

Effects of temperature, body size, and starvation on feeding in a major echinoderm predator

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Abstract The common sea star, *Asterias rubens*, is a major predator in rocky subtidal ecosystems in the northern Gulf of St. Lawrence and along the Atlantic coasts of Nova Scotia and Newfoundland, Canada. We carried out two laboratory experiments to test the effects of water temperature, starvation, and body size, on mussel (*Mytilus edulis*) consumption and size selection in *A. rubens* from southeastern Newfoundland. Experiment 1 examined rates of consumption of medium (15–30 mm) mussels by small (9–15 cm) sea stars fed or starved moderately (for 3 weeks) at three temperatures representative of late summer highs (8, 11, and 15 °C) and one temperature representative of late winter lows (2 °C). Temperature and starvation did not affect consumption in summer, which was two times higher than in winter. Starvation also did not affect consumption in winter. Experiment 2 examined consumption of small (5–15 mm), medium, and large (30–45 mm) mussels by small and large (25–30 cm) sea stars fed or starved moderately or severely (for 6 weeks). Small sea stars consumed similar proportions of mussels regardless of starvation. However, large, moderately starved sea stars consumed at least two times more mussels than large, fed and large, severely starved individuals, indicating that the need to feed after a short starvation was higher in large than small *A. rubens*. Consumption of small, medium, and large mussels was, respectively, affected by the sea star's size only, size and starvation independently, and size and starvation

interactively. Collectively, our findings indicate that starvation, body size, and their interaction are key modulators of feeding in *A. rubens*, while suggesting that feeding is adaptable to thermal conditions. They also speak of the importance of considering the interplay between organismal traits and ongoing changes in ocean climate to better predict causes and consequences of alterations in predator–prey interactions.

Introduction

For most organisms, biological rate processes scale positively with increasing temperature, body size, and food intake (Brockington and Clarke 2001; Gillooly et al. 2001; Brown et al. 2004). Accordingly, a key aspect of the feeding ecology of ectothermic, specialist predators is the ability to alter feeding rates and prey size selection under thermally variable and other metabolically challenging conditions (Dahlhoff et al. 2001, 2002; Brown et al. 2004; Killen et al. 2011; Begon et al. 2014). Ectothermic specialist predators in high-latitude seasonal seas are generally exposed to considerable intra-annual variation in temperature and prey abundance (Menge and Sutherland 1987; Siddon and Witman 2003; Schiel et al. 2004; Frey and Gagnon 2015). Such predators are therefore continuously challenged, making them valuable model organisms to test predictions about plasticity in feeding rates and prey size selection (Killen et al. 2007; Frey and Gagnon 2015).

The common sea star, *Asterias rubens* (formerly *Asterias vulgaris*, Clark and Downey 1992), is a major predator in rocky subtidal ecosystems in the northern Gulf of St. Lawrence and along the Atlantic coasts of Nova Scotia and Newfoundland, Canada (Himmelman and Steele 1971; Gaymer et al. 2001a, b, 2004; Scheibling and

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Lauzon-Guay 2007). In these ecosystems, the sea star primarily consumes bivalve prey with a strong preference for the blue mussel, *Mytilus edulis* (Gaymer et al. 2001a, 2004; Wong and Barbeau 2005). In laboratory conditions, small (12–16 cm in diameter) 1-week-starved *A. rubens* from the northern Gulf of St. Lawrence: (1) mainly select medium-sized (15–30 mm in shell length) *M. edulis* when exposed to unlimited supplies of small, medium, and large individuals; and (2) reduce feeding without altering mussel size selection in the presence of a major competitor, the northern sea star, *Leptasterias polaris* (Gaymer et al. 2001a, 2002). In mussel beds, variably sized (10–24 cm) *A. rubens* predominantly select medium-sized mussels despite decreasing abundance (Gaymer and Himmelman 2002). The latter three studies and several others in eastern Canada (Himmelman and Dutil 1991; Barbeau and Scheibling 1994b; Gaymer et al. 2004; Wong and Barbeau 2005), the Baltic Sea (Anger et al. 1977), the Wadden Sea (Aguera et al. 2012), and the North Sea (Hancock 1958) demonstrate that *A. rubens* is a highly selective predator even when prey abundance is limiting. They also suggest that feeding can vary seasonally, likely in response to temperature changes.

Knowledge about the effects of temperature on feeding rates of *A. rubens* in eastern Canada is limited to experimental data, suggesting that mussel (*M. edulis*) and scallop (*Placopecten magellanicus*) consumption increases with temperature in individuals from the northern Gulf of St. Lawrence and Nova Scotia (Barbeau and Scheibling 1994a; Gaymer et al. 2002). Yet, this suggestion is based on relatively long (up to 7 days) pre-acclimation of *A. rubens* to experimental temperature treatments (Barbeau and Scheibling 1994a) or data pooled from multiple feeding experiments carried out over several summers with different temperature regimes (Barbeau and Scheibling 1994a; Gaymer et al. 2002). Arguably, shorter temperature acclimation times and replication of experiments within a same year or season to better control for possible confounding effects could yield different feeding rates, and hence different conclusions about temperature effects. Furthermore, both studies used small (8–16 cm) *A. rubens* that were starved for no more than 1 week prior to experimentation to standardize hunger levels (Barbeau and Scheibling 1994a; Gaymer et al. 2002). In natural habitats, the sea star likely undergoes longer starvation while searching for food, especially during winter when it migrates to deeper mussel beds (Himmelman and Dutil 1991; Gaymer et al. 2001b, 2002; Scheibling and Lauzon-Guay 2007). In *A. rubens*, a 3-week starvation is long enough to initiate the release of reserve material from the pyloric caeca, but not so long as to provoke a general autolysis and body shrinkage as seen during longer starvation (Hancock 1958; Jangoux and van Impe 1977). We showed in a concurrent

study that displacement and ability to contact *M. edulis* in small (9–15 cm) *A. rubens* from southeastern Newfoundland differ between fed and 3-week-starved individuals (St-Pierre and Gagnon 2015). Yet, no study has specifically examined plasticity in feeding rates and mussel size selection as it relates to starvation and its interaction with temperature and body size.

