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Metabolism, Consumption Rates, and Scope for Growth of Porcelain Crab (*Petrolisthes galathinus*)

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Porcelain crabs *Petrolisthes galathinus* (Bosc, 1802) can be found at high densities in oyster reefs. To examine effects of diet on metabolism, crabs (N = 32) were fed *Artemia salina* nauplii, mixed microalgae, or algal biofilm extract, or left unfed. Oxygen consumption, ammonia excretion, food consumption rate, and absorption efficiency were determined and scope for growth (SFG) was calculated. Oxygen consumption and food consumption rates were highest in crabs fed *Artemia*. The energy gained from mixed microalgae (47 ± 143 J h^{-1}) and algal biofilm (265 ± 203 J h^{-1}) was less than the energy gained from *Artemia* (9,963 ± 658 J h^{-1}). Energy expenditures (oxygen consumption and ammonia excretion) suggest that *P. galathinus* has a low cost of routine metabolism and is able to consume a broad range of food resources including microalgae, benthic algae, and zooplankton. Consumption rates and SFG suggest that zooplankton, when present, are an important and valuable food source for porcelain crabs.

Suspension-feeding bivalves, crustaceans, and polychaetes can have profound effects on ecosystem processes (Grant, 1996; Gili and Coma, 1998; Prins et al., 1998). Suspension feeders remove suspended particles, nutrients, zooplankton, and phytoplankton from the water column and alter current flow; thus, they also alter energy flow and are essential energy links between primary producers and higher trophic levels (Dame and Patten 1981; Powell 1994; Riisgard and Larsen 2010). The porcelain crab *Petrolisthes galathinus* (Bosc, 1802) is a common suspension feeder found within oyster reef communities in the Gulf of Mexico. Porcelain crabs likely consume algae, zooplankton, detritus, and juvenile invertebrates; however, little is known about the diet or consumption rates of *Petrolisthes* spp. When found at high densities these crabs may affect food-web dynamics by consuming microalgae, zooplankton, and algal biofilms (Hollebone and Hay, 2008).

Studying metabolism provides valuable insights into the dietary needs of organisms. The energy budget of any animal can be reasonably measured by assessing oxygen consumption and ammonia excretion (Gnaiger, 1983). Changes in metabolic rates are the result of the physiological energy demands of ingestion, digestion, absorption, excretion, and growth of new tissues (Jobling et al., 1993). Scope for growth (SFG) is the energy available for growth and reproduction after other energetic costs have been incurred and is based on the energy budget of an organism (Warren and Davis, 1967). It is an instantaneous measure of production that ranges from maximum positive values under optimum conditions (i.e., adequate food/nutrition) and declines to negative values when the organism is severely stressed and utilizing its body reserves for maintenance (Widdows, 1995). SFG can be used to determine if a given diet or food source can sustain an organism. *Artemia salina* nauplii have been used as a proxy for naturally occurring zooplankton in research on feeding behavior and metabolism of anomuran crabs (Gonor and Gonor, 1973; Hartman and Hartman, 1977; Whitman et al., 2001; Barria and Gonzalez, 2008) as well as in the rearing of fish, crustaceans, and mollusks (Warren and Davis, 1967; Webster and Lovell, 1990; Moksnes et al., 1997; Villanueva et al., 2002). In this research we report on consumption rates and metabolism of *P. galathinus* to assess the potential energetic requirements of crabs in natural systems.

Methods

Experimental organisms.—Crabs were collected from East Flats, Port Aransas, TX (27°48′38.04″N; 97°05′53.50″W) and maintained in 0.5-liter glass jars with sterilized oyster shells in filtered seawater (0.5 µm) at 25°C and a salinity of 35 practical salinity units with constant aeration and a photoperiod of 12:12 (day:night) hr.

Artemia nauplii fed to crabs were Great Salt Lake strain of *A. salina* hatched for 24 hr. Mixed microalgae fed to crabs was DT's® live marine phytoplankton, containing *Nannochloropsis oculata, Phaeodactylum tricornutum,* and *Chlorella* spp. with cell sizes of 2–20 µm and a total cell count of

approximately 2.92 million cells ml^{-1}. The biofilm extract, composed of *Enteromorpha* spp., benthic diatoms, and detritus, was collected from cement blocks found in ~0.5 m of water in Oso Bay, Corpus Christi, TX.

