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Climate warming leads to replacement of *Limecola balthica* by *Abra tenuis* on high tidal flats of the Wadden Sea

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ABSTRACT

The present climate warming exerts significant effects on coastal marine communities. These effects include species ranges moving poleward, declining numbers at the warm edge and increasing numbers at the cold edge of the distribution areas. We describe an example of such changes. We monitored the dynamics of two temperature-sensitive bivalve species for almost half a century in a tidal-flat area in the Wadden Sea. In this area, *Abra tenuis* is favored by high temperatures and shows high mortality in cold winters. On the other hand, *Limecola balthica* suffers there from high temperatures and benefits from cold conditions. We tested the hypothesis that the abundance of the former species is increasing, whereas the numbers of the latter one are declining. Our monitoring results corroborated this hypothesis. From literature data, we show that the distribution area of *A. tenuis* is expanding to the northeast, whereas that of L. *balthica* is shrinking at the southern edge of its range. We suggest that climate warming is the common cause of all of these changes. We expect that *A. tenuis* will ultimately become more numerous than L. *balthica* in the Wadden Sea and south of this area.

1. Introduction

The warming climate has serious consequences: species distributions shift poleward (Hiddink et al., 2015; Hale et al., 2017), numbers decline at the warm edge of their distribution area, and numbers increase at the cold edge. Such changes transform the structure of biological communities, reassemble food webs, affect biodiversity and interactions between species (Pinsky et al., 2020). This redistribution of life is now one of the most significant biological responses to climate warming. In most cases, however, poleward distribution shifts lagged behind shifts in sea bottom temperatures (Hiddink et al., 2015). In the Wadden Sea, species numbers of bottom animals were found to increase significantly during the last decades (Beukema and Dekker, 2011), partly as a consequence of higher temperatures in the area. More species enter the area from the south than leave it to the north.

Numerous examples have been published of poleward shifting species ranges, including several in the marine realm (e.g. Bates et al., 2014; Lenoir et al., 2020). In the intertidal, Pitt et al. (2010) documented poleward range extension in a high number of invertebrates on Tasmania. In general, however, relevant data on range changes and changes in abundance near the range edges are in short supply. In particular, long-term data series on abundance of such species in specific areas (particularly at the edges of distribution areas) appear to be almost lacking, making quantification of their temporal trends difficult (Mieszkowska and Sugden, 2016). Fortunately, we are now able to add an extensively documented example of long-term trends in 2 bivalve species in a coastal area: *Abra tenuis* and *Limecola (Macoma) balthica.* In the Wadden Sea, the former species is sensitive to low temperatures and favored by high temperatures (Dekker and Beukema, 1993, 1999), whereas the latter suffers from high temperatures and is favored by low temperatures (Philippart et al., 2003, Beukema et al., 2009, Beukema & Dekker, 2014). In the Wadden Sea, the former species lives near the northern (cold) edge of its distribution area, whereas the latter species lives there in the southern (warm) half of its range. These significant differences offer an opportunity for an interesting comparison of their long-term responses to climate warming. In the Wadden Sea, the warming by about 2° C over the past 50 year has exceeded the global average.

The availability of a continuous long-term (almost 50 years) data series on the abundance of the 2 species from a tidal-flat area in the westernmost part of the Wadden Sea (Beukema and Dekker, 2020b) made this study possible. Such long continuous data series are rare for

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marine invertebrates. In the present paper, we report on the fluctuations and trends in abundance of the 2 species, testing the hypothesis that the numbers of *A. tenuis* were increasing and of *Limecola balthica* were declining. We further hypothesize that distribution areas of the 2 species shifted in a poleward direction. For a documentation of these range shifts, we use published data in the literature.

