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Metabolic rate and growth in the temperate bivalve *Mercenaria mercenaria* at a biogeographical limit, from the English Channel

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Metabolism and growth rate of the hard clam, Mercenaria mercenaria*, were investigated in a population invasive to Southampton Water, southern England. An individual metabolic model expressed as a function of soft tissue dry mass was fitted to data of 18 individuals* ($\log (VO_2) = -1.952 + 0.543 \bullet \log (DM)$; $F_{1,16} = 201.18$, $P < 0.001$, $r^2 = 0.926$). *A von Bertalanffy growth function was fitted to 227 size-at-age data pairs of 18 individuals* ($H_t = 80.13 \bullet (1 - e^{-0.149 \bullet (t - 0.542)})$; $r^2 = 0.927$). *Individual age-specific somatic production was calculated, demonstrating increase with age to a maximum of 3.88 kJ* y^{-1} *at ten years old followed by decrease, and individual age-specific annual respiration was calculated, demonstrating asymptotic increase with age to 231.37 kJ* y^{-1} *at 30 years old. Results found here lie within the physiological tolerances reported across the biogeographical range, suggesting that the species' biogeographical limitation in the UK to Southampton Water results from ecological rather than physiological factors.*

Keywords: respiration, sclerochronology, production, hard clam, northern quahog

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INTRODUCTION

The northern quahog, *Mercenaria mercenaria* (Linnaeus, 1758), occurs over a wide geographical range in North America, from the Bay of Chaleurs, Gulf of St Lawrence, south to the Florida Keys (Harte, 2001), surviving temperatures between 0 and 30°C (McHugh, 1984). Following introduction to England during the late 19th and early 20th Centuries a naturalized breeding population of *M. mercenaria* became established in Southampton Water (Harte, 2001). The population increased from the 1950s, possibly occupying the vacant niche left by the elimination of *Mya arenaria* by cold winters in 1947 and 1962/1963 (Mitchell, 1974). The elevation of estuarine temperatures by industrial and power station cooling water discharges and physiological adaptation to spawning at lower temperatures than populations in areas of origin (Mitchell, 1974), resulted in an increasing population that supported a fishery from the 1960s (Eno *et al.*, 1997).

Recently this fishery has become severely depleted (Eno *et al.*, 1997). Differences between the age–frequency distribution observed in the Southampton Water population and those in other study areas indicate that Southampton Water is a marginal habitat for the species (Fegley, 2001). Poor recruitment observed (Richardson & Walker, 1991) may result from large numbers of animals removed by the fishery and damage to the physical environment (Eno *et al.*, 1997), and/or from adverse environmental conditions, e.g. temperature effects (Loosanoff *et al.*, 1951; Loosanoff, 1959). The status of introduced populations in The Netherlands, Belgium and on the west coast of France is unknown (Fegley, 2001). Data on the physiological ecology of *M. mercenaria*, including metabolic rate and growth across the original North American biogeographical range, have been reviewed by Grizzle *et al.* (2001). Although ontogenetic growth models have been established across a wide latitudinal range in North America, indicating a latitudinal gradient of decreasing growth rate from south to north, no model has been constructed for the naturalized Southampton Water population. Additionally, allometric relationships have been established for *M. mercenaria* indicating increasing oxygen consumption rate with increasing body mass (Loveland & Chu, 1969), and with increasing temperature (Hibbert, 1977). Examination of growth and metabolic rates for the Southampton Water population at the edge of the biogeographical limits may elucidate evidence of the impact of adverse environmental conditions on *M. mercenaria*.

In this study functions for age-specific metabolic rate, growth and derived somatic production and respiration were calculated and compared with other findings from the literature to assess the contribution of physiological impairment to the observed biogeographical limit of *M. mercenaria* in the UK to Southampton Water.

MATERIALS AND METHODS

Sampling and maintenance

Mercenaria mercenaria were collected by local fishermen from onboard a small vessel, from the western shore of

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Southampton Water (50°51.7′N 001°22.7′W), with a small benthic dredge. After sampling, animals were immediately transported to the National Oceanography Centre, Southampton, where they were maintained in a recirculating aquarium at ambient salinities (31 – 35), temperature following seasonal changes (minimum 12; maximum 20°C), and a 12:12-hour dark/light cycle. They were fed a mixed diet of *Phaeodactylum tricornutum*, *Isochrysis galbana*, *Pavlova lutheri*, *Chaetoceros ceratosporum* and *Tetraselmis suecica* microalgal cultures *ad libitum* three times each week, until used in experiments.

