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Differential cold-shock resistance among acclimated European mussel populations

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Abstract

To study differential cold-shock resistance of marine mussel populations (*Mytilus* spp.) from different climatic regions in Europe, we sampled 12 populations, ranging from 43 to 58°N. Minimum critical temperatures for aerobic metabolism (CT_{min}) were determined before and after 3 months of common acclimatization in an outdoor mesocosm. Additionally, chill coma in response to cold shock was used to test for differences in physiological plasticity between the translocated populations. The CT_{min} followed a steep cline, being positively related to the ambient temperatures before translocation ($p < 0.0001$), and became similar between populations after 3 months in the outdoor mesocosms ($p > 0.05$). Differential chill coma responses separated the populations into two groups that were also geographically separated by the English Channel. The southern populations showed a much stronger and faster sensitivity to chill than the northern populations, indicating differential physiological adaptation between the two groups. The results are discussed in relation to the genetic background and climatic isolation of the populations.

Keywords: *Mytilus, metabolism, chill coma, cold adaptation, temperature, climate change*

Introduction

Marine mussels (*Mytilus*) are widespread in the temperate zones of the world. Seasonal changes and daily fluctuations in temperature require ongoing physiological adjustments to the environment, and therefore great plasticity. Such adjustments are costly (Somero 2002) and more regionally adapted populations will be favored. Most studies on the limits in thermal plasticity of mussels have focused on upper thermal tolerance limits, which lie at about 28°C for aerobic metabolism (Hicks and McMahon 2002), with about 36°C causing 100% mortality in <2 h (Rajagopal et al. 2005). Based upon heat tolerance,

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differences in adaptation among *Mytilus* species have been described (Wallis 1975; Hoffmann and Somero 1996). Rather little is known about the low thermal limits of mussels and the differential cold adaptation of separated, divergent populations in particular is largely unexplored. Living in the tidal zone, mussels tolerate temporary exposure to subzero temperatures during low tide (Aarset 1982; Bourget 1983; Murphy 1983). However, the effect of a nearly 0° water temperature on the physiological performance of mussels when submerged has not been reported so far.

Low thermal tolerance limits associated with the biogeography of invertebrate species may be related to the minimum temperature at which aerobic metabolism is supported (Peck et al. 2002, Pörtner 2002). In marine ectotherms, this critical minimum temperature for aerobic metabolism (CT_{min}) lies between 1 and 10°Celsius (Kooijman 2000). A fixed CT_{min} of 5°C has been assumed for *Mytilus edulis* (van Haren 1995) and 6.5°C was assessed for *M. edulis* larvae (Sprung 1984). Studies on other European species found CT_{min} values of 4°C for marine polychaetes (Zielinski and Pörtner 1996; Sommer et al. 1997) and 6–7.7°C for Norwegian Salmon (Forseth et al. 2001). In this study we compared the CT_{min} of mussel populations over a wide geographic range to study their relation with the local climate. Moreover, we carried out an experiment in which we acclimatized mussels from nine populations in Europe to similar climatic conditions, estimating and comparing the level of plasticity in CT_{min} and cold-shock resistance in the experimental populations.

European mussels can be subdivided into three different genetic groups (Hummel 2006). These groups are usually referred to as different species, with *M. galloprovincialis* found south and *M. edulis* found north of the English Channel. The third group is located in the Baltic Sea and is often referred to as *M. trossulus*, a conclusion based on its genetic resemblance to a *M. trossulus* population from Canada (Varvio et al. 1988). In recent years, uncertainty has arisen regarding the taxonomic status of these genetic groups. Zones of transition linking two groups are usually broad and gradual, characterized by extensive hybridization (Riginos and Daguin et al. 2001; Luttikhuizen et al. 2002; Cunningham 2005), in the nature of a single species with divergent clades. Moreover, a strong association between the transition between Baltic Sea and North Sea populations and a salinity gradient suggests that the observed genetic divergence is caused by natural selection (Bulnheim and Gosling 1988). In this study, mussels from the three different groups were used. We refer to them as *Mytilus* spp., and examine the matter of their genetic status, in relation to our results, in the "Discussion" section.

