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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.

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Abstract

The Wadden Sea experiences a warming climate with water temperatures having increased by about 2° C during the last 50 years. We studied possible effects of this temperature rise on the dynamics of a cockle (*Cerastoderma edule*) population in the westernmost part of the Wadden Sea by monitoring the numbers of aged cockles since the early 1970s. We found increased rates of mortality at extreme climatic conditions. In particular, survival declined to close-to-0 in all age classes in severe winters. In the hottest summers, survival was somewhat reduced in older (> 1 y old) cockles. On the other hand, recruitment was enhanced after cold winters, but this was not a direct effect of low temperatures as it was mainly caused by a reduction of the abundance of predators on small spat. The observed decline of the long-term trend in recruitment was compensated by an increasing trend of winter survival, resulting in an absence of any long-term trend in adult numbers.

Introduction

The ongoing global warming is bound to change ecosystems (e.g. Harley et al. 2006) and a study of such changes is urgent. We think that results of detailed studies at the species level should underlie any understanding of system changes. In the Wadden Sea, monthly mean temperatures showed increasing trends for the last 50 years in all seasons (Van Aken 2008, Beukema et al. 2009). The incidence of cold winters became rare in the last 2 decades, whereas the frequency of hot and dry summers increased (present paper). Within the scope of these climate changes, and to predict future responses of the Wadden Sea ecosystem to these changes, we studied the relationship between seasonal temperatures and long-term dynamics of a dominant species of the benthic tidal-flat ecosystem of the Wadden Sea: the edible cockle *Cerastoderma edule* L.

Cockles are widespread along the north-eastern coastline of the Atlantic Ocean, from the Barents Sea to Morocco (Malham et al. 2012) and thus live in a wide range of winter and summer temperatures. The Wadden Sea is situated roughly in the center of the area of distribution. Occasionally, cockles will experience both below-lethal temperatures in winter and above-lethal temperatures in summer. Therefore, the Wadden Sea is a suitable area to study (1) the responses of cockle dynamics (recruitment and subsequent survival) to seasonal temperatures and (2) the long-term changes therein.

Several reports are available of experiments to assess lower and upper tolerance temperatures in cockles collected in the Wadden Sea. The lower thermal tolerance limit was determined in winter after 24-h exposure at -2.4^o C by Kristensen (1957) and at -6.2^o C by Compton et al. (2007). A similar value of -6.7^o C was reported by Kristensen (1957) for 6-h exposure.

Upper tolerance limits were first studied by Kristensen (1957). He found 100% mortality after short (minutes) exposure to 36^o C and almost complete mortality after 12 h at 34^o C. Later studies assessed median lethal temperatures. Ansell et al. (1981) reported such temperatures to be 30 and 37^o C for long (96 h) and short (6 h) exposure, respectively. Compton et al. (2007) found such temperatures to amount to 32 and 34^o C in winter and spring, respectively. Verdelhos et al. (2015) observed such temperatures to be about 28 and 32^o C for prolonged (120 h) and shorter (52 h) exposure, respectively.

In the Wadden Sea area, minimal air temperatures of ≤ -10^o C occurred in 12 out of the 50 years of the 1970 – 2019 observation period. Maximal summer air temperatures of ≥

30^o C occurred in more than half of the 50 years of the observation period. Thus, on the tidal flats the animals were exposed frequently for mostly short periods (some hours) at low tide to below-tolerance and to above-tolerance air temperatures. Cockles live buried in the sediment close to the surface. Hardly anything is known on temperatures within the sediment, but at the surface they may sometimes be more extreme than air temperatures in winter as well as in summer (De Wilde and Berghuis 1979). Kristensen (1957) also found for short periods higher sediment than air temperatures in summer. Because of this lack of exact knowledge on sediment temperatures, no predictions can be made on cockle survival on the base of air or water temperatures, but some extra mortality at extremely cold or hot days appears probable.

The availability of long data series on temperatures as well as on abundance of aged cockles in an area close to the sites of temperature records enabled us to relate winter and summer temperatures to densities of cockle recruits and their subsequent annual survival. We hypothesize that cockle recruitment is negatively related to mild (well above 0^o C) winter water temperatures (on the base of Strasser et al. 2003 and Beukema and Dekker 2014), whereas their survival is positively related to higher winter temperatures (on the base of Beukema 1985) and negatively to high (around 30^o C) temperatures (on the base of Kristensen 1957). Troost and Van Asch (2018) and several newspapers reported on excessive cockle mortality in the hot summers of 2018 and 2019, respectively. As a consequence, we hypothesize that cockle recruitment shows a declining long-term trend and that cockle survival shows an increasing long-term trend. We further hypothesize that the outcome of these opposing trends may be an absence of any long-term trend in the abundance of adult cockles.

Methods

We studied bivalve dynamics at a 50-km^2 tidal flat area called Balgzand, located in the westernmost part of the Wadden Sea, at about 53^o N (between 52^o 53^1 and 52^o 59^1) and 5^o E (between 4^o 48^1 and 4^o 57^1). In this area, we sampled the macrozoobenthos ever since the early 1970s at 15 permanent stations. Details on the environmental conditions and fauna of the 15 sampling stations (12 transects and 3 squares) can be found in Beukema and Cadée (1997).