Metabolic rate

Oxygen consumption rates of unfed (deprived of food for at least 3 days), unstressed and inactive animals were used as a proxy for standard metabolic rate as described by Bayne & Newell (1983). Measurements were taken at aquarium ambient temperature (19.5 ± 0.9°C). The largest size-range of animals available was used for sampling.

Oxygen content of water was assessed using oxygen micro-optodes connected to a Microx TX3 array (PreSens, Germany) and a flow-through system, modified from the intermittent flow system described by Heilmayer & Brey (2003). Oxygen microoptodes were used to record oxygen content of water flowing into and out of the respiration chambers at 30 second intervals. Individual metabolic rates (VO_2) were obtained by comparison with control chambers (no animals) (for details Heilmayer & Brey, 2003).

For size–mass relationships the shell height (H), the greatest distance from the umbo to the dorsal margin (Fritz, 2001), of each animal was measured to the nearest 0.1 mm using vernier callipers before animals were dissected, and soft tissue wet mass was weighed to the nearest mg. Soft tissue dry mass (DM) was calculated (using 1 mg soft tissue wet mass = 0.176 mg soft tissue dry mass (Brey, 2001)) and linear regression analysis was carried out on log-transformed data estimating constant a and height scaling exponent b of the size–mass allometric equation:

$$\log(DM) = a + b \bullet \log(H).$$

The VO_2 was expressed as a function of DM with a model fitted by linear regression analysis after logarithmic transformation of both variables:

$$\log(VO_2) = c = d \bullet \log(DM)$$

where c is constant and d is the mass scaling exponent.

Age and growth

Shell growth bands in bivalves result from seasonal oscillations in growth, but also from changes in food availability, spawning events or predation attempts. Identification and interpretation of annual growth bands in *M. mercenaria* were based on that described by Fritz (2001). Winter growth cessations were indicated by thick microgrowth increment boundaries in the outer shell layer microstructure associated with a V shaped notch in the outer layer, and with dark bands in the middle shell layer microstructure (see figure 2.12 in Fritz, 2001).

Valve preparation followed a method modified from that described by Schöne *et al.* (2005). Prior to analysis the shell was cleaned of organic matter with warm 5% NaOCl solution, rinsed with water and dried. A quick-drying metal epoxy resin (J-B KWIK) was applied to the axis of shell height, and allowed to dry overnight before cutting perpendicular to the annual growth lines with a FKS/E table saw (PROXXON MICROMOT), using a 0.7 mm thick diamond coated cutting disc. The section edge of the left valve was ground and polished using an Alpha dual speed grinder–polisher (Buehler) with 180, 400, 1000, 2400 and 4000 SiC grit, before the number of microscopically visible annual growth bands and correlating shell height were analysed using an SZX12 stereo microscope system with U-CMAD3 camera adapter and Color View I digital colour camera (Olympus), and analySIS 5.0 image-processing software (Olympus).

Valve preparation and growth band identification and analysis were conducted in the Sclerochronology Laboratory at the Alfred Wegener Institute (AWI, Germany). A von Bertalanffy growth function was fitted to the resulting size-at-age data pairs using a non-linear iterative Newton algorithm (Brey, 2001):

$$H_t = H_\infty \bullet (1 - e^{-K \bullet (t - t_o)})$$

where H_∞ is the mean asymptotic shell height in mm, K is the Brody growth coefficient, t the age in years and t_o the theoretical age in years at which shell height equals zero.

Somatic production and respiration

Individual age-specific somatic production (P_s) was calculated from the increment between consecutive age-classes in soft tissue dry mass, derived using the size–mass allometric relationship and von Bertalanffy growth function, and the conversion factor (C) 1 mg dry mass = 18.393 J (Brey, 2001):

$$P_s = (DM_{(t+1)} - DM_t) \bullet C$$

Individual age-specific respiration rate (R) was calculated from the average soft tissue dry mass over consecutive age-classes using the metabolic rate equation:

$$\ln(R) = x + y \bullet \ln(((DM_{(t-1)} + DM_t) \div 2) \bullet C)$$

derived from the size–mass allometric relationship, von Bertalanffy growth function, and using the constant x and mass scaling exponent y from the equation for mass-specific respiration rate:

$$\ln(VO_2/DM) = x + y \bullet \ln(DM)$$

calculated by linear regression analysis, where VO_2 is in J y^{-1} and DM is in J with oxygen consumed converted to energy using 1 ml O_2 = 20.1 J (Brey, 2001).

