

Prey selection and the functional response of sea stars (*Asterias vulgaris* Verrill) and rock crabs (*Cancer irroratus* Say) preying on juvenile sea scallops (*Placopecten magellanicus* (Gmelin)) and blue mussels (*Mytilus edulis* Linnaeus)

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Abstract

Predators in nature include an array of prey types in their diet, and often select certain types over others. We examined (i) prey selection by sea stars (*Asterias vulgaris*) and rock crabs (*Cancer irroratus*) when offered two prey types, juvenile sea scallops (*Placopecten magellanicus*) and blue mussels (*Mytilus edulis*), and (ii) the effect of prey density on predation, prey selection, and component behaviours. We quantified predation rates, behavioural components (proportion of time spent searching for prey, encounter probabilities) and various prey characteristics (shell strength, energy content per prey, handling time per prey) to identify mechanisms underlying predation patterns and to assess the contribution of active and passive prey selection to observed selection of prey. Sea stars strongly selected mussels over scallops, resulting from both active and passive selection. Active selection was associated with the probability of attack upon encounter; it was higher on mussels than on scallops. The probability of capture upon attack, associated with passive selection, was higher for mussels than for scallops, since mussels can not swim to escape predators. Sea stars consumed few scallops when mussels were present, and so did not have a functional response on scallops (the target prey). Rock crabs exhibited prey switching: they selected mussels when scallop density was very low, did not select a certain prey type when scallop density was intermediate, and selected scallops when scallop density was high relative to mussel density. The interplay between encounter rate (associated with passive selection) and probability of consumption upon capture (associated with both active and passive selection) explained observed selection by crabs. Scallops were encountered by crabs relatively more often and/or mussels less often than expected from random movements of animals at all scallop densities. However, the probability of consumption varied with scallop density: it was lower for scallops than mussels at low and intermediate scallop densities, but tended to be higher for scallops than mussels at high scallop densities. When mussels were absent, crabs did not have a functional response on scallops, but rather were at the plateau of the response. When mussels were present with scallops at relatively low density, crabs exhibited a type II functional response on scallops. Our results have implications for the

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provision of protective refuges for species of interest (i.e., scallops) released onto the sea bed, such as in population enhancement operations and bottom aquaculture.

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1. Introduction

Predators in nature often include an array of prey types in their diet. Further, in the presence of multiple prey types, they often select certain prey types over others. Selection for a certain prey type is evident when the relative frequency of that prey type in a predator's diet differs from its relative frequency in the environment (Chesson, 1978). An observed selection may result from predators actively choosing a prey type (a process termed active selection) (Rapport and Turner, 1970; Liszka and Underwood, 1990; Sih and Moore, 1990). Alternatively, an observed selection may simply reflect the prey's vulnerability or catchability (a process termed passive selection) (Patterson, 1981; Sih and Moore, 1990). The observed selection may also result from a combination of both active and passive selection (Barbeau and Scheibling, 1994). Active selection (or active predator choice) occurs when a predator consumes more of a prey type than expected when given a choice of prey types than when not given a choice (Underwood et al., 2004). The prey choice model of foraging theory can be a useful conceptual framework for studying active selection (Sih and Moore, 1990; Barbeau and Scheibling, 1994). The prey choice model predicts that, to maximize energy intake per unit foraging time, a predator consumes prey items of higher profitability (ratio of energy gain to handling time) and ignores items of lower profitability (Stephens and Krebs, 1986). As well, this model predicts that the decision of whether a prey type is attacked or not depends on its profitability and on the encounter rate with other prey types of higher profitability. If maximization of the rate of energy intake does occur in a predator–prey system, then active selection should be influenced by prey profitabilities. Passive selection depends on differential prey vulnerabilities, and is affected by prey morphology (such as body size and shell strength) and prey behaviours (such as escape responses).

To understand predation patterns and observed prey selection, it is useful to describe the predation process mechanistically using the predation cycle. This cycle describes a series of behaviours that characterize predation events, and includes searching for, attacking, capturing, and consuming prey (Holling, 1966; O'Brien, 1979). Based on this cycle, predation rate can be divided into a number of components such as encounter rate, the probability of attack upon encounter ($\Pr\{\text{attack}|\text{encounter}\}$), the probability of capture upon attack ($\Pr\{\text{capture}|\text{attack}\}$), and the probability of consumption upon capture ($\Pr\{\text{consumption}|\text{capture}\}$). These components can be associated with active or passive selection. For example, active selection can be associated with a predator's decision to attack an encountered prey (i.e., $\Pr\{\text{attack}|\text{encounter}\}$). Passive selection, which reflects prey vulnerability, can be associated with encounter rate between predators and prey and with $\Pr\{\text{capture}|\text{attack}\}$. $\Pr\{\text{consumption}|\text{capture}\}$ can be influenced by both active and passive selection, since a predator may decide to reject a captured prey (e.g. Elner and Hughes, 1978) or it may simply not be able to handle the captured prey.

The density of available prey types may influence active selection, passive selection and the resulting dynamics between predators and prey. For example, a predator may avoid or reject a prey type that is at low density and is thus unfamiliar. The prey type at low density would have a reduced $\Pr\{\text{attack}|\text{encounter}\}$ or $\Pr\{\text{consumption}|\text{capture}\}$ compared to a prey type that is at a higher density. Whatever the mechanism, predators can respond to differences in prey density by disproportionately consuming the most abundant prey, a phenomenon termed switching (Murdoch, 1969). Evidence for switching may be apparent when observing prey selection of predators over a range of prey densities.

The presence of alternative prey species may affect the functional response of predators on the target prey

species (Chesson, 1989). The functional response represents the relationship between predation rate of individual predators and density of a prey species (Hassell, 1978). Two types of functional responses are commonly observed: the type II response, where predation rate increases at a decelerating rate as prey density increases and reaches a plateau at high prey density; and a type III response, where predation rate increases at an accelerating rate at low prey density and then at a decelerating rate to a plateau at high prey density. In the presence of an alternative prey species, the plateau of the functional response on the target prey may be lower than in its absence. Also, predator behaviours may change in the presence of an alternative prey, influencing the type of functional response on the target prey.

Sea scallops (*Placopecten magellanicus*) are vulnerable to predation mainly when they are juveniles (<50–60 mm shell height) (Elnor and Jamieson, 1979; Barbeau and Scheibling, 1994). In coastal Atlantic Canada, sea stars (*Asterias* sp.) and rock crabs (*Cancer irroratus*) are major predators of juvenile sea scallops (Barbeau et al., 1996). Large portions of juvenile scallops released (seeded) onto the sea bottom for growth by aquaculturists are often lost to predation. Consequently, aquaculturists are concerned with providing seeded scallops with a refuge from predation. The presence of an alternative prey species may provide such a refuge, as predators may select the alternative prey and consume fewer scallops. Mussels (*Mytilus edulis*) are being considered as alternative prey, since they are less commercially important (Wong et al., in press). Density of both prey species may also play a role in protecting juvenile scallop populations by influencing a predator's functional response on scallops.

The objectives of our study were to examine (i) prey selection of sea stars (*A. vulgaris*) and rock crabs (*C. irroratus*) when offered two prey types, juvenile sea scallops (*P. magellanicus*) and blue mussels (*M. edulis*), and (ii) the effect of prey density on predation, prey selection, and component behaviours. Laboratory experiments were used to quantify predation rate when mussels (2 levels: absence, presence) and scallops (6–9 levels of density) were offered to predators concurrently. The components underlying predation rate, such as the proportion of time spent

searching for prey, encounter rate, $\Pr\{\text{attack}|\text{encounter}\}$, $\Pr\{\text{capture}|\text{attack}\}$ and $\Pr\{\text{consumption}|\text{capture}\}$, were quantified.

We predicted that sea stars and rock crabs would select a particular prey species, since scallops and mussels would differ in escape behaviours, shell strength and profitability. Specifically, we predicted that sea stars would select mussels over scallops, a result of passive selection. The $\Pr\{\text{capture}|\text{attack}\}$ would be lower for scallops than for mussels, since scallops can effectively escape by swimming away from sea stars while mussels cannot. Thus, mussels would be the easiest prey for sea stars to capture. We predicted that rock crabs would select scallops over mussels, a result of passive and active selection. Since scallops do not tend to swim when attacked by a crab (Barbeau and Scheibling, 1994), passive selection would be associated with prey shell strength and not with differential escape capabilities of the prey. Scallops likely have a lower shell strength than mussels, because scallops require a lighter shell for effective swimming escape from predators (Vermeij, 1987). Crabs would be able to open scallops more easily and more often than mussels. Consequently, $\Pr\{\text{consumption}|\text{capture}\}$ would be highest for scallops. Also, handling time would be lower for scallops than for mussels, resulting in scallops being highest in profitability. Active selection would result from crabs having a higher $\Pr\{\text{attack}|\text{encounter}\}$ on scallops than on mussels. Furthermore, we predicted that changes in the density of the target prey would not change prey selection. Based on previous work that investigated sea star and crab predation on scallops in the absence of mussels (Wong, 2004), we predicted the simplest scenario. Specifically, we predicted that with increased density of the target prey, encounter rate between the target prey and a predator would increase, but the proportion of time a predator spends searching, $\Pr\{\text{attack}|\text{encounter}\}$, $\Pr\{\text{capture}|\text{attack}\}$, $\Pr\{\text{consumption}|\text{capture}\}$ and handling time per prey would not change. This would result in a type II functional response on the target prey. We also predicted that the plateau of the functional response on the target prey would be lower in the presence of the alternative prey species than in its absence, since some alternative prey would be consumed.

