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RESEARCH ARTICLE

TOWARDS THE CALIBRATION OF AN ENVIRONMENTAL BIORECORDER

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Abstract: Bivalve molluscs fulfil the prerequisites of environmental archives because they grow by periodic accretion. Owing to its extremely long life span and wide distribution on the continental shelves on both sides of the North Atlantic Ocean, the bivalve, *Arctica islandica* is a prospective model organism for studies of climate change effects in Northern boreal marine systems. Shells of *A. islandica* provide a calcareous archive of lifetime growth history and of the environmental conditions an individual animal experienced over lifetime. For the understanding of the *Arctica* shell archive sound knowledge of species ecology and ecophysiology is needed. Aerobic metabolic rate in bivalves changes with temperature and salinity and presumably impacts animals life history and performance. the present study compared lifetime respiration rates of five *Arctica* populations with different temperature and salinity background to understand the effect of both environmental forcing factors on animal growth and metabolic performance. The study built a model which, on the one hand, calibrated and evaluated the metabolic basis of shell growth and on the other hand, allow to model individual lifetime energy budgets as well as to calculate population energy budgets. This would be one way to couple individual life history and population dynamics to large-scale oceanographic models. Samples were collected from five sites, Norwegian Sea, Kattegat, White Sea, North Sea and Baltic Sea, covering a natural temperature and salinity gradient of 4-10°C and 25-34, respectively. Respiration rates are measured at ambient temperature and salinity as well as 5°C above ambient temperature using a multi channel intermittent flow-system equipped with oxygen microoptodes. Multiple linear regression is used to analyze the relation between respiration rate, temperature, salinity, body mass and individual age. This study was a first approach to model respiration of all 5 populations and showed mass specific metabolic activity of *A. islandica* is significantly higher in higher temperature.

Keywords: Respiration, bivalve, bio-recorder, *A.islandica*, environment

Introduction

Knowledge of past environmental variability is important for understanding the present and forecasting future environmental trends (deMenocal, 2001). Observational records of environmental data are spatiotemporally incomplete and extremely scarce prior to AD 1860 (Hurrell and Trenberth, 1999; Smith and Reynolds, 2003). Large scale environmental variability can be well represented by integrating data from a limited number of geographically scattered indicators or 'proxies' of past climate (Bradley, 1999). Proxy data complement and significantly extend such records in space and time (Jones *et al*,.2001). There are two basic types of proxies: natural (biological, physical) and documentary (written) archives. Tree rings (Briffa *et al.*, 1990; Schweingruber *et al*,. 1991; Grudd *et al.,* 2002) and stalagmites (Frisia *et al.,* 2003; Niggemann *et a.*,2003) have for example permitted reconstructions of summer air temperature and precipitation over the past centuries to millennia. However, these records cannot be used to interpret marine temperatures at the same latitude. Fossil tests of foraminifera recovered from ocean sediment cores have been used as environmental archives to study changes in the past ocean climate at century to millennial scales (Weidman *et al.,* 1994; Williams and Fairbanks, 1979; Jiang *et al.,*

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2001). The temporal resolution of laminated, microfossil-bearing sediments, however, is generally coarser than decades. In addition, marine microfossils cannot provide annually resolved long-term records of seasonal environmental variables because the life span of the organisms is too short (Weidman *et al.,* 1994).