2. Methods

Populations of *A. tenuis* and *Limecola balthica* were sampled twice-annually at 15 fixed stations on Balgzand, a 50-km^2 tidal flat area in the westernmost part of the Wadden Sea (at about 53^o N and 5^o E). In the present paper, we use data from samplings in late summer (mostly in August) at the 4 stations situated in the higher part of the intertidal (i.e. from 0 to 5 dm above MTL, mean tide level; the intertidal ranges from +6 to −8 dm). Among these 4 stations, 2 were 1-km transects and 2 were 30 × 30 m squares. A map of the area is shown in Beukema and Cadée (1997) with the sampled stations marked 1, 2, A, and B. Along the transects 50 equally spaced samples of 0.01 m^2 were taken, within the squares 9 samples of 0.1 m^2 plus 9 samples of 0.01 m^2. These samples were sorted alive in the laboratory and all macrobenthic animals identified and counted. All densities are expressed in n m^{-2}. Averages of the densities at the 4 stations were plotted against year number and best fit lines of the regressions were calculated and statistically evaluated by the *t*-test.

Details on environmental conditions at the sampling stations can be found in Beukema and Cadée (1997). The sampled stations differed from the other Balgzand stations by their higher intertidal levels (above mean-tide level) and mostly higher proportions of mud in the sediment.

Over the 50-year study period, water temperatures in the area rose significantly in all seasons. Annual averages at a rate of 0.045 °C y^{-1}, seasonal rates by about 0.04 °C y^{-1} (Beukema and Dekker, 2020a, 2020b). This resulted in a temperature increase of about 2 °C over the study period, being well above the global average. No consistent changes were observed in other environmental factors such as salinity, intertidal level or mud content.

The presence of *A. tenuis* was almost restricted to the area above MTL. For this species, we chose to use the abundance data of 1-year old individuals. The species spawns in summer and at the late-winter samplings the individuals were still too small to be completely retrieved by the 1-mm square-mesh sieves. Thus, the first occasion for reliable sampling was at an age of 1 year. At that time their shell length was around 5 mm. Older individuals were scarce.

For a good comparison, we used data for L. *balthica* abundance at the same 4 stations and used data for the numbers of their spat (about 3 months old), being of about the same size as most *A. tenuis*. Usually, spat numbers in L. *balthica* were maximal in the area above MTL (Beukema, 1993). Older individuals were generally more numerous at lower intertidal levels, but showed similar trends in abundance. So, the 2 species were sampled in the same habitat and this habitat is optimal for all *A. tenuis* and for spat of L. *balthica*.

3. Results

3.1. Distribution patterns

Limecola balthica is a species with a more northern distribution than *A. tenuis*. The first species is found from the Bay of Biscay (where it is now rare) all along the western European coasts up to the Ice Sea. The latter species occurs from northern Africa (Mauritania) to Scotland and reaches its northern edge in the Wadden Sea (Dekker and Beukema, 1993). Up to some 50 years ago, *L. balthica* occurred also along the Spanish part of the Bay of Biscay (Jansen et al., 2007). By now, the southern limit is around the Gironde estuary, where it has become scarce (Bachelet, 1980).

A. tenuis appears to spread into a northeastern direction in the Wadden Sea. Up to 1990, it was restricted almost exclusively to the western half of the Dutch Wadden Sea, after that year it was found also in most of the eastern part (see distribution map in NDFF: Nederlandse Databank Flora en Fauna). In their species list of invertebrates in the Wadden Sea, Wolff and Dankers (1983) mention the species only for the Dutch part of the Wadden Sea. Compton et al. (2017) do not mention *A. tenuis* among the 37 macrobenthic species they found in 2009–2014 in the Ems-Dollard area (easternmost part of the Dutch Wadden Sea). We found an older record from the eastern half of the Dutch Wadden Sea: Vader (1961) mentions the species from Schiermonnikoog. Further, we received a personal communication by K.H. van Bernem and C.-P. Günther reporting a found in the 1980s of *A. tenuis* from Borkum, the westernmost island of the German Wadden Sea at a short distance from the Dutch Wadden Sea (see map in Dekker and Beukema, 1993). This observation could not be confirmed by I. Kröncke (Senckenberg am Meer). However, she communicates a found in 2018 in the Leybucht and on tidal flats near Langeoog and Spiekeroog (all in the western half of the German part of the Wadden Sea). So far, we found no records of *A. tenuis* for Danish parts of the Wadden Sea.