In response to cold shock, *Mytilus* spp., like most animals, produce endomorphines to maintain homeostasis. Morphines affect the nervous system, and activate nitric oxide synthase in the mitochondria (Cadet et al. 2002; Mantione et al. 2003), so that nitric oxide out-competes cytochrome oxidase by binding oxygen (Brown 1999; Brown and Borutaite 2004). This respiratory failure results in a mitochondrial depression which, if continued, causes the temporary loss of physical function in the animal. Loss of function due to cold shock is referred to as chill coma, a commonly applied measure in physiological studies. In insects it is often measured as loss of locomotion (Bradfisch et al. 1982; Marshall and Chown 1995; Gilbert and Huey 2001; Ayrinhac et al. 2004), and in fish as loss of equilibrium (Bennett and Judd 1992) or mortality (Staurnes 1994). Mussels respond to environmental stressors by closing their protective valves, but because the mantle, byssus organ, and foot appear to be more sensitive to cold shock than the adductor muscle, the trapping of the mantel, byssus or foot tissues between the valves can be one of the first signs of chill coma (personal observation). When cold exposure continues, mussels lose the ability to keep their valves closed. Sub-lethal chill coma significantly reduces the probability of survival in nature because the animals are more vulnerable to predation. Since differences

in physiological adaptation to chill coma have been seen at population level before (Ayrinhac et al. 2004); we used this trait to study differential cold-shock resistance among multiple mussel populations with respect to both their genetic background and climatic history.

Materials and methods

Fieldwork and translocation

For this study we sampled mussels from 12 populations along the European coastline (Figure 1). The ambient conditions at the twelve localities differed in terms of salinity,

Figure 1. Map of Europe with research sites. ASK = Asko, LOM = Lomma, MEC = Mecklenburg Bight, WAD = Waddenzee, GRE = Grevelingenmeer, WES = Westerschelde estuary, GRA = Granville, BST = Brest, AIG = Point d'Aiguillon, BID = Bidasoa estuary, MUN = Mundaka estuary, and MAR = Marseille. NIOO = Netherlands Institute of Ecology. Ambient salinity (PSU) is indicated in the white boxes next to the station names (abbreviations) for each locality. The populations LOM, AIG, and MUN were not included in the translocation experiment.

temperature, and food availability. An overview of the ambient salinity at the sites is provided in Figure 1, and the ambient temperature can be estimated from Figure 2. Food availability at the Mediterranean site was classified as low. High food availability is characteristic for the coastal waters and adjacent estuaries of the Bay of Biscay and North Sea. While the Baltic Sea localities can be described as meso-trophic during most of the year, spring blooms caused high food availability during the sampling period. Mussels were collected in April 2005 from shallow water (<1 m depth) and intertidal (low-shore) habitats. After collection, 25 individuals (30–40 mm) were selected to assess CT_{min} for aerobic metabolism. Those specimens were transported to a nearby laboratory, where they were gently cleaned of epifauna and algae, and stored in aquaria with aerated habitat water kept at approximately field temperature (±3°C). A range of 200–300 individuals of nine populations were stored in foam boxes, covered with the seaweed *Fucus* spp. for preservation, and transported to the Netherlands Institute of Ecology (NIOO), Yerseke, the Netherlands within 48 h of collection. The mussels from Marseille were an exception. They were kept at 10°C, in aquaria with aerated habitat water for 5 days before transportation to NIOO. At NIOO, the mussels from each population were distributed over four sock-shaped nets (mesh size 10 mm^2), commonly used in mussel culture (TM10®). The socks were hung vertically in outdoor mesocosms of 1000 L ($100 \times 100 \times 100\ cm^{-3}$) which were positioned on the waterfront. Water was pumped up from the Oosterschelde and distributed equally into the four tanks. During high tide, each tank received >1500 L of unfiltered seawater per hour, with a stable salinity of 30 PSU. During low tide, no habitat water could be supplied to the mussels for ~4 h per tidal cycle but the water in the tanks was aerated. The effluent water was returned to the