RESULTS

Metabolic rate

The range in shell height and soft tissue dry mass of the 18 animals used were from 14.7 to 92.2 mm and from 14 to 8692 mg, respectively. The allometric relationship of soft tissue dry mass in mg and shell height in mm in *Mercenaria*

mercenaria can be described by the linear model:

$$\log(\mathrm{DM}) = -2.800 + 3.315\bullet\log(\mathrm{H});$$
$$F_{1,16} = 1512.85,\ P < 0.001,\ r^2 = 0.990$$

The effect of soft tissue dry mass in mg on individual metabolic rate in ml O_2 h^{-1} can be described by the linear model (Figure 1):

$$\log(\mathrm{VO_2}) = -1.952 + 0.543\bullet\log(\mathrm{DM});$$
$$F_{1,16} = 201.18,\ P < 0.001,\ r^2 = 0.926$$

The DM range of organisms used corresponded to a VO_2 range from 0.06 to 2.62 ml O_2 h^{-1}.

Age and growth

A total of 227 size-at-age data pairs of 18 specimens were fitted best by the von Bertalanffy equation:

$$H_t = 80.13\bullet(1 - e^{-0.149\bullet(t-0.542)});$$
$$r^2 = 0.927\ \text{(Figure 2)}$$

The range of shell height of animals used was from 14.7 to 92.2 mm. The age range of animals used was from two to 30 years old.

Somatic production and respiration

Individual age-specific somatic production can be described by the equation:

$$P_s = (10\hat{}-2.800 + 3.315\bullet\log(80.13\bullet(1 - e^{-0.149\bullet((t+1)-0.542)}))) - 10\hat{}(-2.800 + 3.315\bullet\log(80.13\bullet(1 - e^{-0.149\bullet(t-0.542)})))) \bullet 18.393$$

and demonstrated increase to a maximum 3.88 kJ y^{-1} at an age of ten years, decreasing thereafter (Figure 3).

Mass-specific respiration rate can be described by the equation:

$$\ln(\mathrm{VO_2/DM}) = 6.004 - 0.457\bullet\ln(\mathrm{DM});$$
$$F_{1,16} = 142.51,\ P < 0.001,\ r^2 = 0.899$$

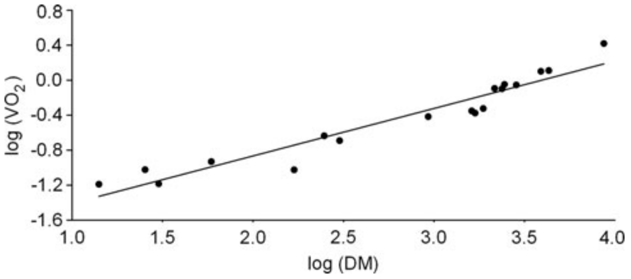

Fig. 1. Linear regression of log (rate of oxygen consumption) over log (dry mass) of *Mercenaria mercenaria* (N = 18) collected from a population in Southampton Water (England): log $(VO_2) = -1.952 + 0.543 \bullet$ log (DM); $F_{1,16} = 201.18$, $P < 0.001$, $r^2 = 0.926$, where VO_2 is the rate of oxygen consumption in mlO_2h^{-1} and DM is the dry mass in mg.