Among 9 areas sampled once along the coasts of France, England and the Netherlands, Bocher et al. (2007) found an increasing trend from north to south in numbers of *A. tenuis* and a declining one in L. *balthica*. South of Brittany, the 2 species were roughly equally abundant, whereas north of Brittany numerical densities of L. *balthica* were in their data set invariably higher (3 to >100 times) than those of *A. tenuis*. In the Bay des Veys, immediately north of Brittany, however, we (pers. obs. JJB) found exclusively *A. tenuis*.

To summarize: recent poleward range shifts were documented in each of the 2 species, for L. *balthica* at the southern range edge and for *A. tenuis* at the northern edge. Moreover, the preponderance of L. *balthica* increases in a poleward direction.

3.2. Changes in abundance

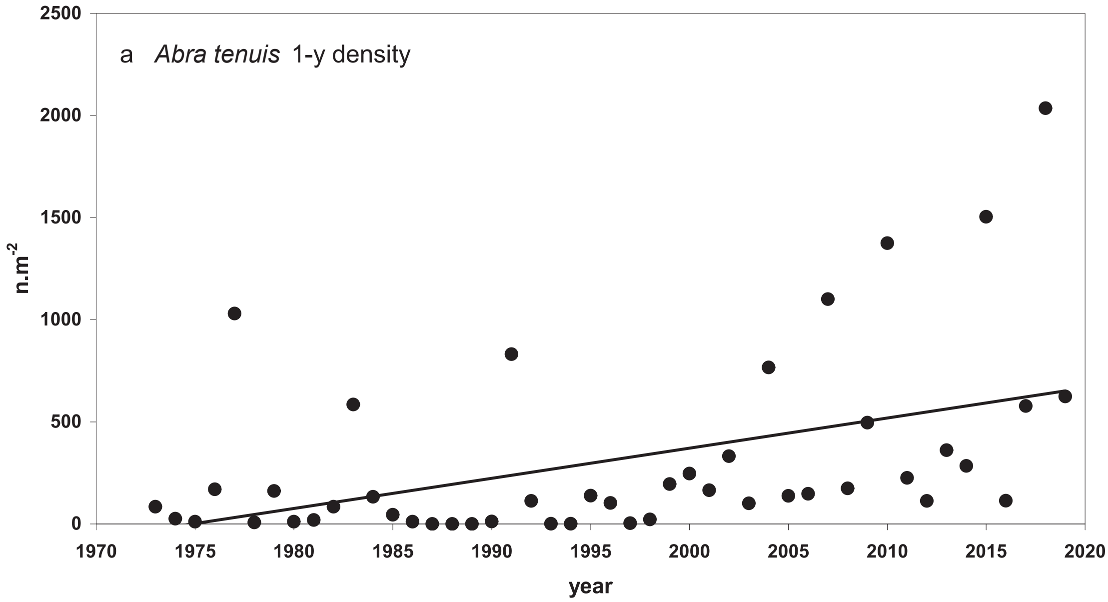
On Balgzand, numerical densities of *A. tenuis* varied strongly from year to year during the 1973–2019 period, but showed a statistically significant increasing long-term trend (Fig. 1a). Close-to-zero values frequently (in about half of the years) occurred before 2000, but were absent after that year. The very low values were found particularly after severe winters (occurring in 1979, 1985, 1986, 1987, and 1996) and lasted 1 or 2 years after these winters. There were no severe winters after 2000 (Beukema and Dekker, 2020a).

