AGEING AND METABOLISM OF *MYTILUS EDULIS*: POPULATIONS FROM VARIOUS CLIMATE REGIMES

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ABSTRACT The aim of this study is to elucidate the impact of age and temperature on metabolic key parameters (respiration rate and mitochondrial marker enzymes) controlling maximal size and longevity in the blue mussel *Mytilus edulis* L. from geographically separated populations of Northern European seas. Mussels from the Barents Sea attain similar maximal sizes as animals from the warmer North Sea. Young animals (<5 y) grow faster in the North Sea, however, inshore Barents Sea mussels grow rapidly even at advanced age. The slowest growth rates were found in a population exposed to strong wave action in the Barents Sea. Respiration rates followed the same age dependent pattern in mussels from all studied populations with low respiration rates in the youngest specimens followed by a rapid increase and then a gradual decline to nearly constant values in the oldest animals. When compared at a common temperature, metabolic rates only of young blue mussels (<7-8 y) are cold compensated with maximal respiration in the most Northern populations. Cold compensated metabolic activities in mussels from Northern populations may support similar patterns of maximal body size and longevity as in the more temperate Southern population.

KEY WORDS: ageing, Barents Sea, citrate synthase, cytochrome C oxidase, growth, environmental temperature, *Mytilus edulis*, North Sea, respiration rate, White Sea

INTRODUCTION

Most eurythermal marine invertebrates of the Northern hemisphere have wide latitudinal distribution and physiological differences between spatially separated populations of one and the same species can be pronounced. In times of rapidly changing regional climate regimes it is a prime concern to study the quality of physiological adaptations, especially in key species like the blue mussel Mytilus edulis. Low ambient temperatures slow down metabolic activity at high latitudes, and there is by now ample evidence that thermal lowering metabolic rates extends life span in ectothermal models like Caenorhabditis elegans (Van Voorhies & Ward 1999) or Drosophila melanogaster (Luckinbill 1998). However, in aquatic ectotherms observations are controversial. Some eurythermal species are distributed over wide latitudinal gradients, and, at least in northern populations, the animals tend to attain bigger body sizes and longer life spans than their southern counterparts (MacDonald & Thompson 1988, Gianniny & Geary 1992, Duchesne & Magnan 1997). In others, no tendency or the opposite trend is observed (Selin et al. 1991, Garvey & Marschall 2003). Although a growing number of publications analyze the ageing process and the influence of age on metabolism in ectotherms with infinite growth (Zolotarev & Ryabushko 1977, Fidhiany & Winckler 1998, Zielinski & Pörtner 2000, Sukhotin et al. 2002, Philipp et al. 2005, 2006), virtually nothing is known about the variation of ageing parameters within a species with a latitudinal distribution.

Latitudinal variations of metabolic rate in aquatic ectotherms were extensively studied and shaped into the hypothesis of metabolic cold adaptation, which suggests a significant elevation of metabolic rate in cold adapted species. This hypothesis has recently been challenged for Antarctic stenotherms (Clarke & Johnston 1999, Peck & Conway 2000), but it has been reemphasized in comparative studies of temperate and subpolar, Northern hemisphere eurytherms (Pörtner 2002a, Pörtner 2004). Notably, eurythermal cold-water animals are characterized by elevated standard metabolic rates in comparison with temperate and tropical confamilial species. The present study addresses the consequences of these patterns for the lifespans of marine bivalves by investigating metabolic changes in the course of ageing in geographically separated populations of the blue mussel Mytilus edulis. M. edulis is a eurythermal species inhabiting European coasts from the French Atlantic coast in the South to the eastern parts of the Barents Sea and the White Sea in the North. We compared growth, metabolic rates and mitochondrial key enzymes of blue mussels from the relatively warm temperate North Sea (Helgoland), the cold subArctic White Sea, where seasonal temperature variations can span up to 15°C, as well as from the cold, but thermally more stable Barents Sea (the seasonal difference in temperature is about 6°C).

