



Macoma balthica in Spain, a few decades back in climate history

Jeroen M. Jansen^{a,*}, Annelies E. Pronker^a,
Sjoerd Wendelaar Bonga^b, Herman Hummel^a

^a Netherlands Institute of Ecology (NIOO), Korringaweg 7, P.O.-box 140, 4400 AC Yerseke, The Netherlands

^b Radboud University, Faculty of Science, Institute IWW, Toernooiveld 1, P.O.-box 9010, 6500 GL Nijmegen, The Netherlands

Received 17 August 2006; received in revised form 17 November 2006; accepted 28 December 2006

Abstract

The marine bivalve *Macoma balthica* has disappeared from the Spanish part of the Bay of Biscay during the past four decades. Investigating the possible role of climate change in forcing this species up north, we translocated it down south, back into two Spanish estuaries, and followed the thermal acclimatization of the metabolic rate during spring, summer and autumn. Our results reveal that in natural populations the respiratory response to temperature becomes down-regulated during summer and autumn. The respiration rate in the southward translocated populations became down-regulated to a safe level at very high temperatures (31 °C), but remained high at average temperatures instead. These translocated populations showed a gradual reduction of the condition-index, down to the level of starvation at the end of summer. Combined with an increased metabolic rate this indicates that the translocated specimens suffered from elevated maintenance rates. We conclude that short-term but frequent exposure to >30 °C in the Spanish estuaries, induces elevated maintenance rates in *M. balthica*, and ultimately starvation. *M. balthica* indeed disappeared from the northern Spanish coast due to increasing summer maxima during the last decades. We prospect that the southern distribution limit of *M. balthica* will shift further north, and that the clam will eventually disappear from the entire Bay of Biscay with future increases in summer temperatures.

© 2007 Elsevier B.V. All rights reserved.

Keywords: Climate change; Respiration; Temperature; Tolerance; Translocation

1. Introduction

Macoma balthica is a sand-dwelling bivalve that may dominate benthic communities of the marine and estuarine coastal zone. It is found throughout north-western Europe, from fully marine to nearly freshwater conditions. Its present limit to its southern distribution in Europe is the Gironde estuary, situated halfway down the Bay of Biscay (Bachelet, 1980). In 1972 however, Otero and Millan reported populations of *M. balthica* present

in Galicia, Spain. The clam has disappeared from this area and is missing from the southern part of the Bay of Biscay ever since (Lastra et al., 2006; Rodriguez et al., 2003; Rodil et al., 2006). Thus, over the past 35 years, the southern distribution limit of *M. balthica* shifted at least 300 km to the north. This shift may be associated with climate change in Western Europe given the increasing heat anomalies and sea water temperatures in the Bay of Biscay (Beaugrand and Reid, 2003; Koutsikopoulos et al., 1998). In this study we aim to assess the role of climate change in forcing the southern distribution of European *M. balthica* populations towards the North.

* Corresponding author. Tel.: +31 113577466; fax: +31 113573616.
E-mail address: j.jansen@nioo.knaw.nl (J.M. Jansen).

Despite inhabiting sediment, *M. balthica* populations may experience great fluctuations in habitat temperature due to daily and tidal cycles in their shallow water and intertidal habitats. Assessment of sediment temperature profiles from *M. balthica* habitats has shown that the summer temperature fluctuates from ~ 12 to ~ 25 °C at Dutch localities (52.9° N), and from ~ 13 to ~ 29 °C at the species distribution limit (45.6° N), with daily fluctuations in habitat temperature that frequently exceed $\Delta 10$ °C (Drent, 2004). Peaks in habitat temperature of 29 °C lie remarkably close to the heat tolerance limit of *M. balthica* (31–34 °C), beyond which mortality occurs (Kennedy and Mihursky, 1971). Yet, it is still unknown what causes failure in *M. balthica* beyond its heat tolerance limit and whether it would endure temperatures above this limit below the southern edge of its geographical distribution range.

Hummel et al. (1996) hypothesized that the migration of *M. balthica* into the warmer habitats beyond its southern distribution limit is constrained by the thermal acclimatization range of its metabolic rate. Increased respiration rates during hyperactivity cannot be compensated for by the energy-substrate ingestion rate, leading to starvation. Contrastingly, Pörtner (2001) has hypothesized that at excessive metabolic rates, ventilation becomes insufficient and results in a declining respiration rate, followed by a depression of

the aerobic metabolism of the organism. So, although different mechanisms have been proposed, the common expectation is that beyond its warmth-tolerance limits the metabolic rate of *M. balthica* will become hampered. The aim of this study was to find evidence for this expectation in the field. To this end we carried out an experiment in which we translocated subpopulations of *M. balthica* from a southern marginal population to beyond their southern distribution limit, into two Spanish estuaries where they occurred naturally less than 40 years ago (Fig. 1). Aiming to simulate what has happened just a few decades back in climate history, we studied detailed habitat temperature profiles, and compared the seasonal changes in the respiratory metabolism and the corresponding reserve dynamics of two translocated populations and, for comparison, a marginal and a core *M. balthica* population.