2. Materials and methods

2.1. Experimental materials

Four experiments were conducted at Huntsman Marine Science Centre, in St. Andrews, New Brunswick, Canada, to examine prey selection and functional response of sea star (*Asterias vulgaris*) and rock crab (*C. irroratus*) predators when offered juvenile sea scallops (*P. magellanicus*) and blue mussels (*M. edulis*) (Table 1). Juvenile scallops were obtained from Sea Perfect Cultivated Products, Arichat, Nova Scotia, Canada. Mussels were collected from the intertidal zone at Brandy Cove and Indian Point, St. Andrews, New Brunswick, Canada. Epibionts were cleaned from mussel shells during collection. Prior to the experiments, a sample of scallop and mussel shells were ink blotted onto graph paper to determine surface area, and then regressed by shell height (scallops) or shell length (mussels). In all experiments, we used this information to obtain scallops and mussels that were equivalent in surface area. Both prey types were held in 260 L tanks for 2–10 days prior to the beginning of experiments. Before and during each experiment, scallops and mussels were batch fed algae paste (Innovative Aquaculture Products Ltd.) at an approximate concentration of 1.0×10^4 cells per mL (Hollett and Dabinett, 1989) for 30–60 min each day.

All predators originated from Passamaquoddy Bay in the Bay of Fundy, New Brunswick, Canada. Sea stars were collected from a local wharf, and were held in holding tanks for 1 week prior to experiments. Sea stars were fed periwinkles (*Littorina littorea*) before being starved for ~3 days prior to an experiment, to standardize predator hunger level. Only intact sea stars with all of their 5 arms were used. Sea stars were measured as the distance between the tip of an average sized arm to the centre of the oral region, multiplied by two (Table 1). Rock crabs were obtained from local lobster and crab fishers. Rock crabs were acclimated for 1 week directly in the experimental tanks prior to the experiments. Crabs were fed beef chunks (from a local grocery store) and then starved for 2 days before the beginning of each experiment, to standardize hunger levels. Only male crabs with both chelae and all walking legs were used. Crab carapace width was measured as the distance between the two most distal marginal teeth (Table 1). During the

Table 1
Details of experiments that investigated the effect of scallop density and the presence of an alternative prey species on predation of juvenile sea scallops (*Placopecten magellanicus*) by sea stars (*Asterias vulgaris*) and rock crabs (*Cancer irroratus*)

Experiment	Date (dd/mm/yy)	Scallop size ± S.D. (mm)	Mussel size ± S.D. (mm)	Predator size (mm)	Scallop density as # unit ⁻¹ (# m ⁻²)	Mussel density as # unit ⁻¹ (# m ⁻²)	Water temperature ± S.D. (°C)	Total time observed (min unit ⁻¹)
Sea stars: one-factor experiment	24/09/02–7/10/02	14.8 ± 2.7	20.0 ± 4.8	110–160	2–20 (11–111)	10 (56)	14.0 ± 0.2	720
Sea stars: two-factor experiment	20/10/02–02/11/02	16.2 ± 2.9	22.2 ± 5.2	130–160	2–62 (2–56)	62 (56)	11.0 ± 1.7	450
Rock crabs: one-factor experiment	23/06/02–07/07/02	36.5 ± 4.9	49.0 ± 4.7	90–120	2–20 (11–111)	10 (56)	10.7 ± 0.4	1380
Rock crabs: two-factor experiment	22/07/02–03/08/02	34.1 ± 4.2	49.4 ± 4.5	100–110	2–55 (2–50)	55 (50)	12.7 ± 0.3	660

The alternative prey species was the blue mussel (*Mytilus edulis*). Scallop size was measured as shell height, and mussel size as shell length. The experimental units were small glass tanks (30 cm wide × 60 cm long × 30 cm high) for the one-factor experiments, and large circular fiberglass tanks (120 cm diameter × 25 cm high) for the two-factor experiments. Experimental animals were maintained in flow-through sea water, which was sand-filtered to 20 µm and regulated between 0.5 and 1.5 L min⁻¹ (one-factor experiment) and between 1 and 3 L min⁻¹ (two-factor experiment). The light regime during all experiments was 14 h light: 10 h dark.

experiments, black plastic covered 25% of the tank to provide shelter for crabs.

2.2. Experimental design

One-factor experiments with sea stars and with rock crabs were conducted in small tanks (bottom area = 0.18 m²), and used a high range of scallop densities (9 levels between 11 and 111 scallops m⁻²) with a constant mussel density (Table 1). A complete randomized design was used, in which one predator was placed per tank and offered a constant mussel density and a particular scallop density. Four replicates were randomly allocated into 36 tanks. Additional treatments were set up to directly investigate active selection: individual predators were offered scallops or mussels alone, or scallops and mussels together (10 animals per tank); four replicates of these treatments were allocated into 12 tanks. Three tanks with both prey types and no predator were also used as controls to determine natural prey mortality; none occurred.

Two-factor experiments with sea stars and with rock crabs were conducted in larger tanks (bottom area = 1.1 m²) than the one-factor experiments to achieve lower scallop densities (6 levels between 2 and ~50 scallops m⁻²) (Table 1). Additionally, the range of scallop densities was offered to individual predators in the presence and absence of a constant mussel density. This allowed direct comparison of the functional response on scallops with and without mussels. A complete randomized design was used, with four replicates randomly allocated into 48 tanks. Two densities of scallops in the two-factor experiments with sea stars (11 and 56 scallops m⁻²) and with rock crabs (11 and 50 scallops m⁻²) overlapped with the one-factor experiments. Three additional tanks containing both prey types and no predator were used as controls to determine natural mortality; natural mortality was minimal (only 2 scallops died in the experiment with rock crabs).

2.3. Collection of data

2.3.1. Predation and selectivity data

In all experiments, the number of scallops and mussels eaten by each predator was monitored twice daily. The appropriate prey densities were maintained

by replacing consumed prey with live ones. Predation rate was calculated for each predator as the total number of prey eaten during an experiment divided by the number of days of the experiment (i.e., number eaten per day). A selection index was calculated using this information:

$$\alpha_i = \frac{r_i/n_i}{\sum_{j=1}^q r_j/n_j}, \quad i = 1, \dots, q \quad (1)$$

(Chesson, 1978) where both i and j denote prey type, α is the deviation from random sampling, r is the number of prey in the predator's diet, n is the number of prey in the environment, and q is the total number of prey types available for consumption by the predator (Chesson, 1978). This measure is scaled between 0 and 1, where $\alpha_i = 1$ when only prey type i is consumed, $\alpha_i = 0$ when no prey type i is consumed, and $\alpha_i = 0.5$ when there is no selection. This measure is useful as it is not influenced by prey density.

2.3.2. Behavioural data

Throughout the experiments, predator and prey behaviours were quantified during continuous 30-min periods (Table 1). A blind was used when observing crabs to avoid observer effects. Foraging behaviours (searching and handling prey) and non-foraging behaviours (stopping, climbing, walking) were quantified (Wong and Barbeau, 2003). The proportion of time for each foraging behaviour was calculated as total duration of the behaviour divided by the total observation time. Handling time per prey was calculated as the total time taken to manipulate a single prey item, from encounter to the end of consumption.

Encounters between predators and prey, and the outcomes of the encounters, were also quantified (Wong and Barbeau, 2003). Encounter rate was calculated as the total number of encounters divided by predator search time. For sea stars, encounters with prey could result in avoidance, pre-capture escape, rejection or consumption of prey. These encounter behaviours were used to calculate conditional probabilities that underlie predation rate. For sea stars, $\Pr\{\text{attack}|\text{capture}\}$ was calculated as $[(\text{encounters} - \text{avoidances})/\text{encounters}]$; $\Pr\{\text{capture}|\text{attack}\}$ as $[(\text{rejections} + \text{consumptions})/(\text{pre-capture escapes} + \text{rejections} + \text{consumptions})]$; and $\Pr\{\text{consumption}|\text{capture}\}$

as $[\text{consumptions}/(\text{rejections}+\text{consumptions})]$. For rock crabs, encounters could result in pre-capture escape, post-capture escape, rejection or consumption of prey. For rock crabs, $\text{Pr}\{\text{capture}|\text{encounter}\}$ was calculated as $[(\text{post-capture escapes}+\text{rejections}+\text{consumptions})/\text{encounters}]$, and $\text{Pr}\{\text{consumption}|\text{capture}\}$ as $[\text{consumptions}/(\text{post-capture escapes}+\text{rejections}+\text{consumptions})]$. $\text{Pr}\{\text{capture}|\text{encounter}\}$ in the crab experiments encompassed both $\text{Pr}\{\text{attack}|\text{encounter}\}$ and $\text{Pr}\{\text{capture}|\text{attack}\}$, as we did not observe crab assessment of prey. Thus, $\text{Pr}\{\text{capture}|\text{encounter}\}$ probably has both active and passive selection components. See Wong and Barbeau (2003) for detailed descriptions of predator foraging and encounter behaviours.