Basal metabolism trials.—To examine basal metabolism, crabs were maintained unfed in an incubator for 5 d; then oxygen consumption and ammonia excretion were measured (N = 21). Crabs were separated into three treatment groups: morning (0700–0900 hr), afternoon (1200–1400 hr), and evening (1900–2100 hr). Data were collected during two trials completed 2 wk apart and results were pooled. Three crabs were excluded from analyses because they lost chelae, released larvae, or because of insufficient oxygen consumption data.

Scope for growth trials.—To examine the effect of diet on SFG, crabs were incubated unfed for 3 d followed by 4 d of daily feeding (N = 32). Due to logistical constraints, four crabs, one per treatment, entered into the experiment each day, staggering the days in which SFG data were collected. The treatment diets included 1 ml of DT phytoplankton, 300 *A. salina* nauplii in approximately 10 ml of seawater, 1 g wet weight of biofilm extract, or filtered seawater as a control. Four crabs molted, two from *Artemia* treatments and two from control, and these crabs were excluded from statistical analyses.

Oxygen consumption.—To determine energy expended, oxygen consumption (μmol hr^{-1}) was measured for 15–30 min using a photo-optic probe (Ocean Optics Inc.) in a static environment (sealed 35-ml glass jar filled to the top with seawater filtered to 0.5 μm) at 25°C ± 0.4°C.

Oxygen consumption rates were converted to energy expenditures using oxycaloric equivalents of 472.64, 439.04, and 428.48 kJ mol^{-1} for carbohydrates, fats, and proteins, respectively (Crisp, 1971; Elliott and Davison, 1975). Equivalency values were calculated for each diet on the basis of the biochemical content (Webster and Lovell, 1990). The biochemical content of the biofilm extract could not be calculated so a generalized oxycaloric value of 450.0 [kJ $(mol\ oxygen)^{-1}$] was used (Gnaiger, 1983). Because crabs starved for short periods of time predominantly use carbohydrate reserves the oxygen consumption rates of control crabs were converted to energy expenditures using the oxycaloric value of 472.64 kJ $(mol\ oxygen)^{-1}$ (Wallace, 1973; Vinagre and De Silva, 1992).

Ammonium excretion.—Two hours after crabs were transferred to 35-ml glass jars for oxygen consumption measurements, a 5-ml water sample was removed for ammonia (mg l^{-1}) determinations. Ammonium excretion rates were converted to energy expenditures using the factor 0.0832 cal $(\mu mol\ ammonium)^{-1}$ and converted to joules using the value 4.1840 J cal^{-1} (Elliot and Davison, 1975).

Consumption rates.—On the last day of feeding consumption rates were calculated. Crabs fed mixed microalgae or biofilm diets were removed from jars 1 hr after diet was added, rinsed, and the remaining water was passed through preweighed filter paper and dried at 50°C. Dry weight was compared with the average of four controls to determine the dry weight of mixed microalgae or biofilm consumed. To calculate the consumption rate of crabs fed the *Artemia* nauplii diet, crabs were removed after 1 hr, and the remaining *Artemia* were passed through a sieve (3.0 μm) and counted. For statistical comparison consumption rates of *Artemia* were converted to gram dry weight using the value 0.00158 mg $(individual\ nauplii)^{-1}$ (Paffenhofer 1967).

Absorption efficiency (AE).—To determine ash content, samples of each diet were passed through 0.45-μm mixed cellulose ester filters, rinsed with deionized water, dried, and ashed at 550°C for 3 hr. To determine calories (g dry $weight)^{-1}$ of diets, samples of each diet were rinsed with deionized water, dried at 50°C for 4–7 d, and combusted in a Parr® 1640 bomb calorimeter. Energy absorbed as food was found using crab consumption rates and the caloric content of diets on the basis of bomb calorimetry. AE was calculated on the basis of Conover's ratio method (Conover, 1966). AE of crabs fed biofilm extract were negative, which suggests that ash content of biofilm was not measured accurately. AE was compared among diets but was not applied to calculations of energy absorbed.