MATERIAL AND METHODS

Animals

Field sampling of blue mussels Mytilus edulis L. was carried out in 3 main areas: (1) Barents Sea (Kola Peninsula, Yarnyshnaja Bay 69°06'N, 36°04'E), (2) White Sea (Chupa Inlet of Kandalaksha Bay, 66°20'N, 33°40'E) and (3) North Sea (at Helgoland Island, 54°11'N, 7°53'E) (Fig. 1a). Salinity of surface waters range from about 24 ppt in the White Sea to 28-32 ppt in the Barents and the North seas. The three selected sampling locations form a cline of temperature conditions. The warmest is the North Sea, whereas the White and the Barents Seas are characterized by far lower winter and summer temperatures, respectively (Fig. 1b). At each site dense or dispersed settlements of Mytilus edulis are found in intertidal and upper subtidal zones. Sampling was performed from intertidal dense mussel beds at about 0.7-1 m above 0 tidal level in each of the three sampling areas. The mussel bed in Yarnyshnaja Bay (Barents Sea, BSi) is situated in the innermost part of a narrow bay, which penetrates about 6 km into the Kola Peninsula shoreline and is thus protected from wave action. In the White Sea sampling

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Figure 1. Map of study area and sampling sites of mussels (a) and monthly average temperature in the North Sea (http://bah. wdc-mare.org), Barents Sea (Matishov et al. 1998) and White Sea (Babkov, 1982).

area (WS) *Mytilus edulis* forms a dense multilayer population on the southern shore of a small island, which is also sheltered from direct wave action, whereas exposed to strong tidal currents. In the North Sea (NS) mussels were collected from the rocky intertidal on the NW coast of Helgoland Island. This site is exposed to wave action at N to NE wind directions.

Mussels were collected in October (BSi and WS) and November (NS) 2002. Sea water temperature was +5.5°C and +9°C, respectively. Furthermore, mussels were sampled from an intertidal population situated in the outer part of Yarnyshnaja Bay of the Barents Sea (BSo). This area is exposed to strong wave action. In addition, a small sample of mussels from the most Eastern part of the Barents Sea was kindly collected by Dr. P.P. Strelkov. These mussels were sampled from subtidal population in 6-m depth near the Vajgach Island (Barents Sea, Novaya Zemlya Archipelago, 69°44'N, 59°30'E) in August 2002 at a water temperature of +3°C.

Molluscs from all sites were transported alive to the Alfred-Wegener Institute (Bremerhaven, Germany) and maintained in aquaria at 30 ppm salinity and +5.7°C temperature. Age was determined for all mussels by counting the rings of winter growth delays on the outer shell surface. This method has previously been verified in studies carried out in the White Sea by comparing the number of internal rings and seasonal growth of individually marked mussels (Chemodanov & Maximovich 1983, Sirenko &

Saranchova 1985). Respiration measurements were performed in January 2003.

Growth

Growth rings of mussels from all four populations were measured from the umbo to the most distant edge of the shell to the nearest 0.1 mm for reconstruction of the growth history of mussels. Linear growth of mussels was approximated using the von Bertalanffy model

$$L_{t} = L_{\infty} \cdot (1 - \exp^{-k \cdot (t - t_{0})}),$$

in which L_t is length (mm) at the age t (years), L_{∞} , k and t_o are constants.

Experimental Procedure

Mussels from all populations were sorted by age with considerable variability in animal size within each age class. The BSi group included age classes from 3-15 y (12 and 14 y age classes were missing) ranging in size from 0.187-4.740 (mean = 1.03) g wet tissue weight. The BSo group was represented by 4-8-y-old mussels (0.095–0.479, mean = 0.29 g wet tissue weight). Mussels from the White Sea (WS) were 1–10 y old (0.046–2.40, mean = 0.72 g wet tissue wt) whereas the North Sea sample (NS) comprised animals from <1 to 11 y of age (0.206–4.036, mean = 1.58 g wet tissue wt). Vajgach sample (Vajgach) was represented by only 8 specimens 5–11-y-old (0.249–1.374, mean 0.75 g wet tissue wt). Mussels from this sample were used only for respiration rate measurements.

