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Physiological basis of inter-population, inter-familiar and intra-familiar differences in growth rate in the green-lipped mussel *Perna canaliculus*

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ABSTRACT

In New Zealand, three quarters (by value) of national aquaculture exports are based on the production of an endemic species, the green-lipped mussel, *Perna canaliculus*, yet there remains a paucity of information describing its underpinning biology. The majority of seed stock is still derived from wild capture from two main geographic locations, however commercial hatchery production has just begun. An established selective breeding programme, now in its 7th generation, has created family lines selected for desirable production traits, including growth rate. The current study therefore used animals derived from selectively bred lines, as well as animals produced in the hatchery from the two geographically distant populations used for commercial spat-catching, which are observed to have differences in growth rates, to explore the key energetic and morphological parameters that may determine fast and slow growth and growth efficiency. Metabolic rates, clearance and assimilation parameters, and morphological characteristics were established for mussels from 3 distinct levels of relatedness; comparing *populations*, full sib *families* (selected a priori for fast or slow growth rate), and inter-*individual* differences between siblings within families displaying heterogeneous growth rates.

Scaling parameters were also determined for metabolic rate, clearance rate, and gill-surface area in the two wild populations of mussels, for comparison of the allometry of the populations, and for size standardization of data. No significant inter-population differences were found in the scaling exponent for any of the parameters, indicating that the size-dependency of physiological rates was effectively the same for mussels from the different geographic areas. However, in contrast, significantly different mass-specific clearance rates were seen in mussels from the two different populations, indicating enhanced energy balances for mussels derived from the Golden Bay population. In the inter- and intra-family experiments, significant differences were found between fast-growing and slow-growing mussels both in terms of anatomy (condition index and relative size of the digestive gland), and in physiological traits such as clearance rate, routine metabolic rate, scope for growth, growth efficiency and metabolic costs of feeding and growth. These results point towards a relatively higher food processing capacity in the gut of faster-growing mussels, and a generally higher metabolic cost of feeding and growth in slower growing mussels. Overall these results reveal the strength of the genetic factors in determining inter-individual variations in physiological performance affecting growth potential, and reinforce the notion that selection of breeding stock both with regard to origin or family provides considerable scope for improvement in mussel production.

1. Introduction

In New Zealand the mussel aquaculture industry is based upon the on-growing of the endemic green-lipped or Greenshell™ mussel, *Perna canaliculus*. This industry has expanded rapidly, and now represents three quarters (by value) of all New Zealand aquaculture exports, exceeding USD$190m p.a. in value (Anon., 2014). However, despite the economic importance of *P. canaliculus* there is a relative paucity of information describing its underpinning biology. Much of the mussel industry's expansion has been fueled by the ability to source very large

Abbreviations: AE, absorption efficiency; AR, absorption rate; CFG, cost of feeding and growth; CI, condition index; CR, clearance rate; GA, gill-surface area; GGE, gross growth efficiency; OIR, organic ingestion rate (rate of ingestion of organic matter); PIM, particulate inorganic matter; POM, particulate organic matter; SFG, scope for growth; SL, shell length; TDW, total dry weight of soft tissues; TPM, total particulate matter; VO_2, rate of oxygen consumption; WDG, weight of digestive gland

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volumes of beach-cast juveniles ("spat") from a single location: Ninety Mile Beach, in the Kaitaia region of northern New Zealand, for subsequent relocation and on-growing throughout the country (Alfaro and Jeffs, 2002). The availability of beach-cast spat is highly seasonal and varies erratically between years (Alfaro et al., 2010), adding uncertainty to the aquaculture industry. In recent years there has also been increasing awareness that spat collected from Kaitaia grow more slowly than locally-caught spat in the main mussel growing area of the Marlborough Sounds, which may be due to reduced baseline condition and cumulative stress from transport and/or translocation (Heasman, 2013), or less favourable genetic characteristics (Camara and Symonds, 2014). Two key strategies have been adopted to mitigate the risk of reliance upon a single seed-source and to capture the genetic potential within other populations. The first strategy has been to deploy spat catchers in other regions known to host significant breeding populations of *P. canaliculus*; notably, farmers catch spat in Golden Bay (South Island, New Zealand; Fig. 1), and have identified these as having faster somatic growth and gonad maturation characteristics when grown in the Marlborough Sounds, compared to Kaitaia derived spat (D. McCall, SPATNZ, pers. comm.; Camara and Symonds, 2014). The second strategy has been to move towards full domestication of *P. canaliculus*, closing the life cycle by conditioning and spawning adults and raising larvae to first settlement in land-based facilities (Ragg et al., 2010). A selective breeding programme established by the Cawthron Institute, has created over 400 family lines spanning 7 generations (Camara and Symonds, 2014; Camara and King, in press). This breeding programme, now the "BreedCo Ltd. Green-lipped mussel selective breeding programme", is being up-scaled in a commercialisation project run by SPATNZ Ltd., with a substantial hatchery operation aiming to supply around 30% of commercial spat requirements (equating to around 30,000 t of annual production), by 2026 (Anon., 2015).