In the present study, we carried out two laboratory experiments with *A. rubens* from southeastern Newfoundland to test the hypotheses that (1) feeding rate upon the blue mussel scales positively with temperature and starvation and (2) feeding rate and mussel size selection scale positively with sea star body size and starvation (see “Materials and methods” for specific predictions). In southeastern Newfoundland, *A. rubens* withstands marked changes in sea temperature from a stable annual minimum of 0–2 °C from January to April, to 15–17 °C peaks in late August. Drops and rises of up to 8 °C over the course of only a few hours to days are frequent from June to October (Blain and Gagnon 2013; Gagnon et al. 2013; Frey and Gagnon 2015). In addressing the first hypothesis, we tested the ability of *A. rubens* to maintain feeding rates under such a thermal regime by incorporating natural thermal history into trials.

Materials and methods

Collection and acclimation of organisms prior to experimentation

Both experiments in the present study (Experiment 1 and Experiment 2) were conducted with *Asterias rubens* hand-collected by divers in January, February, May, and August 2013 at depths of 6 to 15 m between Kings Cove and Lower Horse Cove in Conception Bay (47°35′36.49″N, 52°53′21.75″W), Newfoundland (Canada). Sea stars were transported in large containers filled with seawater to the Ocean Sciences Centre (OSC) of Memorial University of Newfoundland. Upon arrival at the OSC (<6 h after collection), the sea stars were transferred to 330-L holding tanks supplied with ambient flow-through seawater pumped in from a depth of ~5 m in the adjacent embayment, Logy Bay. We kept all five-armed individuals with a body diameter of 9–15 cm (hereafter “small,” for use in Experiments 1 and 2) or 25–30 cm (hereafter “large,” for use in Experiment 2) that clung or displaced readily in the tanks, indicating that the podia functioned normally. In the present study, sea star diameter is the length of the longest axis between two opposing arm tips, as measured with a vinyl tape with a precision of 0.5 mm. We chose these size classes because (1) individuals of these sizes are sexually mature (Nichols and Barker 1984; Himmelman and Dutil 1991), therefore eliminating variation in foraging from potential behavioral

differences between mature and non-mature individuals, and (2) they were the most frequent at times of collection.

All sea stars used in the experiments were offered live blue mussels, *Mytilus edulis*, in the first 3 days of captivity to standardize hunger levels. They were then divided in three acclimation groups: “fed,” “starved for 3 weeks,” and “starved for 6 weeks.” Fed sea stars received live *M. edulis* during the 6 weeks preceding the trials. Sea stars starved for 3 weeks received live *M. edulis* during 3 weeks and were unfed during the following 3 weeks. Sea stars starved for 6 weeks were unfed during 6 weeks prior to experimentation. The two experiments were conducted over several weeks, which required the creation and maintenance of multiple groups of sea stars at various stages of starvation within the holding tanks. For small sea stars, this was done by isolating individuals of a same acclimation group and designated week of usage in 10-L plastic containers, with eight to 10 individuals per container. Each container was covered with nylon netting of 1 mm mesh to prevent escape and allow water circulation. Large sea stars were too big for the containers. They were kept in 330-L holding tanks according to their acclimation group and designated week of usage, with 16 individuals per tank. Fed sea stars in each container and tank received, respectively, 100 to 150 and 200 to 250 live mussels of 15–45 mm in shell length every 3 or 4 days. Empty mussel shells were removed prior to adding new mussels.

Sea stars are generally tolerant to prolonged (>7 weeks) periods of starvation (Valentinčič 1973; McClintock and Lawrence 1985; Rochette et al. 1994). In *A. rubens*, a starvation of 2–4 weeks is long enough to initiate the release of reserve material from the pyloric caeca (Jangoux and van Impe 1977). However, a starvation of more than 4 weeks may trigger general autolysis after depletion of reserve material (Hancock 1958; Jangoux and van Impe 1977). Accordingly, we starved sea stars for 3 and 6 weeks to measure, as required, effects of moderate (3 weeks) and severe (6 weeks) starvation on mussel consumption and size selection in *A. rubens*. There was no physical sign of autolysis, autotomy, and cannibalism during starvation in the holding tanks and during trials. Mussels were hand-collected by divers at Foxtrap (47°30′47.51″N, 52°59′50.71″W) and Petty Harbour (47°27′50.78″N, 52°42′25.47″W). They were transported in large containers filled with seawater to the OSC and kept separately in 330-L holding tanks supplied with ambient flow-through seawater.

Temperature and starvation (Experiment 1)

To test the hypothesis that feeding rate of *Asterias rubens* upon *Mytilus edulis* scales positively with temperature and starvation, we used a factorial experiment (Experiment

1), in which small *A. rubens* fed or starved 3 weeks were allowed to consume live *M. edulis* in seawater at three temperatures: 8, 11, and 15 °C. Our primary objective was to examine feeding during the last few weeks of summer, when *A. rubens* increasingly moves toward, and aggregates on, shallow mussel beds in eastern Canada (Himmelman and Dutil 1991; Gaymer and Himmelman 2002; Gaymer et al. 2002). We used 3-week-starved sea stars because we were interested in the effect of moderate starvation and its interaction with temperature at a time of year when prey are relatively abundant (Gaymer et al. 2001b; Gaymer and Himmelman 2002), and most *A. rubens* are unlikely to exhibit more advanced starvation. We chose these temperature treatments for they reflect the typical sea temperature range in southeastern Newfoundland, including the area where we collected *A. rubens*, at the time we ran the experiment (Blain and Gagnon 2013; Gagnon et al. 2013; Frey and Gagnon 2015).