Oxygen consumption was measured at +5°C in closed 150–200 mL respirometers, containing 1–6 mussels. Oxygen concentration was monitored using Clark type oxygen electrodes (Eschweiler, Kiel, Germany). After the measurements mussels were cut open, gills were dissected, blotted dry on tissue paper, weighed to the nearest 0.1 mg and deep frozen in liquid nitrogen for further analyses of enzyme activities. The residual tissues were also weighed. Respiration rate was expressed in μ mol O₂ g⁻¹ tissue wet wt h⁻¹.

Analyses

Citrate synthase (CS, EC 2.3.3.1) activity was measured spectrophotometrically at 412 nm using an enzymatic test (Sidell et al. 1987). Powdered tissue (about 100 mg) was homogenized in 75 mM Tris+1mM EDTA buffer (pH 7.6) at a 1:9 w/v ratio. After centrifugation (10 min, 9,500 g, at 0°C) CS activity in the supernatant was measured in 100 mM Tris-HCl buffer (pH 8.0) containing 20mM acetyl-CoA, 20 mM oxaloacetate and 5 mM DTNB. Absorbance was monitored at 412 nm using a spectrophotometer (LKB Pharmacia) with cuvettes thermostatted at +25°C.

Cytochrome C oxidase (COX, EC 1.9.3.1) activity in mussel gill tissue was determined according to Hardewig et al. (1999). Powdered tissue (1:9 w/v) was homogenized in 20 mM Tris-HCl +1mM EDTA + 0.1% Tween 20 buffer (pH 7.4). Enzyme activity was measured in the assay buffer (20 mM Tris-HCl, pH 8.0 + 0.5% Tween 20 + 50 μ M reduced cytochrome c) at +25°C. The decrease of absorbance was determined spectrophotometrically (LKB Pharmacia) at 550 nm. Cytochrome C, dissolved in 20 mM Tris-HCl, pH 8.0 was reduced by sodium dithionite, which was removed by gel filtration in a Sephadex G-25 column. Enzyme activities were expressed in U g⁻¹ tissue wet wt.

Calculations and Statistics

One-way ANOVA was used to compare densities, biomasses, respiration rates and enzyme activities between populations. Post-

hoc comparisons were made by Tukey HSD Test for unequal N. Age effects on respiration rates and enzyme activities were tested by Kruskal-Wallis nonparametric test. Age distributions in the studied populations were compared by the Chi-square test. The F-test was used for comparisons of linear growth equations in different samples.

RESULTS

Growth

Mussels from NS and WS populations grew rapidly during the first 4-5 y but growth tended to level off hereafter (Fig. 2). Molluscs from the Barents Sea displayed similar growth strategies in both populations until the 5th year, when animals from the open shore (BSo) slowed their growth, whereas mussels from the sheltered part of the bay (BSi) continued intensive growth until the age of about 10 y, whereafter a decrease in growth rate was observed. In terms of absolute shell length increment, mussels from the North Sea had the fastest growth of all populations in the first 2-3 y after settlement, attaining over 30-mm body length during young age. Hereafter their growth rate diminished to that of mussels from the other sites. The most rapid growth at advanced age (over 5-y-olds, beyond 20-mm body length) was found in the Barents Sea population from the protected site in Yarnyshnaja Bay (BSi). Pairwise comparisons showed that growth curves of mussels from the White Sea (WS) and from the open part of the Yarnyshnaja Bay (BSo, Fig. 2) did not differ statistically (P = 0.246, F-test). Both demonstrated an abrupt decrease of growth rate after reaching 5 y of age. Growth rates of BSi mussels differed significantly from both BSo and WS specimens at P = 0.0012 and P < 0.001, respectively, whereas NS animals differed from all others at P < 0.001 (F-test).

Respiration Rate

The effect of body size on respiration was approximated using 5-y-old individuals from all 3 stations, because this age class was in the middle of the age range and also one of the most abundant (except for the juveniles) in the studied populations (unpublished data). Respiration rate (RR, µmol O₂ g⁻¹ wet wt h⁻¹) of 5-y-old *M. edulis* decreased as a function of tissue wet weight (W, g)



Figure 2. Von Bertalanffy growth curves in mussel populations. NS, North Sea; $L_t = 62.8 \cdot (1 - exp^{-0.197(t+0.34)})$, n = 215, BSi, Barents Sea; innermost (sheltered) part of the bay: $L_t = 412.0 \cdot (1 - exp^{-0.014(t-1.380)})$, n = 194, BSo, Barents Sea; outer (open) part of the bay: $L_t = 126.2 \cdot (1 - exp^{-0.035(t-1.206)})$, n = 30, WS, White Sea; $L_t = 39.3 \cdot (1 - exp^{-0.181(t-1.160)})$, n = 238. Data are mean \pm SE.

$$RR = 3.8 W^{-0.356}$$
 (r = -0.838, p < 0.001, N = 15).