Periodic accretions of biological hard parts produces distinct growth patterns, which form in time intervals of near equal duration and are referred to as "growth increments". These hard parts archive environmental information as both physical and chemical properties of the growth increments (Schöne *et al,*. 2003). They are formed by periodic accretion and preserve the environmental information during growth, thus building the environmental 'bio-archive' (Schöne *et al.,* 2002, 2003). Most bivalve molluscs fulfil the prerequisites of environmental archives because they grow by periodic accretion (e.g. Pannella and MacClintock , 1968; Clark, 1975) and record the environmental information during growth (Epstein *et al.,* 1953; Jones *et al.,*1989). The bivalve *A. islandica* regularly accretes carbonate to its shell, and demonstrates annual growth breaks (Jones, 1983), which allow assigning precise calendar dates to each part of the shell. This kind of fast-growing biogenic material is particularly suitable for the reconstruction of climate variability (Ortlieb *et al.,* 2003). Thus, *A islandica* has potential to function as the 'Tree of the North Atlantic shelf' (Thompson and Jones, 1977). Shells of *A. islandica* can be used to determine the annual bottom water temperature to fill the existing gaps of instrumental recordings (e.g. Levitus *et al.,* 2000; Schöne *et al,*. 2005) and interannual variability during past centuries (Weidman *et al.,* 1994; Marsh *et al.,* 1999; Schöne *et al.,* 2003). Despite many papers dealing with the life history traits, sclerochronology (the marine equivalent of dendrochronology in organisms hard structures), and isotope geochemistry of *A islandica* (Cargnelli *et al.,* 1999), the full capabilities of this species for an ideal biorecorder and/or as an environmental proxy, have not yet been fully demonstrated (Schöne *et al.,* 2002, 2003, 2004). The use of the bivalve, *A.islandica*, as an environmental biorecorder raises the necessity of more regional calibration over the entire distribution range. Especially, more precise knowledge of *A. islandica* physiology, growth and complete energy budget from different environmental settings including low and high salinity and warm and cold habitats are required. The Ocean quahog Arctica islandica inhabits the continental shelves and slopes on both sides of the North Atlantic Ocean, spanning a wide depth (4 – 482 m) and latitudinal range (Cape Hatteras ~35°N to the Barents Sea ~70°N) (Nicol, 1951; Thompson *et al.,* 1980 a,b); Murawski *et al.,* 1982; Jones, 1983). *A. islandica* tolerates between 0 and 16°C and has an optimal temperature range between 6 and 16°C (Mann, 1982; Cargnelli *et al*., 1999). Quahog maximum recorded age is close to 400 years and individuals over 100 years are abundantly found in the North Atlantic (Schöne *et al*., 2004, 2005c; Strahl *et al.,* 2007). Therefore, the main aim of this paper is to establish models of respiration vs temperature, body size and age of the long lived bivalve *A. islandica* from a range of populations living under different environmental conditions (Norwegian Sea, Kattegat, North Sea, White and Baltic Sea).

Materials and Methods

In 2006, bivalve *Arctica islandica* were collected from five different geographic locations covering a temperature and salinity gradient of 4 - 10°C and 25 - 34, respectively (Table 1).

Table 1. Location, experimental temperature (HT: mean annual habitat temperature; ET: Elevated temperature) and sample size for respiration and growth measurement for each population

Population	Location	Salinity	Temperatures (°C)		Samples size	
			HT	ET	HT	ET
Norwegian Sea	69°39´N 18°57´E	33	4	9	35	23
Kattegat	56°10´N11°48´E	31	8	13	29	16
White Sea	66°18´N 33°38´E	25	4	9	12	12
Baltic Sea	54°32´N10°42´ E	25	10	15	28	24
North Sea	54°09´N 07°47´E	31	10	15	8	10

All animals were transported alive to the Alfred Wegener Institute (AWI, Germany) and were kept for 4 - 6 weeks at mean annual habitat temperature for the respective sampling site. Animals of each population were assigned to two different groups. The first subsample (HT) was maintained at mean annual habitat temperature, while the second subsample (ET) was stepwise acclimated to 5°C above the mean habitat temperature (Table 1). Acclimated bivalves were kept for at least four weeks at the elevated temperatures prior to measurements.

Oxygen consumption was taken as a proxy of standard (resting) metabolism. Bivalves were allowed to accommodate to the respiration chambers overnight prior to measurement. Respiration chambers were small Perspex cylinders with a movable lid to adjust chamber volume between 150 – 600 ml to animal size (Heilmayer and Brey, 2003). Experimental temperature was maintained stable (± 0.5°C) by placing the chambers in a water bath within a water jacketed container in which temperature was controlled by a thermocirculator (Julabo FP 40). Three respiration chambers with one animal each (similar size) and a control chamber (without animal) were measured simultaneously in every experiment. Oxygen content in the chambers was monitored continuously with oxygen microoptodes connected to a MICROX TX 3 array (PreSens, Neuweiler, Germany). After the measurements, animals were dissected immediately, and soft tissue wet mass (WM) was determined to 0.001g precision after carefully blotting it dry on paper. The soft tissue was dried at 68°C for at least 48h to obtain dry mass (DM). Dried tissues were combusted at 500°C 24h and ash free dry mass (AFDM) was calculated. Individual age was inferred from shell growth bands.