Along each of the 12 transects of 1 km length, 50 cores were taken twice-annually at equal intervals to a depth of about 30 cm. In February-March, when cores of 0.019 m^2 were used, the sampled area per transect covered a total of 0.95 m^2. In August (when densities are higher than in late winter), using cores of nearly 0.009 m^2, 0.45 m^2 were covered per transect. At the squares, we took 9 samples of 0.1 m^2 plus 9 of 0.01 m^2. Bivalves were sorted from the sieved (1-mm mesh size) samples, assigned to age classes, and counted. Ages of recruits were about 0.2 year in August and about 0.8 year in late winter (counted from the start of their benthic life in late May: Dekker and Beukema 2014). Numerical densities were expressed as 15-station averages in n m^{-2}. Because the recruit densities (numbers of 0-group animals as estimated in August) covered a wide range (from close to 0 to >1000 m^{-2}) and the distribution of these numbers was far from normal, they were plotted and evaluated at a ^{10}log scale. Numbers of annual data about densities were 48 or 49.

Survival was expressed in a percentage: the proportion of the members of an age group still alive 1 year later. This was done both for summer to summer as well as for winter to winter samplings, to study effects of winter and summer temperatures, respectively. Data for years with < 5 cockles m^{-2} at the start of the year were excluded to avoid unreliable values. Resulting numbers of data on annual survival were thus <50, ranging from 35 to 48.

The data sets on *Cerastoderma edule* numbers analyzed during the present study are available from the corresponding author on reasonable request.

Data on water temperatures were derived from a NIOZ data base with monthly averages recorded at a permanent sampling station in a deep channel (the NIOZ jetty) at the south coast of the island of Texel, where water temperatures are recorded ever since 1860 (Van Aken 2008). It is situated at about 5 km from Balgzand. Data on air temperatures for the 50 years of the 1970 – 2019 period were derived from a KNMI web page “weergegevens.nl” for the De Kooy weather station. It is situated at < 1 km from Balgzand.

Statistical methods used were simple Pearson correlation tests. Linear regression lines and their formulae were depicted in the various graphs.

Results

a. Temperature changes

Both winter (Jan/Feb, Fig. 1a) and summer (July/Aug, Fig. 1b) water temperatures showed a significantly increasing trend over the 50 years of the 1970 – 2019 observation period. Annual mean increases amounted to 0.04 to 0.05° C y^{-1}, respectively, or to about 2° C for the entire period of observation. As a consequence of these common trends, winter and summer temperatures were significantly positively related: July/August temperatures = 17.7 + 0.19 x January/February temperatures ($r = 0.30$, $n = 49$, $p < 0.05$). Cold winters, with mean Jan/Feb water temperatures of < 2° C, were found only before 2000 and were totally absent during the last 20 years (Fig. 1a). Hot summers, with mean July/Aug water temperatures of > 20° C, were found only after 2000, whereas all 24 summers before 1994 showed mean water temperatures of < 19.5° C.

Numbers of days with extreme air temperatures (Figs 1c and 1d) showed the trends to be expected from the above trends. The declining trend of the occurrence of extreme (< -10° C) winter temperatures was non-significant (Fig. 1c). Such cold days occurred in about half of the years in the first half of the observation period and became rare after 1997. The numbers of hot days (> +29.5° C) significantly increased: they were rare before 1990 and frequently occurred 2 or more times per year in the second half of the observation period (Fig. 1d). We did not choose these temperatures of -10° and +29.5° C because they exactly represent critical thermal limits, but because they are close to such limits and in particular because they characterize the numbers of days with extreme temperatures in each year. Any other chosen nearby temperature would have yielded Figures showing similar patterns as in Figs 1c and 1d, but with points at higher or lower levels.

Very cold days (minimal air temperatures < -10° C) occurred exclusively in January and February. The numbers (n) of such days were significantly correlated with Jan/Feb water temperatures (T): $n = 3.7 – 0.74\ T$ ($r = -0.64$, $n = 50$, $p < 0.0001$). Very hot days (air temperatures > +29.5° C) occurred mostly in July and August (2 times in September). The numbers (n) of such days were significantly correlated with July/Aug water temperatures (T): $n = -7.8 + 0.47\ T$ ($r = 0.38$, $n = 50$, $p < 0.01$). In the following, we use mean water temperatures for Jan/Feb and July/Aug for quantification of winter and summer character. The above correlations show that mean 2-monthly water temperatures of the most extreme months well reflect extreme air temperatures and thus can be used for correlations between weather and cockle recruitment and survival.

b. Temperatures and cockle survival

Increased winter temperatures significantly (positively) affected survival in both juvenile as well as adult cockles (Figs 2a and 2b). At mean water temperatures below +1.5° C in the coldest months (Jan/Feb) hardly any cockles survived in the 5 years with such severe winters. Thus, in on average 1 out of 10 years, the cockle population on the tidal flats became almost extinct. In the years with higher winter temperatures cockle survival was on average an order of magnitude higher than in the severe winters.

High summer temperatures had a much smaller (negative) influence on cockle survival (Figs 3a and 3b) and this effect was statistically significant only in adult cockles (Fig. 3b). Survival in these older cockles was about twice as high in the coolest than in the warmest summers (Fig. 3b). We did not find any significant correlation between cockle (juveniles or older) survival and number of hot (maximal air temperature >+29.5° C) days. Such correlation was also non-significant if only days were included with low tide in the afternoon (when high temperatures will exert maximal influence on bottom temperatures).

Figs 2a and 3a shows a few points indicating oddly-high (>100%) survival rates in these years, asking for an explanation of impossible survival rates. The cause was a late (after the August samplings, thus not counted in the summer samples) appearance of (very small) cockle spat late in these years. In other years, proportions of very small spat were much lower or negligible. The explanation of one extremely high point is an influx of high numbers of spat to our sampling sites from a nearby very dense bed of cockle recruits (pers. obs. RD).

c. Temperatures and cockle recruitment

The relationship between winter water temperatures and the subsequent (half a year later) recruitment strength was significantly negative (Fig. 4a). On average, recruit densities were only one tenth after the mildest winters as compared to the coldest ones.

