended completely near that time (2004) and, in some areas (such as Balgzand: 1993), several years before. Stock declines continued after the fishery had stopped, and stock increases were found in the eastern Dutch Wadden Sea for the years just before 2004. We conclude that no consistent effects of fisheries on *L. balthica* abundance can be discerned.

An influence of the warming climate could be shown for the period before survival and recruitment strongly declined: throughout the Dutch Wadden Sea we found negative correlations (with *r*-values of around -0.6) between winter temperatures and subsequent recruitment. On Balgzand survival also declined with increasing temperatures (Beukema et

al. 2009, 2017). After around 1995, however, the influence of catastrophic mortality rates became overwhelming, obscuring possible temperature effects. A return to the usual survival rates appears to still be incomplete. Whenever survival recovers to more normal values, we would expect a somewhat lower abundance of *L. balthica* with the ongoing climate warming, as a consequence of lower recruitment and survival at the mostly higher temperatures. Caution, however, is warranted in predictions of temperature effects. As van der Meer et al. (2013) have shown, the effects of temperature change on benthic fauna in the Wadden Sea are poorly predictable.

Acknowledgements. We are grateful to K. Essink and R. Koeman for their generous help in retrieving monitoring reports and data files.

LITERATURE CITED

- ✦ Beukema JJ (1976) Biomass and species richness of the macro-benthic animals living on the tidal flats of the Dutch Wadden Sea. *Neth J Sea Res* 10:236–261
- ✦ Beukema JJ, Cadée GC (1997) Local differences in macrozoobenthic response to enhanced food supply caused by mild eutrophication in a Wadden Sea area. Food is only locally a limiting factor. *Limnol Oceanogr* 42:1424–1435
- ✦ Beukema JJ, Dekker R (2005) Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. *Mar Ecol Prog Ser* 287:149–167
- ✦ Beukema JJ, Dekker R (2014) Variability in predator abundance links winter temperatures and bivalve recruitment: correlative evidence from long-term data in a tidal flat. *Mar Ecol Prog Ser* 513:1–15
- ✦ Beukema JJ, Meehan BW (1985) Latitudinal variation in linear growth and other shell characteristics of *Macoma balthica*. *Mar Biol* 90:27–33
- ✦ Beukema JJ, Essink K, Michaelis H (1996) The geographic scale of synchronized fluctuation patterns in zoobenthos populations as a key to underlying factors: climatic or man-induced. *ICES J Mar Sci* 53:964–971
- ✦ Beukema JJ, Honkoop PJC, Dekker R (1998) Recruitment in *Macoma balthica* after mild and cold winters and its possible control by egg production and shrimp predation. *Hydrobiologia* 375/376:23–34
- ✦ Beukema JJ, Dekker R, Essink K, Michaelis H (2001) Synchronized reproductive success of the main bivalve species in the Wadden Sea: causes and consequences. *Mar Ecol Prog Ser* 211:143–155
- ✦ Beukema JJ, Dekker R, Jansen JM (2009) Some like it cold: populations of the tellinid bivalve *Macoma balthica* (L.) suffer in various ways from a warming climate. *Mar Ecol Prog Ser* 384:135–145
- ✦ Beukema JJ, Dekker R, Philippart CJM (2010) Long-term variability in bivalve recruitment, mortality, and growth and their contribution to fluctuations in food stocks of shellfish-eating birds. *Mar Ecol Prog Ser* 414:117–130
- ✦ Beukema JJ, Dekker R, van Stralen MR, de Vlas J (2015) Large-scale synchronization of annual recruitment