Energy budget calculations.—The energy budget or SFG for aquatic animals, on the basis of work by Winberg (1960), can be defined as:

$$C - F = \mathrm{Ab} = R + U + P,$$

where C = energy consumed as food; F = energy lost as feces; and P = the energy available for growth and reproduction, i.e., SFG.

The balanced equation can be written as:

$$P = \mathrm{Ab} - (R + U)$$

where Ab = energy absorbed from food; R = energy lost as respiration; and U = energy lost as excretion.

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TABLE 1. Scope for growth (SFG) (J), oxygen consumption (μmol h^{-1}), and ammonia excretion (μmol h^{-1}) of crabs fed *Artemia* nauplii, biofilm extract, mixed microalgae, and unfed controls showing mean and standard deviation (N = 32). Porcelain crab average carapace width with standard deviation was 8.0 ± 1.2 mm in *Artemia* treatment, 8.1 ± 2.3 mm in biofilm treatment, 8.3 ± 1.0 mm in phytoplankton treatment, and 8.7 ± 1.2 mm in control.

Diet	SFG (J h^{-1}) mean	SD	Oxygen (μmol h^{-1}) mean	SD	Ammonia (μmol h^{-1}) mean	SD
Artemia nauplii	9,963.1	658.3	4.21	2.03	0.0278	0.0144
Algal biofilm	264.5	202.8	2.48	2.00	0.0270	0.0136
Mixed microalgae	46.69	142.8	3.25	0.92	0.0572	0.0386
Control	−1.53	0.44	3.64	1.30	0.0263	0.0153

Statistical analyses.—Basal oxygen consumption and ammonia excretion rates were analyzed using a 2-way analysis of covariance (ANCOVA) with a covariate of carapace width, fixed main effect of time (morning, afternoon, evening), random main effect of reproductive condition (male, gravid female, nongravid female), and compared using Tukey–Kramer post hoc tests (N = 21).

Scope for growth, food consumption, and AE were compared using a 2-way ANOVA with fixed main effects of diet (phytoplankton, *Artemia,* biofilm, or control) and random main effect of sex (male or female), and compared using Tukey's post hoc tests. SFG, food consumption, and AE were also analyzed using a 1-way ANOVA by separating males and females of each diet, creating eight levels (e.g., female-*Artemia,* male-*Artemia*), and these were compared using linear contrasts. Oxygen consumption and ammonia excretion were compared using a 2-way ANCOVA with a covariate of carapace width, fixed main effect of diet (phytoplankton, *Artemia*, biofilm, or control), and random main effect of sex (male or female), and compared using Tukey–Kramer post hoc tests. All statistical analyses were performed using SAS® 9.2 software.

RESULTS

Basal metabolism.—Oxygen consumption and ammonia excretion were not significantly different at different times of day (morning, afternoon, evening) (ANCOVA F = 0.42, $P = 0.67$, F = 0.57, $P = 0.58$, respectively, N = 21). Carapace length, wet weight, and dry weight were highly significant determinants of oxygen consumption (ANCOVA F = 8.18, $P = 0.016$, F = 13.60, $P = 0.0036$, F = 8.32, $P = 0.015$, respectively, N = 21) and ammonia excretion (ANCOVA F = 4.68, $P = 0.053$, F = 8.59, $P = 0.014$, F = 5.79, $P = 0.035$, respectively, N = 21). Oxygen consumption and ammonia excretion were not significantly different among crabs of different sex (ANCOVA F = 0.25, $P = 0.79$, N = 21) or reproductive condition (ANCOVA F = 0.07, $P = 0.93$, N = 21).

Scope for growth.—Oxygen consumption was significantly higher in crabs fed *Artemia* nauplii than in crabs fed biofilm extract, mixed microalgae, or control crabs (ANCOVA F = 3.33, $P = 0.037$, N = 32) (Table 1). Energy content of the diets on the basis of bomb calorimetry was significantly different (ANOVA F = 517.15, $P < 0.001$, N = 27) (Table 2). The ash content of the diets was significantly different (ANOVA F = 4.26, $P < 0.001$, N = 12), whereas the ash content of the feces was not (ANOVA F = 3.40, $P = 0.176$, N = 32). Average AE of crabs fed *Artemia* nauplii and mixed microalgae was 97.1 ± 0.61 and 88.9% ± 4.1% respectively.