The obtained power coefficient (-0.356) was then used for a weight correction of the respiration data to a mean wet tissue weight (= 1.00 g) for comparisons between mussels of different ages and populations. The correction was as follows $R_{corrected} = R_{observed} \times (1/W)^{-0.356}$.

Although the Vajgach population was subtidal and therefore differed from the other populations, it was included in the interpopulational comparisons of mussels' respiration as the most distant outpost with the lowest ambient temperatures. The factor "population" had a significant (P < 0.001, ANOVA) effect on weight-corrected respiration rates. Figure 3a presents respiration rates of mussels from 5 populations as means of all ages. Respiration increased in the following rank order: NS < WS = BSi = BSo < Vajgach. Compared at a common experimental temperature of 5°C, NS mussels were characterized by significantly (P < 0.01, Tukey HSD) lower respiration rates than their more northern counterparts, whereas Vajgach animals exceeded NS, WS and BSi ones by respiration at P < 0.05. The factor "population" affected mussel respiration in the separate age classes: 2, 4, 5, 6 and 7 y (P < 0.05, Kruskal-Wallis test), whereas at ages 1, 3 and older than 7 y the difference between populations was below significance (Fig. 3b).

Because age classes in Vajgach sample were represented by too



Figure 3. Respiration rates of mussels from studied populations—all age classes combined together (a) and in different age classes (b). NS, North Sea; BSi, Barents Sea; innermost (sheltered) part of the bay, BSo, Barents Sea; outer (open) part of the bay, WS, White Sea; Data are mean \pm SE, evaluated at 5°C.

few specimens this population was not included in the analysis of age influence on respiration. Age effects on mussel respiration rates were significant at P = 0.026, P = 0.047, P = 0.004 and P = 0.010 (Kruskal-Wallis test) for BSi, BSo, NS and WS populations, respectively (Fig. 3b). The shape of the curves describing the age dependence of respiration rates in mussels was similar for NS and WS molluscs. In these groups respiration rates were low at young age (0–1-y-old) followed by a significant increase in 2-y-old specimens. Older mussels were characterized by a gradual decrease of respiration with age, with constant rates in age classes 3–5 in both WS and NS molluscs. The oldest (10–11-y-old) specimens from the NS displayed insignificantly higher respiration rates than 6–9-y-old animals from that same site. However, the sample size was too small for meaningful statistical analyses.

The respiration rate of the youngest mussels in the BSi group (3-y-old) was somewhat, but nonsignificantly, lower than that of 4-y-old specimens, which displayed the highest respiration rates in this population. A rapid 2-fold decrease in respiration rate was recorded between age classes 4 and 6 followed by a gradual decline to the lowest values seen in 15-y-old specimens.

The age range of mussels from the BSo population was much narrower than that of the other populations and included only age classes 4–8 y. Animals older than 8 y were never found on the BSo site. On the other hand, young specimens (0–3-y-old) were too small to be included in the experiments (mean shell length of 3-y-olds from BSo was 6.1 mm). The respiration rate of BSo mussels was similar in all age classes

Enzyme Activities

CS activity in gill tissue of *M. edulis* varied from 2.15–8.24 U g^{-1} wet tissue wt, whereas COX activity was in the range 0.44–1.65 U g^{-1} wet tissue wt. The activity of both enzymes appeared positively correlated (Spearman R = 0.517, *n* = 125, *P* < 0.001) (Fig. 4). Size effects on the activity of citrate synthase and cytochrome C oxidase were tested using regression (enzyme activity vs. body mass) analyses in separate age groups of different populations. No significant trend was found for either CS or COX.