Summer temperatures had a much lower (if any) influence on recruitment success (Fig. 4b). When the recruitments in the summers after the coldest winters (open points in Fig. 4b) were excluded, the relationship with summer temperatures was weak ($r = -0.13$ only) and no longer significant.

d. Long-term trends in survival and recruitment

On the base of the significantly increasing long-term trends in both winter and summer water temperatures (Figs 1a and 1b), the above relationships of survival and recruitment with water temperatures are bound to cause long-term trends in cockle survival and recruitment.

Indeed, we found positive long-term trends in survival (Figs 5a and 5b), though statistically significant only in juvenile cockles (Fig. 5a). Note in Fig. 1a that all winters with water temperatures of <1.5° C (with very low cockle survival: Fig. 2) occurred before 1998, being the first half of the observation period. In this initial period, cockle survival was very low in about one third of the years (Fig. 5). After 1997, incidences of very low cockle survival were a less frequent phenomenon.

The expected negative long-term trend in cockle recruitment was highly significant (Fig. 5c). At the end of the observation period, recruit densities were on average only one quarter of those at the start. Really successful recruitments (>200 recruits m^{-2}) were almost restricted to the initial half of the observation period (with the notable exception for 2011; for an explanation see Beukema and Dekker 2014), and so were the recruit densities of >100 m^{-2} (Fig. 5c).

The combined effects of declining recruitment and increasing survival resulted in an absence of a long-term trend in adult densities (Fig. 5d).

Discussion

We found that temperatures in winter as well as in summer were related to the numbers and changes therein of cockles *Cerastoderma edule*. Extremely low winter temperatures resulted in reductions of survival in cockles of all ages, but promoted subsequent recruitment. Extremely high summer temperatures reduced survival in adult cockles. Of course, several other factors (such as numbers of predators) also affected recruitment and survival, explaining the relatively high scatter in Figs 2 – 4.

Recruitment success (as assessed in summer) significantly declined with higher temperatures in the foregoing winter (Strasser et al. 2003; Fig. 4a of present paper), but was not significantly related to summer temperatures (Fig. 4b). Effects of winter temperature on cockle recruitment were reported and discussed at length in Beukema and Dekker (2005, 2014): the effect was indirect via lower predation pressure on tiny spat by shrimps and shore crabs in springs after cold winters. Moreover, the reduced size of adult stocks after cold winters may have contributed to the subsequent recruitment success (Beukema and Dekker 2018). Further, we observed some negative overall effect of high summer temperatures on recruitment, but this effect disappeared when the data from (relatively cold) summers after cold winters were excluded (Fig. 4b). A seeming effect of summer temperature on recruitment thus originated from the character of the foregoing winter. Annual recruitment success was assessed in summer, but it was established already in spring (Beukema and Dekker 2014) and apparently it did not change by temperatures in the following summer.

Survival significantly increased in cockles of all ages with increasing winter temperatures (Figs 2a and 2b). In the coldest winters, hardly any cockle survived on the tidal flats. Similar severe-winter mass mortalities in cockles were observed in British waters (Hancock and Urquhart 1964), in the Dutch Wadden Sea (Beukema 1979, 1985), in the German Wadden Sea (Dörjes et al. 1986; Strasser et al. 2001) and in the Danish Wadden Sea (Smidt 1944).

The relationship between summer temperatures and cockle survival was negative (but hardly significantly so) in older cockles only (Fig. 3b). Such relationship was absent in juvenile (about 1 year old) cockles (Fig. 3a), as it apparently was in the youngest age group of spat too (Fig. 4b). Although generally juveniles of marine invertebrates appear to be more sensitive than adults to lethal effects of warming (Pandori and Sorte 2019), the reverse was thus true in cockles. In experiments, Kristensen (1957) also observed a greater sensitivity of older than younger cockles to high water temperatures.

In the course of the almost 50 years of the present study, climate became substantially warmer. Mean water temperatures increased by about 2° C in both winter and summer (Figs 1a and 1b) and the numbers of very cold days in winter declined and the numbers of very hot days in summer significantly increased (Figs 1c and 1d). The long-term effects on cockle abundance included: a significant decline of annual recruitment (Fig. 5c) and a significantly increase of subsequent survival (Fig. 5a), both as an effect of increasing winter temperatures. These 2 trends had opposite effects on abundance of older cockles and indeed resulted in an absence of any long-term trend in densities of older cockles (Fig. 5d). Neither annual values of total cockle biomass (Beukema and Dekker 2019) nor annual cockle production (Beukema and Dekker 2015) showed significant long-term trends. Changes in underlying processes (annual recruitment and survival) thus could not always be detected from end-results at the ecosystem level such as productivity.

Cold winters exerted a much stronger negative influence on cockle numbers than hot summers. Therefore, longevity of cockles may be expected to increase in the course of the 50-year observation period. Indeed, we found a few 8 year old cockles in 2016 and several of this age in 2019, whereas the oldest cockles found in all of the earlier years (1970-2015) were at most 6 years old. The presence of so many very old cockles in 2019 will partly have been caused by the exceptional strength of the year class born in 2011 (Beukema 1989).

In a community-wide study in Germany, Pansch et al. (2018) showed that half of the species were tolerant to heat waves and that the populations of only a few species responded strongly negative. These few species included *Limecola (Macoma) balthica*, a species known to be sensitive in several ways to high (as opposed to low) temperatures (Beukema et al. 2009). Crespo et al. (2017) showed in a Portuguese estuary that benthic communities are able to cope with a warming that remains below 2° C: they found no significant impacts of such a rise. Their study, however, lasted only a month. From the above results on *C. edule* and those on *L. balthica* (Beukema et al. 2009) it is clear that a temperature rise of 2° C can result in significant effects on the dynamics of some important species. It should be added that a temperature rise of 2° C is already realized in the Wadden Sea area. Similar rates of increase of about 0.3 to 0.4° C per decade were observed in various European seas (Philippart et al. 2011). We stress that effects of such temperature rises on ecosystems and their components should be studied by long-term (many years) observations rather than by short experiments or short observations of ecosystem changes.