Consumption rate was significantly different among the diets, there were no differences detected between the sexes, and the interaction term was significant (ANOVA F = 404.0, $P < 0.0001$, F = 0.23, $P = 0.6387$, F = 6.50, $P = 0.0022$, respectively, N = 32). On the basis of Tukey's comparisons, consumption rate of *Artemia* was significantly higher than in those fed biofilm or microalgae ($P < 0.0001$) (Table 2). Consumption

TABLE 2. Consumption rate (g dry weight hr^{-1}), energy content [kJ (g dry weight)$^{-1}$], and ash content (%) of the *Artemia* nauplii, biofilm extract, and mixed microalgae showing mean, standard deviation, and sample size.

Diet	Consumption rate (mg dry weight hr^{-1}) mean	SD	Energy content [kJ (mg dry weight)$^{-1}$] mean	SD	Ash content (%) mean	SD
Artemia nauplii	459.8 (N = 7)	28.2	21,737 (N = 12)	919	8.3 (N = 5)	0.28
Biofilm extract	54.66 (N = 9)	36.7	5,104 (N = 7)	1,745	82.6 (N = 5)	3.7
Mixed microalgae	0.156 (N = 9)	0.332	17,491 (N = 8)	425	25.2 (N = 5)	6.7

of mixed microalgae and biofilm were not significantly different or different from control ($P = 0.185$, $P = 0.997$, $P = 0.154$, respectively). When analyzed using a 1-way ANOVA and linear contrasts, consumption of biofilm was significantly higher in female crabs ($F = 12.62$, $P = 0.0016$), consumption of *Artemia* nauplii was significantly higher in male crabs ($F = 6.83$, $P = 0.0153$), and consumption of biofilm was significantly higher than mixed microalgae ($F = 4.37$, $P = 0.0473$).

Absorption effieciency was significantly different among diets, between the sexes, and the interaction term was significant (ANOVA $F = 12.15$, $P < 0.0001$, $F = 5.31$, $P = 0.0302$, $F = 5.63$, $P = 0.0046$, respectively, $N = 32$). When analyzed using a 1-way ANOVA and linear contrasts, AE was not significantly different between males and females feeding on *Artemia* ($F = 0.00$, $P = 0.96$), was higher in males feeding on biofilm ($F = 18.82$, $P = 0.0002$), and was higher in crabs fed mixed microalgae than in crabs fed biofilm ($F = 4.99$, $P = 0.0351$).

Scope for growth was significantly different among diets, between the sexes, and the interaction term was significant (ANOVA $F = 4{,}509.9$, $P < 0.0001$, $F = 29.94$, $P < 0.0001$, $F = 43.88$, $P < 0.0001$, respectively, $N = 32$) (Table 1). On the basis of Tukey's comparisons, SFG of crabs fed *Artemia* was significantly higher than in those fed biofilm or microalgae ($P < 0.0001$). SFG of crabs fed mixed microalgae and biofilm were not significantly different or different from unfed control ($P = 0.551$, $P = 0.955$, $P = 0.339$, respectively).

Discussion

In this study, the low cost of routine metabolism in *P. galathinus* was sustained by consumption of *A. salina* nauplii, mixed microalgae, or algal biofilm. In unfed crabs, starvation did not significantly alter energy expenditures on the basis of oxygen consumption and ammonia excretion. Crabs feeding on *Artemia* expended more energy (measured by oxygen consumption), consumed more biomass than crabs feeding on other diets, and had the highest SFG.

Porcelain crabs, barnacles, calanoid copepods, and most branchiopods use filter setae to capture particles (Riisgard and Larsen, 2010). On the basis of their size and structure, filter setae only capture particles of certain sizes, shapes, and surface chemistry (Palmer et al., 2004), making them more selective than pump systems. This innate selectivity provides a mechanism by which organisms can capture food items that contain more energy and necessary nutrients. When reared in a laboratory environment larvae of *Petrolisthes* spp. are fed *A. salina* nauplii almost exclusively (Gore, 1972; Fujita et al., 2002; Kraus et al., 2004). *Pagurus longicarpus*, another anomuran crab, completed development when fed only *Artemia* but did not survive to adult stages when given only algal food (Roberts, 1974). In these studies *Artemia* was used as a proxy for naturally occurring zooplankton, not just because of their size and behavior, but also because of their energetic and nutritional composition.