2. Materials and methods

2.1. Fieldwork

In April 2004, 400 and 1000 *M. balthica* specimens were collected respectively, from the Westerschelde estuary and at Point d'Aiguillon (Fig. 1). The mean size of the clams from the Westerschelde estuary was 13.7 mm (S.D.: 1.7) and from Point d'Aiguillon 16.9 mm

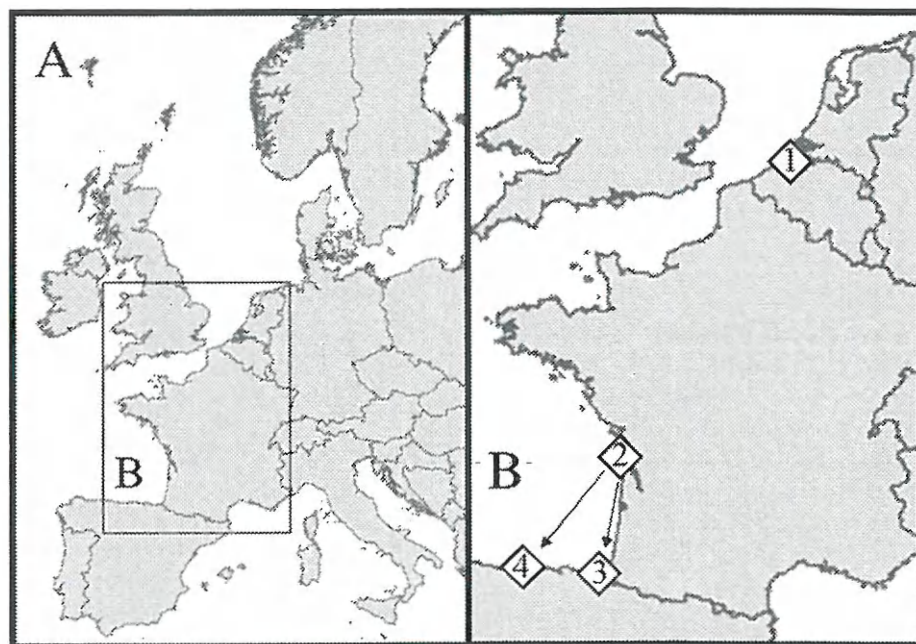


Fig. 1. Overview of the research area and the sampling stations. A) Map of Europe, with B) research area. Diamonds 1, 2, 3 and 4 represent the Westerschelde estuary, Point d'Aiguillon, the Bidasoa estuary and the Mundaka estuary, respectively. Arrows indicate the translocation experiments.

(S.D.: 0.9). For initial measurements, 100 specimens from both sites were transported to a nearby laboratory. The remaining 300 specimens from the Westerschelde estuary were caged in their original habitat. The same was done with 300 specimens from Point d'Aiguillon. The other 600 specimens from Point d'Aiguillon were translocated: 300 into the Bidasoa estuary and 300 into the Mundaka estuary (Fig. 1). The clams were kept in foam boxes with habitat sand during transportation. As part of the caging procedure, the 300 specimens per research site were distributed evenly over six plastic boxes (300×400×12 mm). Each box was filled up with sediment from the field and 50 specimens were positioned on top to bury themselves in the sediment surface. This resulted in a density of about 400 ind/m², at which no intraspecific competition for space or resources was expected (Kamermans et al., 1992). After the animals had disappeared into the sediment, the boxes were closed off with mesh (5 mm²). The boxes were placed in the sediment in such a way that the surface of the box was flush with the sediment surface. Special attention was paid to the positioning of these cages in the tidal zone. This was done at the low water line during neap tide. At Point d'Aiguillon and in the Bidasoa estuary, temperature loggers (HOBO® Water Temp Pro) were positioned next to the boxes in the immediate vicinity of the caged *M. balthica* specimens. The ambient temperature was registered every 30 min. After 1, 3 and 6 months, two boxes were removed from each research location and transported to a nearby laboratory. During this transportation the clams remained buried in the boxes. Upon arrival at the laboratory the boxes were submerged in aerated habitat water until further treatment.

