Contents lists available at ScienceDirect



Comparative Biochemistry and Physiology, Part A

journal homepage: www.elsevier.com/locate/cbpa



Effect of meal size and body size on specific dynamic action and gastric processing in decapod crustaceans



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ARTICLE INFO

Article history: Received 11 June 2013 Received in revised form 23 July 2013 Accepted 23 July 2013 Available online 1 August 2013

Keywords: Crab Digestion Feeding Size Specific dynamic action

ABSTRACT

Meal size and animal size are important factors affecting the characteristics of the specific dynamic action (SDA) response across a variety of taxa. The effects of these two variables on the SDA of decapod crustaceans are based on just a couple of articles, and are not wholly consistent with the responses reported for other aquatic ectotherms. Therefore, the effects of meal size and animal size on the characteristics of SDA response were investigated in a variety of decapod crustaceans from different families. A 6 fold increase in meal size (0.5%-3% body mass) resulted a pronounced increase in the duration of increased oxygen consumption, resulting in an increase in the SDA of Callinectes sapidus, Cancer gracilis, Hemigrapsus nudus, Homarus americanus, Pugettia producta and Procambarus clarkii. Unlike many other aquatic ectotherms a substantial increase between meal sizes was required, with meal size close to their upper feeding limit (3% body mass), before changes were evident. In many organisms increases in both duration and scope contribute to the overall SDA, here changes in scope as a function of meal size were weak, suggesting that a similar amount of energy is required to upregulate gastric processes, regardless of meal size. The SDA characteristics were less likely to be influenced by the size of the animal, and there was no difference in the SDA (k]) as a function of size in H. americanus or Cancer irroratus when analysed as mass specific values. In several fish species characteristics of the SDA response are more closely related to the transit times of food, rather than the size of a meal. To determine if a similar trend occurred in crustaceans, the transit rates of different sized meals were followed through the digestive system using a fluoroscope. Although there was a trend towards larger meals taking longer to pass through the gut, this was only statistically significant for P. clarkii. There were some changes in transit times as a function of animal size. The foregut clearance times for Cancer magister increased with increasing body size, while smaller Carcinus maenas cleared the hindgut region at a faster rate than larger individuals. Unlike fish there was no clear relationship between transit rates and any of the SDA characteristics. While the fluoroscopy method is useful for assessing foregut activity and food passage, it is limited when inferring connections between nutrient assimilation and post-absorptive processes in crustaceans. Therefore, at least with respect to meal size, transit rates do not make a good proxy for determining the SDA characteristics in crustaceans.

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1. Introduction

During the past two decades there has been a resurgent interest on the effects of feeding on metabolism and the various factors that modulate these postprandial metabolic processes (reviewed in Secor, 2009). The increase in metabolic rate, usually measured as an increase in oxygen consumption, is termed the specific dynamic action of food or SDA. It represents the sum of activities associated with food handling and mechanical breakdown in the gut and the subsequent extracellular and intracellular digestion of nutrients (Carefoot, 1990a; Houlihan et al., 1990; Mente, 2003). The characteristics of the SDA response that are typically measured include the time to reach peak oxygen consumption, the difference between basal and peak metabolism (scope), the duration that the postprandial metabolism remains elevated and the actual energy equivalent of the metabolic response (SDA) expressed in kilojoules (Secor, 2009).

Meal size is known to be an important factor in determining the SDA response, and there is a linear increase in the scope, duration and the SDA as a function of meal size across a broad range of taxa (reviewed in Secor, 2009). For example, a two to four fold increase in meal size results in an increase in the scope, duration or the time to peak oxygen

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consumption in a variety of aquatic ectotherms (Jobling and Davies, 1980; Soofiani and Hawkins, 1982; Lucas and Priede, 1992; Secor and Faulkner, 2002; Fu et al., 2005a,b, 2006; Secor and Boehm, 2006; Wang et al., 2012). However, an eight fold increase in meal size in the green crab, *Carcinus maenas*, only affects the duration and thus the SDA, but has no effect on the time to reach peak oxygen consumption, or the scope of the response (Houlihan et al., 1990). As this is the only paper on effects of meal size on the characteristics of the SDA response of decapod crustaceans it is unclear whether this response is specific to decapods.

The size of an individual also affects the characteristics of the SDA, the general trend is that larger sized ectotherms exhibit greater SDAs (Boyce and Clarke, 1997; Secor and Faulkner, 2002; Katersky et al., 2006; Luo and Xie, 2008). The effects of animal size on the characteristics of the SDA response tend to be more variable: scope increases with animal size in the toad, Bufo marinus (Secor and Faulkner, 2002) and the rattlesnake, Crotalus horridus (Zaidan and Beaupre, 2003. Katersky et al. (2006) report higher scopes in medium sized flounder, Paralichthys dentatus, while there is no effect of animal size on the scope, or time to reach peak oxygen consumption in plunderfish, Harpagifer antarcticus (Boyce and Clarke, 1997), cod, Gadus morhua (Hunt von Herbing and White, 2002), catfish, Silurus meriodionalis (Luo and Xie, 2008) or cuttlefish, Sepia officinalis (Grigoriou and Richardson, 2008). The duration of the response increases with animal size in some animals (Sims and Davies, 1994; Boyce and Clarke, 1997; Hunt von Herbing and White, 2002; Zaidan and Beaupre, 2003), while no significant differences are reported for other aquatic organisms (Katersky et al., 2006; Grigoriou and Richardson, 2008; Luo and Xie, 2008). The effects of body size on SDA of crustaceans are also confined to one article: the isopod Ligia pallasii exhibits an increase in SDA with increasing body mass, but this only occurs when they consume one specific diet (Carefoot, 1990b). Since studies on the effects of body size and meal size on SDA of crustaceans are scant and some SDA characteristics do not follow the trends observed for other ectotherms, the first aim of this study was to determine the effect of meal size and body size on the characteristics of SDA in crustaceans. The majority of decapod crustaceans are opportunistic scavengers feeding on a variety of animal and plant material. Therefore, in order to encompass a variety of animals a systematic approach was taken and animals were selected from several common decapod families.

