

The effects of starvation and acute low salinity exposure on food intake in the Dungeness crab, *Cancer magister*

Daniel L. Curtis · Cheryl H. Vanier ·
Iain J. McGaw

Received: 22 June 2009 / Accepted: 9 November 2009 / Published online: 25 November 2009
© Springer-Verlag 2009

Abstract Adult *Cancer magister* make forays into hyposaline estuarine habitats during times of high food abundance. However, as weak osmoregulators, they are poorly equipped to deal with the concurrent demands of osmoregulation and digestion. Therefore, the potential interaction between nutritional status and feeding in a physiologically challenging environment was investigated. Changes in the proportion of crabs feeding, the amount of food consumed, the time spent feeding, and the efficiency with which a meal was consumed were examined in response to the length and severity of hyposaline exposure, and the duration of starvation. Reductions in the (a) number of animals feeding, (b) the amount of food consumed, and (c) the time spent feeding were observed in salinities where *C. magister* actively osmoregulates the concentration of its internal fluids. Although this reduction in feeding was likely a stress response, the crabs were able to evaluate the level of salinity stress: there was a dose-dependent reduction in feeding, and they were able to discriminate between salinities separated by as little as 3.5‰. The likelihood that animals would feed in low salinity increased with starvation. Thus, the aversion to food uptake in

physiologically stressful conditions may be overridden by the need to procure nutrients. In the natural environment, we suggest that *C. magister* are employing an ‘eat and run’ strategy, moving into the estuary, consuming a meal, and retreating to higher salinities to digest.

Introduction

The decision to forage and subsequently feed results from a trade-off between the benefits and risks associated with feeding under a given set of conditions (Stephens and Krebs 1986). When food sources become scarce animals may endure additional risks in order to obtain food. Much of the work associated with foraging theory has focused on animals foraging under the risk of predation (Lima and Dill 1990). Using behavioral titrations, some of these studies have even determined an energetic equivalence for predation risk by investigating how much food needs to be available before an individual will enter into an area where predation risk is high (Abrahams and Dill 1989; Webster and Dill 2006). A number of studies have assessed this trade-off for benthic or intertidal marine scavengers feeding under a perceived increased risk of predation, namely dead conspecifics (Stenzler and Atema 1977; McKillup and McKillup 1995; Moore and Howarth 1996). Recently, it has been shown that similar trade-offs may exist between foraging and challenging environmental conditions (Webster and Dill 2006; Webster and Dill 2007).

For crustaceans living in estuaries, salinity is a key environmental factor affecting their behavior and distribution (Kinne 1966). Salinity regimes may change tidally and seasonally (Curtis and McGaw 2008) and as such, osmoregulatory ability may dictate an animal’s capacity to exploit estuarine habitats (Barnes 1967; Spaargaren 1973).

Communicated by H. O. Pörtner.

D. L. Curtis (✉) · C. H. Vanier
School of Life Sciences, University of Nevada, Las Vegas,
4505 Maryland Parkway, Las Vegas, NV 89154, USA
e-mail: curtisd4@unlv.nevada.edu

D. L. Curtis · I. J. McGaw
Bamfield Marine Sciences Centre,
Bamfield, BC V0R 1B0, Canada

I. J. McGaw
Ocean Sciences Centre, Memorial University of Newfoundland,
St. John’s, NL A1C 5S7, Canada

Decreases in salinity have profound effects on the physiology and subsequently the growth of many estuarine inhabitants. Typically, for crustaceans that are classed as efficient osmoregulators, low-salinity exposure results in an increase in heart rate and oxygen uptake (Taylor et al. 1977). Such responses are thought to aid the additional energetic requirements for active ion uptake and regulation of membrane permeability. For weaker osmoregulators and osmoconformers, low-salinity exposures in the field are often acute (Curtis & McGaw 2008), and the resulting decrease in heart rate and/or cardiac output may minimize the gradient for diffusive ion loss (Cornell 1974; McGaw and McMahan 1996; Curtis et al. 2007). Recent work has shown that these physiological responses to hyposaline exposure may be compromised when crabs feed and subsequently digest in such conditions (Legeay and Massabuau 2000; McGaw 2007). Consequently, for crustaceans unable to balance the demands of several physiological systems, hyposaline exposure may cause an alteration in feeding rate and energetic demands, leading to a reduction in the scope for growth (Guerin and Stickle 1997; Normant and Lamprecht 2006).

Despite these physiological effects, crabs that are classed as weak osmoregulators or even osmoconformers can be found in habitats prone to episodes of low salinity (Curtis et al. 2007). It is thought that individuals enter into these areas in response to increased food abundance (Sugarman et al. 1983; Stevens and Armstrong 1984; Curtis and McGaw 2008). Increased competition generated by a lack of resources may also force animals to feed in sub-optimal habitat conditions (Hoffman and Parsons 1993). Previous work has shown that benthic marine scavengers are more likely to forage and feed under increased predation risk when they are starved (Stenzler and Atema 1977; McKillup and McKillup 1994; Moore and Howarth 1996). As energetic reserves are depleted, the level of hunger and the necessity for feeding increase (Wang et al. 2006). We therefore hypothesized that the necessity for feeding may force decapods of poor osmoregulatory ability to feed in low salinity.

The Dungeness crab, *Cancer magister*, is classified as a weak osmoregulator (Engelhardt and Dehnell 1973). This species commonly occurs in estuaries during juvenile stages (Gunderson et al. 1990; Holsman et al. 2006; Curtis and McGaw 2008). Adult crabs are less common in estuaries, and only appear to make brief excursions into these habitats (Curtis and McGaw 2008). While this recent work has empirically shown that crabs are entering into the estuary during times of high food abundance, there is little substantiation as to what crabs are actually doing while in low salinity. Based on these observations, we hypothesized that adult crabs were making short forays into low-salinity areas to forage. However, feeding in low salinity can be

stressful for adult crabs: *C. magister* is unable to balance the simultaneous physiological costs of feeding and osmoregulation, and postprandial crabs experience higher mortality rates in severe low salinity (McGaw 2006). We further hypothesized that the necessity of procuring a meal must be great before crabs will endure the additional costs of digestion in low salinity. To investigate these questions, we examined changes in the amount of food ingested, the time spent feeding, and the likelihood of feeding in response to (1) the degree of low-salinity exposure, (2) the duration of low-salinity exposure, and (3) the time since the last meal (degree of starvation).

Materials and methods

Animals

Adult male intermolt Dungeness crabs, *Cancer magister*, of 300–750 g were trapped in Barkley Sound British Columbia, Canada, from June to October 2005. Animals were transported to the Bamfield Marine Sciences Centre and held in running seawater (SW) of $32 \pm 1\text{‰}$ and at a temperature of $12 \pm 1^\circ\text{C}$ for a minimum of 1 week prior to experimentation. Crabs were fed fish (*Lepidopsetta bilineata*) every other day. Salinity and temperature regimes were monitored using an YSI-30 conductivity meter (YSI Inc., Yellow Springs, OH).