2.2. Survival and condition

In the laboratory, all *M. balthica* specimens in the boxes (M_t) were collected by sieving, and counted, and the percentage of survivors (M_s) was estimated to the nearest 5% using the following equation: $M_s = M_a / M_t * 100$. In which M_a is the number of *M. balthica* specimens found alive. The condition index (CI), describing the relation between the soft tissue biomass and the volume of the shell cavity, was calculated per individual specimen using the following equation: $CI = W / L_v * 1000$. In which W is the lyophilized (shell-free) dry weight (estimated to the nearest mg), and L_v is the volumetric length, (estimated to the nearest tenth of a mm). The volumetric length of specimens that originated from Point d'Aiguillon was calculated as the maximum shell length [cm] raised to the power of 3.277. For specimens that originated from the Wester-

schelde estuary, maximum shell length was raised to the power of 2.848. These volumetric lengths are based on the allometric relation we assessed between shell length, measured to the nearest tenth of a mm, and the true volume of the shell cavity, for these specific populations. The true volume of the shell cavity was assessed by measuring the weight of the amount of fine and dry sand (to the nearest mg) that was needed to completely fill up the empty valves, and dividing this weight by the density of the sand.

2.3. Respiratory response to temperature

Respiration rates of *M. balthica* from a specific site and at a specific temperature were assessed with respiration chambers of 154 ml made out of tanned Plexiglas to avoid light stress, and Clark-type electrodes. For each measurement, seven individuals of a representative size range were positioned in a respiration chamber that was filled up with filtered and aerated habitat water. The respiration chambers were situated in a thermostated water basin, which kept the water temperature inside the chambers stable with an accuracy of 0.5 °C. Depending on the experimental temperature, measurements continued from 30, to 90 min, until approximately 30% of the oxygen was consumed. The oxygen tension of the water was monitored by the sensors at a frequency of 70 Hz and average values were registered by the computer every 30 s. Experimental animals were frozen and subsequently lyophilized for 72 h, after which the soft-tissue shell-free dry weight (W) was measured. Parallel to each measurement a control chamber (c) without animals was used. The respiration rate (R) was calculated using the following equation: $R = ([O_2]_{t0} - [O_2]_{t1}) - ([O_2]_{c0} - [O_2]_{c1}) / W$, in which $[O_2]_{t0}$ and $[O_2]_{t1}$ are initial oxygen concentration and the concentration after 1 h, respectively. In this way, 2–4 replicate measurements were carried out for all sites at 17, 24 and 31 °C. To compare the sensitivity to temperature of the metabolic rate, the temperature quotient (Q_{10}) was calculated with the following equation: $Q_{10} = (k_1 / k_2)^{10 / (t_1 - t_2)}$, in which k_1 and k_2 are the metabolic rates determined at high and low temperatures, t_1 and t_2 respectively.

2.4. Statistical analysis

To test whether the respiratory response to temperature was different in the translocated populations, a three-way ANOVA was carried out in Statistica® with season, locality and experimental temperature as independent variables. The null hypothesis was that

season and locality have no significant effect on the respiratory response of *M. balthica* to temperature. In this analysis, the interactions between locality and temperature were of particular interest, since we expected *M. balthica* specimens to respond differently to thermal variation in the southern part of the Bay of Biscay. One-way ANOVA's and Bonferroni's multiple comparison tests were used to test for differences in the condition index between different localities and seasons.

To test the effect of caging, additional specimens were collected at Point d'Aiguillon, next to the cages in the field. Both the condition index of these specimens and their respiratory response to temperature did not differ significantly from those of the caged specimens ($P > 0.05$).

3. Results

3.1. Temperature regimes

The ambient temperature, registered by temperature loggers, greatly fluctuated at both research sites (Fig. 2). In April these fluctuations in temperature appeared stronger in the Bidasoa estuary than at Point d'Aiguillon. The high air temperatures in the Basque country caused the habitat temperature to rise to 25 °C in early April and up to 27 °C in late April. At Point d'Aiguillon the maximum temperature in early April was 17 °C and 21 °C in late April. Despite of the difference in maximum temperatures, the average temperature at both localities was similar during this

month. This was due partly to cold Atlantic water that filled up the Bidasoa estuary at high tide and partly to the occurrence of low tide during some relatively cold nights. At Point d'Aiguillon, peaks in habitat temperature that exceeded 25 °C occurred only from the second half of May onwards. During the entire experiment, temperature peaks at Point d'Aiguillon ranged from 25 to 30 °C, while in the Bidasoa estuary these peaks fell between 30 and 34 °C. The mean temperature difference between both sites, over the six month period, was 1.03 °C.

