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Effects of acclimation and acute temperature change on specific dynamic action and gastric processing in the green shore crab, *Carcinus maenas*

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The effects of temperature acclimation and acute temperature change were investigated in post-prandial green shore crabs, *Carcinus maenas*. Oxygen uptake, gut contractions and transit rates and digestive efficiencies were measured for crabs acclimated to either 10 °C or 20 °C and subsequently exposed to treatment temperatures of 5, 15, or 25 °C. Temperature acclimation resulted in a partial metabolic compensation in unfed crabs, with higher oxygen uptake rates measured for the 10 °C acclimated group exposed to acute test temperatures. The Q_{10} values were higher than normal, probably because the acute temperature change prevented crabs from fully adjusting to the new temperature. Both the acclimation and treatment temperature altered the characteristics of the specific dynamic action (SDA). The duration of the response was longer for 20 °C acclimated crabs and was inversely related to the treatment temperature. The scope (peak oxygen consumption) was also higher for 20 °C acclimated crabs with a trend towards an inverse relationship with treatment temperature. Since the overall SDA (energy expenditure) is a function of both duration and scope, it was also higher for 20 °C acclimated crabs, with the highest value measured at the treatment temperature of 15 °C. The decline in total SDA after acute exposure to 5 and 25 °C suggests that both cold stress and limitations to oxygen supply at the temperature extremes could be affecting the SDA response. The contractions of the pyloric sac of the foregut region function to propel digesta through the gut, and contraction rates increased with increasing treatment temperature. This translated into faster transit rates with increasing treatment temperatures. Although pyloric sac contractions were higher for 20 °C acclimated crabs, temperature acclimation had no effect on transit rates. This suggests that a threshold level in pyloric sac contraction rates needs to be reached before it manifests itself on transit rates. Although there was a correlation between faster transit times and the shorter duration of the SDA response with increasing treatment temperature, transit rates do not make a good proxy for calculating the SDA characteristics. The digestive efficiency showed a trend towards a decreasing efficiency with increasing treatment temperature; the slower transit rates at the lower treatment temperatures allowing for more efficient nutrient absorption. Even though metabolic rates of 10 °C acclimated crabs were higher, there was no effect of acclimation temperature on digestive efficiency. This probably occurred because intracellular enzymes and digestive enzymes are modulated through different control pathways. These results give an insight into the metabolic and digestive physiology of *Carcinus maenas* as it makes feeding excursions between the subtidal and intertidal zones.

1. Introduction

The increase in metabolism associated with feeding, usually measured as an increase in oxygen uptake, is termed the specific dynamic action of food or SDA (Secor, 2009). It represents the sum of activities associated with food handling, mechanical breakdown in the gut and the subsequent extracellular and intracellular digestion of nutrients (Carefoot, 1990; Houlihan et al., 1990; Mente et al., 2003). In decapod crustaceans SDA results in a 2–4 fold increase in oxygen uptake that can persist for up to 72 h (Houlihan et al., 1990; McGaw and Reiber, 2000; Whiteley et al., 2001; Robertson et al., 2002; McGaw, 2006b; Romero et al., 2006; Curtis and McGaw, 2010). The characteristics of the SDA typically quantified include the peak rise in oxygen uptake, the duration of the response and the magnitude or integral energy equivalent (Jobling, 1981). There has

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been a resurgent interest during the last decade on the effects of feeding on physiology, in particular, the interactions of digestion with other physiological processes (reviewed in Secor, 2009). Recent work on different crustacean species shows that during changes in the physicochemical environment digestion can pose additional demands on physiological systems (Legeay and Massabuau, 1999, 2000; Robertson et al., 2002; McGaw, 2005, 2006a,b; McGaw et al., 2009). If the animals are unable to balance the demands of several processes it can lead to an increased mortality rate (Legeay and Massabuau, 2000; McGaw, 2006a; McGaw et al., 2009).

Temperature is an important environmental factor affecting the physiology, behaviour and distribution of aquatic ectotherms, and in general metabolic rate is positively correlated with temperature (Willmer et al., 2005). Decapod crustaceans routinely experience seasonal, diel or short term changes in temperature (Lagerspetz and Vainio, 2006) and exhibit different physiological and behavioural reactions depending on whether the temperature change experienced is acute or chronic (Lagerspetz and Bowler, 1993; Whiteley et al., 1997; Cuculescu et al., 1998; Lagerspetz, 2003). In addition to directly affecting metabolic rate, temperature influences protein synthesis rates in crustaceans, although the relationship is affected by thermal experiences and rates of temperature change (Whiteley et al., 1990; Whiteley et al., 2001; Whiteley and Fraser, 2009). This is important because the majority of the increased oxygen uptake associated with the SDA is connected with post-absorptive metabolic processes such as protein anabolism and turnover (Mente, 2003).