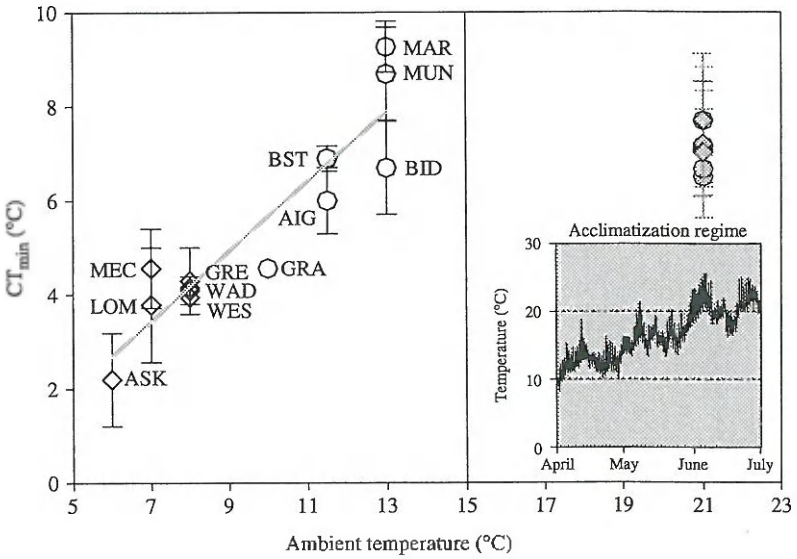

Figure 2. Minimum temperature for aerobic metabolism (CT_{min}) as a function of the ambient temperature. The circles and diamonds represent the populations from the south and the north of the English Channel, respectively. Abbreviations of the location names are explained in the caption of Figure 1. The grey circles and diamonds in the right part of the figure represent the measurements taken after 3 months of common acclimatization in the outdoor mesocosms. The temperature regime that the mussel populations experienced during common acclimatization is superimposed.

Oosterschelde via sand filters with an area of approximately 1.3 m^2. The sand filters were cleaned on a weekly basis and deposited sediment and mussel faeces were removed from the mesocosms twice, at four and eight months after the experiment started. We failed to transplant mussels from Askö successfully. Despite an applied stepwise acclimation to the increased salinity, all mussels from this area died soon after translocation. In the other translocated populations mortality was less than 10%. After 3 months in the outdoor mesocosms, mussels were sampled and carefully cleaned of epifauna and algae, and used for cold-shock resistance experiments.

CT_{min}

To estimate the CT_{min} for aerobic metabolism for the different mussel populations, we assessed respiration rates at 8 different temperatures (2, 4, 6, 8, 10, 12, 14 and 16°C). Rates of oxygen consumption were determined with 264 mL respiration chambers filled with filtered habitat water previously aerated to 100% air saturation. The temperature inside the respiration chambers was kept constant (±0.2°C) using a water cooler (Tamson TLC 10B, Fisher®). For each incubation, 3 mussels of 30–40 mm were placed together in a ring-shaped enclosure positioned halfway down a respiration chamber. Water movement was provided by a magnetic stirrer, and the open center of the ring-shaped enclosures allowed a constant water flow (vortex) throughout the entire chamber. The oxygen concentration in the chambers was monitored with polarographic oxygen sensors (Clark-type electrodes). The mean electrode output was computed every minute by Testpoint software. Three replicate measurements were taken per experimental temperature for each population. Following the measurement, the mussels were frozen at −20°C and subsequently lyophilized for 72 h to a constant weight. For the dried mussels, the shell-free dry weight was determined to the nearest milligram. Control measurements were carried out using the same experimental setup, without mussels, and the results were used for correction. From these data, the mass specific respiration rates were calculated from the tangent of a linear regression line using Microsoft Excel. Mean respiration rates were plotted as a function of the experimental temperature and CT_{min} was determined as the onset of the slope of respiration rates increasing with temperature.