The structure of porcelain crab filter setae are suited for capturing both small food items such as microalgae and larger planktonic food items such as zooplankton (Hartman, 2003; Hollebone and Hay, 2008). In this study, *Petrolisthes galathinus* was able to consume and maintain normal metabolism on a mixed microalgal diet with cell sizes of 2–20 μm. They were likely able to consume microalgae due to the spacing of their filter setae. The third maxillipeds of *Petrolisthes* spp. form a fanlike structure with large setae forming a framework around which smaller setae are attached. In a closely related species, *P. cinctipes*, the spacing among smaller filter setae ranged from 3 to 30 μm, depending on the size of the animal, with an average spacing of 21 μm in distal regions of setae and 9 μm in proximal regions of setae (Wicksten, 1973). Spacing between larger setae is much greater and allows the capture of larger prey items such as zooplankton. A common estuarine copepod, *Acartia tonsa*, ranges from about 400 to 800 μm in length (Stottrup et al., 1986). *Artemia* nauplii, by comparison, are approximately 400 to 500 μm in length (Leger et al., 1987).

Both adult zooplankton such as copepods, and invertebrate larvae such as crustacean nauplii, vary in size, shape, and behavior (Zaret and Suffern, 1976; Pangle et al., 2007) and porcelain crabs should be able to capture and consume many different types and sizes of zooplankton. *Petrolisthes cinctipes* consumed diatoms, ciliated protozoans, and *Artemia* nauplii in a laboratory environment (Wicksten, 1973). *Pagurus longicarpus* was stimulated to feed by the presence of and able to feed on *Artemia* nauplii, the first zoea of Say's mud crab *Dyspanopeus sayi*, green crab *Carcinus maenas*, long-armed hermit crab *Pagurus longicarpus*, marsh grass shrimp *Palaemonetes vulgaris*, and the veligers of slipper shell *Crepidula plana* (Whitman et al., 2001). Although copepods make up the bulk of zooplankters around oyster reefs during the day, planktonic crustacean larvae comprised about 5% of the oyster reef zooplankton community in Maryland (Breitburg et al., 1995) and decapod zoea were numerically important in Virginia (Harding, 2001). The diet of porcelain crabs should

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include any of these zooplankters depending on the size and abundance in space and time.

Porcelain crabs can be extremely abundant on oyster reefs and may compete with oysters for some food resources but not for others. Oysters, like many bivalves, feed using laterofrontal cirri to create currents, or a pump system, that directs food particles to the mouth (Riisgard and Larsen, 2010). *Crassostrea virginica* is able to consume suspended particles 1–12 μm in diameter and optimally consumes those between 3 μm and 4 μm (Haven and Morales-Alamo, 1970). Particles between 2 μm and 3 μm in diameter are not easily captured by *C. virginica* because this size closely matches the spacing of laterofrontal cirri (Haven and Morales-Alamo, 1970). The spacing of filter setae in *Petrolisthes galathinus* and other porcelain crabs is probably similar to that noted in *P. cinctipes* (average 21 μm; Wicksten, 1973), and because it is wider than that of oysters competition for food resources should be minimal.

Few studies have investigated the trophic position or diet of porcelain crabs in the natural environment. As measured by $\delta^{15}N$, the trophic position of *Petrolisthes armatus* in a Florida oyster reef was nearer that of other crabs including shore crab *Pachygrapsus transversus* and juvenile mud crabs, demonstrating that porcelain crab diets are likely different or more varied (or both) than resident bivalve filter feeders (Yeager and Layman 2011). The higher $\delta^{15}N$ value of *Petrolisthes armatus* indicated that higher trophic level prey, such as copepods and invertebrate larvae, were an important food resource for these crabs. As this study demonstrated, porcelain crabs consume other food resources as well, such as microalgae and algal biofilms, but these may only maintain routine metabolism and not provide for additional energetic costs such as molting, limb regeneration, and reproduction. Zooplankton may be important components of porcelain crab diets because they provide enough energy to meet the metabolic costs of growth and reproduction. As a consequence of their potential reliance on zooplankton, porcelain crabs may also influence the populations of a variety of other invertebrates that inhabit oyster reefs.