2.3.3. Data on prey characteristics

Measurements of prey characteristics (energy content, handling time per prey, prey profitability, shell strength) were made to help determine the mechanisms underlying observed prey selection. To quantify energy content per animal, we dried tissue from mussels and scallops ($n=49-75$) for 45 h at 80 °C. Dry tissue weight was multiplied by literature values to determine energy content per animal, and then averaged over all samples for each experiment. Literature values used were chosen to reflect seasonal changes in gamete maturity. For mussels used in sea star experiments, mean energy per dry gram somatic tissue and gonadal tissue (20.75 kJ g⁻¹ dry weight, Lowe et al., 1982; Newell, 1982) was used since mussel gonads were close to full (T. Lander, personal communication). For mussels used in rock crab experiments, energy per dry gram somatic tissue (22.11 kJ g⁻¹ dry weight, Newell, 1982) was used since mussels had recently spawned (T. Lander, personal communication). For scallops, dry weight was multiplied by 24.5 kJ g⁻¹ dry somatic tissue in all experiments (MacDonald and Thompson, 1985), because our juvenile scallops were not sexually mature. As indicated above, handling time per prey was measured during the experiments. Prey profitability was calculated by dividing mean energy (kJ) per prey by mean handling time per prey (Stephens and Krebs, 1986); this calculation assumes that all energy was assimilated. Scallop and mussel prey types were then ranked by profitability to determine whether they should be attacked by a predator using encounter rates during searching time and the algo-

rithm provided by Stephens and Krebs (1986, Eq. (2.11)). Encounter rates were calculated using an encounter rate model based on random movements of animals in a two-dimensional environment (Holling, 1966), which has been shown to accurately model sea star and crab encounter rates with scallops in previous experiments (Barbeau and Scheibling, 1994; Wong, 2004). Shell strength was determined using a Monsanto Tensometer to quantify the force (N) needed to crack one valve.

2.4. Statistical analysis

2.4.1. Effect of prey density and of presence of an alternative prey species

The selectivity index, predation rate and behavioural data were analysed using analysis of variance (ANOVA). For the one-factor experiments, one-way ANOVAs were used with scallop density as the fixed factor. For the two-factor experiments, two-way ANOVAs were used with scallop density and environment (mussels present or mussels absent) as fixed factors. For all analyses, Cochran's test was used to test the assumption of homogeneity of variances. When this assumption was violated, transformations such as square root or $\log(\text{datum}+1)$ were used to obtain homogeneous variances. ANOVAs were performed in cases where this could not be achieved, with awareness of increased probability of type I error (Underwood, 1997). In two-way ANOVAs, we investigated interactions with a $p \leq 0.1$ as a conservative measure to ensure that main effects were not inappropriately interpreted in the presence of a possible interaction (e.g. Hamilton, 2000; Wong and Barbeau, 2003). Simple and main effects were evaluated at $\alpha=0.05$. For multiple comparisons, Student–Newman–Kuel's (SNK) test was used when there were ≤ 3 means or when means were evenly spaced; Ryan's Q test was used when there were > 3 means that were not evenly spaced (Day and Quinn, 1989; Underwood, 1997).

2.4.2. Identification of occurrence of prey selection and active selection

When predators consumed both prey types, a one-sample t -test at each scallop density was used to determine if the selectivity index differed significantly from 0.5 (no selection). If prey selection was ob-

served, active selection was detected by comparing the number eaten when both prey types were present (choice situation, observed frequencies) to the number eaten when one prey type was present (non-choice situation, expected frequencies), using χ^2 tests with Yate's correction for continuity (Liszka and Underwood, 1990; Zar, 1996). Expected frequencies were calculated as:

$$E_i = R \left(\frac{S_i}{S_i + S_m} \right)$$

$$E_m = R \left(\frac{S_m}{S_i + S_m} \right)$$

where E_i and E_m are the expected numbers of scallops and mussels eaten, respectively; R is the number of scallops plus the number of mussels eaten when presented together; S_i and S_m are the numbers of scallops and mussels eaten when presented alone, respectively (Liszka and Underwood, 1990). A significant χ^2 value indicated that active selection was evident. Note that this test is subject to increased type I error, since expected values are estimated from samples.

To identify mechanisms underlying observed prey selection, two sample t -tests were used to compare shell strength, energy content, and handling time per prey of scallops and mussels. $\text{Pr}\{\text{attack}|\text{encounter}\}$ of sea stars and $\text{Pr}\{\text{consumption}|\text{capture}\}$ of crabs were also compared between scallops and mussels using two sample t -tests. The other encounter probabilities were not compared statistically between scallops and mussels because of low variation or lack of data. To assess if encounter rate may be important in explaining observed selection, the ratio of observed encounter rate with scallops to observed encounter rates with mussels was visually compared to an expected ratio. This expected ratio was calculated using an encounter rate model based on random movements of animals (Holling, 1966; see Section 2.3.3 above), as expected encounter rate with scallops to expected encounter rates with mussels.

2.4.3. Identification of the functional response and model fitting

When observation of the predation rate data indicated a functional response, a modified type II

functional response model was fit (for a detailed explanation of the diagnostic steps taken to identify the type of functional response see Wong (2004). This model was the classic type II functional response model (Holling, 1959) extended to include multiple prey species (Hassell, 1978; Chesson, 1989):

$$C_i = \frac{a_i N_i T}{1 + a_i N_i h_i + d_m N_m} \quad (2)$$

where i and m denote prey type, C is the number of prey consumed per predator per unit time, a is rate of successful search, h is handling time per prey, d is a parameter equivalent to $a \cdot h$, N is prey density, and T is proportion of time spent foraging (searching + handling). From our behavioural data, T was fixed at 0.02 for crabs. Since we were interested in the functional response of predators on scallops, we set prey type i to represent scallops and prey type m to represent mussels. Note that our use of d modified the original multiple prey species model; this simplification was appropriate since mussel density was constant. The model assumes that parameters a and h are constant over prey density, and that prey depletion over time is negligible. Models have been developed for when these assumptions are not met (Hassell, 1978; Chesson, 1989).

Functional response models are intrinsically non-linear (Williams and Juliano, 1985), so we used non-linear regression for model fitting (Bates and Watts, 1988). After model fitting, a_m (rate of successful search on mussels) was calculated using estimated values of d_m and observed values of h_m (handling time per mussel). Regressions used full data sets (i.e., 4 replicates per scallop density); however, the fitted curves were overlaid with the means \pm standard error (S.E.) for clear presentation. Parameter standard errors were estimated assuming asymptotic normality.

3. Results

3.1. Sea stars

3.1.1. Sea star prey selection and predation rate

Sea stars strongly selected mussels over scallops in both the one-factor and two-factor experiments (Fig. 1a,c). The selectivity index did not change over scal-

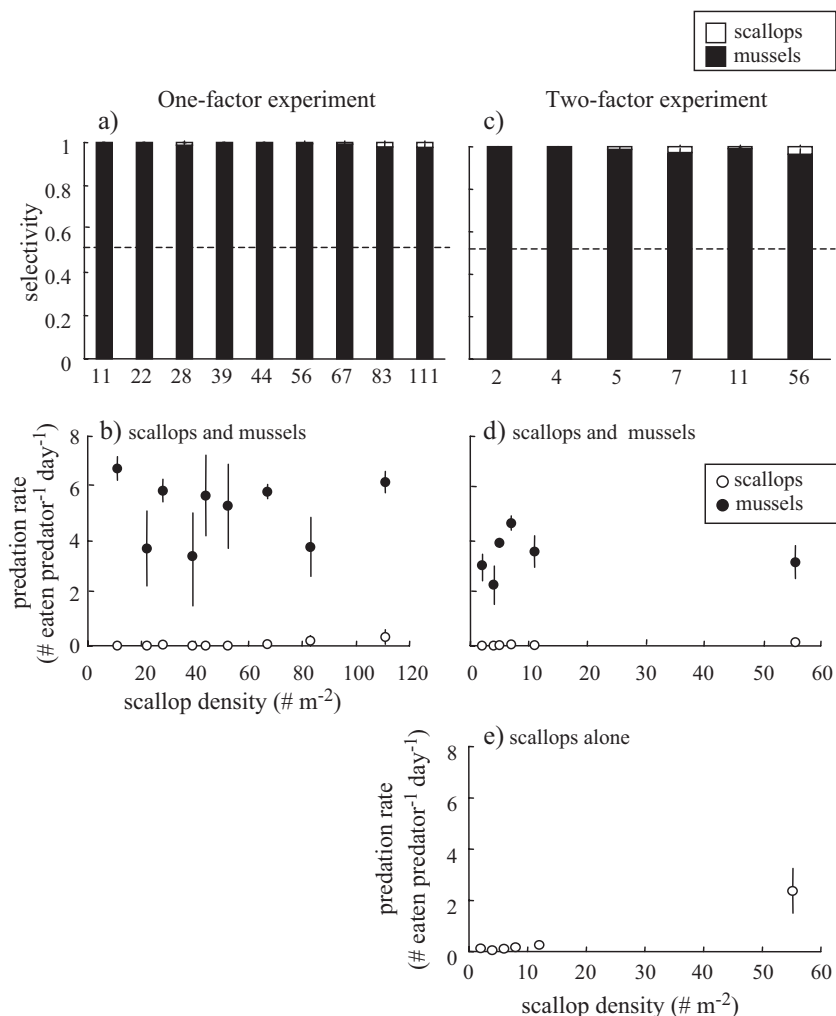


Fig. 1. Prey selection (measured by the selectivity index, α) and predation rate of sea stars (*A. vulgaris*) on juvenile sea scallops (*P. magellanicus*) and blue mussels (*M. edulis*) in the one-factor experiment (a, b) and the two-factor experiment (c, d, e). Dashed line indicates no prey selection ($\alpha=0.5$). Mean \pm 1 S.E., $n=4$.

lop density (Tables 2 and 3), even when scallop density was higher than mussel density (i.e., 67, 83, 111 scallops m⁻² in the one-factor experiment). Active selection was detected underlying observed selection (one-factor experiment: $\chi^2_1=370.3$, $p<0.001$; two-factor experiment: $\chi^2_1=113.1$, $p<0.001$).

In the presence of mussels, predation rate on scallops was very low and not affected by scallop density (Tables 2 and 3, Fig. 1b,d). However, predation rate on scallops when mussels were absent was significantly greater at 56 scallops m⁻² than at lower den-

sities (two-factor experiment: Table 3, Fig. 1e). Predation rate on mussels was fairly constant across all scallop densities in both experiments (Tables 2 and 3, Fig. 1b,d).