Ethical statements

There was no funding for this study. The 2 authors declare that they have no conflicts of interest. This article does not contain any studies with animals performed by any of the authors.

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Legends

Fig 1 Long-term (the years 1970 – 2019) records of winter and summer water temperatures (T) at the NIOZ sampling station at the south coast of Texel (a, b) and number (n) of days with extremely low or high air temperatures at the KNMI weather station De Kooy (c, d),

a. Means for the coldest 2-month periods January/February. Best fit: $T = -82 + 0.04\ y$ ($r = 0.37$, $n = 50$, $p <$ **0.01**);
b. Means for the warmest 2-month periods July/August. Best fit: $T = -80 + 0.05\ y$ ($r = 0.65$, $n = 50$, $p <$ **0.0001**);
c. Numbers of days with minimal temperatures below -10° C. Best fit: $n = 51 – 0.025\ y$ ($r = -0.18$, $n = 50$, $p = 0.20$);
d. Numbers of days with maximal temperatures above +29.5° C. Best fit: $n = -97 + 0.049\ y$ ($r = 0.47$, $n = 50$, $p <$ **0.001**).

Fig. 2 Relationships between winter (January/February) water temperatures T and annual survival (i.e. percentage % of numbers m^{-2} observed at Balgzand in the foregoing summer that were still alive in the subsequent summer) for:

a. Juvenile cockles (0.2 year old in the foregoing summer). Best fit: survival % = $4.9 + 7.1\ T$ ($r = 0.35$, $n = 48$, $p <$ **0.02**);
b. Older cockles (1.2 or more years old in the foregoing summer). Best fit: survival % = $11.3 + 6.7\ T$ ($r = 0.50$, $n = 42$, $p <$ **0.001**).

Fig. 3 Relationships between summer (July/August) water temperatures T and annual survival (i.e. percentage % of numbers m^{-2} observed at Balgzand in the foregoing winter that were still alive in the subsequent winter) for:

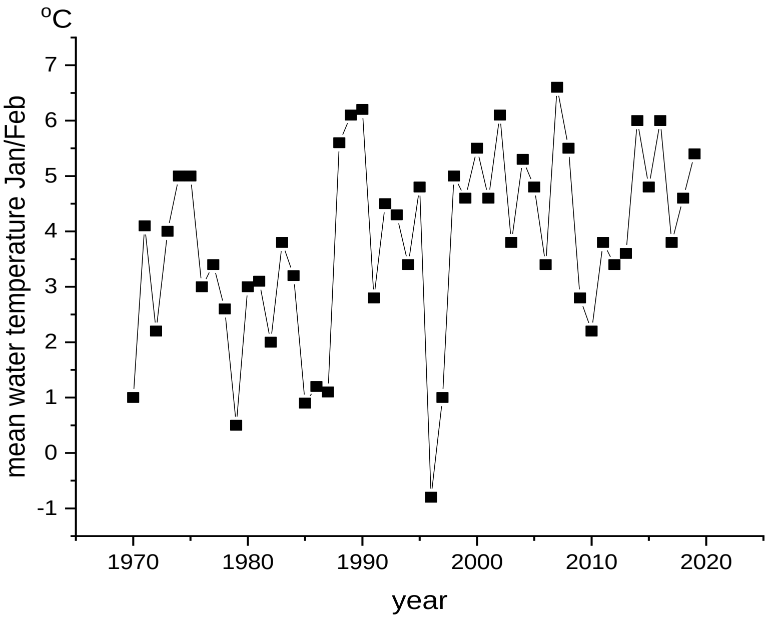
a. Juvenile cockles (0.8 year old in the foregoing winter). Best fit: survival % = $82 – 1.8\ T$ ($r = -0.05$, $n = 36$, $p = 0.8$);
b. Older cockles (1.8 or more years old in the foregoing winter). Best fit: survival % = $171 – 6.9\ T$ ($r =-0.37$, $n = 35$, $p <$ **0.05**).

Fig. 4 Relationships between water temperatures (T) and recruit (0.2-y olds) density found in August (n) for:

a. Winter (Jan/Feb) temperatures. Best fit: n = 187 – 22 T ($r = -0.45$, $n = 49$, $p <$ **0.01**).
b. Summer (July/Aug) temperatures. Open points for the 7 years starting with a cold winter, closed points for the other 41 years. Best fits: all 49 years: n = 681 – 31 T ($r = -0.19$, $n = 49$, $p = 0.2$); for 42 years starting with normal or mild winter: n = 534 – 24 T ($r = -0.13$, $n = 42$, $p = 0.4$).