Numerical densities of spat of L. *balthica* were also highly variable and showed a significantly declining long-term trend (Fig. 1b). Low values (of <100 m^{-2}) were almost restricted to years after 2003. The declining trend was not limited to the spat numbers shown, but was found also in adults (Beukema et al., 2017a, 2017b). They recorded declines in abundance of L. *balthica* all over the Dutch Wadden Sea since the 1990s. Kröncke (pers. comm.) observed a general decrease in abundance of L. *balthica* all over the East-Frisian Wadden Sea between the 1980s and 2018 (publication in preparation).

4. Discussion

In accordance with the poleward shift of climate zones, the distribution of *A. tenuis* and *Limecola balthica* shifted northward. These shifts were found to be well documented in the literature. Shifts were apparent at the northern border of *A. tenuis* which moved in the Wadden Sea to the northeast and at the southern border of L. *balthica* which moved north. The speed of the shifts could not well be deduced from the published records. Further shifts may be expected: at the southern edge around the Gironde estuary L. *balthica* is declining in abundance and at the northern edge on Wadden Sea tidal flats *A. tenuis* shows increasing abundance.

In accordance with the climate warming (amounting to no less than 2° C for the last 50 years), *A. tenuis* became gradually more abundant on Balgzand in the last 50 years. In particular the very low numbers, as



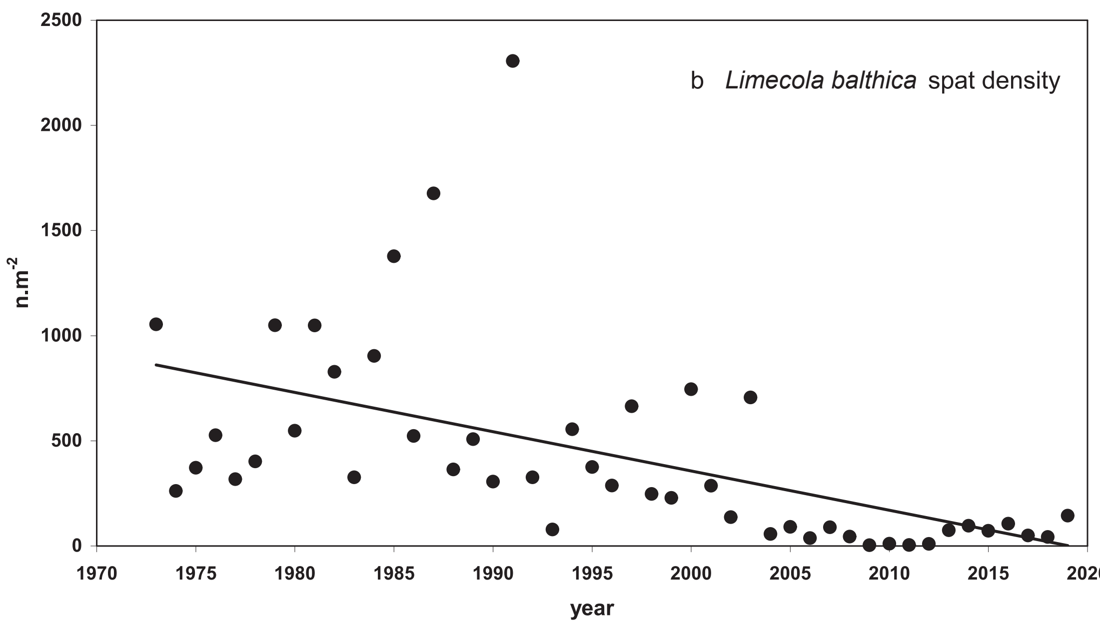


Fig. 1. Numerical densities (D) of 2 species at the high intertidal sampling stations on Balgzand for the 47 years of the 1973–2019 period. Means of 4 stations in n m^{-2}. Linear best fit shown by a straight line. For both lines, the slope differs significantly ($p < 0.01$) from 0.
a. *Abra tenuis*, 1-y old individuals. Best linear fit: D = −29150 + 14.8 y;
b. *Limecola balthica*, spat of about 3 months old. Best linear fit: D = +37722–18.7 y.