Protocol

The interactive effects of the degree of low-salinity exposure, the duration of low-salinity exposure, and the duration of starvation on (1) the proportion of *C. magister* feeding, (2) the amount of food consumed, and (3) the amount of time spent feeding were investigated. Prior to experimentation, the crabs were removed from the holding tanks, transferred to a 300 l tank, and allowed to feed ad libitum on rock sole (*L. bilineata*) for 1 h. After ensuring that each individual had fed, the food was removed, and crabs were starved for 2, 5, or 21 days. These starvation periods were chosen to correspond with physiological changes. A 2 days starvation period is the minimum time period used in physiological and behavioral studies (Elner and Hughes 1978); at this point, the meal has been cleared from the foregut (McGaw and Reiber 2000). At 5 days starvation, the physiological effects of the previous meal have passed, and metabolism has returned to basal levels (Wallace 1973; McGaw and Reiber 2000). Following 21 days starvation, there is a further decrease in metabolic rate that is thought to be associated with switching of metabolic substrates (Wallace 1973), and an increased urgency for feeding (Wang et al. 2006). Once the

animals had been starved for the required period, they were transferred to a sea table (150 × 70 × 20 cm), which was divided into ten equal sized chambers and allowed to settle for 3 h after handling. The salinity was then changed to 25, 50, 75, or 100% SW (8, 16, 24, or 32‰, respectively), over a period of 30 min by draining a portion of the tank and replacing it with aerated dilute seawater of the same temperature.

Crabs were exposed to the test salinities for 0.5, 6, or 24 h. A 0.5 h exposure would represent the crab making a brief foray into low salinity to feed (Curtis and McGaw 2008) or being confronted with an abrupt halocline and showing avoidance behaviors. A 6 h exposure is representative of the salinity conditions that *C. magister* would experience during the tidal cycle at a fixed location in the estuary (Curtis and McGaw 2008). A 24 h exposure is representative of chronic low-salinity conditions that persist in the estuary during times of high run-off (Curtis and McGaw 2008); this time period also allows the osmolality of the hemolymph to reach new stable levels (Siebers et al. 1972; McGaw 2006). Following each exposure time, the crabs were presented with a piece of pre-weighed fish muscle (approximately 10% of their body mass). The fish had been soaked for 6 h prior to experimentation in the treatment salinity, which minimized changes in wet mass during the course of the experiment. When a crab ceased feeding for more than 15 min, the feeding bout was considered finished, and the amount of time spent feeding was recorded. Crabs that did not feed within 1 h of being presented with food were scored as non-feeders. The uneaten food was then removed and weighed, and the amount of food consumed was calculated. This three-way design resulted in a total of 27 separate treatment combinations, in which each of the 3 variables was measured. A minimum of 20 crabs were used for each treatment, and treatments were repeated until at least 5 crabs had fed so that an estimate of variance could be obtained. A total of 570 individuals were tested.

Data analysis

The effect of salinity, starvation, and acclimation on the proportion of crabs feeding for each trial was determined using a generalized linear model with binomial error. The main effects and all two-way interactions were included as fixed effects. The three-way interaction was not included due to sample size limitations on the complexity of the model. The model was estimated using PROC GLIMMIX in SAS v.9.1 (SAS Institute 2002–2003).

The effects of salinity, starvation, and acclimation time on (1) the amount of food consumed, (2) time spent feeding, and (3) efficiency (the amount of food consumed in a given time) were initially examined with identical mixed

model ANOVAs (PROC MIXED; SAS v.9.1). Fixed effects included main effects of salinity, starvation and acclimation, and all two- and three-way interactions, in addition to each individual's wet weight as a covariate. Two- and three-way interactions with the covariate were included in the initial model, but these terms were dropped when they had high *P* values ($P > 0.20$) due to concerns about sample size effects on accuracy of the model. Trial nested within each salinity–starvation–acclimation time combination was included as a random effect. Only animals that fed were included in the models, and all dependent variables were log₁₀-transformed. Significant effects were followed up using Tukey post hoc tests. Unless otherwise stated, values presented are the overall least squares means and contain all levels of the other two factors. Results are presented with asymmetrical error terms resulting from back transformation of log-transformed values. Significance was determined at $\alpha = 0.05$ for all analyses.

Results

Likelihood of feeding

The proportion of *C. magister* that fed varied with the level of salinity exposure and the duration of starvation (Table 1; Fig. 1). As the salinity decreased, fewer crabs fed in each successively lower salinity (Fig. 1a). *C. magister* would not feed below 40% SW even following 21 days starvation; therefore, the 25% SW treatment was not considered in the analyses. The duration of exposure to low salinity did not have a significant effect on the proportion of crab feeding (Table 1; Fig. 1b). In contrast, the proportion of crabs that fed increased with starvation (Fig. 1c).

There were no statistically significant interactions among salinity, starvation, and acclimation; however, trends were observed that may have been masked by the low power and overall effects associated with other salinities (Fig. 2). When each salinity was examined separately,

Table 1 Effects of starvation, acclimation, and salinity on the proportion of crabs feeding in each trial

Effect	<i>df</i>	<i>F</i>	<i>P</i> value
Starvation	2, 38	8.00	0.0013
Acclimation	2, 38	0.61	0.5483
Salinity	2, 38	50.23	<0.0001
Starvation* acclimation	4, 38	2.18	0.0898
Starvation* salinity	4, 38	1.03	0.4041
Acclimation* salinity	4, 38	0.37	0.8263

The degrees of freedom (*df*) are provided as numerator, denominator *df*; bold phase denotes significant *P* values