3.1.2. Sea star foraging behaviours

The presence of mussels influenced the foraging behaviours of sea stars (Table 3, Fig. 2). The proportion of time a predator spent foraging (searching + handling) was significantly lower when mussels were absent than when mussels were present. When scal-

Table 2

One-factor experiment with sea stars: one-way ANOVA results of sea stars (*Asterias vulgaris*) preying on juvenile sea scallops (*Placopecten magellanicus*) and blue mussels (*Mytilus edulis*)

Dependent variable	Source of variation	Effect MS	Error term MS	$F_{df1,df2}$	p
Predation rate on scallops	D	0.053	0.052	1.03 _{8,27}	0.437
Scallop selectivity index	D	3.5×10^{-4}	4.0×10^{-4}	0.89 _{8,27}	0.536
Proportion of time spent foraging	D	0.074	0.033	2.22 _{8,27}	0.060
Proportion of time spent searching	D	0.001	6.9×10^{-4}	1.65 _{8,27}	0.157
Encounter rate with scallops	D	6.067	3.360	1.81 _{8,20}	0.135
Pr{attack encounter} on scallops	D	0.136	0.173	0.78 _{8,11}	0.628
Predation rate on mussels	D	6.140	5.537	1.11 _{8,27}	0.388
Encounter rate with mussels	D	42.25	60.96	0.69 _{8,20}	0.693
Pr{consumption capture} on mussels	D	0.111	0.061	1.82 _{8,14}	0.157

Encounter rate on scallops was square root transformed. Predation rate on scallops and scallop selectivity index could not be transformed to satisfy assumptions, so raw data were used. Pr{capture|attack} and Pr{consumption|capture} on scallops, and Pr{attack|encounter} and Pr{capture|attack} on mussels were not tested statistically, since there were few observations or little variation in the data. The df1=numerator df, df2=denominator df. D=scallop density (per m²).

Table 3

Two-factor experiments with sea stars: two-way ANOVA results (scallop data) and one-way ANOVA results (scallop selectivity index, mussel data) of sea stars (*Asterias vulgaris*) preying on juvenile sea scallops (*Placopecten magellanicus*), when presented alone and with mussels (*Mytilus edulis*)

Dependent variable	Source of variation	Effect MS	Error term MS	$F_{df1,df2}$	p	Post-hoc comparisons
Predation rate on scallops	E	2.746	0.261	11.1 _{1,36}	0.002	
	D	1.833	0.261	7.01 _{5,36}	<0.001	
	ExD	1.499	0.261	5.74 _{5,36}	<0.001	E1: D4 D5 D2 D7 D11 D56 E2: D2 D4 D5 D11 D7 D56 D2: E2 E1 D4: E2 E1 D5: E2 E1 D7: E2 E1 D11: E2 E1 D56: E2 E1
Scallop selectivity index	D	8.5×10^{-4}	8.3×10^{-4}	1.03 _{5,18}	0.429	
Proportion of time spent foraging	E	0.910	0.033	2.72 _{1,5}	<0.001	E1 E2
	D	0.121	0.033	3.63 _{5,36}	<0.009	D2 D5 D4 D11 D7 D56
	ExD	0.049	0.033	1.46 _{5,36}	0.227	
Proportion of time spent searching	E	2.419	0.018	133.2 _{1,36}	<0.001	E2 E1
	D	0.039	0.018	2.16 _{5,36}	0.080	
	ExD	0.025	0.018	1.37 _{5,36}	0.259	
Encounter rate with scallops	E	221.6	33.00	19.1 _{1,34}	<0.001	E2 E1
	D	629.3	33.00	1.87 _{5,34}	<0.001	D2 D5 D7 D4 D11 D56
	ExD	61.81	0.123	0.179 _{5,34}	0.125	
Pr{attack encounter} on scallops	E	0.022	0.123	0.179 _{1,29}	0.678	
Predation rate on mussels	D	2.583	1.186	2.18 _{5,18}	0.102	
Encounter rate with mussels	D	11.09	25.04	0.44 _{5,16}	0.812	
Pr{consumption capture} on mussels	D	0.029	0.099	0.30 _{5,12}	0.907	

Predation rate and encounter rate on scallops, and scallop selectivity index could not be transformed to satisfy assumptions, and raw data were used. Pr{attack|encounter} on scallops was pooled over density to provide enough data for analysis. Pr{capture|attack} and Pr{consumption|capture} on scallops, and Pr{attack|encounter} and Pr{capture|attack} on mussels were not tested statistically since there were few observations or little variation in the data. df1=numerator df, df2=denominator df. E=environment (E1=scallops alone, E2=scallops and mussels present); D=scallop density (per m²). Post-hoc comparison results used SNK test (encounter rate with scallops, proportion of time spent foraging) and Ryan's Q test (predation rate on scallops). Treatment level means are listed in increasing magnitude; those sharing a common underline do not differ significantly.

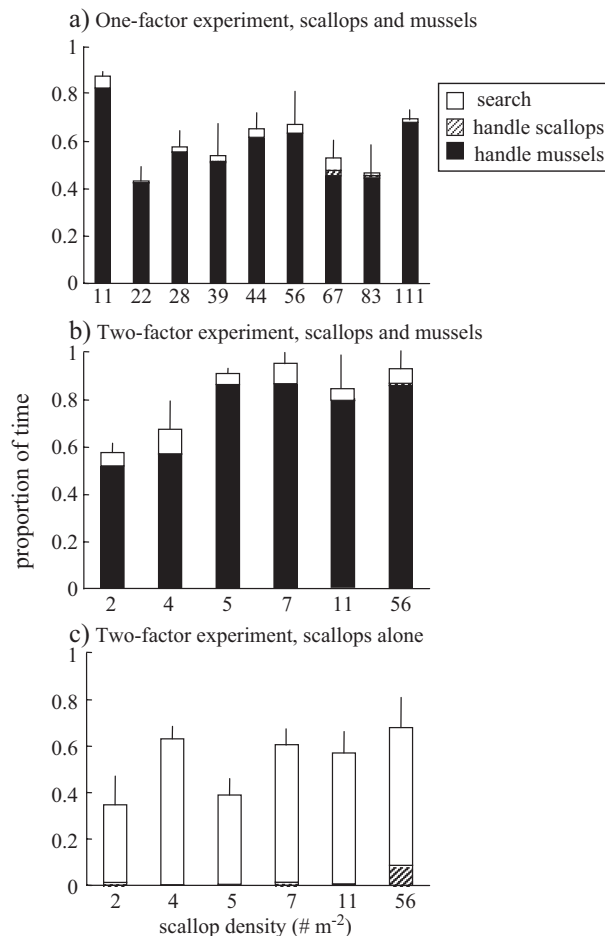


Fig. 2. Mean proportion of time that sea stars (*A. vulgaris*) spent foraging (searching+handling) for juvenile scallops (*P. magellanicus*) and blue mussels (*M. edulis*) in the one-factor experiment (a) and the two-factor experiment (b, c). In all cases, sea stars were inactive or moving but not foraging for the remainder of time. Error bars are 1 S.E. for proportion of time spent foraging. $n=4$.

lops were alone, sea stars spent most of their time searching for prey, whereas in the presence of both scallops and mussels, sea stars spent 40–80% of their time handling mussels. Only small proportions of time (5–10%) were spent searching for prey or handling scallops when mussels were present.

The effect of scallop density on proportion of time spent foraging was marginally non-significant in the one-factor experiment (Table 2), and was significantly lower at 2 scallops m⁻² than at higher scallop densities in the two-factor experiment (Table 3, Fig. 2). Scallop density did not significantly affect the proportion of time spent searching for scallops in either experiment.

3.1.3. Encounter behaviours between sea stars and prey

Most observed encounters with scallops ended in a sea star avoiding the scallop, or the scallop escaping before it was captured (Fig. 3a,c,e). The presence of mussels affected encounter rate with scallops in the two-factor experiment (Table 3, Fig. 3c, e); this encounter rate was significantly higher when mussels were absent than when mussels were present. $\Pr\{\text{attack}|\text{encounter}\}$ on scallops was not significantly affected by the presence or absence of mussels (Tables 2, 3 and 4a; Wong, 2004).