occurring after cold winters, became less frequent by the absence of such winters after 1997 (compare Fig. 1a in Beukema and Dekker, 2020a). Dekker and Beukema (1993, 1999) already observed that mortality rates of the species were higher in cold than in mild winters (with almost complete die out in really severe winters). Recruitment and growth were found to be better in warm than in cool summers. There is thus abundant evidence for a positive influence of temperature on the abundance of *A. tenuis.* In the course of the last half century, winters became milder and summers warmer (Beukema and Dekker, 2020a). Dekker and Beukema (1993) rightly concluded that temperatures are limiting the distribution of this species near the northern border of its distribution area. The temperature sensitivity explains the distribution shift at the cold edge of its distribution area. No other trends in environmental conditions were observed that could explain the increasing abundance of this species.

The northward shift of the distribution of L. *balthica* at the southern edge will have been caused by elevated temperatures, causing high respiration and maintenance rates whereby they reach extremely low weights and finally die (Hummel et al., 2000; Jansen et al., 2007). With further increase in summer temperatures, the shift in southern distribution edge has to go on. Jansen et al. (2007) expect the species to disappear from the entire Bay of Biscay. Such disappearance appears to be unavoidable. The observed decline in numbers in the Wadden Sea can at least partly be explained by higher temperatures which negatively affect survival as well as recruitment in this species (Beukema et al., 2009). However, an infectious disease will have aggravated the decline in abundance observed after 1996 (Beukema et al., 2017a; Dairain et al., 2020). It is unknown whether the spread of this disease has anything to do with rising temperatures.

In conclusion: all changes in distribution area as well as abundance are consistent with the hypothesis that climate warming is the common cause. This is so, because *A. tenuis* is a southern species that is sensitive to low winter temperatures and L. *balthica* is a more northern species that is sensitive to high temperatures. On this physiological base, in the former species, a poleward extension of its range is expected as well as an increase in its abundance near the poleward edge of its range. In the latter species, a range reduction is expected at the equatorial edge of its range and a decrease of its abundance in the warmer part of its area of distribution.

Declaration of Competing Interest

We state that there are no conflicts of interest whatever are involved.

References

Bachelet, G., 1980. Growth and recruitment of the tellinid bivalve *Macoma balthica* at the southern limit of its geographical distribution, the Gironde Estuary (S W France). Mar. Biol. 59, 105–117.

Bates, A.E., et al., 2014. Defining and observing stages of climate-mediated range shifts in marine systems. Glob. Environ. Change 26, 27–38.

Beukema, J.J., 1993. Successive changes in distribution patterns as an adaptive strategy in the bivalve *Macoma balthica* (L.) in the Wadden Sea. Helgol Meeresunters 47, 287–304.

Beukema, J.J., Cadée, G.C., 1997. Local differences on 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, J.J., 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. Progr. Ser. 513, 1–15.

Beukema, J.J., Dekker, R., 2011. Increasing species richness of the macrozoobenthic fauna on tidal flats of the Wadden Sea by local range expansion and invasion of exotic species. Helgol. Mar. Res. 65, 155–164.

Beukema, J.J., Dekker, R., 2020a. Winters not too cold, summers not too warm: long-term effects of climate change on the dynamics of a dominant species in the Wadden Sea: the cockle *Cerastoderma edule* L. Mar. Biol. 167, 44.

Beukema, J.J., Dekker, R., 2020b. Half a century of monitoring macrobenthic animals on tidal flats in the Dutch Wadden Sea. Mar. Ecol. Prog. Ser. 656, 1–18.

Beukema, J.J., Dekker, R., Jansen, J.M., 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, J.J., Dekker, R., Drent, J., 2017a. 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, 18–30.