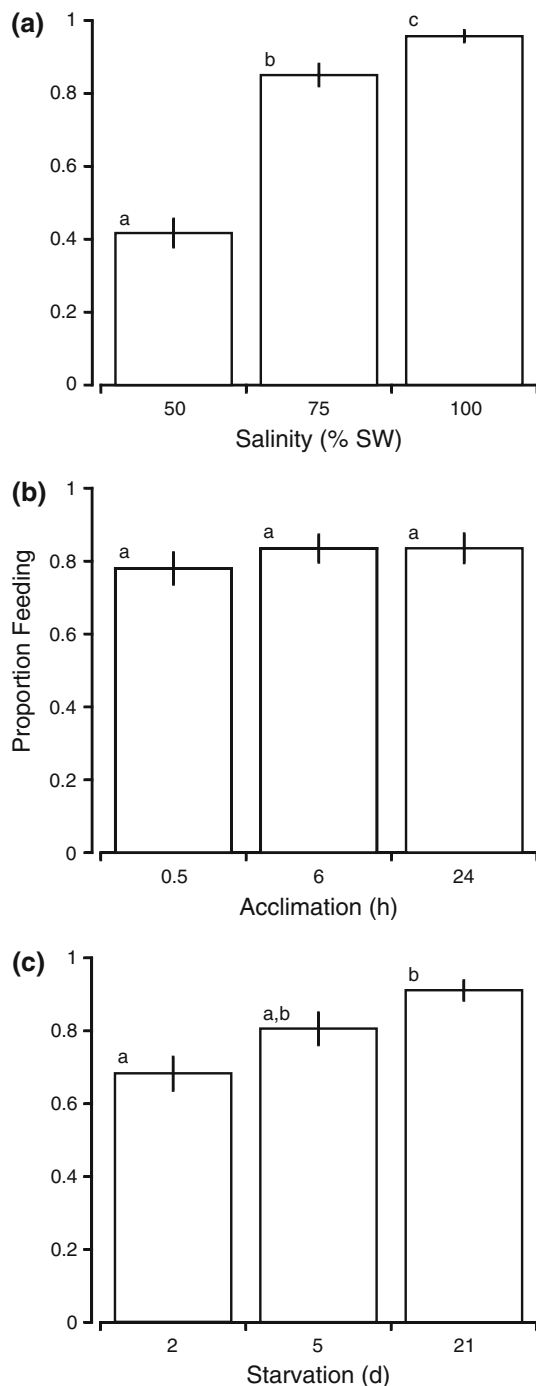


Fig. 1 The overall mean proportion (\pm SE) of crabs feeding following exposure to **a** 50, 75, or 100% SW for **b** 0.5, 6, or 24 h after **c** 2, 5, or 21 days starvation. Different letters indicate significantly different treatments

differences were observed in the 50% SW treatments; here, 21 days starvation increased the proportion of crabs feeding by threefold over the proportion that fed after 2 days starvation. This difference was significant when a post hoc test was applied ($t = 5.04$, $df = 38$, Tukey-adjusted

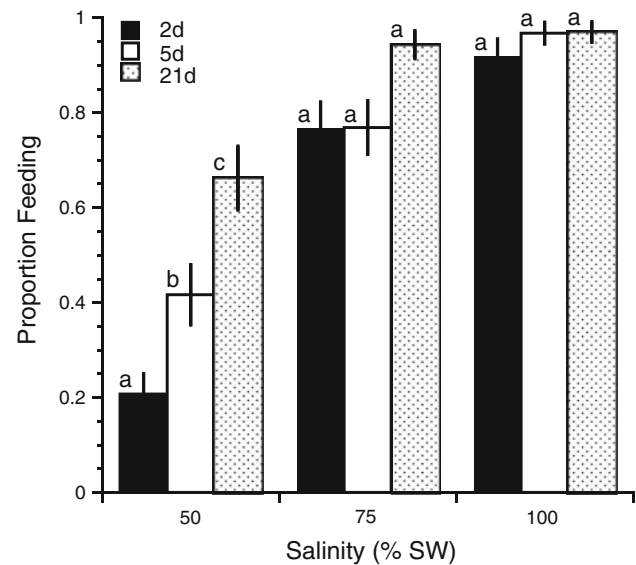


Fig. 2 The mean proportion (\pm SE) of crabs feeding following 2, 5, or 21 days starvation within each level of salinity. Within each level of salinity, different letters indicate significantly different values. Values include all levels of exposure time

$P < 0.0004$). In contrast, there was no effect of starvation time on the proportion of crabs feeding in 75 or 100% SW.

Food consumption

Given that a crab started feeding, the amount of food that it consumed varied with salinity and starvation, but not with the duration of low-salinity exposure (Table 2). The amount of food consumed by crabs in 50% SW was significantly reduced relative to those in 100% SW (Fig. 3a). There were no significant interactions among any of the treatments. Crab mass was positively related to the amount of food consumed (Table 2) and varied with the level of starvation (Table 3). This relationship resulted from

Table 2 Effects of starvation, acclimation, and salinity on the amount of food consumed

Effect	<i>df</i>	<i>F</i>	<i>P</i> value
Starvation	2, 29	7.59	0.0022
Acclimation	2, 29	1.58	0.2224
Salinity	2, 29	4.14	0.0263
Starvation* acclimation	4, 29	0.46	0.7672
Starvation* salinity	4, 29	1.85	0.1457
Acclimation* salinity	4, 29	0.38	0.8215
Starv* acclim* salin	8, 29	0.71	0.6797
Crab mass	1, 333	51.06	0.0000
Crab mass* starvation	2, 333	6.46	0.0018

The degrees of freedom (*df*) are provided as numerator, denominator *df*; bold phase denotes significant *P* values

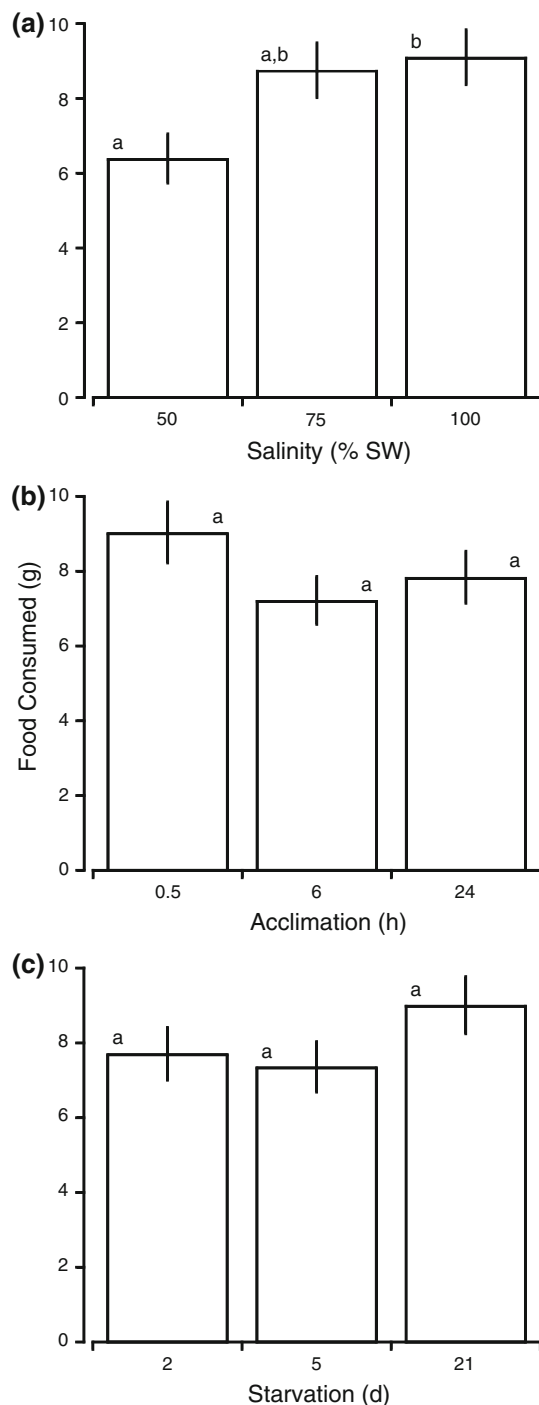


Fig. 3 The overall mean amount of food consumed (\pm SE) following exposure to **a** 50, 75, or 100% SW for **b** 0.5, 6, or 24 h after **c** 2, 5, or 21 days starvation. Different letters indicate significantly different values

smaller crabs consuming relatively larger meals following 21 days starvation (Fig. 4). Additionally, this relationship likely contributed to the significant overall effect of starvation on the amount of food consumed but masked differences between the levels of starvation (Table 2, Fig. 3a).