Chill coma

When exposed to cold shock, mussels closed their valves. After a certain level and duration of cold stress, the adductor muscle became paralyzed and the mussels were unable to close their valves tightly. At this point, opening of the valves was observed, and in most cases the mantle tissue retracted slightly. Mussels with their valves open were tested for chilling coma by pushing their valves together repeatedly with large forceps. When a mussel no longer responded to this external stimulus by keeping its valves closed, it was considered to be in chill coma condition.

Statistical analysis

Linear regression was used to test whether assessed CT_{min} values were proportional to ambient temperatures. The percentages of chill coma, assessed as a function of cold exposure time, were used to calculate Euclidean distances between the populations. Based on these distances, cluster analysis was carried out with the purpose of visualizing the comparability of the cold shock response from the different populations. Cluster analysis was based upon group average linkage, carried out with Primer 5 software.

Subsequently, two-way ANOVAs with Bonferroni multiple comparison tests, were used to test in which treatments (exposure times) the main differences between the groups of populations occurred, and to assess the contribution of interaction in the overall variance.

Results

CT_{min}

The mussels collected from the field in April 2005 exhibited decreasing CT_{min} values with ambient temperatures (Figure 2). Linear regression revealed a significant slope ($CT_{min} = 0.7423\,T - 1.7576$; r^2: 0.852; $p < 0.0001$), and indicated that the CT_{min} may become zero at temperatures ranging from −0.5 to 4.0°C. After 3 months of common acclimatization to increasing summer temperatures in an outdoor mesocosm in the Netherlands (temperature regime is superimposed in Figure 2), all translocated populations exhibited mean CT_{min} values ranging from 6.5 to 7.7°C (Figure 2 at $T = 21$), and no differences between populations were observed ($P > 0.05$).

Chill coma

Chill coma occurred in all populations during the experiment (Figure 3). The fraction of the population in chill coma exceeded 70% in all populations originating from localities south of the English Channel 10 to 25 h after the start of the experiment. The population from Brest revealed the poorest resistance, exhibiting 90% of chill coma after 10 h of cold exposure and no recovery after 200 h. Situated halfway along the English Channel, the population from Granville showed an intermediate response. The number of specimens in chill coma increased gradually with time in this population up to >80% after 40 h of cold exposure, after which it did not increase further.

Populations originating from more northern localities showed more resistance to sudden cold exposure. This difference was particularly obvious in the first part of the experiment. A large fraction (>80%) of the mussels from the Mediterranean Sea and the Bay of Biscay entered the chill coma state shortly after the start of the experiment, while in the North Sea and Baltic Sea populations, the fraction in chill coma condition increased more gradually, and the maximum number of specimens in chill coma did not exceed 75%. The Baltic Sea population from the Mecklenburg Bight appeared most cold-shock resistant, showing a maximum chill coma fraction of approximately 40% between 50 and 100 h of exposure and recovery after 200 h.

Cluster analysis confirms that, based on cold-shock response, the experimental mussel populations can be divided into two main groups (Figure 4). One group (A) formed by MAR, BID, BST and GRA, the other group (B) by WES, GRE, WAD and MEC (see Figure 1 for abbreviations). Plotting group means and standard deviations showed that group A (the more southern populations) was significantly more vulnerable to cold shock than group B (Figure 5). The significant interaction "main group"-"exposure time" contributed 6.6% of the total variance ($P = 0.0244$). This interaction demonstrates that the main groups responded in a different way to cold shock exposure. Group specific differences were significant at the shorter exposure times; from 6–30 h ($p < 0.001$). Also recovery after 200 h was significantly different between A and B ($p < 0.0001$).