Age of the mussels had no influence on either CS or COX activities (Kruskal-Wallis test) (Fig. 5a). The factor "population" significantly affected the activity of both enzymes (ANOVA, P < 0.01 for CS and P < 0.001 for COX) resulting in a decrease in activity in the order NS > WS > BSi \ge BSo (Fig. 5b). NS mussels differed from both Barents Sea populations (P < 0.05, Tukey HSD



Figure 4. Relationship between cytochrome C oxidase and citrate synthese activities in mussels analyzed at 25° C.



Figure 5. The effect of age (a) and population (b) on cytochrome C oxidase and citrate synthase activities in mussels (enzyme activities analyzed at 25° C).

test) with respect to COX and from BSi (P < 0.05, Tukey HSD test) with respect to CS activities.

DISCUSSION

Growth patterns and maximal size observed in the NS and WS populations are typical for mussels from intertidal habitats of the respective areas (see for comparison, for the North Sea: Craeymeersch et al. 1986; Munch-Petersen & Kristensen 2001, for the White Sea: Savilov 1953, Maximovich 1989). On the exposed rocky shore (BSo) mussels colonize crevices in the rocks, where they are protected from strong wave action. Maximal size of mussels in this habitat is obviously limited by the sheltered space available, because animals sticking out from crevices are mechanically removed by waves and winter ice. Strong hydrodynamic action on open shores provide better conditions for growth of mussels from different species than sheltered bays, however, in extreme cases growth on exposed habitats is inhibited and longevity is reduced (McQuaid & Lindsay 2000, Steffani & Branch 2003). Growth of mussels from the BSo population is similar to that of their conspecifics from the sheltered BSi population until the animals reach about 20-mm shell size at 5-6 y. Older BSo animals grow significantly slower than BSi mussels and have only 2 y of further life expectancy. Thus, maximum size and longevity of mussels from the exposed intertidal of the Barents Sea are likely determined by wave action and firmly limited to a maximal size of 30-35 mm reached after 8 y.

In contrast, animals from BSi do not seem to be limited by any mechanical factor and reach maximal old age and maximal attainable size among all studied populations. Although before 3–4 y of age they grow slower than NS and WS mussels with smaller annual growth increments, they keep growing by about 5–6-mm per year until they are about 13-y-old and, eventually, outgrow and outlive mussels from all other populations of this study.

NS mussels exceeded all other populations in shell size within each age class. This difference is grounded in a significant distinction in body size reached by the end of their first growth season in all four populations. *Mytilus* spat in the NS had grown to a mean size of 12.9 mm by the beginning of winter, whereas newly settled mussels in the WS, BSi and BSo attained on average 1.1, 0.81 and 0.60 mm during their first growth season. This parameter (the size of the first ring) depends on two factors: growth rate and duration of the growth season. In the North Sea (at Helgoland, see Sprung, 1983) *Mytilus* settlement starts already in midMay resulting in a 4–5 mo long initial growth season for the spat in a relatively warm sea. In the White Sea and the Barents Sea mussels spat settles in August and even later, leaving not more than 1.5–2 mo for growth before seasonal cooling starts.

According to Bergmann's rule (originally elaborated for mammals and birds, Ray 1960) animals tend to increase their average body size with increasing latitude. Among Northern hemisphere aquatic ectotherms following this rule are fishes Squalus mitsukurii (Taniuchi et al. 1993), and the gastropod mollusc Acanthina punctulata (Gianniny & Geary 1992). Some weaker but significant trends to grow bigger at higher latitudes are recorded for the giant scallop Placopecten magellanicus (MacDonald & Thompson 1988) and the deep-sea gastropod Troschelia berniciensis (Olabarria & Thurston 2003). There are however numerous deviations from this rule (e.g., Gilbert 1973, Selin et al. 1991, Duchesne & Magnan 1997, Garvey & Marschall 2003). The largest specimens of mussels found in our samples from the NS and BSi populations were 60.0 and 71.4 mm length (4.32 and 4.74 g wet tissue weight), respectively. Although mussels from the northern population (BSi) in our study reach the biggest shell size, they attain only similar maximal soft body masses as NS mussels. Therefore, our data do not support Bergmann's rule as well as the expectations of slower growth and longer life of mussels from Arctic compared with temperate populations.