3.2. Respiratory response to temperature

The respiratory response to temperature of *M. balthica* from the Westerschelde estuary and Point d'Aiguillon changed with the seasons (Fig. 3A–B). In April, the oxygen consumption rate of *M. balthica* at 17 °C was slightly higher at Point d'Aiguillon than in the Westerschelde estuary. At the higher experimental temperatures (24–31 °C) that normally did not occur in the field in April, the respiration rates were relatively high at both localities (> 1.5 mg O₂/g/h), with temperature quotients (range 17–24 °C) of 3.25 and 1.29 for Westerschelde and Point d'Aiguillon clams, respectively. In May, the respiration rate at 17 °C of clams from the French population decreased to less than 1.0 (mg O₂/g/h), but the sensitivity to elevations in temperature increased ($Q_{10} (17-24\text{ °C}) = 3.43$). In July and October, after frequent exposure to temperatures > 25 °C, the respiration rate decreased further and the thermal sensitivity had vanished

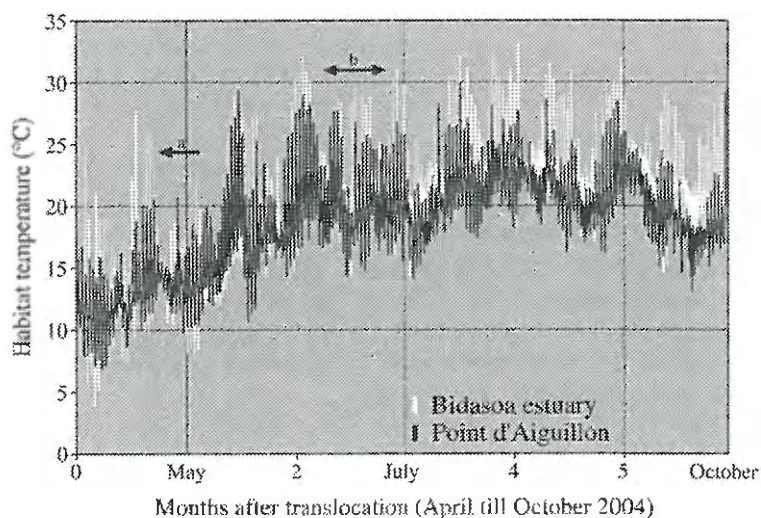


Fig. 2. The habitat temperature measured in the Bidasoa estuary (white) and at Point d'Aiguillon (black) during the experiment. The black arrows point to the peak temperatures measured in the Bidasoa estuary. Samples were taken and measurements were carried out in April, May, July and October 2004.

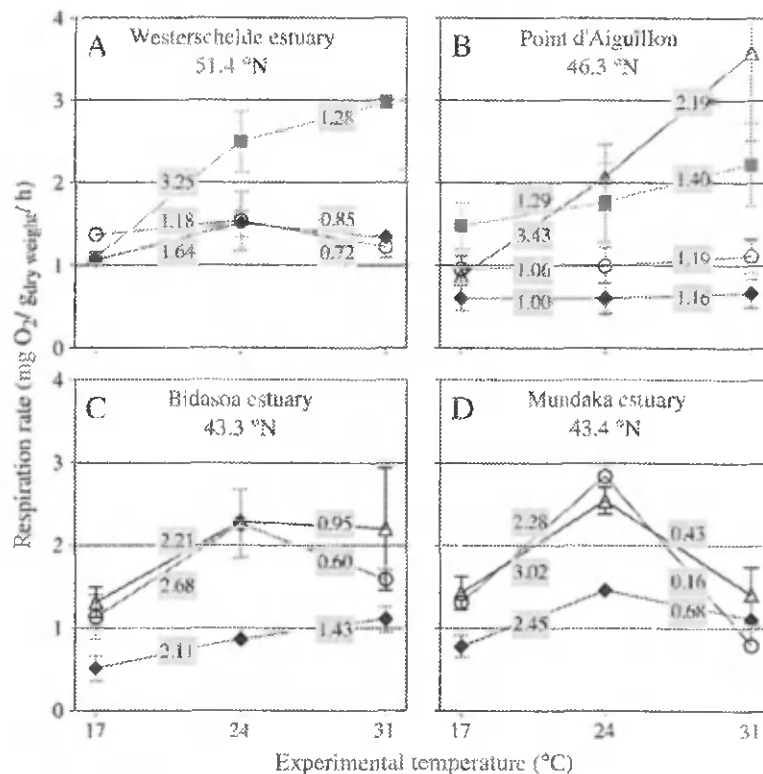


Fig. 3. A, B, C, D: Seasonal variation in the respiratory response to temperature of experimental *M. balthica* specimens from the Westerschelde estuary (A), Point d'Aiguillon (B), the Bidasoa estuary (C) and the Mundaka estuary (D). The squares, triangles, circles and diamonds represent measurements done in April, May, July and October, respectively. The Q_{10} values are plotted in the grey boxes on the corresponding connection lines.

completely (Q_{10} (17–24 °C) July: 1.06, and October: 1.00). In May, no measurements were taken for clams from the Westerschelde estuary. The respiratory responses to temperature measured for this population in July and October followed the same seasonal trend as the responses of the clams from Point d'Aiguillon. The observed differences in respiration rates between the different seasons were significant ($P < 0.001$).