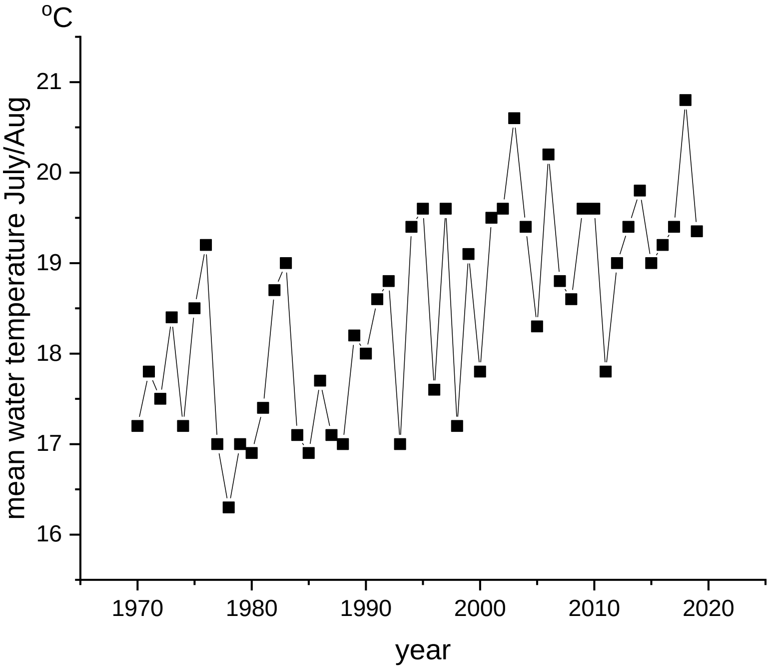
Fig. 5 Long-term (1970 – 2018) trends in:

a. Annual survival (in %) of juvenile cockles (0.2-y olds at start of year). Best fit: % = -1671 + 0.85 y ($r = 0.34$, $n = 48$, $p <$ **0.02**).
b. Annual survival (in %) of older cockles (1.2 or more years old at start of year). Best fit: % = -549 + 0.29 y ($r = 0.16$, $n = 42$, $p = 0.26$).
c. Densities of recruits (N in n m^{-2}) observed in August. Best fit (on ^{10}log scale): N = 3045 – 1.5 y ($r = -0.36$, $n = 49$, $p <$ **0.01**).
d. Adult (age 1^{+}) density (N in n m^{-2}) observed in August. Best fit: N = -173 + 0.10 y ($r = 0.03$, $n = 48$, $p = 0.8$).



ºC
mean water temperature Jan/Feb
-1
0
1
2
3
4
5
6
7
1970
1980
1990
2000
2010
2020
year

Fig. 1a



ºC
mean water temperature July/Aug
16
17
18
19
20
21
1970
1980
1990
2000
2010
2020
year

Fig. 1b

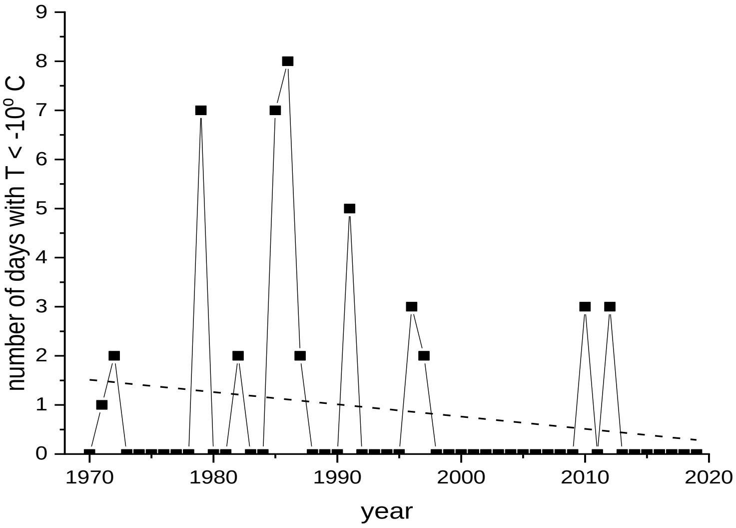

number of days with T < -10° C
0
1
2
3
4
5
6
7
8
9
1970
1980
1990
2000
2010
2020
year

Fig. 1c

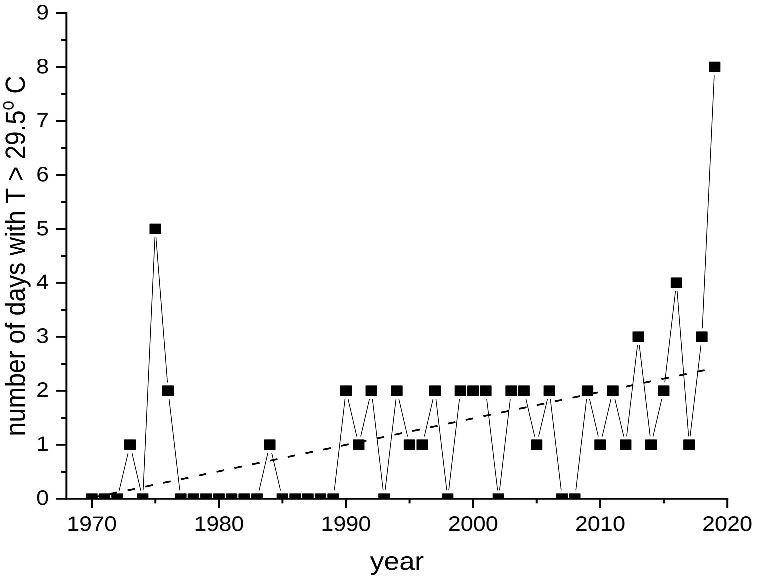

number of days with T > 29.5° C
0
1
2
3
4
5
6
7
8
9
1970
1980
1990
2000
2010
2020
year