Age effects on respiration rates of mussels were studied in four different populations over a wide age range from 0-15 y. In all populations a similar pattern was observed, namely, low respiration rates in the youngest specimens followed by a rapid increase and then a gradual decline to nearly constant and similar values in the oldest specimens at each site. Initial low respiration values may relate to sexual immaturity of the young animals. It has been shown (Maximovich 1985) that M. edulis in the White and the Barents Seas attain sexual maturity only beyond 15-20 mm shell length (50-100 mg wet tissue weight). 2-y-old mussels from the WS population included in the analysis displayed 160-340-mg tissue wet weight, whereas 1-y-old mussels ranged between 40 and 60 mg. The fact that 2-y-olds were already mature, whereas 1-yolds were immature can explain the difference in respiration rates between mussels of these two age classes. According to Sprung (1983), mussels from Helgoland become sexually mature after 1 or 2 y, which explains low respiration rates in 0-1-y-old specimens from the NS. The youngest mussels (3 and 4-y-old) studied in both Barents Sea populations were mature and displayed high respiration rates.

The age-related pattern of respiration rates is common among all four studied populations. Sexual maturation is accompanied by an increase of weight specific respiration, which is followed by a more or less pronounced decrease of respiration at older age. It is interesting that despite the almost 2-fold difference in maximum lifespan observed in the studied populations (8 and 15 y in BSo and BSi, respectively), the age window of "metabolically most active" mussels is the same in all populations (from the age of sexual maturity to 6-7 y) (Fig. 3b).

A general decrease of weight specific metabolic rate in the course of ageing is reported for homeotherms and insects (see for review McCarter 1995), however, with few exceptions (O'Connor et al. 2002). Data on age-dependence of metabolic rate in infinitely growing species are controversial. Mere age effects on respiration rate (not linked to the influence of body size) were reported for bivalves Crenomytilus grayanus (Zolotarev & Ryabushko 1977), Argopecten irradians irradians (Bricelj et al. 1987), Mytilus edulis (Sukhotin & Pörtner 2001) and fish Cichlasoma nigrofasciatum (Fidhiany & Winckler 1998). However, in other studies this effect was poor or not seen at all (Pérez Camacho et al. 2000, Sukhotin et al. 2002, 2003). This study shows that age effects on metabolic rate of mussels are not straight forward (the older the animal, the lower the metabolic rate). There can be periods with a strong effect of age on respiration (e.g., an increase after maturation or a rapid decrease after 6-7 y of age) and also time intervals when metabolism is virtually independent of age (e.g., in the most metabolically active and also in the oldest specimens). Therefore, comparisons of selected age classes in latitudinal comparisons, seeking for an effect of environmental temperature on metabolic rates may lead to erroneous interpretations. Further, our data suggest that the agerelated decline in respiration is more pronounced in cold-adapted subArctic animals (BS and WS) than in North Sea mussels. Moreover, in warm-acclimated (summer) animals (Sukhotin et al. 2002; 2003) the age effect may not appear as pronounced as in late autumn (this study) and winter.

Respiration rates of mussels from the investigated populations are indicative of metabolic cold compensation in Mytilus edulis from Northern latitudes. This compensation of respiratory capacity in cold adapted ectotherms from the Northern hemisphere is achieved by an increase of mitochondrial density or inner membrane surface area as well as mitochondrial capacity (Tschischka et al. 2000, Sommer & Pörtner 2002, 2004). Mussels from intermediate reproductive age classes from the more northern populations had higher specific respiration rates than those from the North Sea. By contrast, old and presumably also very young mussels had lower and uniform respiration rates in all populations so that population differences were abolished in the old animals (Fig. 3b). In other words, cold adaptation, specifically latitudinal differences in metabolic rates according to different temperatures manifests especially in the most metabolically active specimens, possibly because of active somatic growth and substantial reproductive effort, which are costly in terms of assimilated energy. When combined, both findings support the view that in the Northern Mytilus populations lifetime energy expenses peak early in life to support reproductive output in young animals, whereas metabolic activity declines rapidly thereafter. This may be an adaptation to the harsh environmental conditions and may also reflect an age-related decrease of energy demands for somatic growth and reproduction, until a baseline level of energy turnover is reached as required for maintenance that allows no further reduction in the old animal.