The metabolism of the translocated specimens adjusted to novel habitat temperatures in a way that differed from their population of origin (Fig. 3C–D). Especially in July, the populations from the Bidasoa and Mundaka estuary showed strongly increased respiration rates at 24 °C, compared to the population from Point d'Aiguillon ($P < 0.001$). The temperature quotient (range: 17–24 °C) of the metabolic rate of *M. balthica* specimens from the Bidasoa estuary was 2.68 compared to 2.28 at the Mundaka estuary. In May, 1 month after translocation, the clams showed slightly higher respiration rates at 17 °C than at Point d'Aiguillon; similar rates at 24 °C, and lower respiration rates at 31 °C. In October, the respiration rates of the translocated clams were lower

at 17 and 24 °C than in the previous months, yet still higher than in the French population. The thermal sensitivity of the clams, translocated into the Mundaka estuary, remained high (Q_{10} (17–24 °C) = 2.45), but was lower than in the Bidasoa estuary (Q_{10} (17–24 °C) = 2.11).

3.3. Survival and condition

One month after caging, the percentage of surviving clams was high at all locations (around 80 to 95%); (Fig. 4). During May and July this remained unchanged, indicating that the cages were suitable habitats for *M. balthica*. In October there was still 80% survival at Point d'Aiguillon. However, in the translocated populations the mortality was high. The condition index of *M. balthica* specimens caged in their original habitat significantly increased in springtime and early summer, from 7.7 in April to 11.5 in July and remained constant during the rest of the experiment ($P < 0.001$). No increase in condition index was found in the translocated populations. Instead a significant decrease in condition during the experiment became obvious from July

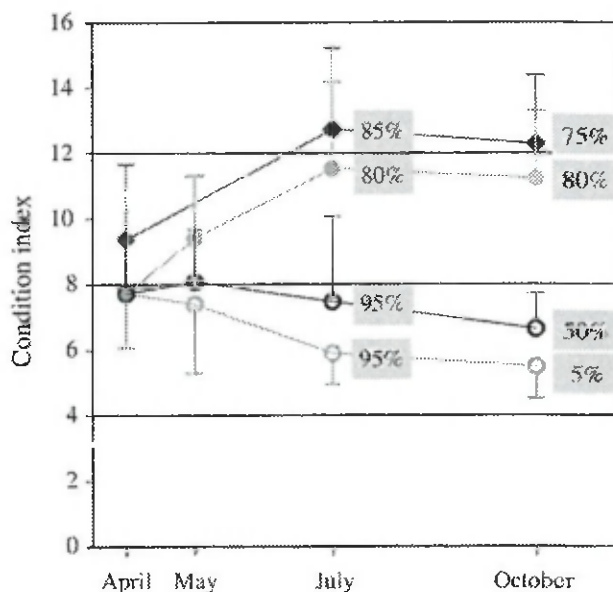


Fig. 4. Seasonal change in mean condition-index (Soft tissue dry weight/shell volume [$\mu\text{g}/\text{ml}$]) for experimental *M. balthica* specimens from the Westerschelde estuary (black diamonds), Point d'Aiguillon (grey circles), the Bidasoa estuary (open grey circles) and the Mundaka estuary (open black circles), 0 (April), 1 (May), 3 (July) and 6 (October) months after caging and translocation. Error bars indicate standard deviations. The values plotted in the grey boxes represent the percentage of surviving specimens in the cages in July (left) and October (right).

onwards, down to 5.5 in the Bidasoa estuary and 6.6 in the Mundaka estuary ($P < 0.001$).

4. Discussion

4.1. Respiratory response to temperature

The respiratory response to temperature of *M. balthica*, in natural populations, was down-regulated during the summer. Since the largest differences between July and April/May occurred at high ambient temperatures (24–31 °C), we concluded that down-regulation was mainly a form of self defense against peak temperatures. Sokolova and Pörtner (2003) found a similar response in a North Sea population of *Littorina saxatilis*. After acclimation to 4 °C, these gastropods showed no metabolic rate protection when exposed to high experimental temperatures. In contrast, a White Sea population performed metabolic down-regulation at high experimental temperatures, irrespective of the acclimation temperature.