We carried out the experiment three times between September 3 and 28, 2013, hereafter termed “summer” runs. Trials lasted 90 h (preliminary trials showed demonstrable mussel consumption over this period) and were conducted in three adjacent water baths (GD120L; Grant). The volume of each bath enabled running simultaneously four replicates of each of the six experimental treatments. Temperature treatments were assigned randomly to each bath in each of the three runs. On the first day of each run, four fed and four starved *A. rubens* were each introduced randomly to one of the eight 1-L plastic containers in each bath pre-filled with seawater from the holding tanks. The eight containers in each bath formed a grid of 2 × 4. Mean daily water temperature in the holding tanks varied from 11.1 to 13.6 °C (mean = 12.8 ± 0.1 °C). As a result, sea stars underwent a change in temperature of 1.5–5.4 °C. The largest changes, 4.5–5.4 °C in 33 % of trials, may qualify as a shock. However, they do occur in southeastern Newfoundland in late summer, with frequent drops and rises of up to 8 °C over the course of only a few hours to days (Blain and Gagnon 2013; Gagnon et al. 2013; Frey and Gagnon 2015).

We did not acclimate the sea stars to the experimental temperature treatments because incorporating their natural thermal history into trials was a more accurate representation of natural processes affecting sea star feeding over the short term. Moreover, the variable thermal environment to which the sea stars were exposed prior to trials made it impossible to determine a proper acclimation time for each temperature treatment. Nevertheless, the water in each container was gradually cooled or warmed to the desired experimental temperature over the 3 h that preceded the onset of each trial to facilitate the thermal transition. Upon reaching the assigned temperature treatment, 25 live mussels of 15–30 mm in shell length were added to

each container. Preliminary trials indicated that these mussel number and size class were sufficient to avoid complete depletion of mussels over 90 h. This mussel size class is also one of the preferred and readily consumed by small *A. rubens* (Gaymer et al. 2001a, 2002). At the end of each trial, we determined the number of mussels consumed by each sea star from the number of entirely eviscerated pairs of valves. We used numbers of mussels consumed in each container to calculate the mean proportion of mussels (out of 25) consumed for each temperature and starvation treatment.

We carried out a shortened version of Experiment 1 three times between March 8 and April 3, 2013, hereafter termed “winter” runs, to test the prediction that feeding in *A. rubens* is higher in summer than winter and in starved than fed individuals. This prediction stems from the argument that in ectothermic organisms metabolic rates, and hence the necessity to feed, increases with temperature and presumably starvation (Jangoux and van Impe 1977; Hart and Chia 1990; Gillooly et al. 2001; Brown et al. 2004). Sea temperature in southeastern Newfoundland is at a stable annual minimum of 0–2 °C from January to April (Blain and Gagnon 2013; Gagnon et al. 2013). Accordingly, in the winter trials we measured consumption of *M. edulis* by fed and 3-week-starved *A. rubens* at one temperature only, 2 °C. We used the same procedures as in the summer runs, except that each of the three winter runs was carried out with one water bath at 2 °C. Mean daily water temperature in the holding tanks varied from 1.2 to 2.5 °C (mean = 1.8 ± 0.1 °C). All sea stars were thus exposed to small and likely inconsequential changes in temperature of <0.8 °C. Regardless, the water in each container was gradually cooled or warmed to 2 °C during the 3 h that preceded the onset of each trial to be consistent with the summer trials.

Each of the two winter treatments and six summer treatments were replicated 12 times with four replicates in each of the three runs in each season. In both winter and summer trials, a gentle stream of air bubbles was pushed continuously in each container with aquarium pumps (Maxima, Hagen) to maintain oxygenation. Each trial was run with new sea stars and mussels.

Body size and starvation (Experiment 2)

To test the hypothesis that feeding rate and size selection of *Asterias rubens* upon *Mytilus edulis* scale positively with sea star body size and starvation, we used a factorial experiment (Experiment 2) in which small and large *A. rubens* fed or starved 3 or 6 weeks were allowed to consume live *M. edulis* in three size classes (shell length, in mm): 5–15 (small), 15–30 (medium), and 30–45 (large). We carried out the experiment during the first few weeks of

summer, when *A. rubens* exhibits sustained feeding in eastern Canada (Gaymer and Himmelman 2002; Gaymer et al. 2004; Himmelman et al. 2005). We used sea stars of different sizes and starvations to test the prediction that mussel consumption is higher in large than small individuals and increases with duration of starvation. This prediction stems from the argument that in ectothermic organisms, metabolic rates scale positively with body size and, presumably, starvation (Jangoux and van Impe 1977; Gillooly et al. 2001; Brown et al. 2004). We used 3- and 6-week-starved sea stars because both starvation levels are likely at this time of year when *A. rubens* recovers from prolonged (~5 months) exposure to cold water at over-wintering depths where mussels are largely absent (Himmelman and Dutil 1991; Blain and Gagnon 2013; Gagnon et al. 2013). We used mussels ≤ 45 mm because *A. rubens* feeds primarily on mussels below this size (Gaymer and Himmelman 2002), and most mussel beds accessible to *A. rubens* in southeastern Newfoundland are dominated by individuals below this size (P. Gagnon, unpubl data). We predicted that small *A. rubens* would select smaller mussels than large *A. rubens* and that the sea star would be less and less selective with increasing duration of starvation regardless of body size.