Weight specific activities of metabolic enzymes as citrate synthase and cytochrome C oxidase often vary between warm and cold adapted mollusks or between summer and winter specimens in one and the same population. Interestingly, whole animal respiration in our study did not follow the same trend as the mitochondrial key enzymes in gills. Enzyme activities in gills were highest in the North Sea population (25°C assay temperature) but whole animal respiration at 5°C was lower at Helgoland than in WS and BS animals. Higher enzyme activities at low whole animal respiration rate would suggest higher mitochondrial densities or capacities in gills of the warmer North Sea animals despite low respiration rate measured at 5°C. This apparent contradiction might suggest that the metabolic requirements in gills vary independently from those of the whole animal. It appears conceivable that food demand and associated gill activity are high at the higher temperatures of the North Sea such that gill metabolic capacity is set high. Moreover, according to the temperature regime seen at Helgoland roads (Wiltshire & Manly 2004: 3°C to 20°C, mean $T = 9^{\circ}C$) the temperature applied during respiration analyses is low for Helgoland indicating that metabolic rate was measured at the low end and enzyme capacities were analyzed beyond the high end of the thermal window. Future analyses should compare mussel metabolism and enzyme activities at the same and within the range of habitat temperatures.

Aerobic enzyme capacities in other invertebrates have been found to vary in line with the cost of cold eurythermy hypothesis (Pörtner et al. 2000, Pörtner 2004). Among scallops, COX activity ranged significantly higher in *Aequipecten opercularis* from the warmer Irish Sea than in cold adapted stenothermal *Adamussium colbecki* from the high Antarctic, whereas CS activities were similar in both species (Philipp et al. 2006). In contrast, cytochrome C oxidase (COX) activity was 10-times higher during summer in cold adapted eurythermal lugworms *Arenicola marina* from the White Sea at 6°C than in North Sea specimens measured at 11°C (Sommer & Pörtner 2002). Seasonal influences may modulate this picture. Sommer and Pörtner (2004) and Keller et al. (2004) found that mitochondrial respiratory capacity was significantly higher in prespawning and lower in postspawning summer animals than in winter. Concomitantly, CS activities in North Sea lugworm tissue during summer versus winter were equal prespawning or lower postspawning. A seasonal comparison of the related horse mussels, *Modiolus modiolus*, (Mytilidae) from shallow subtidal environment (10-m depth) of New Hampshire, Isle of Shoals, United States (Lesser & Kruse 2004) found somewhat but significantly higher respiration in summer than winter animals, however, again with CS concentration per g tissue significantly increased in the winter. This may reflect reduced whole animal respiration rates caused by metabolic depression in winter, whereas enhanced CS levels and COX activities during winter (Lesser & Kruse 2004) are in line with elevated capacities of mitochondria in seasonal cold and may also meet additional metabolic requirements on top of supporting mitochondrial capacity (Pörtner 2002b).

In conclusion, the compensatory increase of metabolic rate in cold adapted Northern hemisphere mussels manifests especially in the most metabolically active individuals and is less apparent at advanced age. Our data suggest compensation for latitudinal cold during summer in blue mussel *Mytilus edulis* Northern populations. Cold compensation is mostly reflected in active whole animal respiration rates, in line with the cold eurythermy hypothesis (cf. Pörtner et al. 2000, Sommer & Pörtner 2004). According to our data, growth and longevity in blue mussels relate to temperature variability within the climatic range covered in this study as well as to local environmental factors. Similarity of maximal life spans of mussels from latitudinally separated populations can be explained by similar metabolic rates at ambient temperature caused by metabolic cold compensation in animals at high Northern latitudes.

ACKNOWLEDGMENTS

The authors thank Dr. P. Strelkov for invaluable help during field work at the Barents Sea. This study was supported by Hanse-Wissenschaftskolleg (Delmenhorst, Germany), which provided a fellowship to AAS.

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