Time spent feeding

The amount of time crabs spent consuming a meal varied with salinity (Table 4; Fig. 5). *Cancer magister* spent almost twice as much time feeding in 100 or 75% SW compared to 50% SW (Fig. 5a). There was no significant effect of acclimation or starvation on the amount of time spent feeding, nor were there any significant interactions among the effects (Table 4; Fig. 5b, c). Larger crabs spent significantly more time feeding (Tables 3, 4; Fig. 6).

Feeding efficiency

The efficiency (food consumed in a given amount of time) with which crabs consumed a meal varied with salinity (Fig. 7; Table 5). Crabs consumed a given amount of food faster in 50% SW than in 75% SW, and there was a trend toward crabs being more efficient in 50% SW than in 100% SW, which fell just short of significance ($P = 0.08$). Starvation, acclimation time, and crab mass did not have significant effects on feeding efficiency, nor were there any interactions among the variables (Table 5).

Discussion

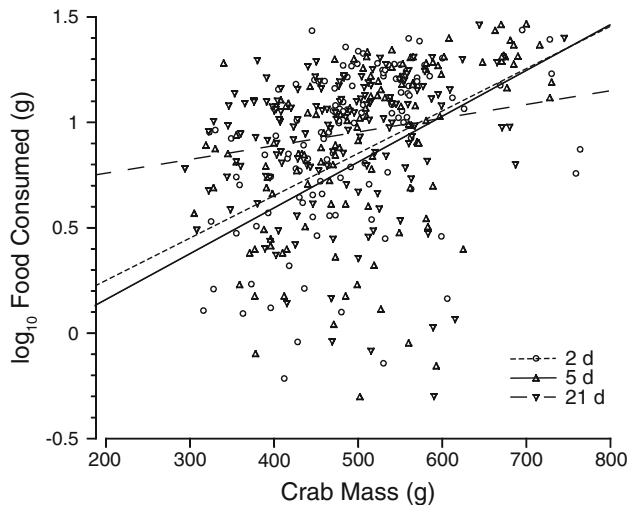
Estuaries are a habitat rich in prey and sparse in predators that provide a valuable resource for juvenile Dungeness crabs (Stevens et al. 1984; Gunderson et al. 1990). However, much less is known about the use of these habitats by adult animals. Forays into estuarine habitats by adult Dungeness crabs are most prevalent during times of high food abundance (Sugarman et al. 1983). During these forays, crabs may either actively enter into areas of low salinity or be passively exposed with the changing tide (Curtis and McGaw 2008). In either case, salinity plays a key physiological role, and it appears that *C. magister* is poorly adapted to deal with the demands of digestion while exposed to hyposaline conditions (McGaw 2006). Therefore, the benefits of feeding in such conditions must outweigh the physiological challenges (Lima and Dill 1990). The results of this study suggest that there is an interaction between the aversion to feeding resulting from low-salinity exposure and the immediacy for procuring a meal.

For such an interaction to exist, animals must be able to integrate associated environmental signals. Decapod crustaceans are able to integrate complex chemosensory signals (Cromarty and Derby 1997) via input from olfactory sensilla (Hallberg et al. 1997). Changes in environmental salinity are detected by hair-peg organs located on the legs (Schmidt 1989) and the antennules (Van Weel and Christofferson 1966), as well as receptors in the branchial chamber (Hume and Berlind 1976; Dufort et al. 2001).

Table 3 Intercept and slope for the equation: $\log_{10}(\text{dependent variable}) = \text{intercept} + \text{slope} \times \text{crab mass}$ for each significant effect, where food mass and crab wet mass were expressed in grams, and time spent feeding was expressed in minutes

Dependent variable	Duration of starvation (days)	Intercept (SE)	Slope (SE)		r^2
Food mass	2	0.2220 (0.1419)	0.0015 (0.0002)	b	0.2167
	5	0.1348 (0.1311)	0.0016 (0.0002)	b	0.3645
	21	0.7453 (0.1180)	0.0005 (0.0002)	a	0.0807
Time feeding		0.0011 (0.0002)	0.8739 (0.0956)		0.0724

Significant differences among slopes are denoted by *different letters*

**Fig. 4** The relationship between crab mass and the amount of food consumed following 2, 5, or 21 days starvation. *Trend lines* are shown for significant relationships (see Table 3 for regression details)**Table 4** Effects of starvation, acclimation, and salinity on the time spent feeding

Effect	<i>df</i>	<i>F</i>	<i>P</i> value
Starvation	2, 29	0.33	0.7220
Acclimation	2, 29	0.67	0.5193
Salinity	2, 29	8.40	0.0013
Starvation* acclimation	4, 29	0.11	0.9771
Starvation* salinity	4, 29	1.43	0.2498
Acclimation* salinity	4, 29	0.38	0.8205
Starv* acclim* salin	8, 29	0.33	0.9464
Crab mass	1, 335	23.58	0.0000

The degrees of freedom (*df*) are provided as numerator, denominator *df*; bold phase denotes significant *P* values

Cancer magister was able to discriminate between salinities separated by less than 3.5‰; the crabs would feed in 50% SW, but not in salinities lower than 40% SW. A substantial reduction in the number of crabs feeding in 50% SW compared with 75% SW suggests that crabs are integrating the degree of low-salinity exposure (Fig. 1a).

Immediately after detecting a drop in environmental salinity, *C. magister* displays behavioral (Sugarman et al. 1983; McGaw et al. 1999) and cardiovascular adjustments (McGaw and McMahon 1996). These adjustments are sensitive indicators of stress (Florey and Kriebel 1974) and take place well before any marked decrease in hemolymph osmolality, which can take over 24 h to reach new stable levels (Siebers et al. 1972; McGaw 2006). In salinities below 75% SW, *C. magister* showed a similar aversion to feeding regardless of the duration of exposure and subsequent changes in the internal milieu (Fig. 1b). Given their ability to detect small changes in external salinity (Sugarman et al. 1983) and integrate complex chemosensory signals, it seems reasonable that crabs are responding to low salinity as a nociceptive stimulus rather than decreases in hemolymph osmolality.

