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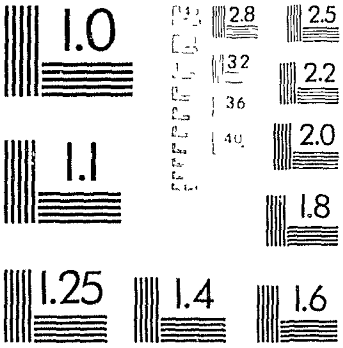

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PREDATOR-PREY INTERACTIONS BETWEEN JUVENILE SEA SCALLOPS (*Placopecten magellanicus*) AND PREDATORY SEA STARS (*Asterias* spp.) AND CRABS (*Cancer irroratus*)

by

Myriam A. Barbeau

Submitted in partial fulfillment of the requirements
for the degree of Doctor of Philosophy

at

Dalhousie University
Halifax, Nova Scotia
April, 1994

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by Myriam Barbeau

in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

Dated May 5, 1994

External Examiner

Research Supervisor

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AUTHOR: Myriam Andrée Barbeau

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ABSTRACT

This study examines the effects of biological and physical factors on predation of juvenile sea scallops (*Placopecten magellanicus*; 5-28 mm shell height) by two major predators, sea stars (*Asterias* spp.) and crabs (*Cancer irroratus*). Predator-prey size laboratory experiments with sea stars (30-150 mm diameter) showed that predation rates increased with increasing sea star size and decreasing scallop size. Preference for small scallops by sea stars was determined by prey vulnerability resulting from differential probabilities of capture upon encounter, even though the probability of capture was <0.20 since scallops usually actively escaped from sea stars. In predator-prey size experiments with crabs (45-120 mm carapace width), predation rates were independent of crab size and increased with scallop size. Preference for large scallops by crabs was due to a combination of prey vulnerability resulting from differential encounter rates, and active selection of large scallops over medium scallops. The probability of capture upon encounter was generally >0.20, since scallops often closed their valves upon encounter with crabs. In laboratory experiments, predation rates on preferred prey sizes increased with water temperature (3-15°C) with Q_{10} values of 6.9 and 2.1 for sea stars and crabs, respectively. The increase in predation rate with temperature was attributable to increased foraging activity of sea stars and crabs, and decreased escape effectiveness of scallops with sea stars. In a field experiment manipulating scallop density, crab predation rate increased with scallop density, but crab density did not, indicating a functional response. Sea star predation rate on scallops was not affected by scallop density. In a series of experiments with different size classes of scallops tethered at different sites and water temperatures (seasons), and in different densities of predators and free-living scallops, the effects of covariates on scallop survival times were assessed using the statistical procedure of survival analysis. Since the tethering technique affected crab and sea star predation differently, the competing causes of scallop mortality were analysed separately. Water temperature, site, and scallop density were the important variables affecting crab predation. There was a significant interaction between temperature and site, such that crab predation on scallops increased with temperature at one site and was independent of temperature at the other site. Predation by crabs also increased with scallop density and, to a lesser extent, with crab density. Water temperature and scallop size were the primary variables affecting sea star predation. Sea star predation on scallops increased with temperature and decreased with scallop size. The results of this study further our understanding of predator-prey interactions in the marine benthic environment as well as suggest options for minimizing predation of scallops by crabs and sea stars in bottom culture operations.

LIST OF ABBREVIATIONS AND SYMBOLS

Abbreviation	Meaning
χ^2	chi-square statistic
°C	degrees Celsius
cm	centimeter
d	day
df	degrees of freedom
F	F statistic
G	Goodness-of-fit statistic
h	hour
L	litre
m	meter
ml	millilitre
min	minute
mm	millimeter
µm	micrometer
MS	mean square
n	sample size
P	probability
$^{\circ}/_{\circ\circ}$ or ppt	parts per thousand
Q_{10}	relationship between a rate function and temperature (*i.e.*, $Q_{10} = \text{rate}_{\text{temperature+10}}/\text{rate}_{\text{temperature}}$)
r	Pearson's correlation coefficient
r^2	proportion of variance in the dependent variable accounted for in a regression
s	second
SD	standard deviation
SE	standard error
t	t statistic
wk	week
yr	year

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PUBLICATIONS

The research described in Chapter 2 is also described in:

Barbeau, M.A. and R.E. Scheibling. In press. Behavioral mechanisms of prey size selection by sea stars (*Asterias vulgaris* Verrill) and crabs (*Cancer irroratus* Say) preying on juvenile sea scallops (*Placopecten magellanicus* (Gmelin)). *J. Exp. Mar. Biol. Ecol.* Written permission was obtained from Elsevier Science Publishers B.V. for non-commercial use of this material in the thesis.

The research described in Chapter 3 is also described in:

Barbeau, M.A. and R.E. Scheibling. In press. Temperature effects on predation of juvenile sea scallops (*Placopecten magellanicus* (Gmelin)) by sea stars (*Asterias vulgaris* Verrill) and crabs (*Cancer irroratus* Say). *J. Exp. Mar. Biol. Ecol.*

The research described in Chapter 4 is also described in:

Barbeau, M.A. and R.E. Scheibling. Accepted. Procedural effects of prey tethering experiments: predation of juvenile scallops by crabs and sea stars. *Mar. Ecol. Prog. Ser.*

CHAPTER 1: General Introduction

Predation is an important ecological process affecting population and community structure and dynamics (Taylor 1984, Begon *et al.* 1986). Traditionally, predator-prey interactions have been investigated by simply measuring predation rates. However, since the 1960's, there has been an increased consideration of the integral components determining the complex nature of predator-prey interactions in terrestrial systems (Holling 1959a, b, 1965, 1966). Later, attention became focused mostly on the behavioural components of foraging, resulting in the development of optimal foraging theory (Charnov 1976a, b, Stephens and Krebs 1986). More recently (1980's in aquatic systems (*e.g.*, Pastorok 1981, Cooper *et al.* 1985, Peckarsky and Penton 1989) and 1990's in marine benthic systems (*e.g.*, Pennings 1990)), researchers have begun in earnest to investigate predation rate in terms of a combination of ecological and behavioural elements in the predator-prey interaction. This approach recognizes that a predator performs a series of sequential behaviours (termed the predation cycle) which includes locating, attacking, capturing and ingesting prey (O'Brien 1979, Riessen *et al.* 1984, O'Brien 1987). Based on this cycle, predation rate can be divided into three components: 1) encounter rate between predator and prey, 2) probability of capture upon encounter and 3) probability of consumption upon capture. In some studies, these components have been subdivided further to better describe the predator-prey system (Riessen *et al.* 1984, O'Brien 1987, Osenberg and Mittelbach 1989). By analyzing a predation event through its components, the mechanisms that underlie the observed patterns of prey selection can be elucidated. Once the mechanisms acting on a predator-prey interaction are understood, one is better able to model the interaction and to predict predation rates in the predator-prey interaction for a particular set of environmental conditions. This knowledge is important for understanding the distribution and abundance of predators and prey, and for successful conservation and harvesting of animal populations.

With sea scallops (*Placopecten magellanicus* (Gmelin)), as with other marine bivalves, predation on the juvenile stage is usually high (Jensen and Jensen 1985, Naidu and Cahill 1986, Boghen 1989, Juanes 1992, Picard 1992, Hatcher *et al.* In press a). However, in contrast to many marine bivalves which are sessile, most species of scallops (including *P. magellanicus*) have a remarkable ability to swim by jet propulsion to escape predators (Thomas and Gruffydd 1971, Stephens and Boyle 1978, Peterson *et al.* 1982, Dadswell and Weihs 1990, Manuel and Dadswell 1991). In addition, scallops have extensible tentacles on the mantle edge around the periphery of the shell, with chemo- and mechanoreceptors, which may be used to detect predators (Moir 1977, Stephens 1978b, Beninger and Le Pennec 1991), and non-cephalic image-forming eyes which can detect movement (Land 1984b, Wilkens 1991). Such mobility and sensory abilities allow for behavioural flexibility in response to predator attack, and thus make scallops a particularly interesting prey organism to study in the marine benthic environment. In light of this flexibility in prey behaviour, the approach of examining components of the predation cycle should prove very useful for assessing the relative importance of predator and prey characteristics in determining predation rates.

Sea scallops are also an important commercial species for fisheries and aquaculture in Atlantic Canada and the northeastern United States (Naidu *et al.* 1989, Brand 1991). Two methods of aquaculture are presently under trial: suspended culture, which consists of placing scallops in cages or attached to lines suspended in the water column, and bottom culture, which consists of releasing scallops onto the seabed (seeding) and harvesting them when they reach commercial size. Both methods of culture have advantages and disadvantages. Suspended culture results in high rates of growth and survival, but is capital and labour intensive. Bottom culture produces lower yields due to lower survival, to dispersal beyond the seeded area, and perhaps to slower growth rates (although, Kleinman (1994) observed no significant differences in growth rate between free-living and suspended scallops in Lunenburg Bay), but has lower costs (Tremblay 1988, Wildish *et al.*

1988). Economic feasibility studies indicate that bottom seeding sea scallops is the only viable option (Wildish *et al.* 1988). Bottom culture of other scallop species in the Far East, Europe, Australia, and New Zealand have been successful, but usually after a period of growth in suspended culture (Ventilla 1982, Bull In press, Dao *et al.* In press, Thomson In press). Although bottom culture or a combination of suspended and bottom culture (intermediate culture) may be the most cost-effective method of sea scallop aquaculture, knowledge of the processes affecting juvenile scallop mortality, growth and movement in natural benthic habitats is limited. To fill this gap, my research focused on one of these processes, namely predation.