We carried out the experiment three times between June 22 and July 11, 2013. Trials lasted 72 h, which allowed sea stars to consume a few but not all mussels as determined from preliminary trials. They were conducted in 75-L glass tanks [62 × 31 × 43 cm (L, W, H)] supplied with ~ 1 L min⁻¹ of flow-through seawater. Water depth in each tank was ~ 40 cm. Each tank was surrounded by an opaque canvas to eliminate light and visual stimuli from the laboratory. One incandescent, 100-W light bulb (Soft White, SYLVANIA) located at 45 cm above the water in each tank and controlled with rheostat and timer was used to create similar light conditions among tanks. We used a daily cycle of 16 h of light from 0500 to 2100 hours and 8 h of darkness from 2100 to 0500 hours to be consistent with the natural photoperiod when the experiment was run. Each sea star in each tank was offered one aggregate of 60 mussels in the centre of the tank. Each aggregate consisted of 20 individuals in each size class (small, medium, and large) intermingled in a 10-cm Petri dish. Aggregates were introduced to the tanks 15 min prior to the start of trials. Each trial began with the introduction to each tank of one sea star on top of the mussel aggregate. Sea stars were placed on the mussels to eliminate searching time and provide each sea star with the same amount of time (72 h) to consume mussels. At the end of each trial, we determined the number of mussels consumed by each sea star in each size class from the numbers of entirely eviscerated pairs of valves. We used numbers of mussels consumed in each size class to calculate the mean proportion of mussels (out of 60) consumed for each sea star body size and starvation treatment.

Each of the six treatments was replicated 12 times with four replicates in each of the three runs. In each run, the tanks were grouped in four blocks of six tanks. Each tank in each block was randomly assigned to one of the six treatments. Tanks were scrubbed with towels, emptied, and filled with new seawater in the hours preceding each trial. Mean daily water temperature in the tanks varied from 6.9 to 11.5 °C (mean = 8.9 ± 0.05 °C). Each trial was run with new sea stars and mussels.

Statistical analysis

Experiment 1: We used a two-way ANOVA with the factors Temperature (8, 11, and 15 °C) and Starvation (fed or starved sea stars) to examine the effects of temperature and starvation on the proportion of mussels consumed by *Asterias rubens* during summer. We treated this analysis as a particular case of the generalized linear model to correct for heteroscedasticity and deviation of residuals from normality detected in the first place with a classical linear model. We used a binomial distribution of the residuals because the response variable was a proportion (McCullagh and Nelder 1989; Bolker et al. 2008). No binomial variation was detected. Prior to running this two-way ANOVA, we used a one-way ANOVA (generalized linear model with a binomial distribution) with the factor Run (each of the three runs of four replicates of each treatment) to determine whether results differed among runs. There was no significant effect of Run ($\chi^2 = 0.58$, $p = 0.753$), and hence, we ran the two-way ANOVA on data pooled from all runs. One starved sea star died during one of the trials at 11 °C. This data point was excluded from the analysis, yielding a sample size (n) of 71. We used a two-tailed t test (two-sample assuming unequal variances) to determine whether the proportion of mussels consumed differed between fed and starved sea stars during winter ($n = 24$).

We carried out a randomization (permutation) test (Sokal and Rohlf 2012) to test for a difference in the proportions of mussels consumed between winter and summer. We determined the probability of obtaining the observed difference between group means ($D_0 = 21.7\%$) by calculating the proportion of values higher than D_0 (one-tail test) in a frequency distribution of 999 randomized differences. Each randomized difference was the difference between means for two groups of proportions ($n = 24$ and 71) drawn randomly from the 95 original proportions (24 in winter and 71 in summer) of mussels consumed. We preferred this statistical approach over a Student's t test because it involves no assumption about the frequency distribution of the test statistic, and hence is a more robust approach to dealing with non-normal residuals and unequal sample sizes (Sokal and Rohlf 2012). All analyses were applied to the raw data.

Experiment 2: We used a two-way ANOVA with the factors Size (small or large sea stars) and Starvation (fed, starved for 3 weeks, and starved for 6 weeks) to examine the effects of body size and starvation on the proportion of mussels consumed by *A. rubens* regardless of mussel size. Prior to running this two-way ANOVA, we used a two-way ANOVA with the factors Run (each of the three runs of four replicates of each treatment) and Block (each of the four blocks of one replicate of each treatment within a run) to determine whether results differed among runs and blocks. There was no significant effect of Run ($F_{2,62} = 0.38$, $p = 0.687$) or Block ($F_{3,62} = 1.68$, $p = 0.181$), and hence, we ran the two-way ANOVA on data pooled from all runs and blocks. Three large fed sea stars spawned during trials, and we miscounted the initial number of mussels offered to one large 3-week-starved sea star. These four data points were excluded from the analysis, yielding a sample size (n) of 68.

We used a two-way MANOVA with the factors Size (small or large sea stars) and Starvation (fed, starved for 3 weeks, and starved for 6 weeks) to examine the effects of body size and starvation on the proportion of mussels in each of three size classes (small, medium, and large) consumed by *A. rubens*. Prior to running this two-way MANOVA, we used a two-way MANOVA with the factor Run (each of the three runs of four replicates of each treatment) and Block (each of the four blocks of one replicate of each treatment within a run) to determine whether results differed among runs and blocks. There was no significant effect of Run ($F_{2,62} = 0.65$, $p = 0.691$) or Block ($F_{3,62} = 0.65$, $p = 0.753$), and hence, we ran the two-way MANOVA on data pooled from all runs and blocks. We excluded the same four data points as in the analysis described above, yielding a sample size (n) of 68. All analyses were applied to the raw data.