An interaction between low salinity and starvation also requires that animals are able to integrate nutritional status. Correspondingly, as the time since their last meal increased, so did the proportion of crabs feeding (Fig. 1c). This pattern was most apparent in 50% SW, and the increase in the proportion of crabs feeding following 21 days starvation appeared, to a large extent, to offset the decrease resulting from low-salinity exposure (Fig. 2). However, this interaction had a threshold, as crabs would not feed below 40% SW, even after 21 days starvation. This strategy would be advantageous given that postprandial crabs show increased mortality at salinities below this level (McGaw 2006). An animal's nutritional status may, therefore, tip the behavioral balance in favor of enduring low-salinity exposure in order to obtain urgently needed sustenance. A similar trade-off between nutritional status and feeding while exposed to a nociceptive stimulus has been observed for a number of benthic scavengers when presented with food and the scent of dead conspecifics (Stenzler and Atema 1977; McKillup and McKillup 1994; Moore and Howarth 1996). Thus, it appears that some of the concepts applied to animals foraging in the face of predation (Lima and Dill 1990) may also be applicable to animals foraging when exposed to environmental challenges such as low salinity (Webster and Dill 2006).

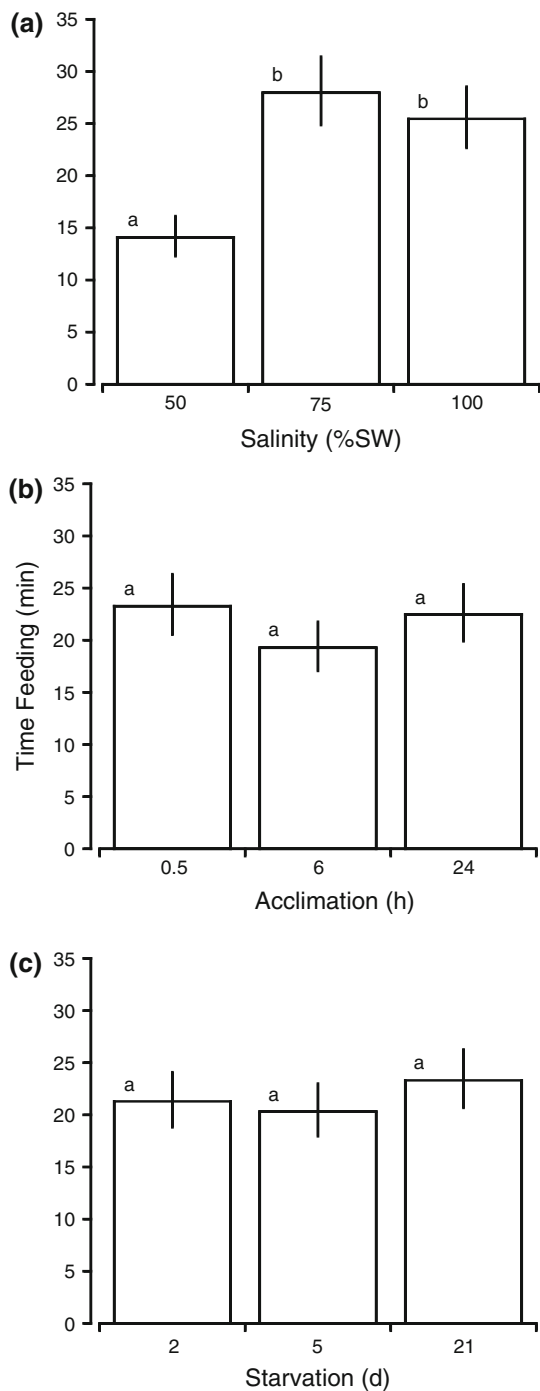


Fig. 5 The overall mean time spent feeding (\pm SE) following exposure to **a** 50, 75, or 100% SW for **b** 0.5, 6, or 24 h after **c** 2, 5, or 21 days starvation. *Different letters indicate significantly different values*

As the time since feeding increases, so too does the urgency for procuring a meal (Wang et al. 2006). When allowed to feed ad libitum, *C. magister* feeds about once per day (Curtis and McGaw, Unpublished obs.), which corresponds closely with the emptying of the foregut (Curtis and McGaw 2009). In many molluscs, appetite is a

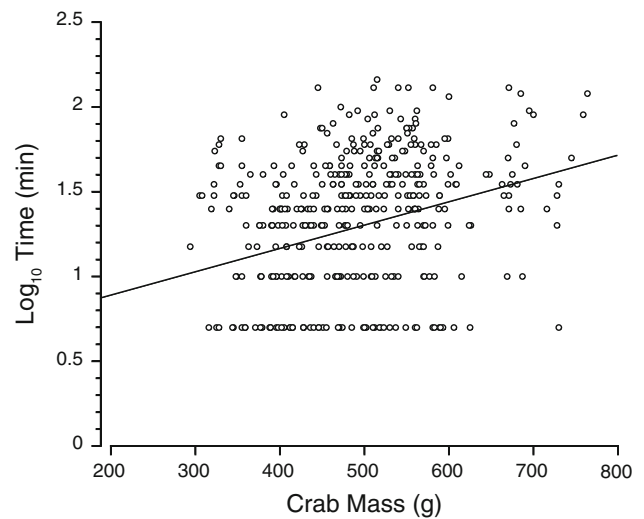


Fig. 6 The overall relationship between crab mass and the amount of time spent feeding. *Trend line* shown for significant relationship (see Table 3 for regression details)

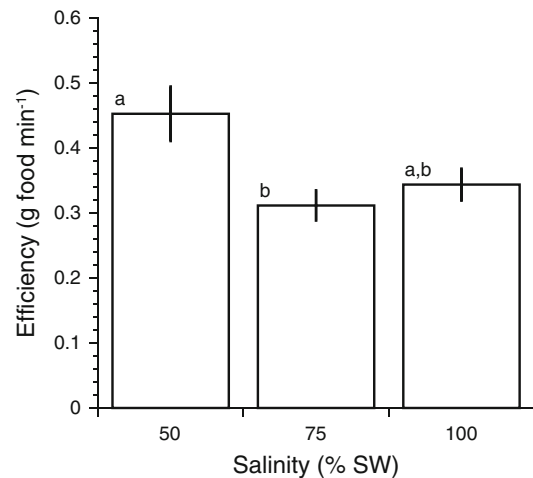


Fig. 7 The overall mean efficiency (\pm SE) with which crabs consumed a meal in 50, 75, or 100% SW. *Different letters indicate significantly different values*