Calculation of metabolic rates: Standard metabolic rates (SMR, µmol O_2 ind^{-1} h^{-1}) were determined from the slope of the oxygen saturation curve after subtraction of the microbial oxygen demand, determined in the blank chamber. Percent O_2 saturation was transformed to micromoles of dissolved oxygen consumption using known values of oxygen solubility (α_{O_2}, µmol dm^{-3}: Benson and Krause, 1984) and converted to microgram O_2 by 32.324 mmol O_2 = 1000 µg O_2 according to:

$$SMR = \frac{satt_o}{satt_{60}} \cdot a_{O_2} \cdot V_{chamber} \quad (1)$$

where $V_{Chamber}$ is the volume of respiration chamber and tubing (dm^3), sat t_0 is the oxygen saturation (%) at the beginning of the experiment and sat t_{60} is the oxygen saturation (%) after 60 min as calculated from linear regression. Metabolic rates were normalized to AFDM by

$$SMR = a \cdot AFDM^b \quad (2)$$

where a is constant/intercept and b the scaling exponent. The model was fitted by linear regression after logarithmic transformation of both variables. Individual mass-specific respiration rates (MSR_{ind}) were calculated according to:

$$MSR_{ind} = \frac{VO_2}{AFDM} \quad (3)$$

Age determination*:* From each bivalve, left valves were cleaned with warm NaOCl (5%) solution, rinsed with demineralized water and dried at 60 °C for 12 h. Each valve was embedded in epoxy resin (Wiko liquid metal FLM-S25), sectioned along the axis of strongest shell growth (LSG) and dried overnight. Smaller valves (< 50mm) were mounted on a plexiglass block for easier handling during the preparation process. Big valves (LSG ≥ 50mm) were cut with a table diamond saw (FK/E PROXXON-28070). Smaller ones were cut with a Buehler low-speed diamond saw. Cross-sections were ground on a Buehler low and high speed Grinder and Polisher, using grits of P400, P1200, P2400 and P4000 grade and subsequently polished using a polycrystalline diamond suspension of 1 and 0.1 µm. The polished shell section was immersed in Mutvei's solution for 20 min at 37°C, following the protocol of Schöne et al. (2005).

Statistical analysis: Relationships between metabolism, temperature and age, as well as differences between populations were evaluated by analysis of variance (ANOVA) and analysis of covariance (ANCOVA). Mahalanobis Jackknife distances (Barnett and Lewis, 1994) was used to identify multivariate outliers to be excluded from further analysis. All analyses were carried out using the statistical package JMP by SAS Inc.

Results

Table 2 summarizes the basic information on the 197 quahogs from the five populations. The number of data available for analysis reduced to 193 after *Mahalanobis* analysis identified 4 outliers. The North Sea population was outstanding because of the lack of small/young animals below 3.7 g and 33y and no detectable nemertean infestation (Table 2) .

Table 2. Total number of measured *A. islandica* in the respiration experiments. M. grossa = infestation with Nemertean *Malacobdella grossa*. n= number of sample, Nd: not determined

Population	Exp. temp (°C)	n	Mass range (g AFDM)	Age range (yrs)	M. grossa (%)
Norwegian Sea	4	35	0.35 – 12.01	6 – 93	68.57
	9	23	0.04 – 12.01	4 – 90	56.52
Kattegat	8	29	1.11 – 2.95	8 – 71	43.75
	13	16	0.91 – 2.95	11 – 45	41.38
White Sea	4	12	0.03 – 0.38	3 – 31	41.67
	9	12	0.12 – 0.42	12 – 53	50.0
Baltic Sea	10	28	0.06 – 1.87	4 – 29	10.71
	15	24	0.08 – 1.42	8-40	8.33
North Sea	10	8	5.04 –7.34	33 –98	0.00
	15	10	3.71 – 6.96	38 –94	0.00

The salinity regime (euhaline vs polyhaline) did not affect metabolic rate, as indicated by a full interaction ANCOVA of ln(MSR) versus ln(M) and the parameter euhaline (yes = Norwegian Sea, Kattegat, North Sea, no = Balic Sea, White Sea).

The initial full factorial interaction ANCOVA model of ln(MSR) versus ln(M) and site detected significant differences (body mass x site; temperature x site), whereas nemertenan infestation (yes/no), and salinity indicated no significant effects of these parameters on mass specific respiration. In addition, ANOVA of the residuals of MSR versus age indicated no significant effect (p=0.11) on mass specific respiration.

Preliminary analysis of the data set indicated that neither the salinity regime (euhaline vs polyhaline) nor nemertenan infestation (yes/no) significantly affected mass specific respiration MSR. The subsequent full factorial interaction ANCOVA of ln(MSR) versus ln(M), 1/T, and site resulted in the model. ln(MSR) = 22.156 - 0.224 * ln(M) - 5831.651 / T + b3 * Site + b4 * Site * ln(M) + b5 * Site / T. (µmol O_2 h^{-1} g^{-1}; g AFDM; K; n= 193, r^2 =0.656; P<0.0001).