In all ANOVA and MANOVA, homogeneity of the variance was verified by examining the distribution of the residuals. Normality of the residuals was verified by examining the normal probability plot of the residuals (Snedecor and Cochran 1989). To detect differences among levels within a factor (ANOVA and MANOVA), we used Tukey HSD multiple comparison tests (comparisons based on least-square means; Sokal and Rohlf 2012). When a factor or interaction between factors was significant in the MANOVAs, we examined the univariate model for the response variables to identify those that contributed to the multivariate effect. This was done by conducting an ANOVA for the response variable with those factors that were significant in the MANOVA (Scheiner and Gurevitch 2001). The Pillai's trace multivariate statistic is more robust than other multivariate statistics to deviations from homoscedasticity and normality of the residuals. It is also more conservative with small and uneven sample sizes. We therefore, used it in the

MANOVA to determine which factor(s) were statistically significant (Scheiner and Gurevitch 2001). A significance level of 0.05 was used in all analyses, which were carried out with R 2.15.2. All means are presented with standard errors (mean \pm SE) unless stated otherwise.

Results

Temperature and starvation (Experiment 1)

Analysis of data from Experiment 1 indicated that the proportion of mussels consumed by small *Asterias rubens* during summer was not affected by temperature within the 8–15 °C range nor differed between fed and 3-week-starved individuals (Table 1). The proportion of mussels consumed varied non-significantly from 28.0 ± 6.5 % in fed sea stars at 8 °C, to 49.1 ± 6.4 % in 3-week-starved individuals at 11 °C (Fig. 1). Consumption during winter in water at 2 °C

Table 1 Summary of two-way ANOVA (generalized linear model with binomial distribution, applied to raw data) examining the effect of temperature (8, 11, and 15 °C) and starvation (fed and starved sea stars) on the proportion (out of 25) of mussels (*Mytilus edulis*) consumed by sea stars (*Asterias rubens*) during summer in Experiment 1

Source of variation	df	χ^2	p
Temperature	2	4.23	0.120
Starvation	1	2.28	0.131
Temperature \times Starvation	2	0.64	0.726

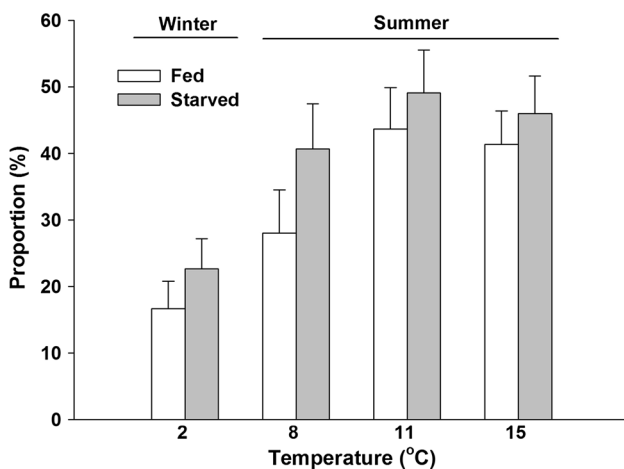


Fig. 1 Mean (+SE) proportion (out of 25) of mussels (*Mytilus edulis*) consumed by small, fed or 3-week-starved sea stars (*Asterias rubens*) in seawater at 2 °C in winter, and at 8, 11, and 15 °C in summer (Experiment 1). Temperature treatments not bracketed by the same horizontal line are different (data pooled across Temperature and Starvation treatments for the winter versus summer comparison; randomization test, $p < 0.001$, $n = 24$ and 71 for winter and summer, respectively)

also did not differ between fed (16.7 ± 4.1 %) and 3-week-starved (22.7 ± 4.5 %) sea stars ($t_{0.05(2),22} = -0.981$, $p = 0.337$; Fig. 1). However, sea stars consumed two times more mussels in summer (41.4 ± 2.5 %) than winter (19.7 ± 3.1 %) (randomization test, $p < 0.001$, Fig. 1).

Body size and starvation (Experiment 2)

Analysis of data from Experiment 2 indicated that the proportion of mussels consumed by *Asterias rubens* varied with body size among levels of starvation (a significant interaction between the factors Size and Starvation, Table 2). The proportion of mussels consumed ranged from 4.6 ± 3.5 % in large fed sea stars, to 30.6 ± 4.3 % in large 3-week-starved individuals (Fig. 2). Starvation had no perceptible effects on small sea stars as shown by the non-significant differences in mussels consumed by fed and starved individuals (Fig. 2). However, starvation affected large sea stars, with six times and two times more mussels

Table 2 Summary of two-way ANOVA (applied to raw data) examining the effect of size (small and large sea stars) and starvation (fed, 3-week-starved, and 6-week-starved sea stars) on the proportion (out of 60) of mussels (*Mytilus edulis*) consumed by sea stars (*Asterias rubens*) in Experiment 2

Source of variation	df	MS	F value	p
Size	1	0.01	0.37	0.546
Starvation	2	0.13	9.09	<0.001
Size \times Starvation	2	0.06	4.19	0.020
Error	62	0.01		
Corrected total	67			

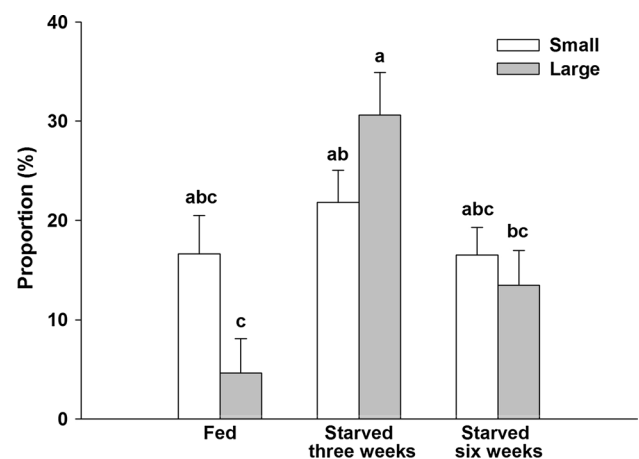


Fig. 2 Mean (+SE) proportion (out of 60) of mussels (*Mytilus edulis*) consumed by small and large, fed or starved sea stars (*Asterias rubens*) (Experiment 2). Bars not sharing the same letter are different (LS means tests, $p < 0.05$; $n = 12$ for each combination of Size \times Starvation, except 9 in large fed sea stars and 11 in large 3-week-starved sea stars)