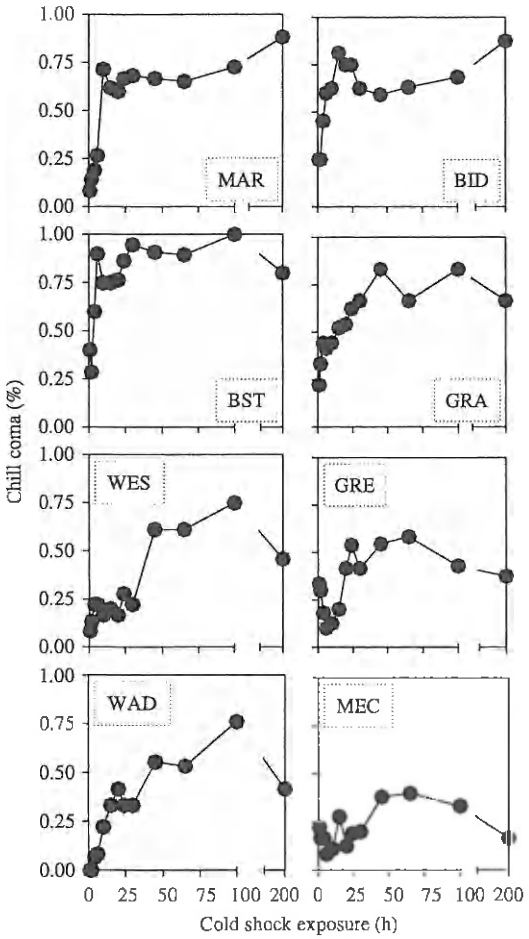

Figure 3. Chill coma (%) as a function of cold-shock exposure time for European mussel populations acclimatized to similar environmental conditions in the outdoor mesocosms. Abbreviations of the location names are explained in the caption of Figure 1.

Discussion

In this study we used cold-shock response to test for differential climatic adaptation, and/or acclimatization among mussel populations. Our results reveal the first overview of CT_{min} values for aerobic metabolism for a range of European mussel populations. As far as we know, this is also the first study that concerns chill coma in bivalves. It proved to be a sensitive measure, detecting small, physiological differences between populations. Marine mussels are often used as a model species so the observed variability in both CT_{min} values and chill coma may apply to other species as well.

CT_{min}

As expected, mussel populations that experience higher ambient temperatures exhibit higher CT_{min} values. Especially in populations from the Mediterranean Sea and the Bay of Biscay, CT_{min} values were higher than assumed in earlier studies

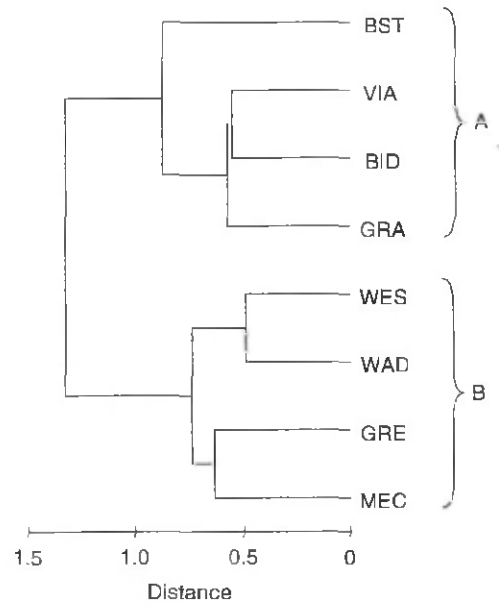

Figure 4. Cluster analysis based upon group average differences in chill coma frequencies after different exposure times. This analysis is based upon Euclidean distances, using untransformed data. Abbreviations of the location names are explained in the caption of Figure 1.