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Literature Cited

Barria, E. M., and M. Gonzalez. 2008. Effect of autotomy and regeneration of the chelipeds on growth and development in *Petrolisthes laevigatus* (Guerin, 1835) (Decapod, Anomura, Porcellanidae). Crustaceana 81:641–652.

Breitburg, D. L., M. A. Palmer, and T. Loher. 1995. Larval distributions and the spatial patterns of settlement of an oyster reef fish: responses to flow and structure. Mar. Ecol. Prog. Ser. 125:45–60.

Conover, R. J. 1966. Assimilation of organic matter by zooplankton. Limnol. Oceanogr. 11:338–345.

Crisp, D. J. 1971. Energy flow measurements, p. 197–279. *In:* Methods for the study of marine benthos. N. A. Holme and A. O. McIntyre (eds.). Blackwell Scientific Publications, Oxford, U.K.

Dame, R. F., and B. C. Patten. 1981. Analysis of energy flows in an intertidal oyster reef. Mar. Ecol. Prog. Ser. 5:115–124.

Elliot, J. M., and W. Davison. 1975. Energy equivalents of oxygen consumption in animal energetic. Oecologia 19:195–201.

Fujita, Y., S. Shokita, and M. Osawa. 2002. Complete larval development of *Petrolisthes unilobatus* reared under laboratory conditions (Decapoda: Anomura: Porcellanidae). J. Crust. Biol. 22:567–580.

Gili, J. M., and R. Coma. 1998. Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol. Evol. 13:316–321.

Gnaiger, E. 1983. Calculation of energetic and biochemical equivalents of respiratory oxygen consumption, p. 337–345. *In:* Polarographic oxygen sensors, aquatic and physiological applications. E. Gnaiger and H. Forstner (eds.). Springer Verlag, New York.

Gonor, S. L., and J. J. Gonor. 1973. Feeding, cleaning, and swimming behavior in larval stages of porcellanid crabs (Crustacea: Anomura). Fish. Bull. 71:225–234.

Gore, R. H. 1972. *Petrolisthes platymerus*: the development of larvae in laboratory culture (Crustacea: Decapoda; Porcellanidae). Bull. Mar. Sci. 22:336–354.

Grant, J. 1996. The relationship of bioenergetics and the environment to the field growth of cultured bivalves. J. Exp. Mar. Biol. Ecol. 200:239–256.

Harding, J. M. 2001. Temporal variation and patchiness of zooplankton around a restored oyster reef. Estuaries 24:453–466.

Hartman, B. H., and M. S. Hartman. 1977. The stimulation of filter feeding in the porcelain crab *Petrolisthes cinctipes* Randall by amino acids and sugars. Comp. Biochem. Physiol. 56:19–22.

Hartman, M. J. 2003. Population dynamics and trophic interactions of *Petrolisthes armatus*, an invasive decapod crustacean. Unpubl. Ph.D. diss., Univ. of South Carolina, Columbia, SC.

Haven, D. S., and R. Morales-Alamo. R. 1970. Filtration of particles from suspension by the American oyster *Crassostrea virginica*. Biol. Bull. 139:248–264.

Hollebone, A. L., and M. E. Hay. 2008. An invasive crab alters interaction webs in a marine community. Biol. Invasions 10:347–358.

Jobling, M., B. M. Baardvik, J. S. Christiansen, and E. H. Jorgensen. 1993. The effects of prolonged exercise training on growth performance and production parameters in fish. Aquacult. Int. 1:95–111.

Kraus, H., A. Hiller, and N. Cruz. 2004. The zoeal stages of *Petrolisthes caribensis* Werding, 1983 reared under laboratory conditions (Decapoda: Anomura: Porcellanidae). Stud. Neotrop. Fauna Environ. 39: 85–90.