Sea scallops (also called giant scallops) range from the coast of Newfoundland to North Carolina (Posgay 1957). They usually occur at depths between 10 to 110 m, but are found in shallower water in the northern part of their range (Naidu *et al.* 1989). Juvenile sea scallops metamorphose from larvae at a size of about 0.3 mm shell height (SH) and reach sexual maturity at a size of ~40 mm SH in 15-25 months (Young-Lai and Aiken 1986, Naidu *et al.* 1989, Dadswell and Parsons 1991). Sea scallops may reach 200 mm SH and live ~20 yr. Predators of sea scallops include sea stars, moonsnails, crabs, lobsters and fish (Table 1.1). In coastal environments where bottom culture is most likely to occur, sea stars and crabs have been observed to be the major predators (Dupouy 1983, Naidu and Cahill 1986, Wildish *et al.* 1988, Picard 1992, Hatcher *et al.* In press a).

Sea stars are non-visual, slow-moving predators that search for food by using distance-chemoreception and/or by relying on chance encounter (Castilla and Crisp 1970, Zafiriou 1972, Sloan 1980a, Sloan and Campbell 1982). Sea stars have an eyespot at the tip of each arm, which detects only changes in light intensity (Yoshida *et al.* 1984). Chemo- and mechanoreceptors are present on the suckers of the tubefeet and along the margins of the ambulacral groove, and are especially prevalent on the sensory tubefeet at the tip of the arms (Valentincic 1973, Sloan 1980b, Valentincic 1983, Barnes 1980). Crabs are

Table 1.1. Reports of predation on sea scallops, *Placopecten magellanicus*.

Predator species	Scallop size (mm)	Comments	Reference
Sea stars:			
Asterias vulgaris	50-80	Laboratory experiment and observation following water temperature fluctuations	Chiasson 1951 and Unpubl. in Dickie and Medcof 1963
	>50	Observations in tracks of trawls and dredges, scallops damaged	Caddy 1968
	75-85, 20-50	Seeding experiment, indirect observation	Wildish *et al.* 1988, Picard 1992
	4-26	Seeding experiment	Hatcher *et al.* In press a
Asterias forbesi	4-26	Seeding experiment	Hatcher *et al.* In press a
Astropecten americanus	0.2-2.5	Gut content, scallops ingested whole	Larson and Lee 1978
Crossaster papposus	14-18	Anecdotal, scallops ingested whole	Medcof and Bourne 1964
Gastropods:			
Lunatia heros	>50	Observation following water temperature fluctuations	Young 1930 in Dickie and Medcof 1963

Table 1.1 continued.

Predator species	Scallop size (mm)	Comments	Reference
Crustaceans:			
Cancer irroratus	>50	Observations in tracks of trawls and dredges, scallops damaged	Caddy 1973
	20-70, 40-110	Laboratory and field experiments	Elner and Jamieson 1979, Jamieson *et al.* 1982
	juveniles	Anecdotal	Auster and Malatesta 1991
	40-60, 20-50	Seeding experiment, indirect observation	Dupouy 1983, Picard 1992
	4-26	Seeding experiment	Hatcher *et al.* In press a
Homarus americanus	?	Gut contents	Squires 1970, Ennis 1973
	20-70, 40-110	Laboratory and field experiments	Elner and Jamieson 1979, Jamieson *et al.* 1982
	20-50	Seeding experiment, indirect observation	Picard 1992

Table 1.1 continued.

Predator species	Scallop size (mm)	Comments	Reference
Fish:			
Gadus morhua	?	Gut contents	Medcof and Bourne 1964
Hippoglossoides platessoides	?	Gut contents	Medcof and Bourne 1964, Kohler and Fitzgerald 1969
	10-59	Gut contents	Naidu and Meron 1986
Anarhichas lupus	?	Gut contents	Medcof and Bourne 1964
Limanda ferruginea	12	Gut contents	Naidu and Meron 1986
Pseudopleuronectes americanus	>50	Observations in tracks of trawls and dredges, scallops damaged	Caddy 1968, 1973
Myoxocephalus spp.	>50	Observations in tracks of trawls and dredges, scallops damaged	Caddy 1968, 1973

fast-moving predators that search for prey mainly through chemical and tactile stimuli received by sense organs on the antennae and walking legs (pereopods) (Elner and Hughes 1978, Hadlock 1980, Blundon and Kennedy 1982, Lawton and Hughes 1985, Juanes and Hartwick 1990). The antennules have high densities of chemoreceptors and are used for distance chemoreception. The dactyls of the pereopods have contact chemoreceptors that are associated with mechanoreceptors (the complex is called the funnel canal) (Blundon and Kennedy 1982, Laverack 1986, 1988, Zimmer-Faust 1989, Rebach *et al.* 1990). Stalked compound eyes aid in the detection of mobile prey (Land 1984a, Cronin 1988).

The predator species studied for my thesis are two congeneric and morphologically similar sea star species (*Asterias vulgaris* Verrill and *A. forbesi* (Desor)), and the rock crab (*Cancer irroratus* Say). *A.vulgaris* ranges from Newfoundland to South Carolina, at depths of 0-900 m (Clark and Downey 1992). Recently, it has been considered to be the same species as *A. rubens* Linnaeus, the common sea star found along the coast of Greenland and Northeastern Atlantic (*i.e.*, Norway to Portugal; Clark and Downey 1992). Along the coast of Nova Scotia and Maine, *A. vulgaris* co-occurs with *A. forbesi*, which can be distinguished by the more rigid body and the bright orange madreporite (Clark and Downey 1992). *A forbesi* ranges from Nova Scotia to Brazil, at depths of 0-150 m (Brinkhurst *et al.* 1975, Clark and Downey 1992). Both sea star species can reach 300 mm in diameter. The rock crab, *C. irroratus*, ranges from Newfoundland to Miami, Florida, at depths of 0-575 m (Squires 1990). Males usually reach a size of 125 mm carapace width (CW) and females, 100 mm CW, although males of up to 140 mm CW have been observed (Bigford 1979, Squires 1990). Crabs grow in increments due to the molting process, with smaller crabs molting more frequently than larger crabs. During molting, which usually occurs in late winter or early fall, crabs stop feeding and lower their activity level (Bigford 1979).

My thesis research comprises a series of laboratory and field experiments designed to examine the effect of biological and physical factors on predation of juvenile sea scallops

(*Placopecten magellanicus*) by sea stars (*Asterias* spp.) and crabs (*Cancer irroratus*). The variables investigated include predator size and density, prey size and density, water temperature, and field site. Predation rates were analyzed in terms of components of the predation cycle. The research addresses the following sets of questions:

1) What are the predator-prey size relationships between juvenile scallops and their major predators? Are certain size classes of scallops more vulnerable to predation than others? Do predators actively select certain prey sizes? What are the mechanisms determining prey selection?

2) How does water temperature, an important environmental variable, affect predation rates of juvenile scallops by their predators? Which predation rate components of the interaction are most affected by temperature?

3) How do changes in scallop density affect predation rates? Do predators exhibit individual increases in consumption rate (*i.e.*, functional responses) and/or increases in local densities (*i.e.*, numerical aggregative responses) in response to increases in scallop density?

4) How do scallop size, scallop density, predator density and water temperature interact to determine scallop survival in the field? To what extent do these factors account for among-site variability in predation rate?

Each group of questions is examined in one of the following chapters. Chapter 2 examines the predator-prey size relationships and describes the behavioural interactions of scallops, sea stars and crabs in laboratory experiments. Chapter 3 examines the effect of water temperature on these predator-prey interactions in the laboratory. The experimental procedure of tethering scallops is assessed in laboratory experiments in Chapter 4, before examining the effects of various biological and physical variables on scallop survival in the field in Chapter 5. The results of the laboratory and field experiments contribute to the theoretical understanding of predator-prey interactions and have implications for aquaculture, as discussed in Chapter 6.

CHAPTER 2: Behavioural mechanisms of prey size selection by sea stars and crabs preying on juvenile sea scallops

Introduction

In recent years, much research has been directed towards describing, understanding and modelling prey selection by predators in aquatic, marine and terrestrial systems (Kerfoot 1980, Kamil *et al.* 1987, O'Brien 1987, Hughes 1990). The resultant body of knowledge can be usefully integrated into a simple and appealing concept. This concept is based on the series of sequential behaviours (termed the predation cycle) that a predator performs during a predation event and that includes locating, attacking, capturing and ingesting prey (O'Brien 1979, Riessen *et al.* 1984, O'Brien 1987). Based on this cycle, predation rate can be divided into components such as encounter rate between predator and prey, probability of capture upon an encounter, and probability of consumption upon a capture (Pastorok 1981, Riessen *et al.* 1984, Cooper *et al.* 1985, Bence and Murdoch 1986, Allan *et al.* 1987, Ryer 1988, Lawton 1989, Osenberg and Mittelbach 1989, Peckarsky and Penton 1989, Pennings 1990, Sih and Moore 1990). Prey selection results from differential predation rates. Mechanisms underlying observed patterns of prey selection can thus be revealed by examining predation rate through its different components.