Scallop density also had a significant effect on encounter rate with scallops in the two-factor expe-

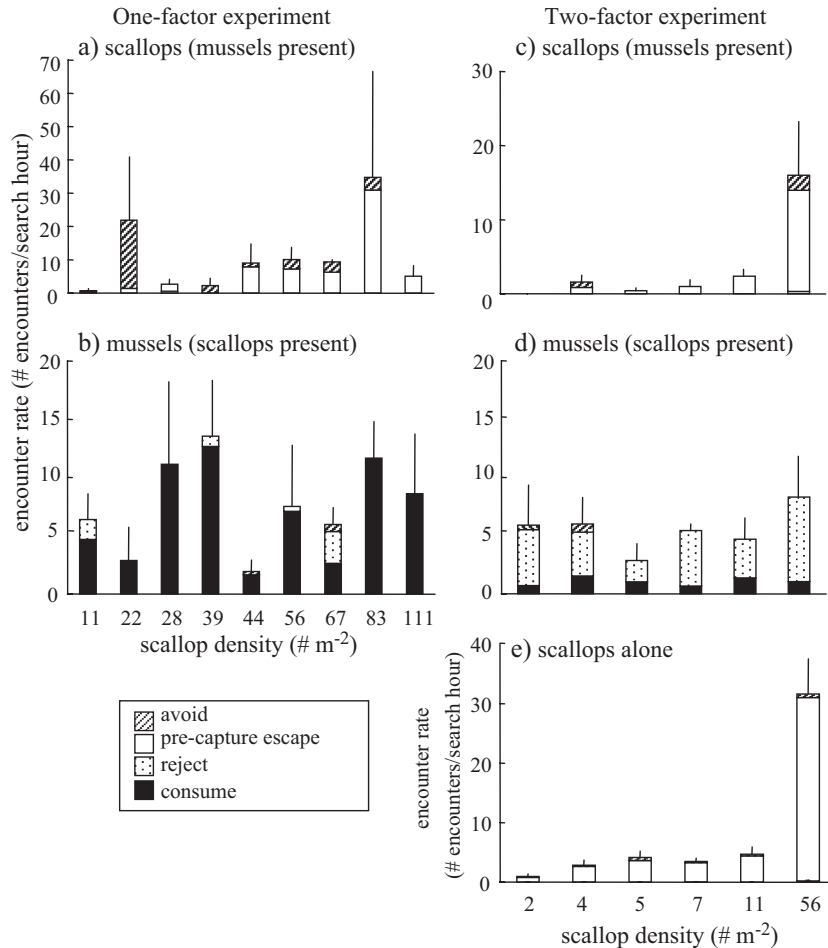


Fig. 3. Mean encounter rate between sea stars (*A. vulgaris*) and juvenile sea scallops (*P. magellanicus*) and blue mussels (*M. edulis*) in the one-factor experiment (a, b) and the two-factor experiment (c, d, e). The portions of each bar represent the outcomes of encounters. In all cases, error bars are 1 S.E. for encounter rate. No encounter was observed at 2 scallops m⁻² in (c). $n=2-4$.

periment: it increased significantly as scallop density increased (Table 3, Fig. 3c,e). At relatively high scallop density (one-factor experiment), encounter rate with scallops was not affected by scallop density (Table 2, Fig. 3a). $\text{Pr}\{\text{attack}|\text{encounter}\}$ on scallops in the presence of mussels was not affected by scallop density and generally ranged between 0.5 and 1 in both experiments (Tables 2, 3 and 4a; Wong, 2004). $\text{Pr}\{\text{capture}|\text{attack}\}$ on scallops in the presence of mussels was very low, zero or not observed (Table 4a; Wong, 2004), and so there were almost no data for $\text{Pr}\{\text{consumption}|\text{capture}\}$ on scallops.

Encounter rate with mussels did not change significantly over scallop density (Tables 2 and 3; Fig. 3b,d).

Most encounters with mussels ended in consumption or rejection, although some were avoided. For mussels, $\text{Pr}\{\text{attack}|\text{encounter}\}$ and $\text{Pr}\{\text{capture}|\text{attack}\}$ were always close to 1, while $\text{Pr}\{\text{consumption}|\text{capture}\}$ varied between 0.2 and 1 (Table 4a; Wong, 2004). $\text{Pr}\{\text{consumption}|\text{capture}\}$ on mussels did not change significantly over scallop density (Tables 2 and 3).

3.1.4. Mechanisms underlying sea star prey selection

Energy content per mussel was significantly higher than that per scallop (Table 5; one-factor experiment: $t_{98}=3.64$, $p<0.001$; two-factor experiment: $t_{97}=3.02$, $p=0.003$). Handling time per mussel was significantly higher than that per scallop in the two-factor expe-

Table 4

Encounter probabilities averaged over all scallop densities (\pm S.E.) for sea star experiments (a) and rock crab experiments (b)

(a)				
Experiment	Prey	Pr{attack encounter}	Pr{capture attack}	Pr{consumption capture}
Sea stars: one-factor experiment	scallops (mussels present)	0.60 ± 0.09 (20)	0.02 ± 0.02 (15)	0.0 (1)
	mussels (scallops present)	0.95 ± 0.04 (24)	1.0 ± 0.0 (23)	0.82 ± 0.06 (23)
Sea stars: two-factor experiment	scallops (mussels present)	0.84 ± 0.09 (9)	0.008 ± 0.008 (9)	0.0 (1)
	mussels (scallops present)	0.98 ± 0.01 (18)	1.0 ± 0.0 (18)	0.22 ± 0.07 (18)
	scallops alone	0.88 ± 0.03 (23)	0.004 ± 0.002 (23)	1.0 ± 0.0 (4)
(b)				
Experiment	Prey	Pr{capture encounter}	Pr{consumption capture}	
Rock crabs: one-factor experiment	scallops (mussels present)	0.80 ± 0.07 (24)	0.46 ± 0.09 (21)	
	mussels (scallops present)	1.0 ± 0.0 (9)	0.28 ± 0.14 (9)	
Rock crabs: two-factor experiment	scallops (mussels present)	1.0 ± 0.0 (12)	0.20 ± 0.11 (12)	
	mussels (scallops present)	1.0 ± 0.0 (5)	0.56 ± 0.10 (15)	
	scallops alone	0.92 ± 0.06 (18)	0.39 ± 0.08 (17)	

Number in parentheses= n .

periment ($t_9=2.74$, $p=0.023$). Profitability of scallops and mussels was similar. Based on encounter rates and profitabilities, both prey types should be attacked except at the two highest scallop densities in the one-factor experiment, where only scallops should be attacked.

For the different scallop densities, the observed ratio of encounter rates with scallops and with mussels (i.e., sea star encounter rate with scallops: sea star encounter rate with mussels) was fairly similar to the ratio of expected encounter rates. For example, at 11 scallops m^{-2} , the observed and expected ratios were 0.3 and 0.2, respectively, and at 56 scallops m^{-2} , 1.6 and 1.0, respectively. Pr{attack|encounter} was greater for mussels than scallops (Table 4a; one-factor experiment: $t_{42}=3.55$, $p<0.001$; two-factor experi-

ment: $t_{25}=2.11$, $p=0.045$). Pr{capture|attack} was much greater for mussels than scallops (Table 4a). Pr{consumption|capture} on scallops was observed too infrequently to conclude anything.

3.1.5. Sea star functional response in the presence of alternative prey

Sea stars did not have a functional response on scallops when mussels were present, because predation rate on scallops was very low.

3.2. Rock crabs

3.2.1. Rock crab prey selection and predation rate

Prey selection by rock crabs differed between experiments (Fig. 4a,c). When scallops were at a

Table 5

Measurements of prey characteristics

Experiment	Prey species	Energy content \pm S.E. (kJ prey ⁻¹)	Handling time per prey \pm S.E. (min prey ⁻¹)	Profitability \pm S.E. (kJ min ⁻¹ prey ⁻¹)	Shell strength \pm S.E. (N)
Sea stars: one-factor experiment	Scallop	0.6 ± 0.04 (50)	—	0.0100 ± 0.003	
	Mussel	1.0 ± 0.1 (50)	105.3 ± 15.0 (23)	0.0095 ± 0.002	
Sea stars: two-factor experiment	Scallop	0.7 ± 0.05 (50)	59.8 ± 11.9 (5)	0.0117 ± 0.004	
	Mussel	2.0 ± 0.4 (49)	168.9 ± 34.7 (6)	0.0118 ± 0.003	
Rock crabs: one-factor experiment	Scallop	13.5 ± 0.6 (75)	8.4 ± 1.7 (19)	1.607 ± 0.4	28.5 ± 1.0 (74)
	Mussel	10.7 ± 0.5 (73)	6.2 ± 3.0 (6)	1.726 ± 0.8	42.0 ± 2.0 (66)
Rock crabs: two-factor experiment	Scallop	10.3 ± 0.5 (50)	4.6 ± 1.0 (12)	2.239 ± 0.1	
	Mussel	11.4 ± 0.5 (50)	6.8 ± 1.5 (19)	1.677 ± 0.07	

Number in parentheses= n . Full handling events were not observed in the one-factor experiment with sea stars, so we used data for handling time per scallop from the two-factor experiment to calculate profitability.

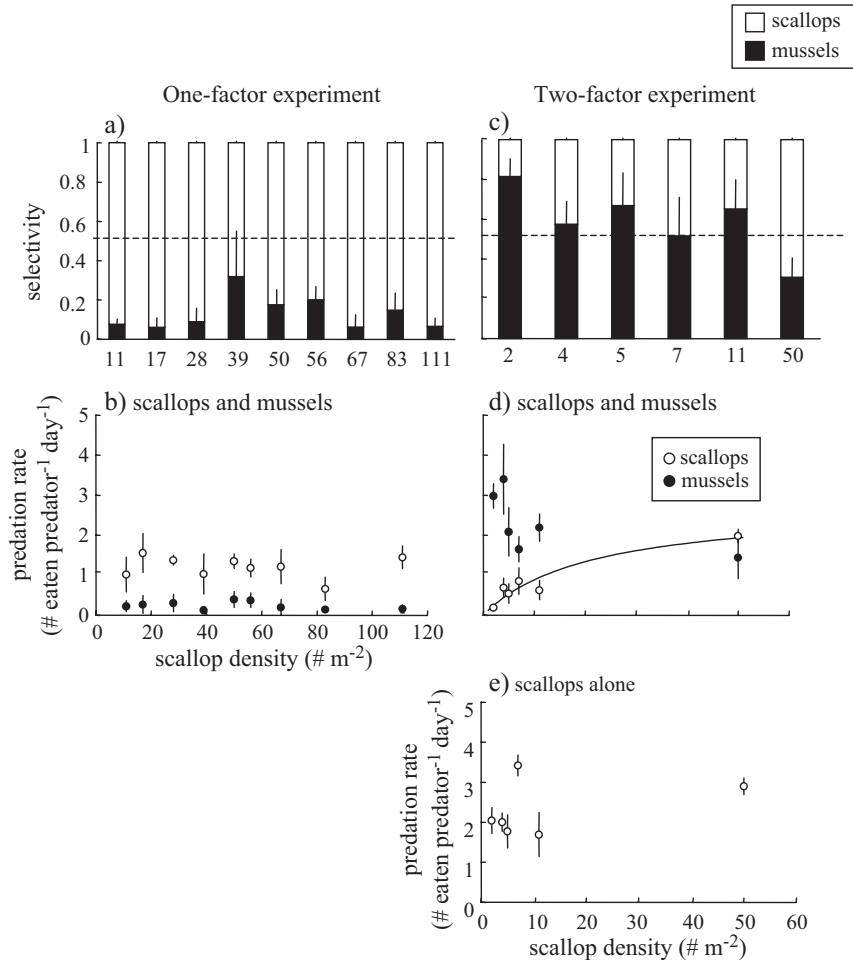


Fig. 4. Prey selection (measured by the selectivity index, α) and predation rate of rock crabs (*C. irroratus*) on juvenile sea scallops (*P. magellanicus*) and blue mussels (*M. edulis*) in the one-factor experiment (a, b) and the two-factor experiment (c, d, e). Dashed line indicates no preference ($\alpha = 0.5$). Mean \pm 1 S.E., $n = 4$.