In some fish species direct correlations between the duration of the SDA response and gastric evacuation rates have been recorded (Jobling and Davies, 1980; Boyce and Clarke, 1997; Fu et al., 2005a,b, 2006), and the gastric evacuation time is considered to be more important than the meal size in determining the duration of the SDA (Fu et al., 2005a,b, 2006). It may also be expected that in crustaceans changes in characteristics of the SDA response would be accompanied by changes in processing times of the meals. In copepods and mysids larger meals move through the gut at a faster rate than smaller meals (Murtaugh, 1984; Dagg and Walser, 1987; Tirelli and Mayzaud, 2005). In contrast, there does not appear to be a common pattern of meal transit times in relation to animal size. Gut transit times are faster in smaller euphausiids, Meganyctiphanes norvegica (Heyraud, 1979) and in the crabs Ucides cordatus (Nordhaus et al., 2006) and Ovalipes catharus (Haddon and Wear, 1987), whereas transit times are longer in small spiny lobsters, Jasus edwardsii (Simon and Jeffs, 2008). In crayfish, Cherax quadricarinatus (Loya-Javellana et al., 1995), prawn, Penaeus subtilis (Nunes and Parsons, 2000) and the shrimps Farfantepenaeus paulensis and Farfantepenaeus aztecus (Soares et al., 2005; Beseres et al., 2006) no difference in transit rates as a function of body size is evident. Only a few studies relate the actual processing of the meal to the SDA (Curtis and McGaw, 2010; McGaw and Whiteley, 2012). It is possible that transit times could be used as a proxy for SDA responses in crustaceans. Therefore, the second aim of the study was to investigate the effects of meal size and body size on transit times of digesta through the gut system and to determine if there was a connection between the characteristics of the SDA response and the transit times of the meal.

2. Material and methods

2.1. Animal collection and housing

Intermoult graceful crabs, C. gracilis (185-220 g), Dungeness crabs, Cancer magister (233-891 g), and kelp crabs, Pugettia producta (195-295 g) were trapped in Barkley Sound, British Columbia, Canada. They were transferred to the Bamfield Marine Sciences Centre and held in running seawater (31-32‰ at 11-12 °C). Purple shore crabs, Hemigrapsus nudus (29-51 g) were collected at Morro Bay, CA, USA, and blue crabs, Callinectes sapidus (190-225 g), were purchased from Gulf Specimens Ltd (Panacea, FL, USA). These two species were housed at University of Nevada, Las Vegas, NV, USA (UNLV) in a recirculating aquarium (Instant Ocean, 31-32%) at 14-15 °C and 18-20 °C respectively. Crayfish, Procambarus clarkii (21-32 g) were trapped at the desert wildlife refuge, Las Vegas, and maintained in freshwater tanks at 18-20 °C at UNLV. Lobsters, Homarus americanus, were donated by Rick Wahle, University of Maine, ME, USA (15-27 g) or purchased from Clearwater®, Nova Scotia (430–520 g); rock crabs, Cancer irroratus (25-242 g), were collected from Bay Bulls, NF, Canada; both species were maintained at 31-32‰ and 12-14 °C. Green crabs, C. maenas (9–110 g) were collected from North Harbour, NL, Canada and kept at 31-32‰ and 14-15 °C. The lobsters, rock crabs and green crabs were housed at the Department of Ocean Sciences, Memorial University of Newfoundland. All the animals were acclimated to laboratory conditions for at least 7 d, and all experiments were carried out at the holding salinities and temperatures. The animals were fed either fish or shrimp twice a week and allowed to feed until satiated, but were isolated from the general population and fasted for 3–6 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). The experimental temperatures used for each species were typical of those in occurring in their habitat during the summer months. Although this precluded direct comparisons of absolute values this protocol ensured the animals were unstressed, would all feed, and that metabolic processes were proceeding at optimal levels (Wieser, 1972; Robertson et al., 2002).

2.2. Oxygen consumption

Oxygen consumption (mg O_2 kg h^{-1}) 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 recirculates the water through the chamber at a rate of 10 L min⁻¹, ensuring that oxygen gradients do not build up within the chamber. During experiments the animals were held in cylindrical chambers and allowed to settle for at least 8 h. Oxygen consumption was calculated during a 20 min decline in oxygen levels while the chamber was sealed, and then the chamber was continuously flushed for 10 min between readings. Data was recorded on a Loligo data acquisition system (Copenhagen, Denmark). The experiments were carried out in constant dim light, which helped reduce any diurnal rhythms and the apparatus were surrounded by black plastic sheeting to avoid visual disturbance to the animal. The resting metabolic rate (post-absorptive, minimal activity) was recorded for a 3 h control period. The animals were then fed a meal of fish (C. gracilis, P. producta) or shrimp muscle (C. sapidus, H. nudus, H. americanus, P. clarkii), all had finished feeding by the time the first postprandial oxygen consumption reading (0.5 h) was completed. Oxygen consumption was recorded until it returned to pre-feeding levels. For each experiment the following parameters were calculated: a) the time to reach peak oxygen consumption

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