Components of predation can be used to determine whether observed preferences exhibited by predators for certain prey types are passive or active. Passive or mechanistic prey selection usually results from physical properties and behaviours of the predator and prey (Hughes 1980a, Rodrigues *et al.* 1987, Hughes 1988), such as body size, movement velocities and habitat overlap of predators and prey, and escape abilities or shell strength of prey. Thus, passive components of predation are generally determined by encounter rate and probability of capture, collectively termed the risk of predation or prey vulnerability (Pastorok 1981, Allan *et al.* 1987, Osenberg and Mittelbach 1989, Peckarsky and Penton 1989, Pennings 1990, Sih and Moore 1990). Active selection occurs when an animal selects a prey type more often than expected when given a choice of prey types than when not given a choice (Rapport and Turner 1970, Liszka and Underwood 1990). As with passive selection, active selection may occur at more than one point in the predation cycle. It may occur in the attack process, *i.e.*, in the predator's decision of whether to attack an encountered prey item or to continue searching (Allan *et al.* 1987, Osenberg and Mittelbach 1989, Pennings 1990, Sih and Moore 1990, Litvak and Leggett 1992), or in the rejection process, *i.e.*, in the predator's decision of whether to accept or to reject a manipulated (and therefore attacked and captured) prey item (Hughes 1979, 1980a, Jubb *et al.* 1983, Allan *et al.* 1987).

A conceptual framework for examining active selection comes from the prey choice model of optimal foraging theory (Osenberg and Mittelbach 1989, Sih and Moore 1990). In this model, predators actively select prey to maximize the rate of energy intake. Prey types are ranked in terms of value to the predator by the ratio of energy gain to handling time, termed profitability of a prey type (Stephens and Krebs 1986). A second prediction of the prey choice model is that to maximize energy intake per unit foraging time, a predator consumes prey items of higher profitabilities and ignores items of lower profitabilities. A third prediction of the model is that the inclusion of a prey type in a predator's diet 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 the active selection component of predation rate should be influenced by prey profitabilities. If prey selection is the result of active selection only, then the consumption rate on different prey sizes (termed the diet curve) may be expected to reflect prey profitabilities (Elner and Hughes 1978, Elner 1980, Jubb *et al.* 1983, Campbell 1987). If observed prey preferences are the result of active and passive components, then profitability should be compared to the active component only (Osenberg and Mittelbach 1989). If, however, prey selection is the result of prey vulnerability (passive components) only, then prey profitabilities are irrelevant to the particular predator-prey system (Pastorok 1981, ap Rheinallt 1986).

The sea scallop *Placopecten magellanicus* (Gmelin) is an important bivalve species in fisheries and aquaculture along the coast of Eastern Canada and Northeastern USA (Naidu *et al.* 1989, Brand 1991). Predation during the juvenile stage of the sea scallop is thought to limit population size (MacKenzie 1979, Young-Lai and Aiken 1986, Tremblay 1988, Naidu *et al.* 1989, Hatcher *et al.* In press a). Although sea stars, crabs, lobsters and several species of fish have been identified as predators of sea scallops (Table 1.1), there is little known about predation rates on juvenile sea scallops and the behavioural mechanisms underlying these rates. Juvenile scallops are thought to be susceptible to most of these predators because of their small size. They reach 5 mm shell height (SH) in 6-8 months after settlement and 20-25 mm SH in 10-18 months (Young-Lai and Aiken 1986, Naidu *et al.* 1989, Dadswell and Parsons 1991). A commercial size of 90 mm SH is reached in approximately 4 years.

The objective of this study was to investigate the predator-prey size relationships between juvenile sea scallops and two of their main predators, the sea star *Asterias vulgaris* Verrill and the rock crab *Cancer irroratus* Say. In a series of laboratory experiments, the effect of predator and scallop size on predation rates, predator foraging behaviours and scallop escape responses were examined. To identify behavioural mechanisms underlying observed predation rates, single prey size (no choice) experiments were conducted, in which I expected predation rates to be affected by only passive or mechanistic selection since alternative prey types were not available, and multiple prey size (choice) experiments, in which I expected predation rates to be affected by both passive and active selection. Only by comparing size-specific consumption rates in single and multiple prey size experiments can active selection be recognized. To determine the relative importance of passive and active prey selection, predation rates were analyzed in terms of specifically defined components: encounter rate, probability of capture upon encounter, and probability of consumption upon capture. Encounter rate was predicted to be a passive component and to reflect body size and movement velocity of predator and prey. The probability of capture upon encounter was also expected to be a passive component since it is a function of prey behaviour (*i.e.*, through the escape response of scallops). The probability of consumption upon capture was viewed as an active component since, once captured, juvenile scallops were without defence against the predator. Based on the third prediction of the prey choice model of optimal foraging (*i.e.*, the inclusion of a prey type in a predator's diet depends on the encounter rate with other prey types of higher profitability), the probability of consumption should approach 1 in the single prey type experiments because alternative prey types were not available, and should vary in the multiple prey size experiments to reflect differential prey profitabilities.

Materials and Methods

EXPERIMENTS

Effects of predator (sea star, rock crab) and prey (juvenile scallop) size on scallop survival and predator foraging behaviour were examined in single prey size and multiple prey size experiments conducted in 54 L (60 cm length x 30 cm width x 30 cm height) glass aquaria. In single prey size predation experiments, 15-20 scallops from one of two or three size classes were presented to a single predator from one of two or three size classes (Table 2.1). In multiple prey size experiments, 15 scallops (5 individuals from each of the three size classes) were offered to a single predator from one of four size classes. The number of replicate aquaria within each scallop-predator combination ranged from 2-4 (Table 2.1). The duration of each experiment ranged from 4-8 d, except for Sea star Experiment 2.2 which was extended to 26 d due to the high individual variability in sea star activity. One to four control aquaria with scallops of single or multiple size classes, but without a predator, were run concurrently in each experiment to monitor non-predatory mortality.

Sea stars *Asterias vulgaris* and rock crabs *Cancer irroratus* used in any given experiment were collected from one site, either Sheet Harbour, Sandy Cove or Lunenburg

Bay, Nova Scotia. Prior to the experiments, predators were held in 140 L seawater tanks for 1-20 weeks (the acclimation period was the same for animals in any given experiment) and fed intact, live mussels (*Mytilus edulis*) *ad libitum*. Sea star size (diameter) was measured (± 2 mm) as the distance between the tip of an average size ray to the mouth multiplied by 2. Crab size was measured (± 1 mm) as the carapace width (CW) between the tips of the two most distal marginal teeth.

Wild juvenile scallops (*Placopecten magellanicus*) were obtained from spat collectors in Passamaquoddy Bay, New Brunswick, through a commercial supplier (The Great Maritime Scallop Trading Co.). Cultured juvenile scallops were obtained from an experimental hatchery at Sandy Cove, Nova Scotia, (Fisheries Resource Development Limited). Scallops were kept in 70 L seawater tanks and continually drip-fed to maintain a concentration of ~1 x 10^4 cells ml^{-1} cultured algae, either *T-Isochrysis galbana* or a mixture of *T-Isochrysis galbana*, *Thalassiosira pseudonana* and *Chaetoceros mülleri* (Hollett and Dabinett 1989). Scallop size was measured (± 0.1 mm) as the shell height (SH) from the middle of the dorsal hinge to the furthest ventral shell edge.

Prior to initiation of predation experiments, predators were starved for 48 h to standardize hunger levels. Individual animals were used only once in an experiment, except for crabs used in Experiments 2 and 3. These crabs were held for 1 month between the two experiments in the pre-experimental conditions described above. Only male crabs were used to avoid potential confounding sex-related variation. To provide shelter for crabs, I used a black plastic sheet to cover one end of the aquarium (shaded 25% of the bottom area). Scallops were acclimated to experimental aquaria for at least 20 h prior to introduction of a predator. Scallops in experimental aquaria were fed 50 ml of concentrated cultured algae (1 x 10^6 cells ml^{-1}) daily. Aquaria were monitored daily in the morning and just before sunset to record the number and size of scallops consumed and to replace consumed scallops.

Table 2.1. Description of predator-prey size laboratory experiments conducted between Sept.1989-Jan.1990 and Nov.1990-Jan.1991 with sea stars (*Asterias vulgaris*) or rock crabs (*Cancer irroratus*). In single prey size experiments, predators of 2-3 size classes were offered juvenile scallops of one of 2-3 size classes in aquaria. In multiple prey size experiments, predators of 4 size classes were offered juvenile scallops of 3 size classes. Scallops were obtained from collectors (wild) or from a hatchery as indicated. The number of scallops offered to a predator in an aquarium, the number of replicate aquaria per treatment combination, and the duration of each experiment are given. Water temperature, averaged over the duration of each experiment, was the ambient seawater temperature. Crab Experiment 2.1 had two temporal blocks; mean water temperature is given for each block. Scallop size was measured as shell height. Predator size classes were measured as diameter for sea stars and carapace width for crabs.