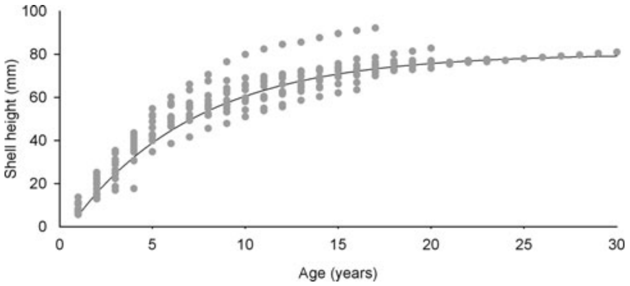

Fig. 2. Von Bertalanffy growth function fitted to 227 size-at-age data pairs of 18 *Mercenaria mercenaria* collected from a population in Southampton Water (England), calculated according to Brey (2001). Growth function parameters are: $H_\infty = 80.13$ mm, $K = 0.149$, $t_o = 0.542$; $r^2 = 0.927$, where H_∞ is the mean asymptotic shell height, K is the Brody growth coefficient and t_o is the theoretical age at which shell height equals zero.

and mean mass-specific respiration rate over the DM range was 5.65 J y^{-1} J^{-1}.

Individual age-specific respiration can therefore be described by the equation:

$$\ln(R) = 6.004 - 0.457\bullet\ln(((10\hat{}-2.800 + 3.315\bullet\log(80.13\bullet(1 - e^{-0.149\bullet((t-1)-0.542)}))) + 10\hat{}(-2.800 + 3.315\bullet\log(80.13\bullet(1 - e^{-0.149\bullet(t-0.542)})))) \div 2)\bullet 18.393)$$

and demonstrated asymptotic increase to 231.37 kJ y^{-1} at an age of 30 years (Figure 3).

DISCUSSION

The broad geographical range over which *Mercenaria mercenaria* occurs naturally in North America, and the broad 0 to 30°C temperature range which this corresponds to, indicate that this species is strongly eurythermal *sensu* Pörtner *et al.* (2005). Reported growth functions from across the species' biogeographical range demonstrate a latitudinal gradient of decreasing growth rate from south to north (Figure 4A), suggesting that temperature is the major cause of this variation. Mean annual growth of *M. mercenaria* has been shown to be highly correlated ($r = 0.88$) to mean annual water temperature (Jones *et al.*, 1989), and previous analysis has evaluated optimum temperature for shell growth as approximately 20°C, with shell growth ceasing below 9°C or

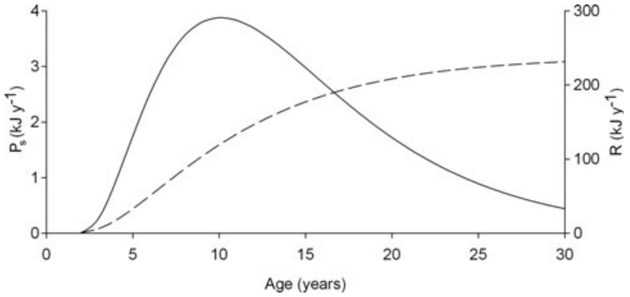

Fig. 3. Somatic production (solid line) and respiration (dashed line) at age of *Mercenaria mercenaria* from a population in Southampton Water (England), calculated according to Brey (2001).

above 31°C (Ansell, 1968). The strong resemblance of the growth function derived in this study to those across the biogeographical range indicates that growth in *M. mercenaria* in Southampton Water is not physiologically impaired. Composite indices of overall growth performance (e.g. log (K) + log (H_∞)) can be used to indirectly compare these non-linear growth patterns (Heilmayer *et al.*, 2004), and support this conclusion (Figure 4B). The maximum longevity of 30 years observed within the population studied here, falls in the range reported for representative sites for North American populations, e.g. 28 years in Florida (Jones *et al.*, 1990) and 46 years in North Carolina (Peterson, 1986). Additionally, the metabolic rate observed falls within the range described by existing models (Figure 5). The absence of physiological impairment of *M. mercenaria* necessitates a consideration of the ecological factors that may influence the biogeographical limitation of the species in the UK to Southampton Water.

Age–frequency data reported for Southampton Water by Richardson & Walker (1991) suggest that environmental constraints on larval development may contribute to the limitation of the species' range. Spawning across the North American distribution of *M. mercenaria* focuses around peak water temperatures, and durations decrease with increasing latitude shifting from semi-annual to annual gametogenic cycles (Eversole, 2001). Annual spawning in the Southampton Water population has been reported at 18°C (Mitchell, 1974), and appears unusually low when compared with spawning temperature amongst natural North American populations. Larval growth rates are significantly affected by temperature with individuals successfully reared from egg to metamorphosis between 18 and 30°C (Loosanoff *et al.*, 1951) reaching metamorphosis after 16–24 days and 5–7 days, respectively (Loosanoff, 1959). Outside this temperature range rates of normal development were low (Loosanoff *et al.*, 1951). Larval development indicates that higher temperatures are more favourable. Southampton Water experiences considerable interannual variability in monthly mean water temperature, rarely exceeding 18°C for three months, and seldom exceeding 20°C (Richardson & Walker, 1991). Peaks in temperature outside the estuary are lower and it therefore appears likely that the effect of temperature on larval development will contribute significantly to the observed limitation of *M. mercenaria* to Southampton Water.