Table 3 Summary of two-way MANOVA (applied to raw data) examining the effect of size (small and large sea stars) and starvation (fed, 3-week-starved, and 6-week-starved sea stars) on the proportion (out of 20) of mussels (*Mytilus edulis*) in three size classes (small, medium, and large) consumed by sea stars (*Asterias rubens*) in Experiment 2

Source of variation	Pillai	F value	NumDF	DenDF	p
Size	0.052	21.69	3	60	<0.001
Starvation	0.277	3.28	6	122	0.005
Size × Starvation	0.270	3.17	6	122	0.006

Table 4 Summary of two-way ANOVAs (applied to raw data) examining the effect of size (small and large sea stars) and starvation (fed, 3-week-starved, and 6-week-starved sea stars) on the proportion (out of 20) of mussels (*Mytilus edulis*) in three size classes (small, medium, and large) consumed by sea stars (*Asterias rubens*) in Experiment 2

Mussel size class	Source of variation	df	MS	F value	p
Small (5–15 mm)	Size	1	0.194	22.61	<0.001
	Starvation	2	0.012	1.34	0.268
	Size × Starvation	2	<0.001	0.08	0.924
	Error	62	0.009		
	Corrected total	67			
Medium (15–30 mm)	Size	1	0.126	5.00	0.029
	Starvation	2	0.123	4.87	0.011
	Size × Starvation	2	0.034	1.33	0.272
	Error	62	0.025		
	Corrected total	67			
Large (30–45 mm)	Size	1	0.379	11.15	0.001
	Starvation	2	0.392	11.55	<0.001
	Size × Starvation	2	0.315	9.28	<0.001
	Error	62	0.034		
	Corrected total	67			

consumed in 3-week-starved individuals than in fed and 6-week-starved individuals, respectively (Fig. 2).

The MANOVA showed that body size and starvation affected the proportion of mussels consumed by *A. rubens* among the three mussel size classes (a significant interaction between the factors Size and Starvation, Table 3). However, effects of body size and starvation differed among mussel size classes (Table 4). Consumption of small (5–15 mm) mussels was influenced by body size only, being five times higher in small (13.2 ± 2.0 %) than large (2.5 ± 0.1 %) sea stars (Table 4; Fig. 3). Consumption of medium (15–30 mm) mussels was affected by body size and starvation independently, being ~1.5 times higher in small (22.2 ± 2.7 %) than large (13.6 ± 3.2 %)

sea stars, and two times higher in 3-week-starved individuals (26.3 ± 4.0 %) than fed (12.6 ± 3.6 %) individuals (Table 4; Fig. 3). Consumption of large (30–45 mm) mussels peaked to 61.4 ± 6.2 % in large 3-week-starved sea stars (Fig. 3) and varied with body size among levels of starvation (a significant interaction between the factors Size and Starvation, Table 4). It varied non-significantly with starvation in small sea stars and was at least two times higher in large, 3-week-starved individuals than in large, fed and 6-week-starved individuals, and small individuals of any starvation level (Fig. 3).

Discussion

The present study demonstrates that body size and starvation strongly affect mussel (*Mytilus edulis*) consumption and size selection in *Asterias rubens* from southeastern Newfoundland. It also shows that mussel consumption is unaffected by short-term (hours to days) variation in water temperature in late summer, when the sea star increasingly moves toward and aggregates on shallow mussel beds in eastern Canada (Himmelman and Dutil 1991; Gaymer et al. 2001b, 2002; Gaymer and Himmelman 2002).

Experiment 1 showed that in September, small (9–15 cm), fed and 3-week-starved *A. rubens* can maintain feeding upon medium-sized (15–30 mm) mussels despite temperature changes of up to 5.4 °C within the 8–15 °C range. Sea temperature in southeastern Newfoundland frequently drops and rises by up to 8 °C over the course of only a few hours to days from June to October (Blain and Gagnon 2013; Gagnon et al. 2013; Frey and Gagnon 2015). Accordingly, we did not acclimate sea stars to their experimental temperature treatments to account for effects of natural thermal history on feeding. Barbeau and Scheibling (1994a) studied effects of temperature on predation of sea scallops (*Placopecten magellanicus*) by *A. rubens* from Nova Scotia. They found that small (8–10 cm) *A. rubens* consumed nearly four times more scallops at 15 than 8 °C during summer, which, contrary to our finding, suggests that feeding in *A. rubens* increases with temperature. Sea stars in the latter study were pre-acclimated for 5–7 days to their experimental temperature treatments (Barbeau and Scheibling 1994a). In general, feeding rates in most ectothermic organisms scale positively with temperature as a result of increased metabolism (Brockington and Clarke 2001; Gillooly et al. 2001; Brown et al. 2004). We propose that the inconsistent outcomes between the present study and that of Barbeau and Scheibling (1994a) are partly caused by differences in metabolic adjustment times of *A. rubens* prior to experimentation. More studies are needed to increase knowledge about the metabolic cascades ensuing from variation in the thermal environment and their effects on