Experiment	Type	Scallop source	No. of scallops per aquarium	Duration (days)	No. of replicate aquaria	Mean (± SD) water temperature (°C)	Scallop size classes (mm)	Predator size classes (mm)
Sea star 2.1	Single prey size	Wild	20	7	2	10.2 ± 0.7	5-8.5	30-45
							10-15	60-75
								120-150
Sea star 2.2	Single prey size	Hatchery	15	26	4	9.7 ± 1.3	5-8.5	80-99
							10-15	125-150
							20-25	
Sea star 2.3	Multiple prey size	Wild	15	7	4	11.9 ± 2.4	5-8.5	35-45
							10-15	55-65
							20-25	80-90
								125-135

Table 2.1 continued.

Experiment	Type	Scallop source	No. of scallops per aquarium	Duration (days)	No. of replicate aquaria	Mean (± SD) water temperature (°C)	Scallop size classes (mm)	Predator size classes (mm)
Crab 2.1	Single prey size	Wild	15	4	2	7.2 ± 0.4	5-8.5	65-75
						4.3 ± 0.9	10-15	90-100
							20-25	110-120
Crab 2.2	Single prey size	Hatchery	15	8	3	8.4 ± 0.8	5-8.5	45-60
							10-15	70-85
							20-25	95-110
Crab 2.3	Multiple prey size	Hatchery	15	5	4	4.3 ± 0.4	5-8.5	50-52
							10-15	70-76
							20-25	89-93
								100-110

Predation rates were measured as the number of prey consumed per day per predator (consumption rate) in all experiments, and as the energy consumed per day per predator, standardized for predator body weight (standardized energy consumption rate) in single prey size experiments. Consumption rate was calculated for individual predators as the total number of scallops consumed by the predator during the experiment divided by the duration (in days) of the experiment. The first day of the experiment was excluded from these calculations to allow the predator to acclimate to the aquarium environment. To determine energy content of consumed scallops, soft tissues of 100 scallops (4.7-28.3 mm SH) were removed from the shell and dried at 80°C for 45 h. The regression of tissue dry weight (y, mg) on shell height (x, mm) based on this sample was:

$$\log_{10}(y) = 3.176\log_{10}(x) - 2.678 \quad (r^2=0.991, \mathrm{df}=1, 98, P<0.001).$$

Shell heights of the experimental scallops were converted to dry weights using this equation. Energy consumption per scallop ingested was estimated using the conversion: 1 g dry weight of body tissue = 24500 J (MacDonald and Thompson 1985). Predators consumed all of the body tissue except in two instances where crabs consumed approximately 75% of the body tissue. Standardized energy consumption rate was obtained by converting consumption rate (*i.e.*, number of scallops consumed d^{-1} predator^{-1}) to energy consumption and dividing by predator dry weight. Predator dry weight was estimated using the following equations:

$$\log_{10}(y) = 0.959\log_{10}(x) - 0.924 \quad \text{for } \textit{Asterias vulgaris};$$

$$\log_{10}(y) = 2.938\log_{10}(x) - 4.226 \quad \text{for } \textit{Cancer irroratus};$$

where y is dry weight in g and x is diameter for *A. vulgaris* or CW for *C. irroratus* in mm (Scheibling and Raymond 1990).

Ambient seawater was sandbed filtered to 50 μm, and the flow to each aquarium regulated at 400-500 ml min^{-1}. Salinity averaged (± SD) 31.2 ± 0.5 ppt during this study. Water temperature was measured twice daily and averaged over the duration of each experiment (Table 2.1). The natural light:dark regime was maintained in all experiments.

Natural lighting was provided through windows and augmented by overhead fluorescent lights.

BEHAVIOURS

To determine the mechanisms underlying observed predation rates, predator and prey behaviours were quantified. Aquaria were monitored by an observer and by video camera. Video camera observation was used to sample behaviours *ad libitum* in all experiments. Visual sampling of behaviours by an observer was *ad libitum* in Sea star Experiment 2.1, Sea star Experiment 2.3 and Crab Experiment 2.1. In Sea star Experiment 2.2, Crab Experiment 2.2 and Crab Experiment 2.3, visual sampling of behaviours by an observer was continuous for 20-30 min intervals at randomly chosen times. Measures obtained from the behavioural observations are presented for Sea star Experiment 2.2, Sea star Experiment 2.3, Crab Experiment 2.2 and Crab Experiment 2.3; total observation periods by an observer in these experiments were 660, 150-300, 250 and 170 min aquarium^{-1}, respectively. A blind was used when observing crabs.

Predator foraging behaviour consisted of searching for and handling scallops. A sea star was characterized as searching when it moved towards scallops, usually along the bottom of the aquarium, with its arm tips curled up and sensory podia extended. Handling was defined to begin once the scallop was caught, usually at the tip of the arm. The sea star then manipulated the scallop to its oral region and assumed a humped, feeding position to extra-orally digest the prey. Handling continued until the sea star completed digestion and moved away, leaving an empty shell (usually the valves were still bound by the dorsal hinge ligament). When not foraging, sea stars were either active (usually walking along the walls of the aquarium near the water surface, and not heading for scallops) or quiescent.

A crab was characterized as searching when it probed the floor of the aquarium with the dactyls of its walking legs. Upon sensing a scallop, the crab positioned it under the abdomen and used the claws in an attempt to seize it. Handling was defined to begin once the scallop was picked up. The crab then opened the scallop. Handling continued until the crab finished eating and walked away. When not foraging, crabs were either active (attempting to climb or walking without probing) or immobile (quiescent or cleaning).

Encounters between predators and scallops may occur with sensory detection before actual physical contact (Curio 1976). However, non-physical encounters were difficult to observe and quantify. As a result, an encounter was only scored when a searching predator came into physical contact with a scallop. Encounters culminated either in prey escape, rejection or consumption (Fig. 2.1). Two types of prey escapes were observed in sea star-scallop interactions: active escapes by scallops and retractions by sea stars. Active escapes occurred when scallops jumped (single claps displacing the scallop along the bottom) or swam (repeated claps propelling the scallop through the water column). Retractions occurred when sea stars curled their arm aborally after encountering a scallop and moved several times alternately away from and towards the scallop before finally moving away. Two types of prey escapes also were observed in crab-scallop interactions: active escapes, in which scallops jumped or swam away, and passive escapes, in which scallops closed their valves and were not picked up by the crabs. Captures occurred when tubefeet of sea stars attached to the shell of a scallop or when the chelae of crabs seized a scallop. Upon capture, predators either rejected the scallop or accepted and consumed it. Handling time was defined as the time from capture to the end of consumption and rejection time was defined as the time from capture to rejection.

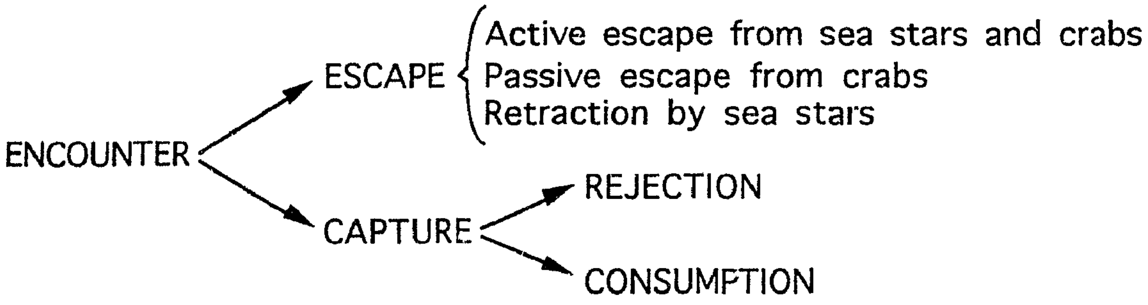


Fig. 2.1. Schematic of the different behaviours following a physical encounter between sea star or crab predators and scallops. See text for a description of the different behaviours.

Encounter behaviours were used to calculate encounter rate during predator searching time, the probability of capture upon encounter, and the probability of consumption upon capture. Encounter rates (*i.e.*, number of encounters/searching time) are presented only for the single prey size experiments, as these are expected to reflect true encounter rates. In other words, after detecting a prey item, a predator may decide to attack or to continue searching. According to the prey choice model of optimal foraging, this decision is based on the availability of other prey types (Stephens and Krebs 1986). Since no other prey types were present in the single prey size experiments, all prey items detected were assumed to be attacked and, hence, physically contacted. The probability of capture was calculated as: (number of rejections + consumptions)/number of encounters. The probability of consumption was calculated as: number of consumptions/(number of rejections + consumptions). Other measures included: 1) percentage of time a predator spent searching (*i.e.*, searching time/observation time x 100), 2) percentage of time a predator spent handling scallops (*i.e.*, handling time/observation time x 100), 3) proportion of active escapes to total escapes in sea star-scallop interactions (*i.e.*, (number of swims + jumps)/(number of swims + jumps + retractions)), 4) proportion of active escapes resulting in swims (*i.e.*, number of swims/(number of swims + jumps)), and 5) proportion of active escapes resulting in collisions with aquarium walls (*i.e.*, number of collisions/(number of swims + jumps)).