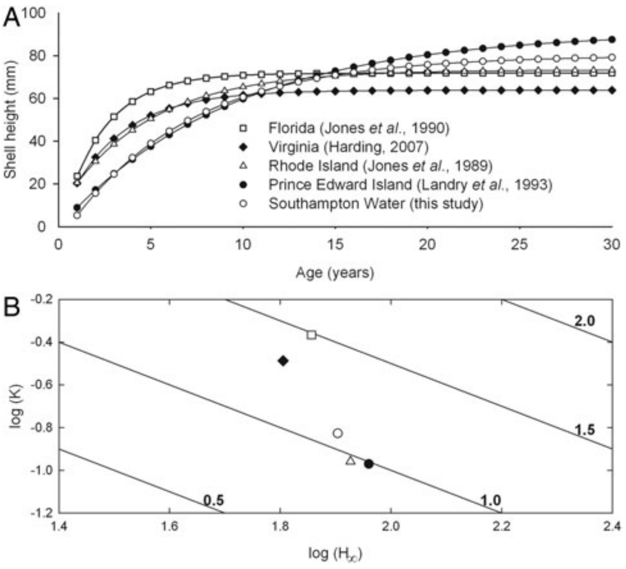

Fig. 4. Comparison of (A) von Bertalanffy growth functions and (B) overall growth performance ($P = \log(K) + \log(H_\infty)$, where K is the Brody growth coefficient and H_∞ is the mean asymptotic shell height in mm) for *Mercenaria mercenaria* from representative sites for North American populations and from Southampton Water: Florida, Matanzas River (Jones *et al.*, 1990); Virginia, York River (Harding, 2007); Rhode Island, Narragansett Bay (Jones *et al.*, 1989); Prince Edward Island, Hillsborough River (Landry *et al.*, 1993); Southampton Water (this study). Shell length (L) to shell height (H) conversions were made using the equation $H = 0.73 + 0.93 \bullet L$, derived from the Southampton Water sample data and comparable to those reported for populations across the geographical range. Diagonal lines indicate isolines of growth performance index.

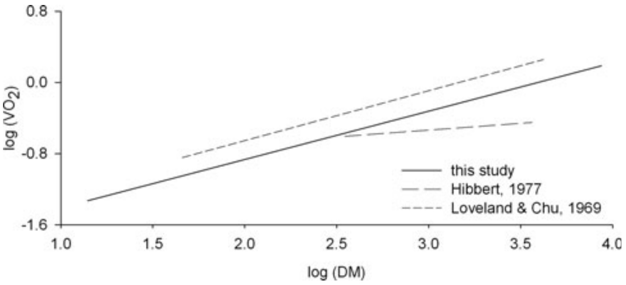

Fig. 5. Comparison of metabolic rate functions for *Mercenaria mercenaria* from New Jersey (Loveland & Chu, 1969), and Southampton (Hibbert, 1977; this study). Shell length (L) to shell height (H) conversions were made using the equation $H = 0.73 + 0.93 \bullet L$ and total wet mass (TWM) to soft tissue dry mass conversions (DM) were made using the equation $\log(DM) = -2.44 + 1.11 \bullet \log(TWM)$, derived from the Southampton Water sample data and comparable to those reported for populations across the geographical range. Functions are presented for sample size-ranges. A Q_{10} translation derived from Hibbert (1977) was applied to the metabolic rate function for the New Jersey population.

Growth and metabolic data presented here yield no indication of physiological impairment of *Mercenaria mercenaria* from the study area. The explanation for the biogeographical limitation of this species in the United Kingdom must therefore lie elsewhere. Further detailed analysis of the ecological factors affecting this species throughout its life cycle is required to clearly establish this.

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