Table 3 shows the site specific values of b3, b4 and b5. Fig 2 visualizes the effects of body mass (negative) and temperature (positive) on MSR. The residuals of the model are distributed randomly (Fig.3), i.e. the model is unbiased. Based on the model, Q10 values (5°C – 15°C) amount to 4.48 for North Sea, 2.63 for Norwegian Sea, 2.34 for White Sea, 1.20 for Kattegat and 1.15 for Baltic Sea respectively.

Table 3. Parameter values of the multiple linear prediction model
ln(MSR) = 22.156 - 0.224 * ln(M) - 5831.651 / T + b3 * Site + b4 * Site * ln(M) + b5 * Site / T (µmol O_2 h^{-1} g^{-1}; g AFDM; K; n= 193, r2 =0.656; P<0.0001).

Population	b3	b4	b5
Norwegian Sea	7.091	0.144	-1923.777
Kattegat	-14.984	0.176	4339.745
White Sea	2.947	-0.483	-967.735
Baltic Sea	-16.272	-0.026	4732.580
North Sea	21.218	0.190	-6180.815

Discussion

Age effect on metabolism: Results show that MSR of long lived *A. islandica* does not correlated with age (p=0.11 ANCOVA). This result contrasts a study with shorter lived *M. edulis* by Sukhotin and Pörtner (2001) where respiration rates were decreased with age. Data analyzing physiological indicators of fitness and senescence in the extremely long lived A. islandica population from Iceland indicated parameters like the mitochondrial marker enzyme CS to be maintained on constant past maturation levels in animals over 33 and up to at least 200 years (Abele *et al.*, 2008). This and the extremely slow accumulation of fluorescent age markers lipofuscin (Strahl *et al.*, 2007) indicated that aging in long lived animals might be significantly slowed and even imperceptible and in this contrasting findings from shorter lived species like the blue mussel. However, the results from different studies are controversial (e.g. Sukhotin *et al.*, 2002), present data supports, age influences respiration rate in bivalves may be only indirectly, due to the age-related gain in body size (e.g. Philipp *et al.*, 2006). The present results concluded that MSR in long-lived bivalves like *A. islandica* do not change with age.

Temperature and mass effect on metabolism: The respiration model in Fig 1 show mass specific metabolic rate of *A. islandica* was significantly higher at higher temperature (Fig. 1).

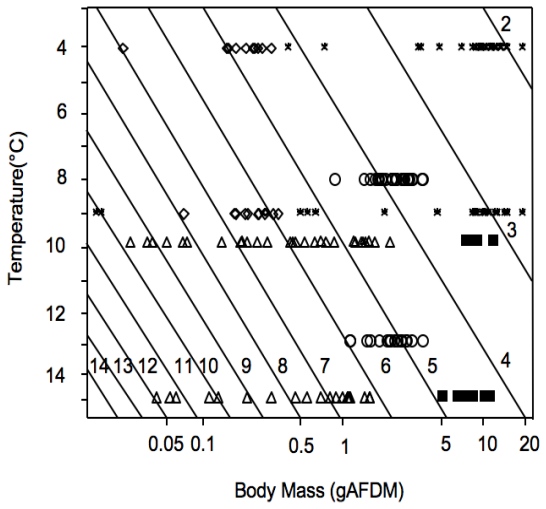

Fig. 1. Visualization of the relationship between MSR (µmol O_2 h^{-1} g^{-1} AFDM), body mass (gAFDM) and temperature (°C) as described by the multiple linear respiration model (table 3), but with site effects neglected. Superimposed are the body mass / temperature data of all MSR measurements. Triangles: Baltic Sea, diamonds: White Sea, squares: North Sea, stars: Norwegian Sea, circles: Kattegat

Temperature is assumed to be the most important environmental modulator of poikilotherm metabolism (Thompson, 1984), so that the metabolism in bivalves can be best described by an Arrhenius model (Peck and Conway, 2000). Index of the dependence of the physiological rate on temperature, Q_{10}, show a four- fold effect of temperature in North Sea, whereas Norwegian and White Sea animals displayed a temperature dependent increase of MSR by the two-fold, and Kattegat and Baltic Sea animals MSR did not change in response to warming. It is assumed that the acute temperature response of the rate of oxygen consumption by North Sea animals is more likely due to its higher body mass of 3-7g AFDM (see Bayne et al., 1976). Lower Q_{10} values (1. 15-1.20) in Baltic Sea, 0.5-2 g AFDM and Kattegat, 1-3g AFDM correlated with comparatively lower body mass (Bayne et al. 1976) and indicated temperature independency. However, the White Sea animals, had lower body mass (0.03-0.42) and a Q_{10} of 2, so the size effect may be only one out of several factors modulating the respiratory response to changing temperature. There is a general tendency when comparing animals adapted to narrow windows of cold temperatures but with polyhaline salinity, to respond more sensitive to environmental change (Bayne, 1971). Mass specific respiration of Arctica islandica follows the well known rule of negative correlation with mass with a common relationship for all investigated populations. The overall exponent between mass (AFDM) and specific respiration (0.224) show in line with mussel exponent scale (Bayne, 1971; Vahl, 1978). The temperature effect on MSR is however different and depends on climatic adaptation and animal mass (Bayne, 1975; Sukhotin et al. 2002).