CALCULATED ENCOUNTER RATES AND PROFITABILITIES

Observed encounter rates were compared to predicted encounter rates between predator and prey. These predicted encounter rates were calculated using Holling's equation (1966), which relates the number of encounters, N_E, during time t, to predator and prey movement velocities, predator and prey size, and prey density in a two-dimensional environment:

$$N_E = [2V_R t(r_A + r_B) + \pi(r_A + r_B)^2]n_B, \qquad (2.1)$$

where V_R is the approximate velocity of predator and prey which equals $(V_A^2 + V_B^2)^{1/2}$; V_A is the velocity of predator; V_B is the velocity of prey; r_A is the radius of predator or of its perceptual field; r_B is the radius of prey; and n_B is the density of prey.

Encounter rates were calculated for Sea star Experiment 2.2 and Crab Experiment 2.2. In the spatially limited environment of an experimental aquarium, with prey continuously present, the water mass was assumed to be homogeneous in its concentration of chemical stimuli emitted by prey. Therefore, distance chemoreception was assumed to be unimportant in prey detection, and the radius of the predator's body contacting the bottom rather than that of its perceptual field was used in the calculation of encounter rate. Sea star radius was calculated as the average diameter in each size class divided by 2. Movement velocities of medium and large sea stars were between 2 and 3 cm min^{-1} when searching. An average of 2.5 cm min^{-1} (or 150 cm h^{-1}) was used in the encounter rate calculations. In crabs, only the tip and setae of walking legs were in contact with the bottom of the aquarium. Each walking leg was estimated to cover an area of the bottom 0.1 cm in diameter. Therefore, crab radius was calculated as 8 walking legs x 0.05 cm = 0.4 cm. Crab movement velocities when searching were 33 ± 9 (SE) cm min^{-1} (or 1980 cm h^{-1}). Scallop radius was calculated as the average shell height in each size class divided by 2. Scallops usually remained stationary until physically contacted by a predator. Therefore, the scallop movement velocity used in the encounter rate calculations was 0 cm h^{-1}. Since prey availability was maintained in the single prey size experiments, scallop density was 15 scallops 1800 cm^{-2}.

To examine whether active prey selection (when it occurred) followed optimal foraging predictions, profitability was calculated for each predator-scallop size combination by dividing the energy (J) obtained from the mean scallop size by mean predator handling time (min). Mean handling time of a given predator-scallop size combination was obtained by combining video camera and experimenter observations in all experiments. The representation of profitability using gross energy rather than net energy assumes that the metabolic costs per unit time of the different handling activities do not differ significantly between the different prey sizes (Pyke 1984, Osenberg and Mittelbach 1989).

STATISTICAL ANALYSIS

Sea star Experiment 2.1 and Crab Experiment 2.1 were randomized block designs. For the sea star experiment, aquaria were located on tables at two heights (2 spatial blocks). For the crab experiment, the blocks (at the same height) were temporal, run one month apart. Blocking factors were non-significant ($P>0.25$) for both experiments; therefore, the blocks were pooled (Underwood 1981). Sea star Experiment 2.2 and Crab Experiment 2.2 were completely randomized designs. The fixed factors were scallop size and predator size. The response variables included: 1) consumption rate and 2) standardized energy consumption rate in Sea star Experiment 2.1, Sea star Experiment 2.2, Crab Experiment 2.1 and Crab Experiment 2.2, 3) percentage of time a predator spent searching for scallops, 4) percentage of time a predator spent handling scallops, 5) encounter rate, 6) probability of capture, and 7) probability of consumption in Sea star Experiment 2.2 and Crab Experiment 2.2, and 8) proportion of active escapes to total escapes, 9) proportion of active escapes resulting in swims, and 10) proportion of active escapes resulting in collisions with aquarium walls in Sea star Experiment 2.2.

The assumption of homogeneity of variance was tested using Cochran's test. When variances were heteroscedastic, the dependent variable was transformed using logarithms or, for proportional data, using arcsine-square root. Transformations were successful in homogenizing variance in all cases. Single prey size experiments were analyzed using two-way, fixed factor analyses of variance (ANOVA). In Sea star Experiment 2.2, analyses of covariance (ANCOVA) were done, in which consumption rate or standardized energy consumption rate was the dependent variable and the ratio of searching time to observation time (an independent measure of foraging activity) was the covariate. A three-way ANOVA was initially done to check for non-significant interactions between the covariate and the fixed factors. (An ANCOVA is not presented for Crab Experiment 2.2, because the relationship between the covariate and consumption rate or standardized energy consumption rate was not significant). Multiple comparisons of the means (at the 0.05 significance level) were performed with a Student-Newman-Keul's test (SNK) when sample sizes were equal, or with the T' or GT2 method when sample sizes were unequal (Sokal and Rohlf 1981). A Bryant-Paulson generalization of Tukey's test was done on the adjusted means of the ANCOVA's (Bryant and Paulson 1976, Bryant and Bruvold 1980). Observed encounter rates were statistically compared to encounter rates calculated from equation 1, and probabilities of consumption were statistically compared to 1 using two-tailed *t* tests. The effect of predator and scallop size on mean handling time of a scallop and on profitability were not statistically tested because observations of handling times came from all experiments.

In the multiple prey size experiments, consumption rates on the different prey sizes were not independent, which precluded the use of ANOVA's or log-likelihood ratio tests (*G*-test). An appropriate test, the multivariate Hotelling's T^2 statistic, was not used because the experimental design (*i.e.*, number of choices = 3, number of replicates = 4) gives little power to this test (refer to Roa 1992). Therefore, I do not present a formal analysis of consumption rates, probability of capture, or probability of consumption in multiple prey size experiments and base my interpretations on visual inspection of the results.

To test whether active choice by a given predator type and size class occurred, the numbers of scallops in each prey size class consumed in multiple prey size experiments (observed frequencies, Sea star Experiment 2.3 and Crab Experiment 2.3) were compared to expected frequencies calculated from the numbers of scallops in the same prey size classes consumed in single prey size experiments (Sea star Experiment 2.2 and Crab Experiment 2.2) using single classification *G*-tests (Sokal and Rohlf 1981, Liszka and Underwood 1990). Note that these *G*-tests are subject to increased Type 1 error (rejecting the null hypothesis when it should be retained) because the expected numbers of scallops consumed is estimated (Liszka and Underwood 1990).

To determine which components of predation rate were important in influencing prey size selection, Pearson product-moment correlation analysis was used to examine the relationship between the mean consumption rates of different predator-scallop size combinations in the multiple prey size experiment and the mean encounter rates, probabilities of capture, and probabilities of consumption measured in either the single or multiple prey size experiments.

Mortality due to causes other than predation was negligible in controls in the six experiments conducted: only one small (6.1 mm) scallop died. Therefore, consumption rates were not adjusted for control mortality rates.

Results

EXPERIMENTS WITH SEA STARS

Behavioural observations

Upon the approach of a sea star, a juvenile scallop fully extended its tentacles, opened its valves widely and closed its mantle edge in a "ready-to-swim" position. In this position, the tentacles extended outwards and upwards over the shell, and criss-crossed dorsally. In contrast, a scallop in the feeding position did not have fully extended tentacles and its mantle edge was open allowing for water circulation. Upon encountering a scallop, the sensory podia of a sea star contacted the scallop's tentacles. This often resulted in the sea star retracting its arm, followed by an attempt to manoeuvre closer to the scallop with its arm raised or curled. After several seconds, the scallop swam or jumped away (active escape), the sea star moved away (retraction), or the sea star successfully attached a few tubefeet on the scallop's upper valve (capture). Valve closure, as a means of escape, occurred infrequently and only with small scallops or scallops that had already swam or jumped repeatedly.

Single prey size experiments

In Experiment 2.1, sea star size and juvenile scallop size had no significant effect on consumption rates (Table 2.2, Fig. 2.2a), although high individual variability and low replication resulted in low power (sea star size: ϕ=1.2, df=2, 6, power=0.3; scallop size: ϕ=1.0, df=1, 6, power=0.2). Several changes were made to the experimental design before performing a second experiment. The duration of the second experiment and the number of replicates were increased, and the small sea star size class was excluded due to its low consumption rate in Experiment 2.2 (Fig. 2.2a). Also, an index of foraging activity, the ratio of searching time to observation time, was used as a covariate in the analysis of consumption rate in Experiment 2.2 since individual variability in sea star activity was high (Fig. 2.3). In Experiment 2.2, small scallops were consumed at a significantly higher rate than medium and large scallops (Table 2.3, Fig. 2.2a). Large sea stars had significantly higher consumption rates than medium sea stars. There was a positive and significant relationship between the ratio of searching time to observation time (covariate) and consumption rate (Table 2.3, Fig. 2.3).