Furthermore, the New Zealand aquaculture industry is committed to expand to a net annual production value of NZD$1bn by 2025, driven substantially by increased revenue from Greenshell™ mussel production (AQNZ, 2006). There is therefore increasing interest in the potential for selective breeding programmes to develop phenotypes that are able to exploit available phytoplankton resources more efficiently, thus increasing the productivity or carrying capacity of existing or potential aquaculture sites (Camara and Symonds, 2014). A major emphasis of the current study was therefore an exploration of the key energetic parameters underpinning fast and slow growth, in an attempt to identify characteristics of more efficient growth performance in *P. canaliculus*, as well as determining the drivers of differences in growth rate between the two major wild spat source populations.

Studies of other mollusc species have established that a significant degree of genetic control is exerted over parameters influencing energy utilization and growth efficiency, including oysters (Bayne et al., 1999b; Parker et al., 2010) and abalone (Gonzalez et al., 2010). Specific mechanisms associated with distinct growth rate or efficiency in bivalves include the efficacies of a) processes of food acquisition and b) metabolic rates both at resting or active state (Bayne, 1999; Bayne, 2000; Bayne et al., 1999a; Bayne et al., 1999b; Pace et al., 2006; Tamayo et al., 2013; Tamayo et al., 2011; Tamayo et al., 2015; Toro and Vergara, 1998).

The present study therefore aimed to characterize physiological performance (metabolism, clearance and assimilation) in groups of mussels showing distinct growth rate characteristics, at three distinct levels of relatedness; comparing *populations* derived from the two major wild spat collecting areas of Kaitaia and Golden Bay (Fig. 1) known to exhibit differences in growth rate, full sib *families* derived from the selective breeding programme, selected a priori for fast or slow growth rate, and inter-*individual* differences between siblings within families displaying heterogeneous growth rates.

Standardization and meaningful comparison of physiological parameters requires knowledge of the corresponding scaling factors (e.g. Nagy, 2005), relating the parameter to animal size (e.g. dry flesh mass). No such information is presently available for *P. canaliculus*. Multiple-parent pooled lots of adults sourced from the two different populations used for wild spat-sourcing (Kaitaia and Golden Bay), were repeatedly spawned to provide multiple cohorts of F1 offspring of different ages and sizes, from the same genetic pools. These different sized cohorts provided a unique opportunity to determine robust scaling functions in this species. Using these differently aged and sized individuals raised under identical conditions, scaling functions were determined for metabolic and clearance rates, as well as gill-surface area from both source populations. These exponential relationships were then used to compare the allometry of the two populations, as well as to allow size standardization of the family data used in inter-family and inter-individual comparisons.

The aims of this study were:

1. To determine the allometric scaling functions for clearance rate (energy acquisition), oxygen consumption (metabolic rate), and gill-surface area, in the green-shell mussel *Perna canaliculus*.
2. To test the existence of significant differences in allometric scaling, or the physiological energetics of growth between Kaitaia and Golden Bay derived green-lipped mussels.
3. To identify the physiological parameters responsible for the existence of differences in the growth potential between mussel families (inter-family differences).
4. To identify the physiological parameters responsible for the existence of differences in the growth potential between individual sibling mussels (intra-family differences).

2. Materials and methods

2.1. Production and selection of mussels

2.1.1. Mussels for the inter-population analysis

Wild juveniles sized approx. 1 mm shell length were captured at the two major commercial spat-catching locations of Kaitaia, and Golden Bay, in the far north of the North Island, and the north of the South Island of New Zealand, respectively (Fig. 1). The spat from different geographic origins were kept separate, but reared to adulthood under identical, standard long-line farming conditions on the same farm located within the Marlborough Sounds (Fig. 1), to be used as "Kaitaia" and "Golden Bay" broodstock. Once mature, these broodstock were brought into the hatchery at Cawthron Aquaculture Park (Fig. 1), and spawned by temperature induction. The F1 "Kaitaia" and "Golden Bay" offspring, were produced by pooling the gametes of 5 males and 5 females from each population (in equal volume per male/female). Thus each 'cohort' could potentially include up to 25 different combinations of parents ("families"). These F1 offspring were created on the same day, and raised in the hatchery under identical conditions. The same broodstock individuals (parents) were allowed to recondition and were subsequently induced to spawn again on four further occasions, 3–5 months apart, to create different aged cohorts of genetically similar individuals from each source population. All cohorts were transferred at a size of 1 mm shell length into identical standard long-line growing conditions on the same farm located in the Marlborough Sounds (Fig. 1). Three of the different age cohorts were used for the current experiments to examine allometric scaling in the different populations; those created in February, June and November of 2013. Thus the animals were aged 5, 10 and 14 months old at the time of assessment.

2.1.2. Selection of mussels for inter and intra-family analysis

Six pedigreed families from the BreedCo Ltd. Green-lipped mussel selective breeding programme, produced in March of 2012 (alias numbers 12, 16, 19, 29, 37 and 39) were selected to perform these experiments. Each "family" consisted of the full sib offspring of individual male and female parent crosses, raised under identical hatchery conditions from the same day of spawning, and subsequently