Leger, P., D. A. Bengtson, P. Sorgeloos, K. L. Simpson, and A. D. Beck. 1987. Nutritional value of *Artemia*: a review. Artemia research and its applications. Ecology, culturing, use. Aquaculture 3:357–372.

Moksnes, P. O., R. N. Lipcius, L. Pihl, and J. Van Montfrans. 1997. Cannibal–prey dynamics in young juveniles and postlarvae of the blue crab. J. Exp. Mar. Biol. Ecol. 215:157–187.

Paffenhofer, G. A. 1967. Caloric content of larvae of the brine shrimp *Artemia salina*. Helgoland Mar. Res. 16:130–135.

Palmer, M., H. Nepf, T. Petterson, and J. Ackerman. 2004. Observations of particle capture on a cylindrical collector: implications for particle accumulation and removal in aquatic systems. Limnol. Oceanogr. 49:76–84.

Pangle, K. L., S. D. Peacor, and O. E. Johannsson. 2007. Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. Ecology 88:402–412.

Powell, C. M. 1994. Trophic linkages between intertidal oyster reefs and their adjacent sandflat communities. Unpubl. M.S. thesis, Univ. of North Carolina, Wilmington, NC.

Prins, T. C., A. C. Smaal, and R. F. Dame. 1998. A review of the feedbacks between bivalve grazing and ecosystem processes. Aquat. Ecol. 31:349–359.

Riisgard, H. U., and P. S. Larsen. 2010. Particle capture mechanisms in suspension-feeding invertebrates. Mar. Ecol. Prog. Ser. 418:255–293.

Roberts, M. H. 1974. Larval development of *Pagurus longicarpus* Say reared in the laboratory. V. Effect of diet on survival and molting. Biol. Bull. 146:67–77.

Stottrup, J. G., K. Richardson, E. Kirkegaard, and N. J. Pihl. 1986. The cultivation of *Acartia tonsa* Dana for use as a live food source for marine fish larvae. Aquaculture 52:87–96.

Villaneuva, R., N. Koueta, J. Riba, and E. Boucaud-Camou. 2002. Growth and proteolytic activity of *Octopus vulgaris* paralarvae with different food rations during first feeding, using *Artemia* nauplii and compound diets. Aquaculture 205:269–286.

Vinagre, A. S., and R. S. da Silva. 1992. Effects of starvation on the carbohydrate and lipid metabolism in crabs previously maintained on a high protein or carbohydrate diet. Comp. Biochem. Physiol. 102A: 579–583.

Wallace, J. C. 1973. Feeding, starvation and metabolic rate in the shore crab *Carcinus maenas*. Mar. Biol. 20:277–281.

Warren, C. E., and G. E. Davis. 1967. Laboratory studies on the feeding, bioenergetics and growth of fish, p. 175–214. *In:* The biological basis of freshwater fish production. S. D. Gerking (ed.). Blackwell, Oxford, U.K.

Webster, C., and R. T. Lovell. 1990. Comparison of live brine shrimp nauplii and nonliving diets as first food for striped bass larvae. Prog. Fish. Cult. 52:171–175.

Whitman, K. L., J. J. McDermott, and M. S. Oehrlein. 2001. Laboratory studies on suspension feeding in the hermit crab *Pagurus longicarpus* (Decapoda: Anomura: Paguridae). J. Crust. Biol. 21:582–592.

Wicksten, M. K. 1973. Feeding in the porcelain crab, *Petrolisthes cinctipes* (Randall) (Anomura: Porcellanidae). Bull. So. Calif. Acad. Sci. 72:161–163.

Widdows, J., P. Donkin, M. D. Brinsley, S. V. Evans, P. N. Salkeld, A. Franklin, R. J. Law, and M. J. Waldock. 1995. Scope for growth and contaminant levels in North Sea mussels *Mytilus edulis*. Mar. Ecol. Prog. Ser. 127:131–148.

Winberg, G. G. 1960. Rate of metabolism and food requirements of fishes. J. Fish. Res. Board Can. 23:1717–1759.

Yeager, L. A., and C. A. Layman. 2011. Energy flow to two abundant consumers in a subtropical oyster reef food web. Aquat. Ecol. 45:267–277.

Zaret, T. M., and J. S. Suffern. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanogr. 21:804–813.

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