Although consumption rates of sea stars feeding on large juvenile scallops were low, the energy obtained from large scallops was higher than that obtained from smaller scallops (Fig. 2.2b). However, predation rates on larger scallops were highly variable: sea stars did not prey or rarely preyed on medium and large scallops in some replicates (Fig. 2.3). Therefore, the effect of scallop size on standardized energy consumption rate was marginally non-significant in Experiment 2.1 (P=0.055) and was non-significant in Experiment 2.2 (Table 2.2 and 2.3). In Experiment 2.1, medium sea stars had the highest standardized energy consumption rate. In Experiment 2.2, there was no significant effect of sea star size on standardized energy consumption rate. The relationship between the covariate and standardized energy consumption rate was significant in Experiment 2.2 (Table 2.3).

Sea stars spent from 11 to 27% of their time searching for juvenile scallops in Experiment 2.2 (Fig. 2.4a). Sea star size and scallop size did not significantly affect the percentage of time sea stars spent searching (Table 2.4). Prey handling time increased with scallop size due to the increased time required to digest larger prey (Fig. 2.5). However, the percentage of time sea stars spent handling scallops did not vary significantly with sea star or scallop size, because it is dependent on the number of prey consumed as well as the individual prey handling times (Table 2.4, Fig. 2.4a). Profitability increased with scallop size (Fig. 2.5), because the energetic content of a scallop increased more rapidly with scallop size than did prey handling time. Rejection times were 1.4 ± 0.4 min (mean ± SE, n=22) for all sea star and scallop size classes combined.

Table 2.2. ANOVA and SNK test results for consumption rate (no. scallops predator^{-1} d^{-1}) and standardized energy consumption rate (J g^{-1} d^{-1}) in Sea star Experiment 2.1. S=small, M=medium and L=large. See Table 2.1 for sea star and juvenile scallop size classes. For the post hoc comparisons, treatment levels sharing a common underline did not differ significantly.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Consumption rate	sea star size	2	6.763	3.27	0.110	
	scallop size	1	6.163	2.98	0.135	
	interaction	2	3.243	1.57	0.284	
	error	6	2.072			
Energy	sea star size	2	467.7	9.80	0.013	scallop sizes pooled: $\underline{\text{S L}}$ M
	scallop size	1	269.3	5.65	0.055	
	interaction	2	113.7	2.38	0.173	
	error	6	47.7			

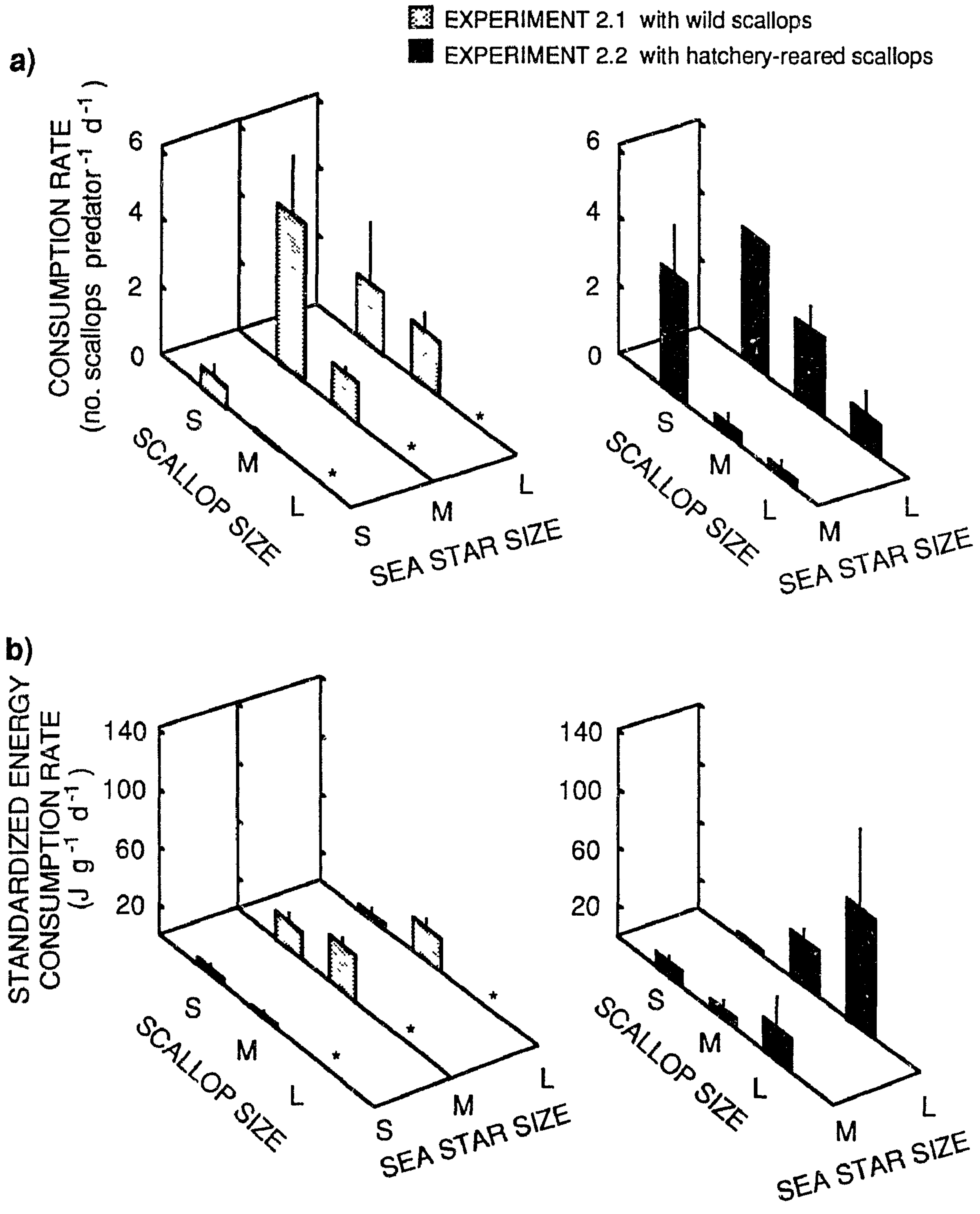


Fig. 2.2. Mean a) consumption rate and b) standardized energy consumption rate (± SE) for each sea star-scallop size combination in single prey size Sea star Experiment 2.1 and 2.2. See Table 2.1 for sea star and scallop size classes. *=no treatment combination.