Table 5 Effects of starvation, acclimation, and salinity on feeding rate (g/min)

Effect	<i>df</i>	<i>F</i>	<i>P</i> value
Starvation	2, 29	0.44	0.6491
Acclimation	2, 29	0.19	0.8290
Salinity	2, 29	4.65	0.0177
Starvation* acclimation	4, 29	0.58	0.6760
Starvation* salinity	4, 29	1.12	0.3670
Acclimation* salinity	4, 29	0.25	0.9073
Starv* acclim* salin	8, 29	1.22	0.3244
Crab mass	1, 335	1.21	0.2714

The degrees of freedom (*df*) are provided as numerator, denominator *df*; bold phase denotes significant *P* values

graded function based on gut fullness (Elliott and Susswein 2002) and recovery from the physiological demands associated with digestion may be linked to the return of appetite in dog fish (Sims and Davies 1994). Accordingly, most work examining the interplay between starvation and feeding motivation in benthic marine scavengers has only looked at a single level of starvation (Stenzler and Atema 1977; McKillup and McKillup 1994; Moore and Howarth 1996), comparing ‘hungry’ vs. ‘not hungry’ responses. In the present study, three starvation periods (2, 5, and 21 days) were used, each corresponding to a physiological change that alters the degree of urgency for procuring another meal (Wang et al. 2006). At 2 days postfeeding, crabs are no longer satiated (McGaw and Reiber 2000). At 5 days postfeeding, the physiological changes associated with digestion have passed, but no large-scale physiological changes associated with starvation have occurred within this time (Wallace 1973). By 21 days postfeeding nutritional stores are depleted, and crabs are likely relying on protein catabolism as their primary means of energy production (Wallace 1973; Sanchez-Paz et al. 2006). In *C. magister*, it appears that feeding motivation is regulated by a more complex system than satiation alone. Based on a satiation model, the crabs should have been equally likely to feed at all levels of starvation because their gut was no longer full (Elliott and Susswein 2002). However, it was not until 21 days starvation that a significant increase in the proportion of animals feeding was observed (Fig. 1c). The degree of nutritional deprivation, rather than gut fullness, appeared to be of prime importance. While a clear internal mechanism for sensing long term changes in nutritional status is difficult to substantiate, many terrestrial arthropods are able to sense nutritional deficiencies in their diet and make compensatory changes in their feeding behavior by selecting food items or portions of prey items that are rich in the deficient nutrient (Mayntz et al. 2005; Pompilio et al. 2006). Additionally, it has been shown that these animals are able to associate olfactory inputs not only with a reward, but also with the degree of reward provided (Behmer et al. 2005).

A definitive neurological or hormonal basis for the trade-off between nutritional status and low-salinity exposure has yet to be shown for *C. magister*, but it appears that both chemosensory stimuli and the degree of nutritional deprivation affect feeding behavior. In the sand fiddler crab, *Uca pugilator*, when the eye stalks are ablated, subsequently removing hormonal control exerted by the sinus gland/X-organ complex, feeding inhibition due to satiation is removed (Sears et al. 1991). This response may be due to the action of a putative hormone referred to as feeding inhibition factor (FIF). Preliminary results suggest that the anorexic effects resulting from low-salinity exposure may also be related to endocrine products originating in the

sinus gland (Curtis and McGaw, In prep.). In the current study, even after a brief (30 min) exposure to low salinity, crabs that refused to feed in low salinity did not regain their appetite for over 4 h following return to 100% SW (Curtis and McGaw, Unpublished obs.). This timing corresponds to the circulating time of FIF (Sears and Rittschof 1991), supporting the assumption that the anorexic effects resulting from low-salinity exposure are the result of a neuro-hormonal release, rather than changes in the internal osmolality of the animal.

After feeding, crabs must subsequently cope with the metabolic demands associated with digestion, referred to as apparent specific dynamic action (SDA; McCue 2006). The scope (Pan et al. 2005) and duration (Ansell 1973; Beamish 1974; Houlihan et al. 1990) of the SDA response increase with ration size, and *C. magister* is no exception (McGaw, Unpublished obs.). Low-salinity exposure resulted in a decrease in the amount of food consumed (Fig. 3a), which likely resulted in a lower overall SDA (Curtis and McGaw 2009). This reduction in SDA may be further aided by a reduction in foregut activity that slows food passage through the gut, subsequently minimizing costly downstream processes such as protein synthesis (Curtis and McGaw 2009).

While a reduction in meal size may help to facilitate foraging in low salinity, reduced caloric intake may have a negative effect on growth rates (Guerin and Stickle 1992). An alternative explanation for reduced meal sizes is that crabs simply lack the energetic resources to consume larger meals while coping with the physiological demands associated with low-salinity exposure. Such a limitation is possible since *C. magister* prioritizes the cardiovascular and ventilatory responses to low-salinity exposure over those associated with digestion (McGaw 2006). Nevertheless, the fact that the crabs consumed a given amount of food faster in low salinity (Fig. 7), and the costs of actually ingesting a meal are low (Rovero et al. 2000), would suggest that this is unlikely.

Following 21 days starvation, smaller *C. magister* consumed larger meals relative to their counterparts that had been starved for 2 or 5 days (Fig. 4). Yet, larger crabs consumed similar meal sizes regardless of starvation. The tolerance of starvation among crustaceans appears to be highly variable, with some species such as the Chinese mitten crab, *Eriocheir sinensis*, routinely surviving periods of starvation greater than 70 days (Wen et al. 2006). Within a species, however, smaller crabs seem to be more prone to food deprivation (Moir and Weissburg 2009). Smaller animals possess relatively fewer energy reserves and have higher mass specific metabolic requirements, meaning that those reserves that they do have will be more rapidly depleted (Clifford and Brick 1983). Therefore, for smaller *C. magister*, consuming larger meals may be a means of compensating for an additional nutritional deficit despite an increased SDA. An increased susceptibility to

starvation may therefore contribute to the prevalence of smaller individuals in hyposaline waters (Stevens et al. 1984).