Fig. 1d

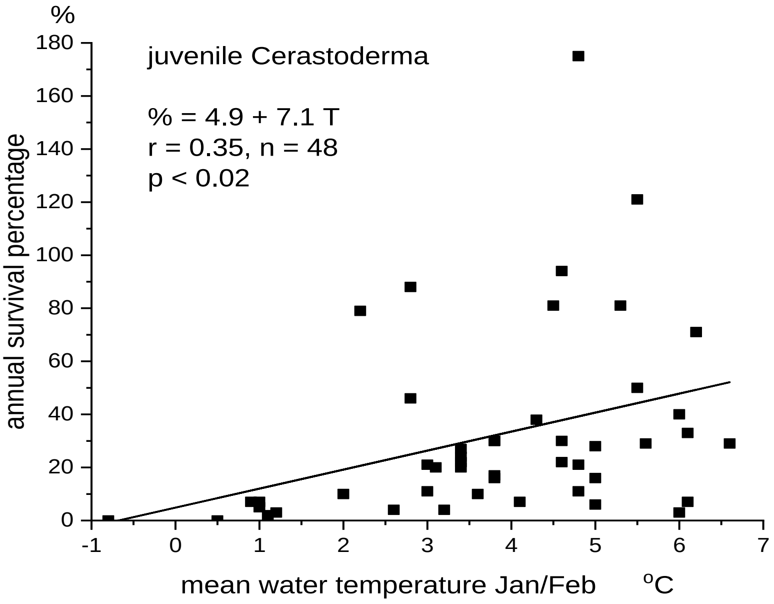

juvenile Cerastoderma
% = 4.9 + 7.1 T
r = 0.35, n = 48
p < 0.02
%
annual survival percentage
0
20
40
60
80
100
120
140
160
180
-1
0
1
2
3
4
5
6
7
mean water temperature Jan/Feb °C

Fig. 2a

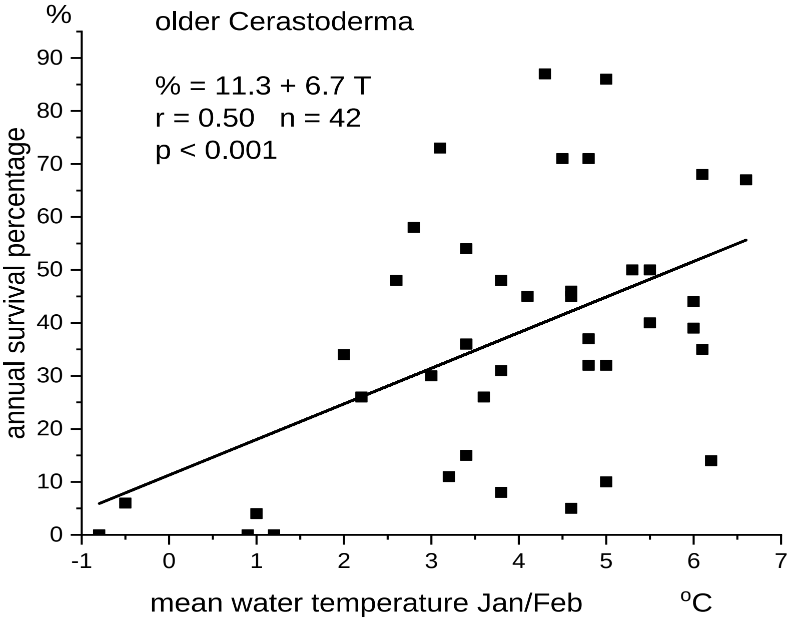

older Cerastoderma
% = 11.3 + 6.7 T
r = 0.50 n = 42
p < 0.001
%
annual survival percentage
0
10
20
30
40
50
60
70
80
90
-1
0
1
2
3
4
5
6
7
mean water temperature Jan/Feb °C

Fig. 2b

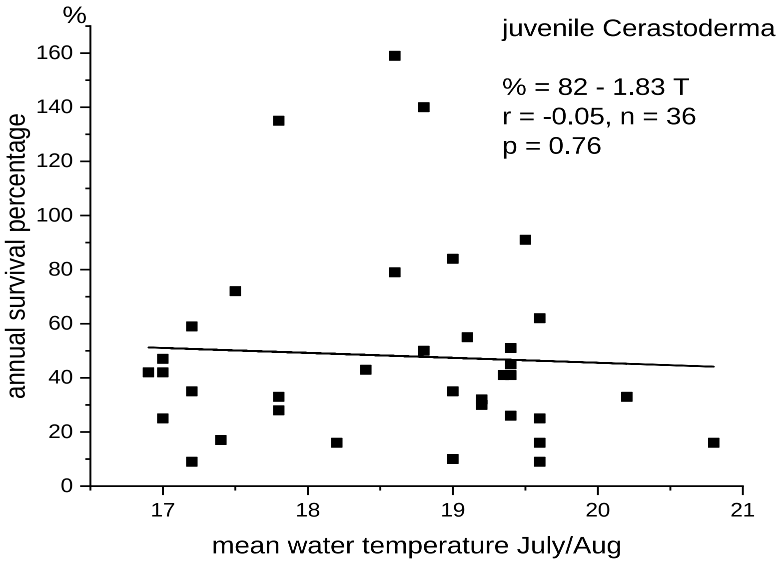

%
160
140
120
100
80
60
40
20
0
annual survival percentage
17
18
19
20
21
mean water temperature July/Aug
juvenile Cerastoderma
% = 82 - 1.83 T
r = -0.05, n = 36
p = 0.76