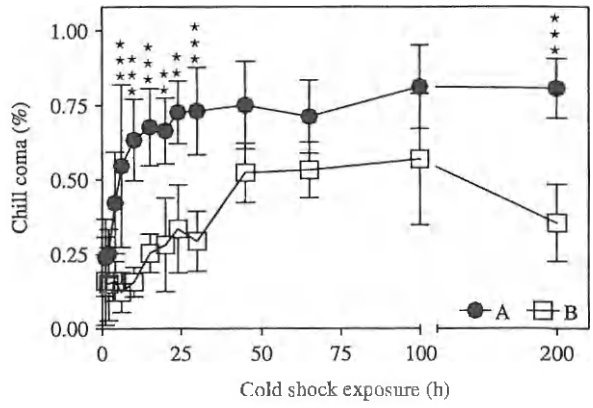

Figure 5. Group average (A and B) chill coma response to cold-shock exposure. The black circles and white squares represent group A (southern populations) and B (northern populations), respectively. Error bars indicate the standard deviations. Significant differences between A and B are indicated by 2 ($p < 0.001$) or 3 ($p < 0.0001$) stars above the error bars.

(Wright et al. 1980; van Haren 1995). They assumed that the CT_{min} for mussels is 5°C. Our data show, however, that in mussels from the central Baltic Sea, CT_{min} values smaller than 5°C should be expected in springtime. The observed linearity between CT_{min} and the ambient temperature gives no indication of a low temperature threshold for aerobic metabolism in acclimatized mussels, and suggests similar adjustment by each population to its local climate.

Interestingly, after 3 months of common acclimatization in an outdoor mesocosm, the CT_{min} values of all the populations became similar, demonstrating the plasticity of this trait. It indicates that CT_{min} values are not constant throughout the year, but subject to seasonal acclimatization. Moreover, the fact that CT_{min} values are linearly related to ambient temperatures argues for uniformity of this mechanistic aspect of thermal acclimatization among the mussel populations used in this study.

Although the ambient temperature at the end of the acclimatization time was about 21°C, mean CT_{min} did not exceed 7.7°C in any of the experimental populations. This means that the CT_{min} values had either reached a maximum, or that summer values have a different relationship with temperature, which would imply that the CT_{min} is not exclusively temperature-dependent.

Chill coma

Chill coma occurred in all mussel populations that were exposed to cold shock in summer. Acclimatized to the winter conditions, mussels might be less sensitive to the 0° treatment, and more severe treatments are probably needed to explore differences in cold adaptation when measuring chill coma. However, the study is, as far as we are aware, the first on chill coma in mussels to show differential adaptation to climate.

In some chill coma experiments, recovery time from coma was used as a physiological trait (Ayrinhac et al. 2004). For mussels this was not useful because recovery in 20°C seawater was rapid. From chill coma state to normal behavior (filtering and byssus organ, movement) took less than one minute for all specimens tested. In fish, primary and secondary chill coma has been distinguished. The first is due to respiratory failure and causes rapid mortality in sensitive species. The second is usually the consequence of osmoregulatory failure, and may result in delayed death (Staurnes, 1994). Mussels are well known to survive short-term respiratory failure (Zwaan and de Eertman 1996), which may explain the rapid recovery in habitat water of 20°C. Changes in osmolite concentrations due to cold shock will cause some level of metabolic depression in mussels, comparable to the effect of changed osmolite concentrations during natural fluctuations in salinity (Kube et al. 2006). The studied populations were all acclimatized to a stable salinity (30 PSU). Observed differences between mussel populations should therefore not be the result of acclimatization to different salinity regimes in their original environments.

Acclimatization to seasonal changes in temperature in the field is expected to have a time lag of ~1–2 weeks (Widdows and Bayne 1971). Since mussels were in a common outdoor mesocosm for 3 months prior to treatment and under close to natural conditions, we are confident that they were acclimatized to similar environmental conditions. The similarity in critical minima for aerobic metabolism after acclimatization suggests that the experimental populations were indeed adjusted to the same temperature regime. The differences in cold-shock resistance that remained after common acclimatization therefore display some level of differential adaptation, indicating that mussels are adapted to their local climates. Furthermore, group-specific interaction with exposure time suggests a differently developed mechanism of cold-shock resistance between the groups of populations found on the opposite sides of the English Channel.