When exposed to low salinity, *Cancer magister* spent less time feeding (Fig. 5a) and consumed a given amount of food faster (Fig. 7). The metabolic costs associated with the act of ingesting a meal are relatively low, accounting for about 2% of the energy gained from the meal (Rovero et al. 2000). It has been postulated that rather than measuring actual energy expenditure, the time spent consuming a meal may be a better metric of the cost of foraging (Juanes 1992). In the laboratory, both fed and postprandial crabs show an equal aversion to low-salinity exposure, preferring the highest salinity offered (Curtis and McGaw 2004); however, after prolonged starvation crabs spend more time in low salinity searching for food (Curtis and McGaw, In prep). Upon finding a meal, *C. magister* does not move the food to areas of higher salinity, but instead remains in these conditions to feed (Curtis and McGaw, Unpublished Obs.), and therefore, they must continue to endure the physiological demands associated with low-salinity exposure. The reduced time spent feeding in low salinity (Fig. 5) may be the result of a trade-off between the tendency toward avoidance behaviors and the necessity of procuring a meal. Additionally, increased feeding efficiency in low salinity (Fig. 7) further suggests that crabs are not energetically restricted, but rather are employing an ‘eat and run’ strategy to minimize exposure. Such a strategy is supported by field observations (Curtis and McGaw 2008). During times of high food abundance, adult *C. magister* move up into the shallow, lower salinity regions of the estuary, presumably to feed. However, these excursions into low salinity typically only last a few hours before the crabs retreat to deeper, higher salinity waters. This ‘eat and run’ behavior would minimize the need to use physiological mechanisms to cope with the simultaneous demands of digestion and osmoregulation.

In resource limited habitats, competition may force animals to reside or forage in challenging environmental conditions (Hoffman and Parsons 1993). We have shown that unless the necessity for feeding is great, inhibitory mechanisms may prevent *C. magister* from feeding in salinities below 75‰ SW. In crabs that do feed in these hyposaline environments, a reduction in the amount of food consumed may reduce the effects of SDA (Curtis and McGaw 2009), thus enhancing their ability to prioritize the physiological responses to low salinity over those of digestion. Additionally, reducing the amount of time spent feeding would minimize exposure to low salinity; while retreating to more favorable salinity conditions would allow them to digest the meal more efficiently (Curtis and McGaw 2009). Though these strategies would provide an immediate reprieve from the challenge of concurrent

osmoregulation and digestion, they may also lead to a substantial reduction in food intake and thus growth if conditions become more ephemeral and low salinity becomes more pervasive.

Acknowledgments We wish to thank the director and staff of the Bamfield Marine Sciences Centre for use of facilities. This work was supported by an NSF grant (IBN #0313765) to IJM and an NSERC postgraduate scholarship to DLC.

References

- Abrahams MV, Dill LM (1989) A determination of the energetic equivalence of the risk of predation. *Ecology* 70:999–1007
- Ansell AD (1973) Changes in oxygen consumption, heart rate and ventilation accompanying starvation in the decapod crustacean *Cancer pagurus*. *Neth J Sea Res* 7:455–475
- Barnes RSK (1967) Osmotic behaviour of a number of grapsoid crabs with respect to their differential penetration of an estuarine system. *J Exp Biol* 47:535
- Beamish FWH (1974) Apparent specific dynamic action of large-mouth bass, *Micropterus salmoides*. *J Fish Res Board Can* 31:1763–1769
- Behmer ST, Belt CE, Shapiro MS (2005) Variable rewards and discrimination ability in an insect herbivore: what and how does a hungry locust learn? *J Exp Biol* 208:3463–3473
- Clifford HC, Brick RW (1983) Nutritional physiology of the freshwater shrimp *Macrobrachium rosenbergii* (Deman). I. substrate metabolism in fasting juvenile shrimp. *Comp Biochem Physiol Physiol* 74:561–568
- Cornell JC (1974) Reduction in water exchange rates in an osmoconforming crab. *Am Zool* 14:1259
- Cromarty SI, Derby CD (1997) Multiple excitatory receptor types on individual olfactory neurons: implications for coding of mixtures in the spiny lobster. *J Comp Physiol Sens Neural Behav Physiol* 180:481–491
- Curtis DL, McGaw IJ (2004) Feeding and digestion in low salinity: behavioural adaptations to avoid physiological multitasking in the Dungeness crab *Cancer magister*. *Integr Comp Biol* 44:686
- Curtis DL, McGaw IJ (2008) A year in the life of a Dungeness crab: methodology for determining microhabitat conditions experienced by large decapod crustaceans in estuaries. *J Zool* 274:375–385
- Curtis DL, McGaw IJ (2009) Respiratory and digestive responses of postprandial Dungeness crabs, *Cancer magister*, and blue crabs, *Callinectes sapidus*, during hyposaline exposure. *J Comp Physiol B* doi: 10.1007/s00360-009-0403-z
- Curtis DL, Jensen EK, McGaw IJ (2007) Behavioral influences on the physiological responses of *Cancer gracilis*, the graceful crab, during hyposaline exposure. *Biol Bull* 212:222–231
- Dufort CG, Jury SH, Newcomb JM, O’Grady DF, Watson WH (2001) Detection of salinity by the lobster, *Homarus americanus*. *Biol Bull* 201:424–434
- Elliott CJH, Susswein AJ (2002) Comparative neuroethology of feeding control in molluscs. *J Exp Biol* 205:877–896
- Elner RW, Hughes RN (1978) Energy maximization in diet of shore crab, *Carcinus maenas*. *J Anim Ecol* 47:103–116
- Engelhardt FR, Dehnel PA (1973) Ionic regulation in Pacific edible crab, *Cancer magister* (Dana). *Can J Zool Revue Canadienne De Zoologie* 51:735–743
- Flore E, Kriebel ME (1974) Effects of temperature, anoxia and sensory stimulation on heart-rate of unrestrained crabs. *Comp Biochem Physiol* 48:285–300