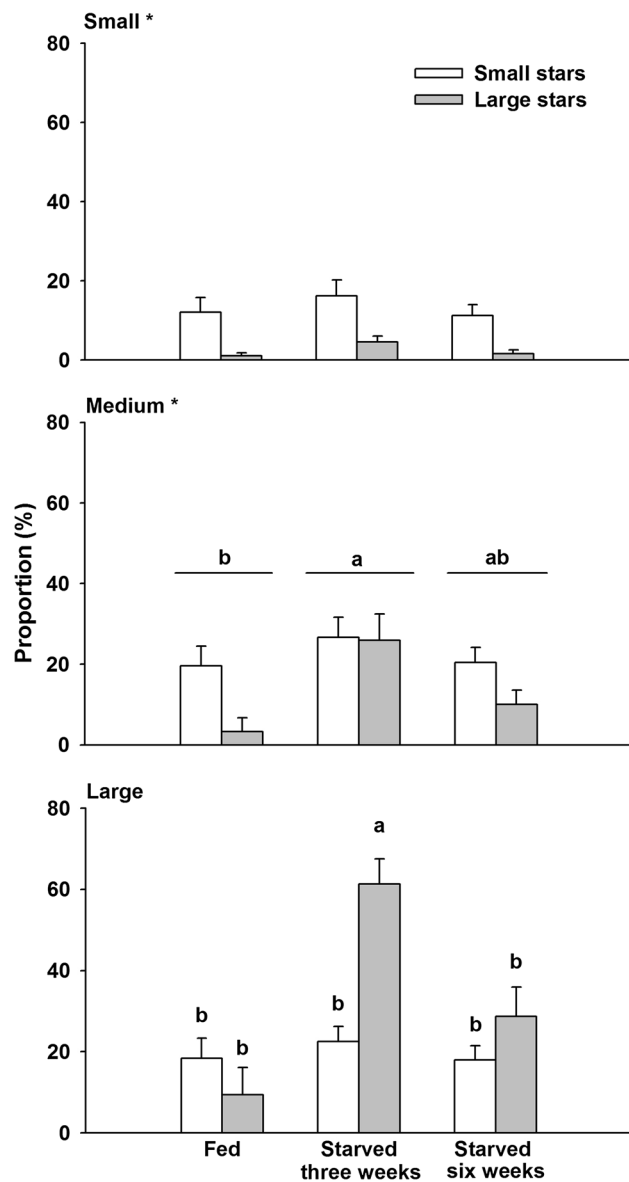


Fig. 3 Mean (+SE) proportion (out of 20) of mussels (*Mytilus edulis*) in three size classes (*small*, *medium*, and *large*) consumed by small and large, fed or starved sea stars (*Asterias rubens*) (Experiment 2). Panels with an asterisk indicate a significant difference in proportions between sea star sizes (small > large; data pooled across Starvation treatments). Bars not bracketed by the same horizontal line or not sharing the same letter (data pooled across sea star sizes for the medium mussel size class) are different (LS means tests, $p < 0.05$; $n = 12$ for each combination of sea star Size \times Starvation, except 9 in large fed sea stars and 11 in large 3-week-starved sea stars)

feeding rates in *A. rubens*. Yet, that mussel consumption in the present study did not vary appreciably with temperature between 8 and 15 °C indicates that *A. rubens* from southeastern Newfoundland can adapt to short-term shifts in water temperature during the warmer summer season.

Our finding in Experiment 1 that *A. rubens* consumed 52 % less mussels in winter than summer, when mean

sea temperature was, respectively, ~2 and ~13 °C, suggests that long-term (seasonal) shifts in temperature have a profound effect on feeding. In northern seas, *M. edulis* meat weight and protein and glycogen contents vary seasonally, being lowest in late winter (Zandee et al. 1980; Okumuş and Stirling 1998). Sea stars in our experiment would have had to consume a greater number of mussels in winter than summer to obtain the same amount of energy, which was not the case. Hence, it appears that the lower feeding rate in winter was largely caused by the prolonged (several months) exposure of sea stars to near-zero temperatures lowering their metabolism, and to a much lesser extent by reduced mussel profitability. Other environmental factors such as day length, salinity, and dissolved oxygen also vary seasonally in northern seas (Pinet 2011) and may have affected *A. rubens*. However, the effect of such factors would have been negligible compared to that of temperature, which is generally regarded as the primary modulator of metabolism and foraging in ectothermic organisms (Gillooly et al. 2001; Brown et al. 2004; Harley 2013). Studies of *A. rubens* in Europe also showed lower feeding in winter than summer (Hancock 1958; Anger et al. 1977; Aguera et al. 2012).

In a concurrent study, Frey and Gagnon (2015) showed that kelp consumption in early summer (June–July) by green sea urchins (*Strongylocentrotus droebachiensis*) from southeastern Newfoundland obeyed a nonlinear, size- and temperature-dependent relationship. Feeding in large urchins was consistently highest and positively correlated with temperature <12 °C and dropped within and above the 12–15 °C tipping range (Frey and Gagnon 2015). As in Experiment 1, urchins in the latter study were not pre-acclimated to experimental temperature treatments, which ranged from 3 to 18 °C. Yet, the authors modeled mean daily rates of kelp bed destruction by urchin fronts over nearly 3 months with an accuracy of 88 % based on temperature-dependent relationships derived from an experiment similar to Experiment 1, sea temperature, and urchin abundance at one subtidal site (Frey and Gagnon 2015). Collectively, these findings speak of the importance of considering natural variation in sea temperature at multiple temporal scales if we are to accurately predict causes and consequences of alterations to predator–prey interactions.