Using *M. balthica* specimens sampled at different shore heights in the Somme estuary (50.2° N) during the summer, Wilson and Elkaim (1991) showed that clams from a high-shore habitat applied metabolic down-regulation between ≈ 15 and 30 °C, while specimens from mid-shore and low-shore levels did not. Although our specimens were caged at mid-shore level, strong down-regulation was observed in the summer; mainly in

clams from Point d'Aiguillon, which was probably due to the southern positioning of this locality. Thus, a more challenging thermal environment, e.g. increased shore height and southern distribution, promotes stronger down-regulation and temperature independence of the metabolic rate, in summer and autumn.

In the translocated populations, seasonal acclimatization developed differently compared their population of origin. The translocated clams remained highly sensitive to temperature changes during the summer, only showing metabolic down-regulation at 31 °C. This resulted in strongly elevated respiration rates at ambient temperatures (2 to 3 $\text{mg O}_2/\text{g dry weight}/\text{h}$), that have never been observed in acclimatized *M. balthica* specimens before. Although the rates of oxygen consumption had returned to the natural range in October, they were still elevated when compared to specimens from Point d'Aiguillon.

Nearly all experimental specimens showed some level of metabolic down-regulation at 31 °C. Decreased respiration rates at 31 °C may indicate the onset of anaerobic metabolism. However, Wilson and Elkaim (1991) demonstrated that under extreme heat exposure (35–40 °C), respiration rate can increase again in this species, reaching unnaturally high rates up to 3.1 ($\text{mg O}_2/\text{g dry weight}/\text{h}$). This capacity shows that reduced respiration rates at 31 °C result from metabolic regulation rather than respiratory failure. It must therefore be concluded that disruption of the respiratory function in *M. balthica*

occurs at much higher temperatures than those found in its natural range.

To achieve a temperature-independent metabolic rate, *M. balthica* needs a rapid mechanism to adjust to fluctuating temperatures. A candidate mechanism works through suppression of mitochondrial respiration by nitric oxide (Brown, 1999). Beneficial control of mitochondrial respiration requires anaerobic metabolic pathways that generate sufficient ATP to meet the (reduced) energy requirements during anaerobiosis (Carroll and Wells, 1995; Hand and Hardewig, 1996; de Zwaan and Ertunan, 1996). Induction of anaerobiosis by nitric oxide may explain why the threshold temperature for anaerobic metabolism does not rise under hyperoxic circumstances, as was shown in for the Antarctic fish *Pachycara brachycephalum* (Mark et al., 2002).

4.2. Survival and condition

An increasing condition index, in the non-translocated populations, during springtime and early summer was in agreement with earlier work on *M. balthica* from the Dutch Wadden Sea (52.9° N) (Beukema and de Bruin, 1977). While clams from the Westerschelde estuary and Point d'Aiguillon showed a similar seasonal trend, the condition index was higher in the more northern population. In the translocated clams, a gradually declining condition index reached ≈ 5 in the Bidasoa estuary in October, corresponding to the minimum reported for *M. balthica* (Honkoop and Beukema, 1997). Since these clams showed 95% mortality, such a low condition index represents starvation.

4.3. Enhanced maintenance costs

Only the clams from the Westerschelde estuary increased in shell length during the experiment (ANOVA, $P < 0.01$). While specimens at Point d'Aiguillon increased their soft tissue biomass, it clearly declined in the translocated clams. When starving, organisms allocate all energy to somatic maintenance. Therefore, the elevated respiration rates and no growth combined with starvation indicate enhanced energy requirements for maintenance that could not be met by energy ingestion. Hummel et al. (2000) also found elevated respiration rates in *M. balthica* specimens, 5 months after translocation (April–August) from the Westerschelde estuary into the Basin d'Arcachon (44.6° N) and the Bidasoa estuary. After 7 months, these elevated rates had vanished. Although these observations were less pronounced, they are in line with our results. Wilson and Elkaim (1991) reported relatively high respiration rates in summer acclimatized *M. balthica*

specimens from their southern-most population, the Gironde estuary (45.6° N). Although the rates they observed were within the natural range (≈ 0.95 mg O₂/g dry-weight/h), it suggests that these specimens had increased energy demands. For the same population, a reduced mean condition index (Hummel et al., 2000) and growth rate (Hummel et al., 1998) has been described. Apparently, the energy requirements could barely be met in this subpopulation.