- Guerin JL, Stickle WB (1992) Effects of salinity gradients on the tolerance and bioenergetics of juvenile blue crabs (*Callinectes sapidus*) from waters of different environmental salinities. *Mar Biol* 114:391–396
- Guerin JL, Stickle WB (1997) Effect of salinity on survival and bioenergetics juvenile lesser blue crabs, *Callinectes similis*. *Mar Biol* 129:63–69
- Gunderson DR, Armstrong DA, Shi YB, McConnaughey RA (1990) Patterns of estuarine use by juvenile English sole (*Parophrys vetulus*) and Dungeness crab (*Cancer magister*). *Estuaries* 13:59–71
- Hallberg E, Johansson KUI, Wallen R (1997) Olfactory sensilla in crustaceans: morphology, sexual dimorphism, and distribution patterns. *Int J Insect Morphol Embryol* 26:173–180
- Hoffman AA, Parsons PA (1993) Evolutionary genetics and environmental stress. Oxford University Press, New York
- Holsman KK, McDonald PS, Armstrong DA (2006) Intertidal migration and habitat use by subadult Dungeness crab *Cancer magister* in a NE Pacific estuary. *Mar Ecol Prog Ser* 308:183–195
- Houlihan DF, Waring CP, Mathers E, Gray C (1990) Protein synthesis and oxygen consumption of the shore crab *Carcinus maenas* after a meal. *Physiol Zool* 63:735–756
- Hume RI, Berlind A (1976) Heart and scaphognathite rate changes in a euryhaline crab, *Carcinus maenas*, exposed to dilute environmental medium. *Biol Bull* 150:241–254
- Juanes F (1992) Why do decapod crustaceans prefer small sized molluscan prey? *Mar Ecol Prog Ser* 87:239–249
- Kinne O (1966) Physiological aspects of animal life in estuaries with special reference to salinity. *Neth J Sea Res* 3:222–244
- Legeay A, Massabuau JC (2000) Effect of salinity on hypoxia tolerance of resting green crabs, *Carcinus maenas*, after feeding. *Mar Biol* 136:387–396
- Lima SL, Dill LM (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Can J Zool Revue Canadienne De Zoologie* 68:619–640
- Mayntz D, Raubenheimer D, Salomon M, Toft S, Simpson SJ (2005) Nutrient specific foraging in invertebrate predators. *Science* 307:111–113
- McCue MD (2006) Specific dynamic action: a century of investigation. *Comp Biochem Physiol Mol Integr Physiol* 144:381–394
- McGaw IJ (2006) Prioritization or summation of events? Cardiovascular physiology of postprandial Dungeness crabs in low salinity. *Physiol Biochem Zool* 79:169–177
- McGaw IJ (2007) Gastric processing and evacuation during emersion in the red rock crab, *Cancer productus*. *Mar Freshwat Behav Physiol* 40:117–131
- McGaw IJ, McMahon BR (1996) Cardiovascular responses resulting from variation in external salinity in the Dungeness crab, *Cancer magister*. *Physiol Zool* 69:1384–1401
- McGaw IJ, Reiber CL (2000) Integrated physiological responses to feeding in the blue crab *Callinectes sapidus*. *J Exp Biol* 203:359–368
- McGaw IJ, Reiber CL, Guadagnoli JA (1999) Behavioral physiology of four crab species in low salinity. *Biol Bull* 196:163–176
- McKillup SC, McKillup RV (1994) The decision to feed by a scavenger in relation to the risks of predation and starvation. *Oecologia* 97:41–48
- McKillup SC, McKillup RV (1995) The responses of intertidal scavengers to damaged conspecifics in the field. *Mar Freshwat Behav Physiol* 27:49–57
- Moir F, Weissburg MJ (2009) Cautious cannibals: behavioral responses of juvenile and adult blue crabs to the odor of injured conspecifics. *J Exp Mar Biol Ecol* 369:87–92
- Moore PG, Howarth J (1996) Foraging by marine scavengers: effects of relatedness, bait damage and hunger. *J Sea Res* 36:267–273
- Normant M, Lamprecht I (2006) Does scope for growth change as a result of salinity stress in the amphipod *Gammarus oceanicus*? *J Exp Mar Biol Ecol* 334:158–163
- Pan ZC, Ji X, Lu HL, Ma XM (2005) Metabolic response to feeding in the Chinese striped necked turtle, *Ocadia sinensis*. *Comp Biochem Physiol Mol Integr Physiol* 141:470–475
- Pompilio L, Kacelnik A, Behmer ST (2006) State dependent learned valuation drives choice in an invertebrate. *Science* 311:1613–1615
- Rovero F, Hughes RN, Chelazzi G (2000) When time is of the essence: choosing a currency for prey-handling costs. *J Anim Ecol* 69:683–689
- Sanchez-Paz A, Garcia-Carreno F, Muhlia-Almazan A, Peregrino-Urriarte AB, Hernandez-Lopez J, Yepiz-Plascencia G (2006) Usage of energy reserves in crustaceans during starvation: status and future directions. *Insect Biochem Mol Biol* 36:241–249
- Schmidt M (1989) The hair peg organs of the shore crab, *Carcinus maenas* (Crustacea, Decapoda): ultrastructure and functional properties of sensilla sensitive to changes in seawater concentration. *Cell Tissue Res* 257:609–621
- Sears MA, Rittschof D (1991) Control of chemically stimulated feeding behavior in sand fiddler crabs *Uca pugilator*: evidence for hemolymph feeding inhibitory factor. *J Chem Ecol* 17:2337–2346
- Sears MA, Rittschof D, Obrien T (1991) Eyestalk factor modulation of chemically stimulated feeding in sand fiddler crabs *Uca pugilator* (Bosc 1802). *J Exp Mar Biol Ecol* 152:1–13
- Siebers D, Lucu C, Sperling KR, Eberlein K (1972) Kinetics of osmoregulation in crab *Carcinus maenas*. *Mar Biol* 17:291–303
- Sims DW, Davies SJ (1994) Does specific dynamic action (SDA) regulate return of appetite in the lesser spotted dogfish, *Scyliorhinus canicula*. *J Fish Biol* 45:341–348
- Spaargaren DH (1973) Effect of salinity and temperature on heart rate of osmoregulating and osmoconforming shrimps. *Comp Biochem Physiol* 45:773–786
- Stenzler D, Atema J (1977) Alarm response of marine mud snail, *Nassarius obsoletus*: specificity and behavioral priority. *J Chem Ecol* 3:159–171
- Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton, NJ
- Stevens BG, Armstrong DA (1984) Distribution, abundance, and growth of juvenile Dungeness Crabs, *Cancer magister*, in Grays Harbor estuary, Washington. *Fish Bull* 82:469–483
- Stevens BG, Armstrong DA, Hoeman JC (1984) Diel activity of an estuarine population of Dungeness Crabs, *Cancer magister*, in relation to feeding and environmental factors. *J Crust Biol* 4:390–403
- Sugarman PC, Pearson WH, Woodruff DL (1983) Salinity detection and associated behavior in the Dungeness Crab, *Cancer magister*. *Estuaries* 6:380–386
- Taylor EW, Butler PJ, Alwassia A (1977) Effect of a decrease in salinity on respiration, osmoregulation and activity in shore crab, *Carcinus maenas*, at different acclimation temperatures. *J Comp Physiol* 119:155–170
- Van Weel PB, Christofferson JP (1966) Electrophysiological studies on perception in antennulae of certain crabs. *Physiol Zool* 39:317–325
- Wallace JC (1973) Feeding, starvation and metabolic rate in shore crab *Carcinus maenas*. *Mar Biol* 20:277–281
- Wang T, Hung CCY, Randall DJ (2006) The comparative physiology of food deprivation: from feast to famine. *Annu Rev Physiol* 68:223–251
- Webster SJ, Dill LM (2006) The energetic equivalence of changing salinity and temperature to juvenile salmon. *Funct Ecol* 20:621–629
- Webster SJ, Dill LM (2007) Estimating the energetic cost of abiotic conditions using foraging behaviour. *Evol Ecol Res* 9:123–143
- Wen XB, Chen LQ, Ku YM, Zhou KY (2006) Effect of feeding and lack of food on the growth, gross biochemical and fatty acid composition of juvenile crab, *Eriocheir sinensis*. *Aquaculture* 252:598–607