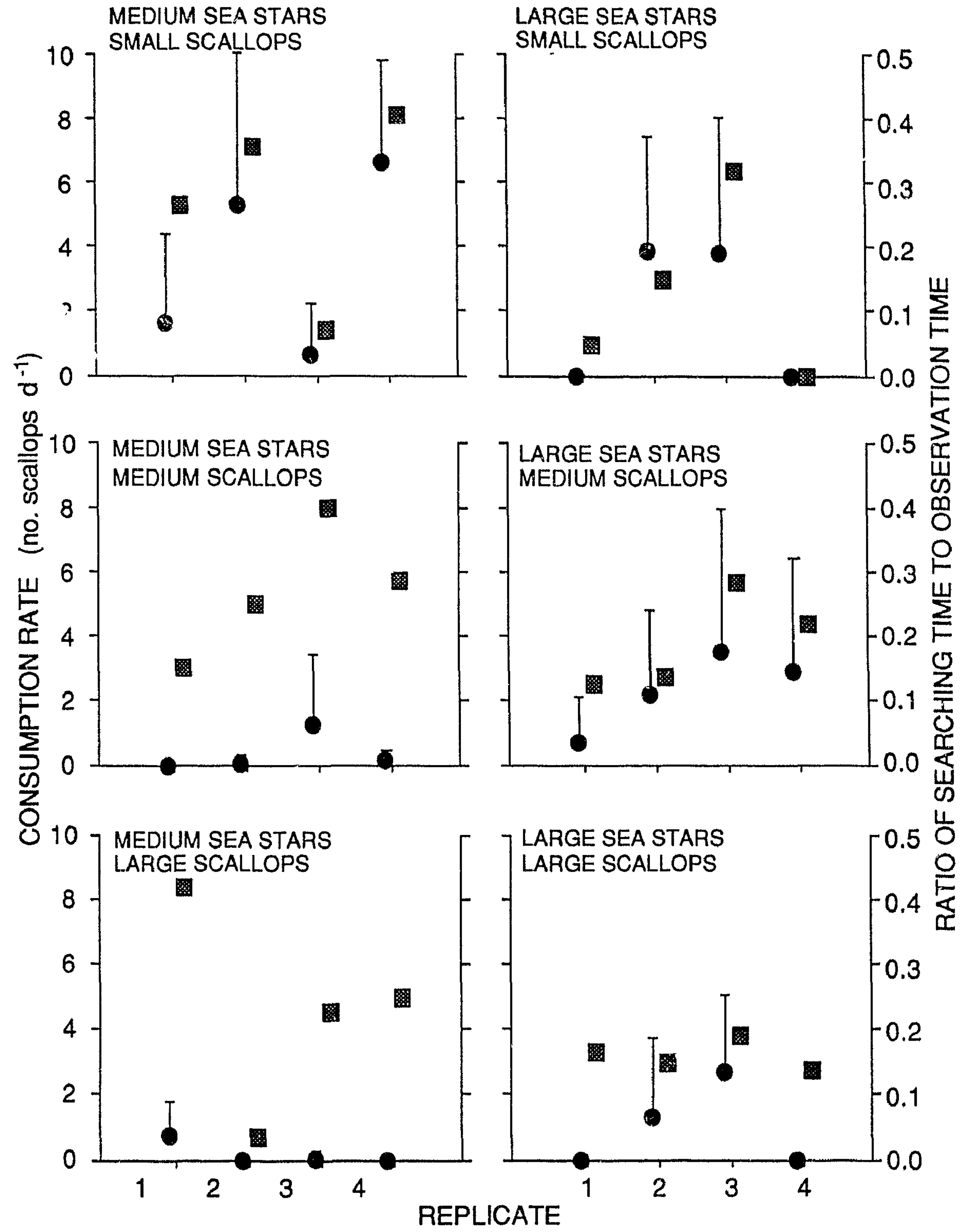


Fig. 2.3. Consumption rate averaged over the duration of the experiment (circles; ± SD) and ratio of searching time to observation time (squares; covariate in the ANCOVA) for each replicate of each treatment combination in single prey size Sea star Experiment 2.2. See Table 2.1 for sea star and scallop size classes.

Table 2.3. ANCOVA and Bryant-Paulson T-test results for consumption rate (no. scallops predator^{-1} d^{-1}) and standardized energy consumption rate (J g^{-1} d^{-1}) (log transformed data) in Sea star Experiment 2.2. The covariate was the ratio of searching time to observation time. S=small, M=medium and L=large. See Table 2.1 for sea star and juvenile scallop size classes.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Consumption rate	sea star size	1	9.462	6.63	0.020	scallop sizes pooled: M L
	scallop size	2	9.697	6.80	0.007	sea star sizes pooled: L M S
	covariate	1	25.986	18.21	0.001	
	interaction	2	4.311	3.02	0.075	
	error	17	1.427			
Energy	sea star size	1	7.650	1.88	0.189	
	scallop size	2	2.448	0.60	0.560	
	covariate	1	39.673	9.73	0.006	
	interaction	2	6.421	1.58	0.236	
	error	17	4.076			

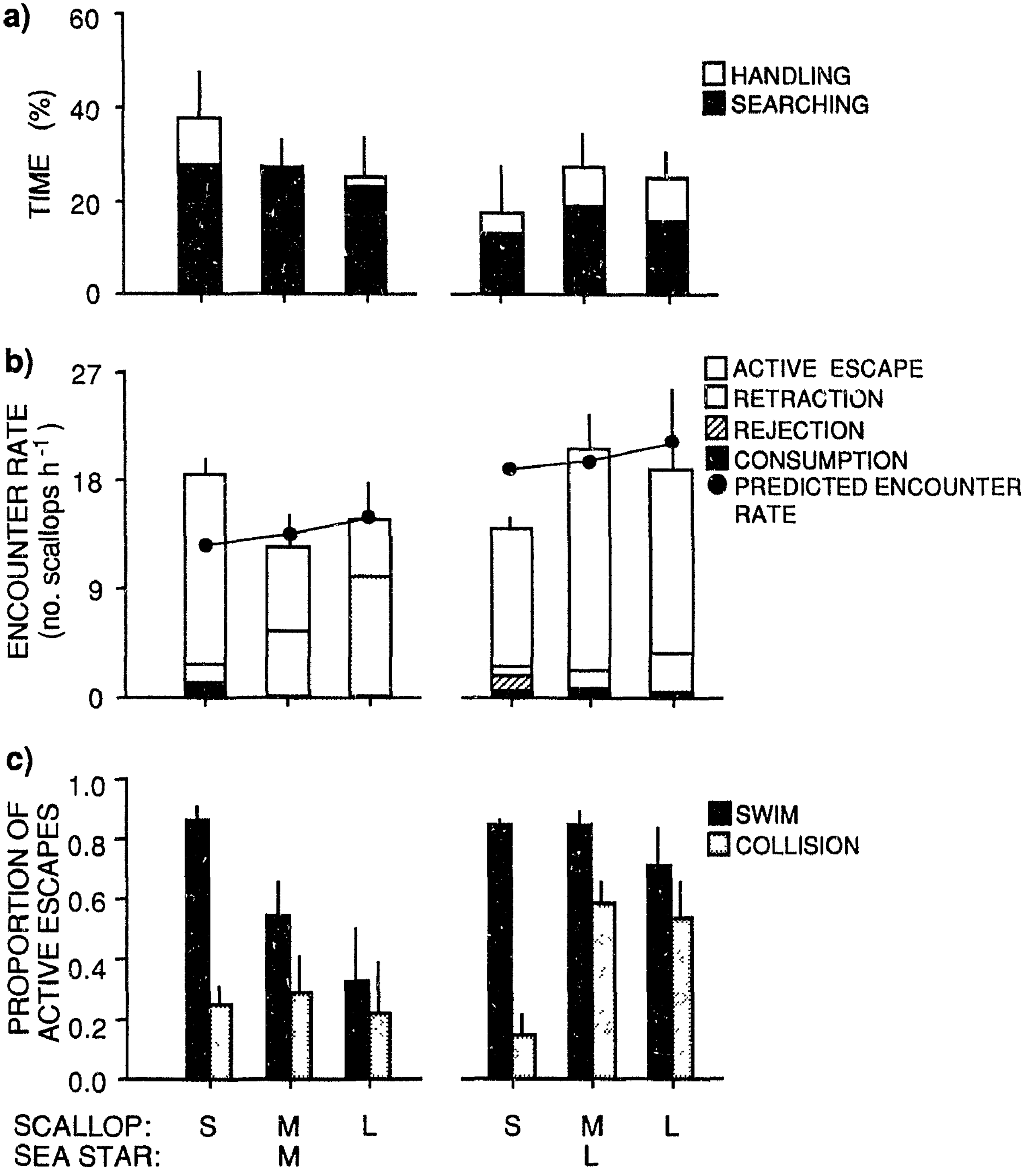


Fig. 2.4. Behaviours observed in each sea star-scallop size combination in single prey size Sea star Experiment 2.2. a) Sea star foraging time (% foraging time = % searching time + % handling time). b) Observed encounter rates (bars), different outcomes of encounter (shadings), and predicted encounter rates (line) based on body size and movement velocity of sea stars and scallops. c) Proportion of active escapes in which scallops swam and in which scallops collided with aquarium walls. Mean shown for all variates; error bars = SE (for % foraging time in a and for observed encounter rate in b). See Table 2.1 for sea star and scallop size classes. Observation time = 660 min aquarium^{-1}.

Table 2.4. ANOVA and T' test results for searching time (%), handling time (%), encounter rate (no. scallops h^{-1}) (log transformed data), probability of capture, probability of consumption, proportion of active escapes to total escapes, proportion of active escapes resulting in swimming, and proportion of active escapes resulting in collisions with aquarium walls in Sea star Experiment 2.2. S=small, M=medium and L=large. See Table 2.1 for sea star and juvenile scallop size classes.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Searching time	sea star size	1	401.21	3.56	0.075	
	scallop size	2	117.48	1.04	0.373	
	interaction	2	0.80	0.007	0.993	
	error	18	112.63			
Handling time	sea star size	1	64.43	1.20	0.289	
	scallop size	2	49.15	0.91	0.419	
	interaction	2	148.30	2.75	0.091	
	error	18	43.87			
Encounter rate	sea star size	1	0.021	0.76	0.367	
	scallop size	2	0.001	0.05	0.950	
	interaction	2	0.063	2.29	0.132	
	error	17	0.027			

Table 2.4 continued.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Capture probability	sea star size	1	0.0078	25.07	0.000	small scallops: M L medium scallops: M L large scallops: M L
	scallop size	2	0.0206	66.54	0.000	medium sea stars: L M S large sea stars: L M S
	interaction	2	0.0016	5.22	0.017	
	error	17	0.0003			
Consumption probability	sea star size	1	1282	0.90	0.368	
	scallop size	2	447	0.31	0.739	
	interaction	2	434	0.30	0.745	
	error	9	1430			
Active escapes	sea star size	1	0.545	15.92	0.001	scallop sizes pooled: M L
	scallop size	2	0.329	9.59	0.002	sea star sizes pooled: L M S
	interaction	2	0.122	3.57	0.051	
	error	17	0.034			

Table 2.4 continued.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Swims	sea star size	1	0.274	8.19	0.011	scallop sizes pooled: M L
	scallop size	2	0.192	5.75	0.013	sea star sizes pooled: $\underline{\text{L}\ \rlap{$\underline{\phantom{\text{M S}}}$}\text{M}}\ \text{S}$
	interaction	2	0.076	2.29	0.134	
	error	16	0.033			
Collisions	sea star size	1	0.164	4.38	0.053	
	scallop size	2	0.110	2.94	0.082	
	interaction	2	0.097	2.60	0.105	
	error	16	0.037			