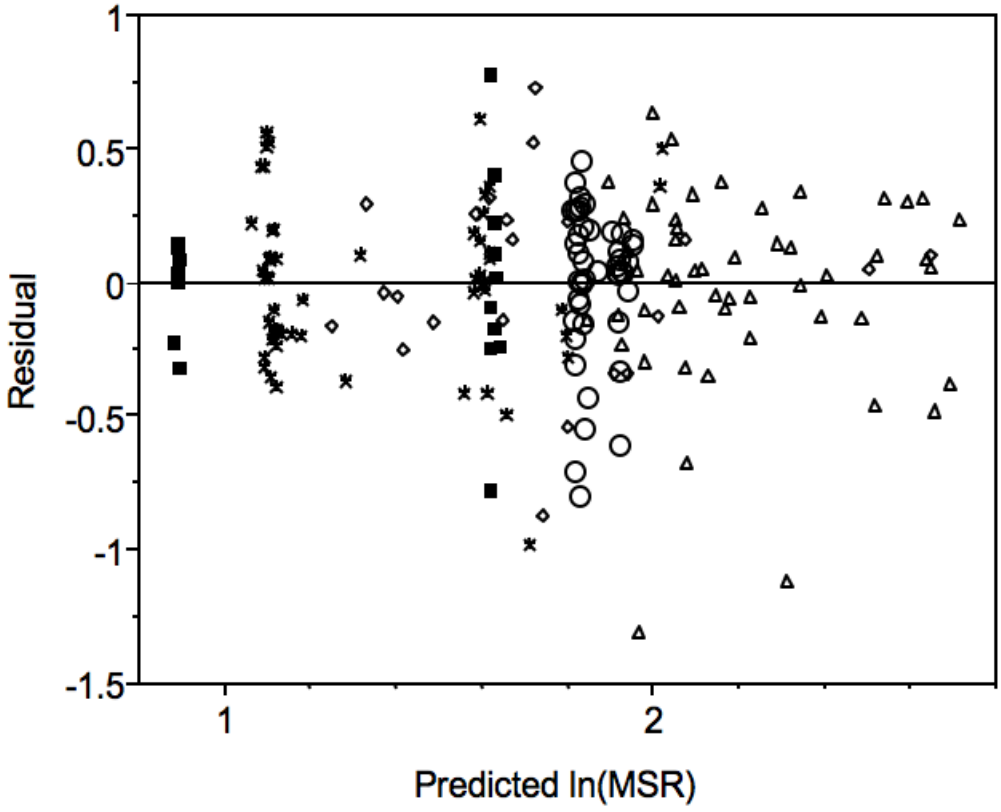

Fig. 2. Residual plot (residual versus predicted values) of the multiple linear model (Table 3). Triangles: Baltic Sea, diamonds: White Sea, squares: North Sea, stars: Norwegian Sea, circles: Kattegat

Conclusion

Bivalves are sensitive environmental bio-indicators. They are abundantly available, easy to obtain and to measure, and can be extremely long lived. In addition, bivalve molluscs offer several advantages over other environmental reconstructions. Therefore the calibration of bivalve is required to model physiological aspects. Present model describes the respiration of *A. islandica* behaves within the underlaying mechanism of temperature and mass. Thus, it can be a reference model for *Arctica* respiration, which depends on regional differences and environmental factors (e.g. temperature). In this research, the metabolic rate and its consequences for ocean quahog *A. islandica* was quantified in the context of their environment (temperature, salinity), available mass range and age between populations. Although it is very difficult to maintain the similar size range from such a wide range of population. Nevertheless, the present study detected, mass specific respiration rate significantly increase with temperature and do not correlated with age while decrease with mass. The principle might be applicable for calibrating the entire bivalve, from tropical to temperate species. The application of bivalve as indicators of coastal zone management and climate change for the south west Bangladesh can be studied. Additionally, it could be applicable to investigate how coastal structures affect (present and predicting future) bio-diversity.

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