4.4. Environmental variables

Several environmental variables may be held responsible for the elevated respiration rates of *M. balthica* at the translocation sites. Besides temperature regimes, salinity, pollution and food availability influence the metabolic rate. However, other dominant bivalve species found at Point d'Aiguillon, were also present at the translocation-sites, indicating a suitable *M. balthica* habitat in terms of sediment structure, food availability and salinity regime. Although in October 95% of the *M. balthica* specimens in the Bidasoa estuary had died, the local sand-dwelling bivalves had flourished inside the cages via natural recruitment. Especially the surface deposit feeder *Scrobicularia plana* reached extreme densities (Mean density: 1220, S.D.: 348 [ind/m²], mean size: 22.4 mm S.D.: 6.4), three times higher than maximum densities for adult *S. plana* in the Bidasoa estuary (Sola, 1997). Such productivity shows that food was certainly abundant during the experiment.

Even though the other bivalve species grew well in the cages in the Bidasoa estuary, *M. balthica* may have suffered from the relatively high degree of environmental pollution in this area, as suggested by Hummel et al. (2000). The Mundaka estuary is much less polluted (Garcia-Albras and Rallo, 2004). Even so, the physiological performance of *M. balthica* from this area was comparable to the subpopulation from the Bidasoa estuary, indicating that pollution was not the main cause of an enhanced energy demand in the translocated clams.

4.5. Peak temperatures

Important differences in maximum temperature between the French and Spanish sites were present. When translocated, the clams may not have been fully prepared for these warmer conditions (Fig. 2 arrow a). Summer peak temperatures were also higher in the Bidasoa estuary than at Point d'Aiguillon (Fig. 2 arrow b). While 30 °C was only reached once at Point d'Aiguillon, ambient temperature frequently exceeded 30 °C, up to 35 °C in the Bidasoa estuary. Since 30 °C is the maximum habitat

temperature of *M. balthica*, and exposure to >33 °C causes rapid mortality in this species (Kennedy and Mihursky, 1971), the peak temperatures occurring at the translocation sites will cause sub-lethal damage, inducing an increased energy demand. Such heat caused stress has been described for *Mytilus trossulus* from Garrison Bay (USA) living in the upper tidal zone (Hofmann and Somero, 1996).

4.6. Conclusion

In conclusion, *M. balthica* applies metabolic down-regulating to protect its metabolic flux when it acclimatizes to warm ambient conditions. This strategy fails beyond its southern distribution limit due to an increased energy demand at excessive temperatures that approach lethal limits. Increasing summer maxima brought on by climate change may therefore be implicated in the disappearance of *M. balthica* from the Atlantic coast of Spain. We expect *M. balthica* to disappear completely from the Bay of Biscay as global temperatures continue to rise.

Acknowledgements

This study, publication no. 3960 Netherlands Institute of Ecology (NIOO-KNAW), was supported by the European Committee (Research Directorate General, Environment Program Marine Ecosystems) through the BIOCOMBE project (contract EVK3-2001-00146). We are grateful to all colleagues that have assisted in the fieldwork and kindly thank Miss S. Barley for improving the English in our manuscript.[SS]