Fig. 3a

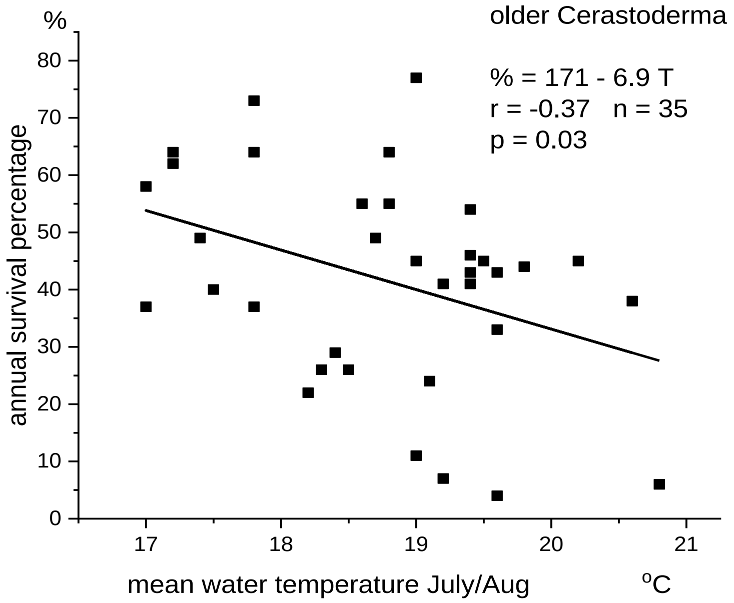

%
80
70
60
50
40
30
20
10
0
annual survival percentage
17
18
19
20
21
mean water temperature July/Aug
°C
older Cerastoderma
% = 171 - 6.9 T
r = -0.37   n = 35
p = 0.03

Fig. 3b

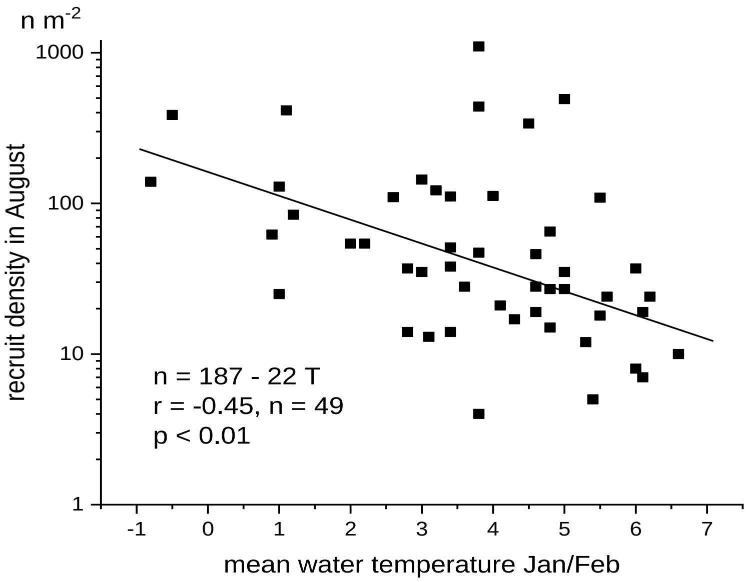

n m-2
1000
100
10
1
recruit density in August
n = 187 - 22 T
r = -0.45, n = 49
p < 0.01
-1
0
1
2
3
4
5
6
7
mean water temperature Jan/Feb

Fig. 4a

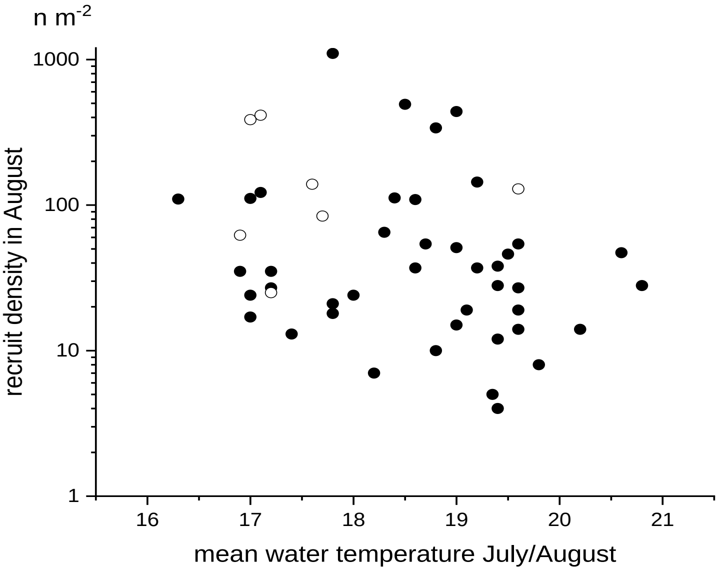

n m-2
1000
100
10
1
recruit density in August
16
17
18
19
20
21
mean water temperature July/August

Fig. 4b

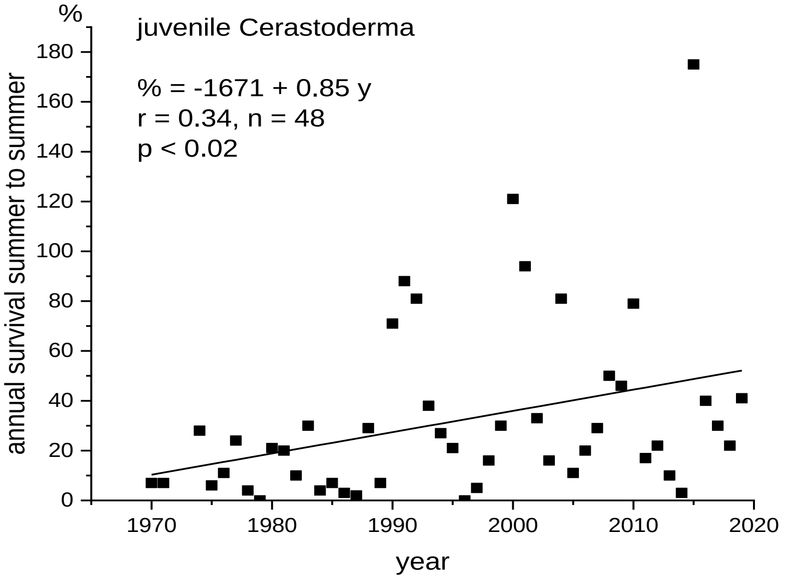

%
juvenile Cerastoderma
% = -1671 + 0.85 y
r = 0.34, n = 48
p < 0.02
annual survival summer to summer
0
20
40
60
80
100
120
140
160
180
1970
1980
1990
2000
2010
2020
year