relatively high density (one-factor experiment), crabs selected scallops over mussels at all scallop densities ($t_3 = 4.01\text{--}15.8$, $p < 0.05$), except one (39 scallops m⁻²; $t_3 = 0.785$, $p = 0.490$). When scallops were at a relatively low density (two-factor experiment), crabs selected mussels over scallops at very low scallop density (2 scallops m⁻²; $t_3 = 3.60$, $p = 0.037$). Crabs tended to select scallops over mussels at 50 scallops m⁻², although this trend was not significant likely due to low power ($t_3 = 2.0$, $p = 0.140$). Crabs did not select a certain prey species at the intermediate densities ($t_3 = 0.64\text{--}1.99$, $p > 0.05$). In visually comparing the overlapping densities between the one-factor experiment and the two-factor experiment (11 and 50 scal-

lops m⁻²), selectivity data matched only at 50 scallops m⁻². Within an experiment, Chesson's selectivity index did not change significantly over scallop density (Tables 6 and 7). Active selection was detected underlying observed selection in the one-factor experiment ($\chi^2_1 = 48.4$, $p < 0.001$) and at 50 scallops m⁻² in the two-factor experiment ($\chi^2_1 = 4.8$, $p = 0.027$).

In the presence of mussels, predation rate on scallops increased with scallop density when scallop density was relatively low (two-factor experiment: Table 7, Fig. 4d), and stayed fairly constant when scallop density was relatively high (one-factor experiment: Table 6, Fig. 4b). When mussels were absent, preda-

Table 6

One-factor experiment with rock crabs: one-way ANOVA results of rock crabs (*Cancer irroratus*) preying on juvenile sea scallops (*Placopecten magellanicus*) and blue mussels (*Mytilus edulis*)

Dependent variable	Source of variation	Effect MS	Error term MS	$F_{df1,df2}$	p
Scallop selectivity index	D	0.038	0.042	0.90 _{8,25}	0.532
Predation rate on scallops	D	0.296	0.503	0.59 _{8,27}	0.777
Proportion of time spent foraging	D	0.001	0.004	0.42 _{8,27}	0.898
Proportion of time spent searching	D	6.8×10^{-4}	0.004	0.19 _{8,27}	0.991
Encounter rate with scallops	D	4.6×10^4	2.7×10^4	1.73 _{8,22}	0.145
Pr{capture encounter} on scallops	D	0.139	0.120	1.16 _{8,15}	0.381
Pr{consumption capture} on scallops	D	0.202	0.173	1.17 _{8,12}	0.389
Predation rate on mussels	D	0.039	0.109	0.35 _{8,27}	0.935
Encounter rate with mussels	D	0.734	1.445	0.51 _{8,22}	0.837

Proportion of time spent foraging and proportion of time spent searching for prey were square root transformed, and encounter rate with mussels was $\log(\text{datum} + 1)$ transformed. Scallop selectivity index could not be transformed to satisfy assumptions, and raw data were used. Pr{capture|encounter} and Pr{consumption|capture} on mussels were not tested statistically since there were few observations or little variation in the data. df1=numerator df, df2=denominator df. D=scallop density (per m²).

Table 7

Two-factor experiment with rock crabs: two-way ANOVA results (scallop data) and one-way ANOVA results (scallop selectivity index, mussel data) of rock crabs (*Cancer irroratus*) preying on juvenile sea scallops (*Placopecten magellanicus*), when presented alone and with mussels (*Mytilus edulis*)

Dependent variable	Source of variation	Effect MS	Error term MS	$F_{df1,df2}$	p	Post-hoc comparisons
Scallop selectivity index	D	0.116	0.077	1.51 _{5,18}	0.236	
Predation rate on scallops	E	26.62	0.354	75.17 _{1,36}	<0.001	
	D	2.676	0.354	7.55 _{5,36}	<0.001	
	ExD	0.758	0.354	2.14 _{5,36}	0.083	E1 : <u>D11 D5 D4 D2</u> <u>D50 D7</u>
						E2: <u>D2 D5 D11 D4 D7</u> D50
						D2: E2 E1
						D4: E2 E1
						D5: E2 E1
						D7: E2 E1
						D11: E2 E1
						D50: E2 E1
Proportion of time spent foraging	E	0.001	0.005	0.24 _{1,36}	0.624	
	D	0.007	0.005	1.33 _{5,36}	0.271	
	ExD	0.004	0.005	0.85 _{5,36}	0.521	
Proportion of time spent searching	E	1.1×10^{-5}	2.3×10^{-5}	0.46 _{1,36}	0.501	
	D	8.4×10^{-6}	2.3×10^{-5}	0.36 _{5,36}	0.871	
	ExD	2.1×10^{-5}	2.3×10^{-5}	0.94 _{5,36}	0.470	
Encounter rate with scallops	E	3.7×10^5	3.5×10^4	10.82 _{1,28}	0.003	E2 E1
	D	3.2×10^4	3.5×10^4	0.94 _{5,28}	0.472	
	ExD	6.7×10^4	3.5×10^4	1.94 _{5,28}	0.119	
Pr{consumption capture} on scallops	E	0.260	0.127	2.04 _{1,27}	0.164	
Predation rate on mussels	D	2.314	1.146	2.02 _{5,18}	0.124	
Encounter rate with mussels	D	132.2	52.33	2.52 _{5,16}	0.072	
Pr{consumption capture} on mussels	D	0.234	0.109	2.14 _{4,10}	0.150	

Encounter rate with mussels and proportion of time spent foraging were square root transformed. Proportion of time spent searching could not be transformed to satisfy assumptions, and raw data were used. Pr{capture|encounter} on scallops and on mussels were not tested statistically because there was little variation in the data; Pr{consumption|capture} on scallops was pooled across density to provide enough data for analysis. df1=numerator df, df2=denominator df. E=environment (E1=scallops alone, E2=scallops and mussels present); D=scallop density (per m²). Post-hoc comparisons used Ryan's Q test. Treatment level means are listed in increasing magnitude; those sharing a common underline do not differ significantly.

tion rate on scallops did not show any pattern with respect to scallop density (Table 7, Fig. 4e). Predation rate on scallops was significantly greater when mussels were absent than when mussels were present. Predation rate on mussels did not vary significantly across scallop density in both experiments (Tables 6 and 7).

3.2.2. Rock crab foraging behaviours

The presence of mussels did not affect crab foraging behaviours (Tables 6 and 7, Fig. 5). Regardless of whether mussels were present or absent, rock crabs spent <6% of their time foraging. The presence of mussels did not significantly affect the proportion of time spent foraging or searching (Table 7). Scallop density also did not significantly affect these foraging behaviours (Tables 6 and 7).

3.2.3. Encounter behaviours between rock crabs and prey

In both experiments, most observed encounters with scallops and mussels resulted in consumption or rejection of prey (Fig. 6). In the two-factor experiment, the presence of mussels influenced encounter rate of crabs with scallops: encounter rate with scallops was lower when mussels were present than when mussels were absent (Table 7, Fig. 6c,e). $\Pr\{\text{capture}|\text{encounter}\}$ and $\Pr\{\text{consumption}|\text{capture}\}$ on scallops were not influenced by the presence of mussels (Tables 4b, 6 and 7).

Scallop density did not influence encounter behaviours with scallops or mussels in either experiment (Tables 6 and 7, Fig. 6). $\Pr\{\text{capture}|\text{encounter}\}$ was usually close to 1 for scallops and was always 1 for mussels in both experiments (Table 4b; Wong, 2004). $\Pr\{\text{consumption}|\text{capture}\}$ showed high variability (Table 4b; Wong, 2004). Moreover, this probability was often zero for mussels (but not for scallops) at relatively high scallop density (one-factor experiment); in contrast, it was often zero for scallops (but not for mussels) at relatively low scallop density (two-factor experiment, when <50 scallops m^{-2}).