Results of Experiment 2 supported the conclusion from Experiment 1 that moderate (3 weeks) starvation has no perceptible effect on mussel consumption by small *A. rubens*. We also found with Experiment 2 that consumption by small, severely (6 weeks) starved sea stars was similar to that by small, fed and moderately starved individuals. In contrast, consumption by large (25–30 cm), moderately starved *A. rubens* was: (1) six times higher than that by large, fed individuals; and (2) two times higher than that by large, severely starved ones. These findings have two

important conceptual implications. Firstly, they indicate that the need to feed after a relatively short period (~3 weeks) of food deprivation is considerably higher in large than small *A. rubens*. Sea stars, including *A. rubens* in eastern Canada, often form dense feeding aggregations in mussel beds (Sloan and Aldridge 1981; Dare 1982; Gaymer and Himmelman 2002; Scheibling and Lauzon-Guay 2007). Once sea star aggregations eliminate mussels and other prey from an area, they move away in search of other prey patches (Sloan 1980; Menge 1982; Robles et al. 1995; Gaymer et al. 2001b). By being less sensitive than large conspecifics to the effects of starvation, small *A. rubens* should be better adapted to low food conditions, and hence resume normal feeding more quickly upon reaching the next patch of prey. Secondly, they indicate that large *A. rubens* attempt to increase prey consumption when starvation does not exceed ~3 weeks, while suggesting greater breakdown of reserve material from specialized organs when starvation exceeds ~3 weeks. This suggestion is based on several studies showing that the release of reserve material from pyloric caeca in *A. rubens* and other species of sea stars occurs during up to 4 weeks of starvation, after which general autolysis occurs (Chia 1969; Jangoux and van Impe 1977; Xu and Barker 1990). If large *A. rubens* in Experiment 2 had pyloric reserves that they could use for up to 6 weeks, then mussel consumption after 6 weeks of starvation would have been at least as high as after 3 weeks of starvation. Yet, consumption was half lower in 6-week-starved sea stars than 3-week-starved sea stars, suggesting that general autolysis had begun between 3 and 6 weeks of starvation. Our results also suggested that small *A. rubens* were much less reliant on pyloric reserves for mussel consumption was similar among small, fed and 3- and 6-week-starved individuals.

The universal quarter-power allometric relationship by which biological rate processes in most animals scale with body size (Gillooly et al. 2001) helps explain why the suggested depletion of pyloric reserves occurred in large but not small *A. rubens*. Indeed, the mass-specific metabolic rate of an organism, B/M , scales with body mass, M , such that $B/M \propto M^{-1/4}$. Accordingly, large sea stars must, in theory, sustain a higher metabolic rate than smaller individuals, and hence deplete their pyloric reserves more quickly. However, Raymond et al. (2007) found that the energetic content (lipids and carbohydrates) of pyloric caeca in *A. rubens* decreased during one spawning season in the northern Gulf of St. Lawrence. We did not measure pyloric caeca in the present study, and hence, we cannot rule out the possibility that pyloric reserves may have been affected by reproduction. We reduced this potential effect by discarding the only sea star that spawned prior to trials, as well as trials during which sea stars spawned (3 out of 72).

Experiment 2 also showed that consumption of small (5–15 mm), medium (15–30 mm), and large (30–45 mm)

mussels by *A. rubens* was, respectively, affected by the sea star's size only, size and starvation independently, and size and starvation interactively. This finding indicates that an increasingly complex set of morphological and physiological variables affects the ability of *A. rubens* to consume mussels as both organisms grow larger. Size therefore matters, which aligns with the empirical demonstration that feeding rates in *A. rubens* from the Baltic Sea increase more than cubically with the size of the sea star and more than linearly with its body mass (Sommer et al. 1999). Hummel et al. (2011) studied consumption of *M. edulis* in five size classes by *A. rubens* from the Wadden Sea. They found that the sea star generally selects mussels smaller than those with the highest profitability (i.e., the ratio of prey energy content to the time required for handling the prey, Emlen 1966; MacArthur and Pianka 1966; Hummel et al. 2011). A similar inclination to feed upon energetically suboptimal prey sizes has been shown in other types of predators, including green crab (*Carcinus maenas*, Johnstone and Norris 2000), Dungeness crab (*Metacarcinus magister*, formerly *Cancer magister*, Juanes and Hartwick 1990), and oystercatcher (*Haematopus ostralegus*, Smallegange and Van der Meer 2003). It is generally regarded as a mechanism to avoid damaging predatory organs when attempting to penetrate or crush larger and harder shelled prey (Juanes and Hartwick 1990; Johnstone and Norris 2000; Smallegange and Van der Meer 2003; Hummel et al. 2011). Small *A. rubens* in Experiment 2 consumed higher proportions of small and medium mussels than large sea stars, which consumed higher proportions of large mussels than small sea stars. Moreover, large, moderately starved sea stars consumed six times more large mussels than large, fed sea stars. These findings support the notion that *A. rubens* selects mussels according to profitability, while demonstrating that starvation can alter the normal pattern of consumption of large mussels by large sea stars.

The present study is the first examination of the factors that cause variation in mussel (*M. edulis*) consumption and size selection in *A. rubens* from southeastern Newfoundland. We conclude that body size and starvation are key modulators of the sea star's inclination and ability to feed. Feeding seems adaptable to thermal conditions, being relatively high and constant in late summer despite considerable variation in sea temperature, and much lower in winter when temperature is stable and about 11 °C lower. Further experimental and mensurative studies of interactions between *A. rubens* and *M. edulis* at multiple sites spanning broad geographical, thermal, and hydrodynamic ranges are required to test the generality of our findings. In a concurrent study, we showed that wave action and starvation modulate displacement, microhabitat selection, and ability to contact mussels in small *A. rubens* from southeastern Newfoundland (St-Pierre and Gagnon 2015). Collectively, these findings speak of the importance of considering the interplay between organismal traits and ongoing changes in

ocean climate to better predict causes and consequences of alterations in predator–prey interactions.

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