Fig. 5a

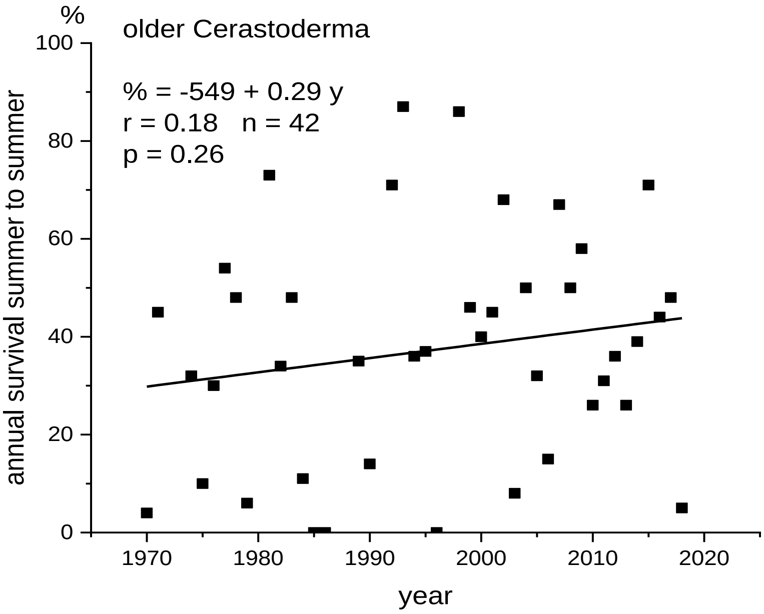

%
older Cerastoderma
% = -549 + 0.29 y
r = 0.18   n = 42
p = 0.26
annual survival summer to summer
0
20
40
60
80
100
1970
1980
1990
2000
2010
2020
year

Fig. 5b

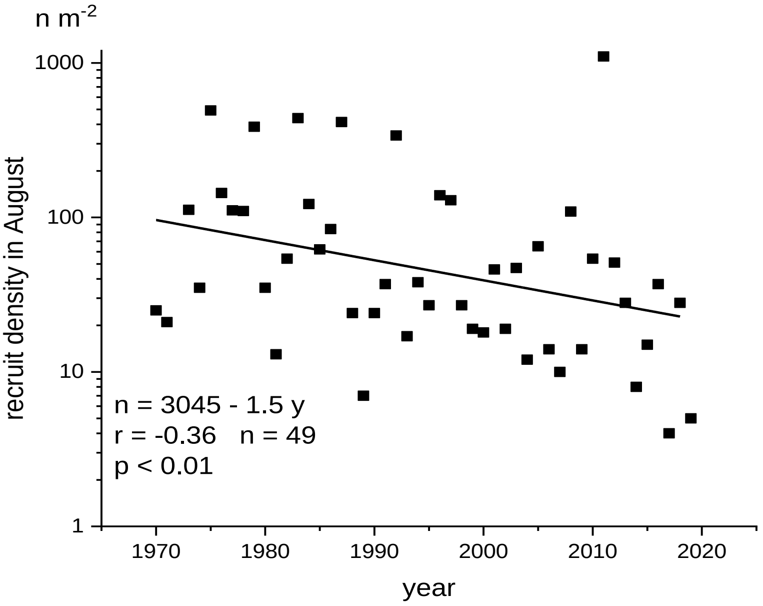

n m-2
recruit density in August
1000
100
10
1
1970
1980
1990
2000
2010
2020
year
n = 3045 - 1.5 y
r = -0.36 n = 49
p < 0.01

Fig. 5c

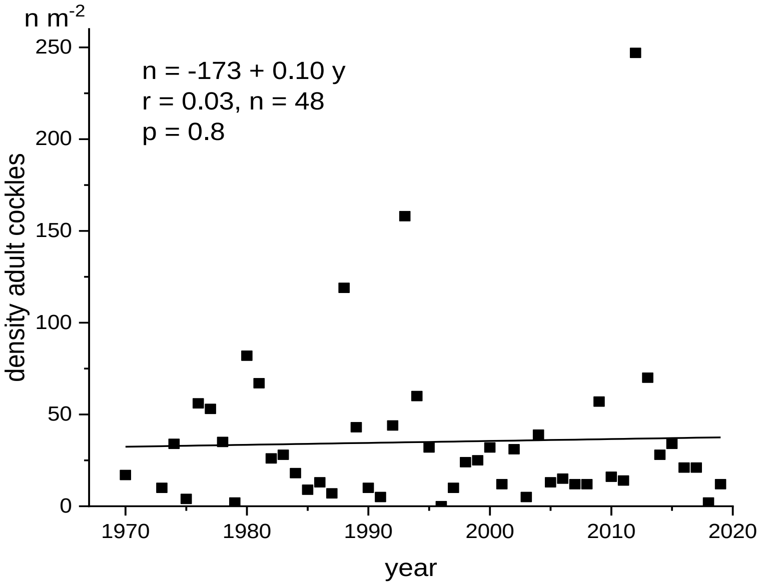

n m-2
density adult cockles
250
200
150
100
50
0
1970
1980
1990
2000
2010
2020
year
n = -173 + 0.10 y
r = 0.03, n = 48
p = 0.8

Fig. 5d