3.2.4. Mechanisms underlying rock crab prey selection

Shell strength (force to crack one valve) was significantly lower for scallops than for mussels (Table 5; $t_{138}=6.21$, $p<0.001$). Energy content per scallop was

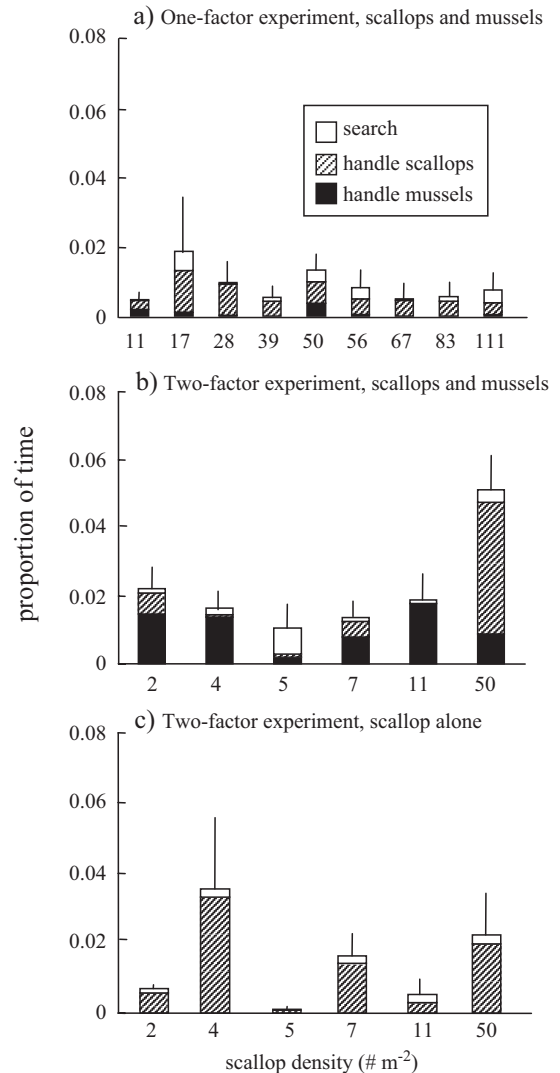


Fig. 5. Mean proportion of time that rock crabs (*C. irroratus*) spent foraging (searching+handling) for juvenile sea scallops (*P. magellanicus*) and blue mussels (*M. edulis*) in the one-factor experiment (a) and the two-factor experiment (b, c). In all cases, crabs were inactive or moving but not foraging for the remainder of time. Error bars are 1 S.E. for proportion of time spent foraging. $n=4$.

significantly greater than that per mussel in the one-factor experiment ($t_{171}=3.87$, $p<0.001$), but was not significantly different in the two-factor experiment ($t_{98}=1.66$, $p=0.099$). Handling time per scallop and per mussel did not differ significantly (one-factor experiment: $t_{23}=0.633$, $p=0.533$; two-factor experiment: $t_{47}=1.317$, $p=0.194$). Profitability of scallops

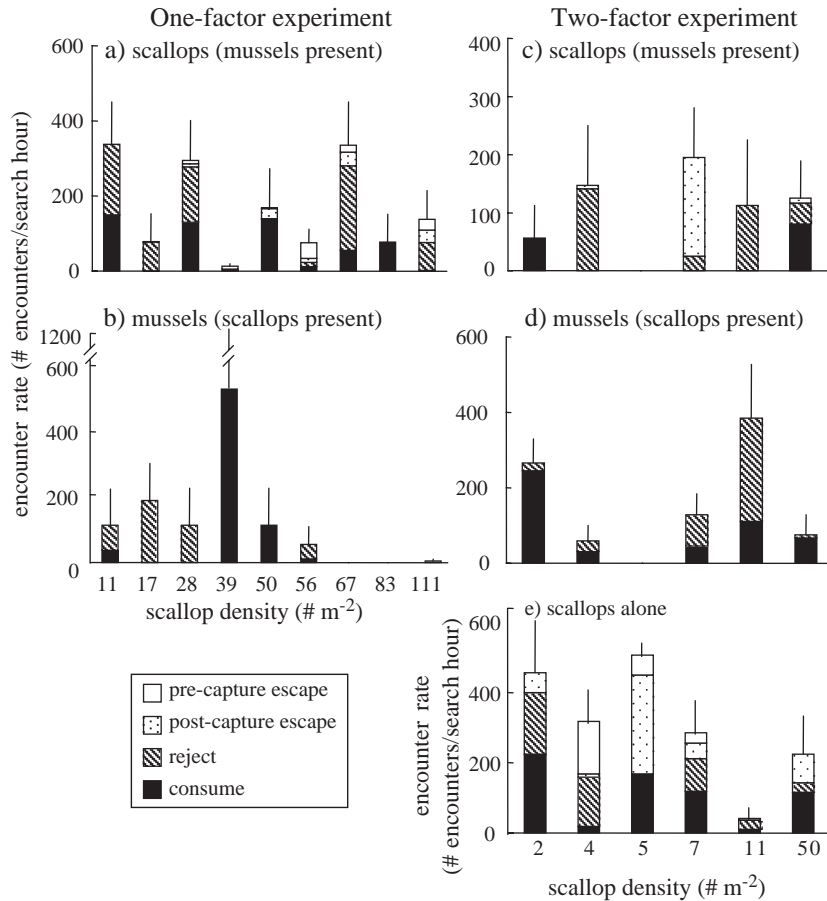


Fig. 6. Mean encounter rate between rock crabs (*C. irroratus*) and juvenile scallops (*P. magellanicus*) and blue mussels (*M. edulis*) in the one-factor experiment (a, b) and the two-factor experiment (c, d, e). The portions of each bar represent the outcomes of encounters. In all cases, error bars are 1 S.E. for encounter rate. No encounter was observed at 5 scallops m⁻² (c, d) or at 67 and 83 scallops m⁻² (b). $n=2-4$.

and mussels was similar in the one-factor experiment; profitability of scallops was higher than that of mussels in the two-factor experiment. Based on encounter rates and profitabilities, the two prey types should be attacked in both experiments, except for the highest scallop density in the two-factor experiment, where only scallops should be attacked.

In both experiments, the ratio of observed encounter rates with scallops and mussels (i.e., crab encounter rates with scallops: crab encounter rates with mussels) was consistently higher than the expected ratio (note: observed ratio was not calculated for 39, 67 and 83 scallops m⁻² in one-factor experiment, and for 5 scallops m⁻² in two factor experiment, because of too few observations or missing data).

Over the different scallop densities, the observed ratio ranged from 0.2 to 7.7, and the expected ratio from 0.03 to 1.6. In both experiments, $\text{Pr}\{\text{capture}|\text{encounter}\}$ was very high and similar for scallops and mussels (Table 4b). $\text{Pr}\{\text{consumption}|\text{capture}\}$ was often zero for mussels at relatively high scallop density (one-factor experiment), and so was generally lower than for scallops (Table 4b; Wong, 2004); however, the difference was not significant due to high variability ($t_{28}=1.03$, $p=0.311$). In contrast, at relatively low scallop density (two-factor experiment), $\text{Pr}\{\text{consumption}|\text{capture}\}$ was significantly higher for mussels than scallops ($t_{25}=2.39$, $p=0.024$, including all data; $t_{23}=2.06$ $p=0.050$, excluding data for 50 scallops m⁻²).

3.2.5. Rock crab functional response in the presence of alternative prey

Rock crabs had a functional response on scallops in the presence of mussels in the two-factor experiment. We successfully fit the modified functional response model for multiple prey species (Eq. (2)) to observed predation rate data ($F_{2,23}=53.7$, $p<0.001$). The regression explained 59.3% of the total variance about the mean (mean corrected R^2), although this statistic is calculated assuming asymptotic normality and is not entirely appropriate for non-linear regression (Draper and Smith, 1998). The estimated rate of successful search (a_i) for scallops was $8.0 \pm 2.2 \text{ day}^{-1}$. The estimated handling time per scallop (h_i) was $0.007 \pm 0.002 \text{ day prey}^{-1}$ (or $\sim 10 \text{ min scallop}^{-1}$), which is similar to that observed experimentally (Table 5). For mussels, the parameter d_m was estimated to be 0.004, which converts to an estimated rate of successful search (a_m) of 0.81 day^{-1} (using the mean observed handling time per mussel).

4. Discussion

4.1. Prey selection

Sea stars (*A. vulgaris*) and rock crabs (*C. irroratus*) selected particular prey species when offered juvenile sea scallops (*P. magellanicus*) and blue mussels (*M. edulis*) concurrently. Components of the predation cycle (encounter rate, encounter probabilities) and prey characteristics (handling time per prey, energy content, shell strength) were quantified to help identify mechanisms underlying the observed selection.

We predicted that sea stars would select mussels over scallops, and that passive selection mechanisms would underlie observed selection. Our predictions were partially supported: sea star selection for mussels was likely determined by a combination of active and passive selection. Active selection was detected since sea stars consumed significantly more mussels than expected when given a choice of prey types than when not given a choice. $\text{Pr}\{\text{attack}|\text{encounter}\}$ appeared to be an important component of active selection, since it was significantly higher for mussels than scallops. Sea stars avoided encountered scallops relatively often (1–66% of encounters), but attacked almost all encountered mussels. From energy content analyses, sea star

active selection may be based on selection of prey with the highest energy content. In our case, prey profitability did not provide a useful framework to understand active selection since it did not differ much between mussels and scallops; differences in handling time compensated for differences in energy content. In both sea star experiments, passive selection was evident in $\text{Pr}\{\text{capture}|\text{attack}\}$. This probability for scallops was very low, whereas for mussels it was always 1. This reflects differential prey escape capabilities: juvenile scallops are effective swimmers that can easily escape sea stars (Manuel and Dadswell, 1993; Barbeau and Scheibling, 1994), while mussels do not have an active escape response. Sea star encounter rates with scallops and mussels did not explain prey selection, since observed encounter rates were fairly similar to expected encounter rates modelled from random movement of animals (Holling, 1966). Finally, we could not conclude anything about $\text{Pr}\{\text{consumption}|\text{capture}\}$, since it was observed very infrequently with scallops. Thus, for our sea star-scallop-mussel system, $\text{Pr}\{\text{attack}|\text{encounter}\}$, a component associated with active selection, and $\text{Pr}\{\text{capture}|\text{attack}\}$, a component associated with passive selection, were the main behavioural mechanisms determining observed prey selection.