- success and stock size in Wadden Sea populations of the mussel *Mytilus edulis* L. *Helgol Mar Res* 69: 327–333
- ✦ Beukema JJ, Dekker R, Drent J (2017) Dynamics of a *Limecola (Macoma) balthica* population in a tidal flat area in the western Wadden Sea: effects of declining survival and recruitment. *Helgol Mar Res* 71:18
- ✦ Burrows MT, Moore JJ, James B (2002) Spatial synchrony of population changes in rocky shore communities in Shetland. *Mar Ecol Prog Ser* 240:39–48
- ✦ Campos J, Bio A, Cardoso JFMF, Dapper R, Witte JJJ, van der Veer HW (2010) Fluctuations of brown shrimp *Crangon crangon* abundance in the western Dutch Wadden Sea. *Mar Ecol Prog Ser* 405:203–219
- ✦ Compton TJ, Holthuijsen S, Koolhaas A, Dekinga A and others (2013) Distinctly variable mudscapes: distribution gradients of intertidal macrofauna across the Dutch Wadden Sea. *J Sea Res* 82:103–116
- ✦ Compton TJ, Bodnar W, Koolhaas A, Dekinga A and others (2016) Burrowing behavior of a deposit feeding bivalve predicts change in intertidal ecosystem state. *Front Ecol Evol* 4:1–9
- De Mesel I, Craeymeersch J, Jansen J, van Zweeden C (2011) Biodiversiteit, verspreiding en ontwikkeling van macrofauna soorten in de Nederlandse kustwateren. IMARES Wageningen Report, C022/11. Wageningen University and Research. IMARES, Ijmuiden
- Dekker R (2009) Het macrozoobenthos op twaalf raaien in de Waddenzee en de Eems-Dollard in 2008. NIOZ Rapport 2009-1, Texel
- Dekker R (2012) Macrozoobenthosonderzoek MWTL, voor- en najaar 2010, waterlichaam: Waddenzee (Balgzand en sublitorale westelijke Waddenzee). NIOZ Rapport 2011-6, Texel/ Rijkswaterstaat, rapportnummer BM10.11
- ✦ Dekker R, Beukema JJ (2007) Long-term and large-scale variability in productivity of the tellinid bivalve *Macoma balthica* on Wadden Sea tidal flats. *Mar Ecol Prog Ser* 337:117–134
- ✦ Folmer EO, Drent J, Troost K, Büttger H and others (2014) Large-scale spatial dynamics of intertidal mussel (*Mytilus edulis* L.) bed coverage in the German and Dutch Wadden Sea. *Ecosystems* 17:550–566
- ✦ Honkoop PJC, van der Meer J (1997) Reproductive output of *Macoma balthica* populations in relation to winter-temperature and intertidal-height mediated changes of body mass. *Mar Ecol Prog Ser* 149:155–162
- ✦ Lagos NA, Tapia FJ, Navarrete SA, Castilla JC (2007) Spatial synchrony in the recruitment of intertidal invertebrates along the coast of central Chile. *Mar Ecol Prog Ser* 350:29–39
- Laufer Y (1992) Long-term development of biomass of intertidal macrozoobenthos at Piet Scheve Plaat (Dutch Wadden Sea). Rapport DGW-92.014, Dienst Getijdewateren, Groningen
- ✦ Liebhold A, Koenig WD, Bjørnstad ON (2004) Spatial synchrony in population dynamics. *Annu Rev Ecol Evol Syst* 35:467–490
- ✦ Magelhães L, Freitas R, de Montaudouin X (2016) Cockle population dynamics: recruitment predicts adult biomass, not the inverse. *Mar Biol* 163:16
- ✦ Philippart CJM, van Aken HM, Beukema JJ, Bos OG, Cadée GC, Dekker R (2003) Climate-related changes in recruitment of the bivalve *Macoma balthica*. *Limnol Oceanogr* 48:2171–2185
- ✦ Piersma T, Koolhaas A, Dekinga A, Beukema JJ, Dekker R, Essink K (2001) Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. *J Appl Ecol* 38:976–990
- ✦ Strasser M (2002) Reduced epibenthic predation on intertidal bivalves after a severe winter in the European Wadden Sea. *Mar Ecol Prog Ser* 241:113–123
- ✦ Strasser M, Dekker R, Essink K, Günther CP and others (2003) How predictable is high bivalve recruitment in the Wadden Sea after a severe winter? *J Sea Res* 49:47–57
- ✦ Tulp I, Bolle LJ, Meesters E, de Vries P (2012) Brown shrimp abundance in northwest European coastal waters from 1970 to 2010 and potential causes for contrasting trends. *Mar Ecol Prog Ser* 458:141–154
- ✦ van Aken HM (2008) Variability of the water temperature in the western Wadden Sea on tidal to centennial scales. *J Sea Res* 60:227–234
- van der Graaf AJ, Tydeman P (2008) Het macrozoobenthos op vijf permanente quadraten op het Groninger wad. Trendanalyse 1998–2007. Rapport 2008-001, Bureau Koeman en Bijkerk, Haren
- van der Graaf AJ, de Vlas J, Herlyn M, Voss J, Heyer K, Drent J (2009) Macrozoobenthos. Thematic Report No. 10. In: Marencic H, de Vlas J (eds) Quality Status Report 2009. Wadden Sea Ecosystem No. 25. Common Wadden Sea Secretariat, Wilhelmshaven
- ✦ van der Meer J, Beukema JJ, Dekker R (2001) Long-term variability in secondary production of an intertidal bivalve population is primarily a matter of recruitment variability. *J Anim Ecol* 70:159–169
- ✦ van der Meer J, Beukema JJ, Dekker R (2013) Using stochastic population process models to predict the impact of climate change. *J Sea Res* 82:117–121
- Wanink JH, Leewis L, Verburg A (2014) Macrozoöbenthosonderzoek in zoute Rijkswateren, MWTL 2014. Rapport 2014-022, Koeman en Bijkerk

Editorial responsibility: Romuald Lipcius,
Gloucester Point, Virginia, USA

Submitted: June 13, 2017; Accepted: October 5, 2017
Proofs received from author(s): December 4, 2017