The green shore crab, *Carcinus maenas*, is native to north-western Europe. Because of its tolerance of a wide range of environmental temperatures it has become an important invasive species (Behrens-Yamada, 2001). It is now found from the cold oceans of the north-western Atlantic into warmer waters of the Mediterranean and Australasia (Carlton and Cohen, 2003; Klassan and Locke, 2007). Although it can survive in temperatures between −1 °C and 31 °C, the limits for feeding and efficient cardiorespiratory functioning are approximately 5–25 °C (Wallace, 1973; Taylor et al., 1978; Taylor and Wheatly, 1979; Camus et al., 2004). *C. maenas* is a recent invader in Barkley Sound, British Columbia, where it has been captured from the high intertidal zone down to about 20 m depth (Behrens-Yamada and Gillespie, 2008; McGaw et al., 2011). A seasonal thermocline exists in Barkley Sound at 12–16 m. The temperature ranges between 8 and 11 °C below the thermocline, while summer temperatures above the thermocline average 14–18 °C, but can rise as high as 21 °C at the surface of the water (Gosselin and Chia, 1995; Curtis and McGaw, 2008; Stillman and Tagmount, 2009). The difference in the vertical distribution of the crabs suggests they may be exposed for prolonged periods (acclimate) to water temperatures varying by as much as 10 °C (McGaw et al., 2011). Because *C. maenas* makes migrations from subtidal habitats into the intertidal (and vice versa) to forage, it is also likely to experience a range of different temperatures (Hunter and Naylor, 1993; Warman et al., 1993). These temperature ranges may be even more pronounced if the animals become stranded in the intertidal zone (Naylor, 1962; Taylor and Wheatly, 1979).

When *C. maenas* is acclimated to different temperatures (7 °C, 15 °C and 25 °C) and fed, the duration of the SDA response is inversely proportional to temperature, the peak rise in oxygen consumption is highest at 15 °C and the magnitude of the SDA is lowest at 7 °C (Robertson et al., 2002). However, there is no information on how long-term temperature acclimation affects physiological responses when *C. maenas* experiences subsequent acute changes in temperature. Therefore, the first aim of the study was to investigate how metabolic changes associated with acclimation and acute temperature change, interact with those occurring as a result of the SDA. Although a fairly extensive literature exists on the effects of temperature on the components of SDA in crustaceans, these tend to concentrate on enzyme activity (Dittrich, 1990; Pavasovic et al., 2004; Diaz-Tenorio et al., 2006) and protein synthesis rates (reviewed in Whiteley et al., 2001; Whiteley and Faulkner, 2005). There is comparatively less work on mechanical digestion and transit rates (Haddon and Wear, 1987). These measures are important indicators of absorption and assimilation rates and animals may be able to alter transit rates, slowing the passage of food to extract nutrients or speeding up transit rates if a meal is nutrient poor (Mitra and Flynn, 2007). In fish direct correlations between gastric evacuation rates and the duration of the SDA response have been recorded (Jobling and Davies, 1980; Fu et al., 2005, 2006). Gastric evacuation time is considered to be more important than either the meal size or nutrient content in determining the duration of the SDA (Fu et al., 2005, 2006). Thus, the second aim of the study was to determine how chronic and acute temperature experience affects gastric processing and how this may be connected to the characteristics of the SDA in crustaceans (Curtis and McGaw, 2010).

2. Material and methods

Adult male, intermoult green crabs, *C. maenas*, of 137–164 g (75–90 mm carapace width) were trapped in Barkley Sound, British Columbia, Canada between May and August 2008. They were transferred to the Bamfield Marine Sciences Centre and held in running seawater (31–32‰). The animals were acclimated to laboratory temperatures of either 10 °C or 20 °C for at least 20 d (Taylor and Wheatly, 1979; Camus et al., 2004). These temperature regimes represent typical summer temperatures below the seasonal thermocline and the upper range of summer temperatures above the thermocline in Barkley Sound, respectively (Gosselin and Chia, 1995; Stillman and Tagmount, 2009). The crabs were fed fish every other day, but were isolated from the general population and starved for 3 d prior to experimentation. This time period allowed all food to be evacuated from the digestive system, but avoided large-scale physiological changes associated with starvation (Wallace, 1973).

2.1. Oxygen uptake

Oxygen uptake was measured using a Qubit D101 intermittent flow respirometry system (Kingston, ON, Canada). This fully automated system is equipped with two pumps; the first pump continually flushes seawater through the chamber while it is open. The chamber is sealed for measurements and a second pump re-circulates the water through the chamber at a rate of 5 l/min, ensuring that oxygen gradients do not build up within the chamber. Crabs ($n=7$ per treatment) were held in a cylindrical chamber of 20 cm diameter × 8 cm depth and allowed to settle for 3 h before experimentation. Oxygen uptake was calculated during a 20 min decline in oxygen levels while the chamber was sealed, then the chamber was continuously flushed for 10 min between readings. Data was recorded on a Loligo systems data acquisition system (Copenhagen, Denmark). The experiments were carried out in constant dim light, which helped reduce any nocturnal activity and the apparatus were surrounded by black plastic sheeting to avoid visual disturbance to the animal. Air diffusers were used to maintain the oxygen levels at or above 16 kPa during experiments. In the first set of experiments the crabs were maintained at 10 °C; following a 3 h control recording period they were fed a piece of shrimp muscle totalling 2.5% of their body mass and allowed to consume the meal for 15 min. The temperature was then changed to 5 °C, 15 °C or 25 °C (at approximately 0.25 °C/min) using a recirculating water bath, and oxygen uptake was recorded for an additional 48 h period.