Rock crabs showed switching behaviour, since selection changed according to the abundances of prey types available (Murdoch, 1969; Chesson, 1978). Based on both our experiments, crabs selected mussels when scallop density was very low, did not select a certain prey species when scallop density was intermediate, and selected scallops when scallop density was high relative to mussel density. So, at relatively high scallop densities (one-factor experiment and the highest density in the two-factor experiment), crab selection for scallops was as we had predicted. This observed selection was likely associated with both active and passive selection mechanisms. Active selection was detected since crabs consumed significantly more scallops than expected when given a choice of prey types than when not given a choice. In the one-factor experiment, $\text{Pr}\{\text{consumption}|\text{capture}\}$ may have been important in determining crab selection for scallops, since this probability varied from 0.175 to 1 for scallops (average=0.46, Table 4b; Wong, 2004), but was often zero for mussels (average=0.28). This probability contains an active

selection component since crabs may be evaluating captured prey (Jubb et al., 1983); evaluation may be based on information that a crab gains during a short manipulation period of a prey item, or on information that the crab obtains from the relative strength of stimuli from the grasped prey item compared to surrounding prey. In the one-factor experiment, energy content was higher for scallops than for mussels, whereas prey profitability did not differ between prey species. In the two-factor experiment, prey profitability was higher for scallops than mussels, and the prey choice model predicted that only scallops should be included in the crab's diet at the highest scallop density. So, either energy content or prey profitability may have been a basis for active selection. Initially, we had predicted that $\text{Pr}\{\text{attack}|\text{encounter}\}$, a component associated with active selection and incorporated in $\text{Pr}\{\text{capture}|\text{encounter}\}$ in our crab study, would be important; however, $\text{Pr}\{\text{capture}|\text{encounter}\}$ did not vary between prey types and so did not help to explain predation patterns.

Passive selection was also important in determining observed selection by crabs for scallops at relatively high scallop densities. In addition to an active selection component, $\text{Pr}\{\text{consumption}|\text{capture}\}$ contains a passive selection component which is related to shell strength, and crabs may have been rejecting captured prey (i.e., mussels) simply because they had difficulty opening them. Moreover, passive selection may have been associated with encounter rate between predator and prey. Based on our comparison of the ratio of observed encounter rates to the ratio of expected encounter rates, scallops were encountered relatively more often and/or mussels less often than expected from random movements. The clumping behaviour of mussels may have influenced these results: mussels often formed clumps of ~5–10 individuals in the middle of the tanks. While the probability of encounter with clumped prey is potentially higher than with solitary prey, crabs would not usually travel over mussel clumps. So even when mussels were more abundant than scallops and clumped in groups, per capita encounter rate between crabs with mussels was often lower than with scallops. Thus, in our rock crab–scallop–mussel system, encounter rate and $\text{Pr}\{\text{consumption}|\text{capture}\}$ were the mechanisms underlying observed prey selection at relatively high scallop densities.

The observed selection by crabs for mussels at low scallop density ($2 \text{ scallops m}^{-2}$) and the lack of selection at intermediate scallop densities ($4\text{--}11 \text{ scallops m}^{-2}$) were also likely related to encounter rate and $\text{Pr}\{\text{consumption}|\text{capture}\}$. At low and intermediate scallop densities, the ratio of observed encounters with scallops and mussels was still consistently higher than the ratio of expected encounters based on random movements of animals. Thus, even though scallops were at a much lower density than mussels, crabs were encountering scallops relatively more often and/or mussels less often than expected from random movements. However, at these scallop densities, $\text{Pr}\{\text{consumption}|\text{capture}\}$ was significantly higher for mussels (0.52 ± 0.11 , $n=13$, mean \pm SE, excluding data for $50 \text{ scallops m}^{-2}$ in the two-factor experiment) than scallops (0.11 ± 0.11 , $n=9$). Therefore, selection may not have been observed at intermediate scallop densities because a low $\text{Pr}\{\text{consumption}|\text{capture}\}$ on scallops compensated for relatively high encounter rates with scallops. At very low scallop density, we may have observed crab selecting mussels because encounter rates with scallops were not high enough to compensate for low $\text{Pr}\{\text{consumption}|\text{capture}\}$ on scallops. In sum, encounter rate and $\text{Pr}\{\text{consumption}|\text{capture}\}$ appear to be the important mechanisms determining prey selection by crabs, whatever the scallop density.

To our knowledge, only one other study has identified selection of prey species resulting from both active and passive selection mechanisms. Cooper et al. (1985) found that a freshwater predator (*Buenoa scimitra*) selected certain species of zooplankton (cladocerans and ostracods) over copepods (specifically *Diaptomus* sp.). Active selection was apparent in $\text{Pr}\{\text{attack}|\text{encounter}\}$, since it was higher for zooplankton than for copepods. Similar to our sea star–scallop system, passive selection was evident in the $\text{Pr}\{\text{capture}|\text{attack}\}$, a result of differential prey escape mechanisms (copepods have a more vigorous escape response than cladocerans and ostracods). Based on this study and ours, different mechanisms can lead to observed selection when both active and passive components are involved. For example, in our study, sea star selection was influenced by $\text{Pr}\{\text{attack}|\text{capture}\}$ and $\text{Pr}\{\text{capture}|\text{attack}\}$, whereas rock crab selection was influenced by encounter rate and $\text{Pr}\{\text{consumption}|\text{capture}\}$. While few studies have identified selec-

tion in terms of both active and passive components, many have identified the importance of passive selection. Based on a survey of aquatic predator–prey interactions, Sih and Moore (1990) found that out of 33 studies, 82% related selection to passive selection components (the remaining 18% related selection to active selection). Encounter rate between predators and prey has often been identified as important. For example, Bergelson (1985) found that dragonfly nymphs consistently attacked prey encountered most often (mayfly nymphs and tubifex worms), and Cooper et al. (1985) found that encounter rate determined most freshwater predator diets of zooplankton (except for *B. scimitra*). Also, a predator's ability to capture mobile prey, reflected in $\text{Pr}\{\text{capture}|\text{attack}\}$ (or $\text{Pr}\{\text{capture}|\text{encounter}\}$), is often identified as the single important behaviour contributing to selection (Allan et al., 1987; Barbeau and Scheibling, 1994; Lang and Gsödl, 2001).

4.2. The effect of alternative prey on the functional response

We predicted that both sea stars and rock crabs would have a type II functional response on scallops (the target prey) in the presence of mussels. This prediction was not supported for sea stars. When mussels were present, sea stars selected mussels and spent a substantial amount of time handling them. Because the term describing mussel consumption ($d_m N_m$) in the functional response model was very large, the time available for searching (and subsequently encountering prey) was reduced (Chesson, 1989). As a result, scallop consumption by sea stars was very low in the presence of mussels, and sea stars did not have a functional response on scallops. This differed from the type III functional response of sea stars observed in another study, where similar densities of scallops were offered in the absence of mussels (as discussed in Wong, 2004).

Our prediction that rock crabs would have a type II functional response on scallops was supported when mussels were present with scallops at relatively low density (two-factor experiment). Crabs did not show a functional response when mussels were present with scallops at relatively high density (one-factor experiment) or when scallops were offered alone at relatively low density (two-factor experi-

ment). In a comparable experiment, where scallops were offered at a high range of densities in the absence of mussels, crabs also did not have a functional response (Wong, 2004). In these cases where no functional response was observed, predation rate may already have been at the plateau. The presence of mussels with scallops at low density may have distracted and slowed the fast moving crabs, causing the entire functional response to be exhibited. As predicted, predation rate at the plateau of the functional response on scallops was lower when mussels were present than when mussels were absent. Whether in the absence or presence of mussels, a functional response on scallops may be more evident if smaller scallops were used (e.g., 15–25 mm SH), since the plateau would be higher (6–10 scallops day^{-1} rather than 2 scallops day^{-1} ; Barbeau and Scheibling, 1994), giving more opportunity to see the initial increase in predation rate.

4.3. Practical implications

Our study has contributed to the understanding of how multiple prey types influence predator–prey interactions. Additionally, it has applications for the bottom aquaculture of scallops. Our study suggests that if sea stars are the main predators of seeded scallops, aquaculturists could seed an additional prey species that can not actively escape predators, since $\text{Pr}\{\text{capture}|\text{attack}\}$ is a dominant mechanism underlying sea star predation rates. If crabs are the main predators at the seeding site, scallop survival may be increased by seeding an alternative prey with a lower shell strength, and/or by decreasing encounter rates between crabs and scallops (e.g., by changing the density of seeded scallops), since $\text{Pr}\{\text{consumption}|\text{capture}\}$ and encounter rate are dominant mechanisms underlying crab selection. A recent field study has shown that seeding an alternative prey (blue mussels) concurrently with scallops can provide seeded scallops with a short-term refuge from predation (Wong et al., in press). In this field study, estimated predation rates by sea stars and crabs on seeded scallops near the beginning of the experiment were highest in plots without mussels, were intermediate in plots with mussels at low density, and lowest in plots with mussels at high density (Wong et al., in press). However, the refuge was only short term: prey were not replenished,

and by the end of the experiment the density of seeded scallops was very low, independent of whether mussels had been seeded concurrently or not. In general, alternative prey has the potential to reduce predation pressure on the prey species of interest. However, care must be taken since increased prey density, independent of prey type, may cause short-term aggregations of predators (a result observed in Wong et al., in press; Taylor, 1984). Also, a predator's reproductive rate may benefit from an enhanced diet, and cause a long-term increase in predator numbers (Holling, 1966).

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