Beukema, J.J., Dekker, R., Drent, J., 2017b. Parallel changes in *Limecola (Macoma) balthica* populations in the Dutch Wadden Sea. Mar. Ecol. Prog. Ser. 585, 71–79.

Bocher, P., Piersma, T., Dekinga, A., Kraan, C., Yates, M.G., Guyot, T., Folmer, E.O., Radenac, G., 2007. Site- and species-specific distribution patterns of molluscs at five intertidal soft-sediment areas in northwest Europe during a single winter. Mar. Biol. 151, 577–594.

Compton, T.J., et al., 2017. Shifting baselines in the Ems Dollard estuary: a comparison across three decades reveals changing benthic communities. J. Sea Res. 127, 119–132.

Dairain, A., Engelsma, M.Y., Drent, J., Dekker, R., Thieltges, D.W., 2020. High prevalence of disseminated neoplasia in the Baltic tellin *Limecola balthica* in the Wadden Sea. Dis. Aquat. Org. 138, 89–96.

Dekker, R., Beukema, J.J., 1993. Dynamics and growth of a bivalve, *Abra tenuis*, at the northern edge of its distribution. J. Mar. Biol. Ass. UK 73, 497–511.

Dekker, R., Beukema, J.J., 1999. Relations of summer and winter temperatures with dynamics and growth of two bivalves, *Tellina tenuis* and *Abra tenuis*, on the northern edge of their intertidal distribution. J. Sea Res. 42, 207–220.

Hale, S.S., Buffum, H.W., Kiddor, J.A., Hughes, M.M., 2017. Subtidal benthic invertebrates shifting northward along the US Atlantic coast. Est. Coasts 40, 1744–1756.

Hiddink, J.G., Burrows, M.T., Molinos, J.G., 2015. Temperature tracking by North Sea benthic invertebrates in response to climate change. Glob. Chang. Biol. 21, 117–129.

Hummel, H., Bogaards, R.H., Bachelet, G., Caron, F., Sola, J.C., Amiard-Triquet, C., 2000. The respiratory performance and survival of the bivalve *Macoma balthica* (L.) at the southern limit of its distribution area: a translocation experiment. J. Exp. Mar. Biol. Ecol. 251, 85–102.

Jansen, J.M., Pronker, A.E., Wendelaar Bonga, S., Hummel, H., 2007. *Macoma balthica* in Spain, a few decades back in history. J. Exp. Mar. Biol. Ecol. 344, 161–169.

Lenoir, J., et al., 2020. Species better track climate warming in the oceans than on land. Nat. Ecol. Evol. 4, 1044–1059.

Mieszkowska, N., Sugden, H.E., 2016. Climate-driven range shifts within benthic habitats across a marine biogeographic transition zone. Adv. Ecol. Res. 55, 325–369.

Pinsky, M.L., Selden, R.L., Kitchel, Z.J., 2020. Climate-driven shifts in marine species ranges: scaling from organisms to communities. Annu. Rev. Mar. Sci. 12, 153–179.

Pitt, N.R., Poloczanska, E.S., Hobday, A.J., 2010. Climate-driven range changes in Tasmanian intertidal fauna. Mar. Freshw. Res. 61, 963–970.

Philippart, C.J.M., Van Aken, H.M., Beukema, J.J., Bos, O.G., Cadee, G.C., Dekker, R., 2003. Climate-related changes in recruitment of the bivalve Macoma balthica. Limnol. Oceanogr. 48, 2171–2185.

Vader, W., 1961. Wadinventarisatie Schiermonnikoog. Verslag Schier I 1960 (Amsterdam, NJN).

Wolff, W.J., Dankers, N., 1983. Preliminary checklist of the zoobenthos and nekton species of the Wadden Sea. In: Dankers, N., Kühl, H., Wolff, W.J. (Eds.), Invertebrates of the Wadden Sea, pp. 24–60 report 4.