References

- Bachelet, G., 1980. Growth and recruitment of the tellinid bivalve *Macoma balthica* at the southern limit of its geographical distribution, the Gironde estuary (SW France). *Mar. Biol.* 59 (2), 105–117.
- Beaugrand, G., Reid, P.C., 2003. Long-term changes in phytoplankton, zooplankton and salmon related to climate. *Glob. Chang. Biol.* 9 (6), 801–817.
- Beukema, J.J., de Bruin, W., 1977. Seasonal changes in dry weight and chemical composition of the soft parts of the tellinid bivalve *Macoma balthica* in the Dutch Wadden Sea. *Neth. J. Sea Res.* 11, 42–55.
- Brown, G.C., 1999. Nitric oxide and mitochondrial respiration. *BBA Bioenerg.* 1411 (2–3), 351–369.
- Carroll, L., Wells, M.G., 1995. Strategies of anaerobiosis in New Zealand infaunal bivalves: adaptations to environmental and functional hypoxia. *N.Z. J. Mar. Freshw. Res.* 29, 137–146.
- Drent, J., 2004. Life history variation of a marine bivalve (*Macoma balthica*) in a changing world. *Wiskunde en Natuurwetenschappen. Rijksuniversiteit Groningen, Groningen*, p. 192.
- de Zwaan, A., Eertman, R.H.M., 1996. Anoxic or aerial survival of bivalves and other euryoxic invertebrates as a useful response to environmental stress, a comprehensive review. *Comp. Biochem. Physiol.*, C 113 (2), 299–312.
- Garcia-Albras, L., Rallo, A., 2004. Population dynamics and production of *Streblospio benedicti* (Polychaeta) in a non-polluted estuary on the Basque coast (Gulf of Biscay). *Sci. Mar.* 68 (2), 193–203.
- Hand, S.C., Hardewig, J., 1996. Downregulation of cellular metabolism during environmental stress: mechanisms and implications. *Annu. Rev. Physiol.* 58, 539–563.
- Hofmann, G.E., Somero, G.N., 1996. Interspecific variation in thermal denaturation of proteins in the congeneric mussels *Mytilus trossulus* and *M. galloprovincialis*: evidence from the heat-shock response and protein ubiquitination. *Mar. Biol.* 126 (1), 65–75.
- Honkoop, P.J.C., Beukema, J.J., 1997. Loss of body mass in winter in three intertidal bivalve species: an experimental and observational study of the interacting effects between water temperature, feeding time and feeding behaviour. *J. Exp. Mar. Biol. Ecol.* 212 (2), 277–297.
- Hummel, H., Amiard-Triquet, C., Bachelet, G., Desprez, G., Marchand, M., Sylvand, J., Amiard, B., Rybarczyk, J.C., Bogaards, R.H., Sinke, J., 1996. Sensitivity to stress of the estuarine bivalve *Macoma balthica* from areas between the Netherlands and its southern limits (Gironde). *J. Sea Res.* 35 (4), 315–321.
- 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 (1), 85–102.
- Hummel, H., Bogaards, R., Bek, T., Polishchuk, L., Sokolov, K., Amiard-Triquet, C., Bachelet, G., Desprez, M., Naumov, A., Strelkov, P., 1998. Growth in the bivalve *Macoma balthica* from its northern to its southern distribution limit: a discontinuity in northern Europe because of genetic adaptations in Arctic populations? *Comp. Biochem. Physiol. A.* 120 (1), 133–141.
- Kamerlings, P., van der Veer, H.W., Karczmarski, L., Doeglas, G.W., 1992. Competition in deposit- and suspension-feeding bivalves: experiments in controlled outdoor environments. *J. Exp. Mar. Biol. Ecol.* 162 (1), 113–135.
- Kennedy, V.S., Mihursky, J.A., 1971. Upper temperature tolerances of some estuarine bivalves. *Chesap. Sci.* 12 (4), 193–204.
- Koutsikopoulos, C., Beillois, P., Leroy, C., Taillefer, F., 1998. Temporal trends and spatial structures of the sea surface temperature in the Bay of Biscay. *Oceanol. Acta* 21 (2), 335–344.
- Lastra, M., de La Huz, R., Sanchez-Mata, A.G., Rodil, I.F., Aerts, K., Beloso, S., Lopez, J., 2006. Ecology of exposed sandy beaches in northern Spain: environmental factors controlling macrofauna communities. *J. Sea Res.* 55 (2), 128–140.
- Mark, F.C., Bock, C., Pörtner, H.O., 2002. Oxygen-limited thermal tolerance in Antarctic fish investigated by MRI and 31P-MRS. *Am. J. Physiol., Regul. Integr. Comp. Physiol.* 283 (5), 1254–1262.
- Otero, H.J., Millan, J.F., 1972. Distribucion de los Moluscos: Gasteropodos y Petecipodos marinos de las costas de Galicia. *Cuad. Biol.* 1, 79–93.
- Pörtner, H.O., 2001. Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften* 88 (4), 137–146.
- Rodil, I.F., Lastra, M., Sanchez-Mata, A.G., 2006. Community structure and intertidal zonation of the macroinfauna in intermediate sandy beaches in temperate latitudes: North coast of Spain. *Estuar. Coast. Shelf Sci.* 67 (1–2), 267–279.
- Rodriguez, J.G., Lastra, M., Lopez, J., 2003. Meiofauna distribution along a gradient of sandy beaches in northern Spain. *Estuar. Coast. Shelf Sci.* 58 (1), 63–69.

- Sokolova, I.M., Pörtner, H.O., 2003. Metabolic plasticity and critical temperatures for aerobic scope in a eurythermal marine invertebrate (*Littorina saxatilis*) from different latitudes. J. Exp. Biol. 206 (1), 195–207.
- Sola, J.C., 1997. Reproduction, population dynamics, growth and production of *Scrobicularia plana* da costa (pelecypoda) in the Bidasca estuary, Spain. Aquat. Ecol. 30 (4), 283–296.
- Wilson, J.G., Elkaim, B., 1991. Tolerances to high temperature of infaunal bivalves and the effect of geographical distribution, position on the shore and season. J. Mar. Biol. Assoc. U.K. 71 (1), 169–177.