Cause of differentiation

Physiological differentiation may result from genetic adaptation or physiological adjustments in early development that do not change in adults. This is termed ontogenetic fixation (Qiu et al. 2002). Based on our results, the populations can be

divided into two geographic groups separated by the northern part of the English Channel. The Channel forms a narrow transition zone from the relatively warm Bay of Biscay into the colder North Sea basin. The northern part of the Bay of Biscay can be relatively cold in summertime due to upwelling of deep Atlantic water (Koutsikopoulos et al. 1998; Puillat et al. 2004). Differences in sea water temperature between both sides of the English Channel are therefore particularly apparent in wintertime, when a steep temperature gradient (5–6°C) in sea surface temperature can be found over a relatively small latitudinal range (3°N), and these two climatic regions form distinct habitats. So, on the one hand, ontogenetic adaptation to winter minima may result in the observed grouping of our populations. On the other hand, differential genetic adaptation cannot be excluded as an explanation.

With respect to population genetics research, *Mytilus* forms a very well-studied group (Knowlton 2000). Different genetic markers have described a genetic transition through the English Channel (Daguin et al. 2001; Bierne et al. 2003; Śmietanka et al. 2004). All these genetic studies make use of the species names *Mytilus galloprovincialis* and *Mytilus edulis* to describe these two divergent groups, with *M. galloprovincialis* occurring south and *M. edulis* occurring north of the English Channel.

Mussels have great dispersal potential. First, natural dispersal of planktonic larvae can be extensive in spawning bivalves (Scheltema 1986). Second, European mussels have been transplanted extensively during more than a century of aquaculture. Despite their great dispersal capacity and their transplantations, segregation on the basis of cold shock resistance is preserved. This may indicate that these divergent groups are genetically adapted to different environments.

Due to their anti-tropical distribution, separated *Mytilus* spp. populations occur in the opposing hemispheres during interglacial periods. We speculate that differential cold shock resistance may have evolved in opposite hemispheres. Coexistence of distinct populations in Europe subsequently may have resulted from transequatorial contact between *Mytilus* spp. populations during a glacial period (Hilbish et al. 2000). It is thus possible that differential cold adaptation among European mussel populations coincides with the neutral genetic variation reported.

Comparing chill coma and the CT_{min} results, we see that while the CT_{min} was positively related to the acclimatization temperature, chill coma could be related to developmental differentiation or genetic background. In some other studies, ethological traits also appeared more useful for detecting differential physiological adaptation than other physiological traits (Gilbert and Huey 2001; Castañeda et al. 2004).

Conclusions, implications and recommendations

Mussels acclimatize to local conditions by adjusting closely to the existing thermal environment. As such, mussels are as energy efficient as the environment allows them to be. Furthermore, differences in cold-shock resistance indicate adaptation. As a consequence of climate change, increasing winter minima may cause the invasion of southern genetic groups, as has been observed for mussel populations in the USA (Geller 1999; Wonham 2004) and for certain European bivalve species as well (Diederich et al. 2005). Currently, increasing numbers of mussels are being translocated from southern Europe into the North Sea area for aquaculture industry (Wijsman and Smaal 2006). These large-scale transplantations potentially accelerate the predicted invasions of southern genetic groups.

We recommend repetition of this research in different seasons, and further experiments using multiple populations that are hatched under similar conditions, to further distinguish between genetically embedded adaptive responses and differences due to ontogenetic fixation. For the aquaculture industry we recommend more conservative translocation procedures to avoid an accelerated introduction of genetically distinct mussels adapted to different climatic conditions.

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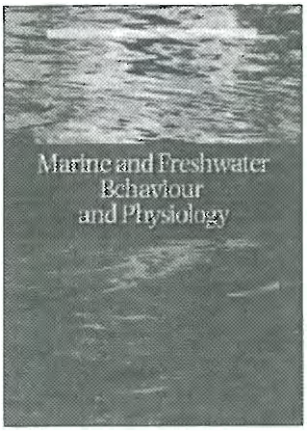

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Differential cold-shock resistance among acclimated European mussel populations

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