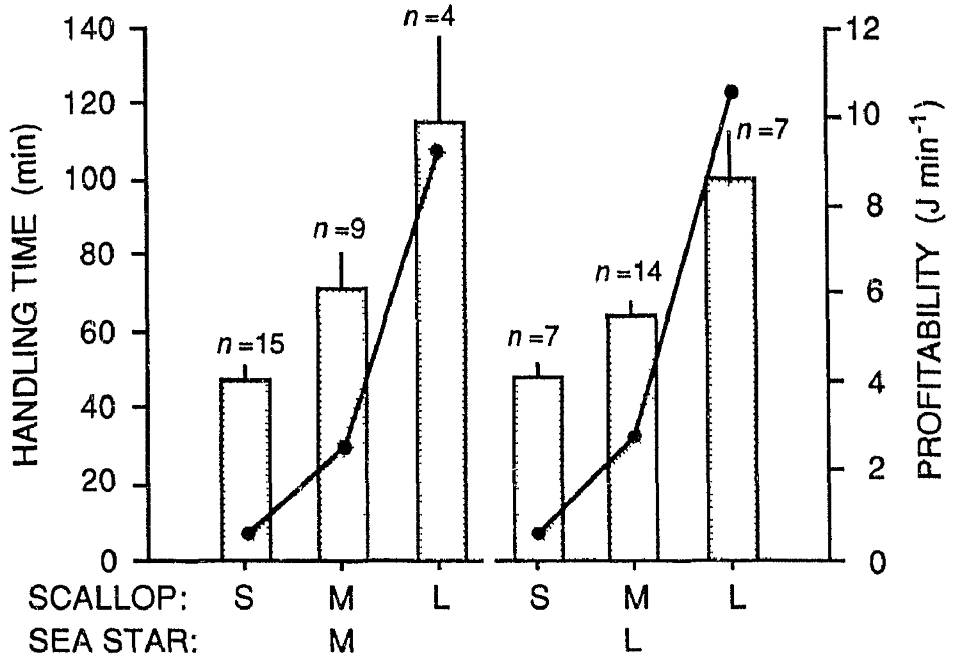


Fig. 2.5. Mean prey handling time (± SE) (bars) and profitability (line) in different sea star-scallop size combinations. The number of observations (*n*) is indicated. Profitability was calculated as the energy obtained from the mean scallop size of a size class divided by mean handling time. Scallop size classes were small=5-8.5, medium=10-15 and large=20-25 mm SH. Sea star size classes were medium=70-105 and large=110-150 mm diameter. Water temperature range: 7.3-12.9°C.

Table 2.5. Probability of capture and of consumption (mean ± SE) in Sea star Experiment 2.2. See Table 2.1 for sea star and scallop size classes. Sample size is shown in parenthesis.

Sea star Size	Scallop Size	Probability of capture		Probability of consumption	
Medium	Small	0.07 ± 0.01	(4)	0.76 ± 0.19	(4)
Medium	Medium	0.003 ± 0.003	(4)	1.00	(1)
Medium	Large	0.002 ± 0.002	(4)	1.00	(1)
Large	Small	0.14 ± 0.01	(3)	0.31 ± 0.19	(3)
Large	Medium	0.03 ± 0.01	(4)	1.00 ± 0.00	(3)
Large	Large	0.02 ± 0.01	(4)	0.50 ± 0.29	(2)

Sea star size and juvenile scallop size did not have a significant effect on observed encounter rates in Experiment 2.2 (Table 2.4, Fig. 2.4b). These encounter rates did not differ significantly from predicted encounter rates ($-0.5<t<0.5$, df=3, $P>0.05$), except for sea stars offered small scallops (medium sea stars: $t=5.2$, df= 3, $P<0.05$; large sea stars: $t=-5.0$, df=2, $P<0.05$) (Fig. 2.4b). I used an average velocity of 2.5 cm min^{-1} in predicting encounter rates with equation 2.1. However, qualitative observations indicated that medium sea stars tended to move faster than large sea stars. When velocities of 3 and 2 cm min^{-1} were used for medium and large sea stars, respectively, observed encounter rates did not differ significantly from predicted encounter rates (medium sea stars: $t=3.1$, df=3, $P>0.05$; large sea stars: $t=-1.4$, df=2, $P>0.05$).

The probability of capture upon encounter was low (<0.15) for all treatment combinations in Experiment 2.2 (Table 2.5, Fig. 2.4b). However, it was significantly higher for small scallops than for medium and large scallops, and for large sea stars than for medium sea stars offered small scallops, resulting in a significant interaction between sea star and scallop size (Table 2.4). The probability of consumption did not vary significantly with sea star and scallop size (Table 2.4), and did not differ significantly from 1 ($-3.6<t<0$, df=1-3, $P>0.05$) (Table 2.5).

In Experiment 2.2, the ratio of active escapes to total escapes increased significantly with decreasing scallop size and with increasing sea star size (Table 2.4). Retractions occurred most often with large scallops and with medium sea stars (Fig. 2.4b). Generally, scallops swam away from sea stars more often than they jumped away (Fig. 2.4c). The ratio of swims to active escapes increased significantly with decreasing scallop size and with increasing sea star size (Table 2.4). Since scallops were confined to aquaria, they did not always realize the full potential of their active escapes: nearly 60% of active escapes collided with aquarium walls in some treatments (Fig. 2.4c). The proportion of active escapes which resulted in collisions with the walls was not significantly affected by scallop size and only marginally affected by sea star size ($P=0.053$) (Table 2.4). Mean (± SD) swimming distance (without colliding with aquarium walls) and maximum swimming distance were 6.9 ± 3.7 cm and 30 cm for small scallops, 15.6 ± 9.1 cm and 55 cm for medium scallops, and 25.6 ± 12.1 cm and 60 cm for large scallops. The mean jumping distance for all scallop sizes combined was 2.8 ± 1.7 cm.

I did not formally compare the effect of scallop source (wild or hatchery) on predation rates and behavioural interactions in one experiment. However, observed behaviours of sea stars and hatchery-reared scallops in Experiment 2.2 (refer to Table 2.4) were generally similar to observed behaviours of sea stars and wild-collected scallops in Experiment 2.1 ($-2.0<t<3.2$, df=3 or 4, $P \geq 0.05$), with the exception of encounter rate. Observed encounter rates were lower in Experiment 2.2 than in Experiment 2.1 ($-15<t<-3.6$, df=3 or 4, $P<0.05$), most likely due to the lower number of scallops present in the aquaria (Table 2.1).

Multiple prey size experiment

When given a choice, sea stars consumed more small scallops than medium or large ones (Fig. 2.6). Overall, consumption rates increased with sea star size. The probability of capture (Table 2.6) showed a similar trend to that in the single prey size experiment (Table 2.5). The probability of consumption was significantly lower than 1 for small scallops (t= -4.9 and -8.5 for medium and large sea stars, respectively, df=2, $P<0.05$), was ~1 for medium scallops (t=-1.9 for large sea stars, df=1, $P>0.05$), and was not observed for large scallops.

The observed numbers of small, medium and large juvenile scallops consumed in the multiple prey size experiment did not differ significantly from the expected numbers calculated from single prey size Experiment 2.2 (Table 2.7), indicating that scallop size selection was not due to active choice by sea stars.

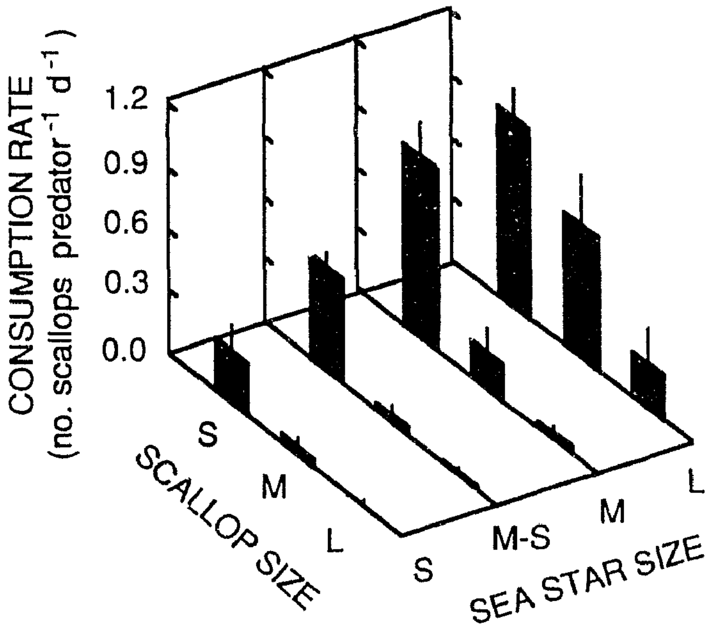


Fig. 2.6. Mean consumption rates (± SE) in multiple prey size Sea star Experiment 2.3. See Table 2.1 for sea star and scallop size classes.

Table 2.6. Probability of capture and of consumption (mean ± SE) in Sea star Experiment 2.3. Small and medium-small sea star size classes are combined. See Table 2.1 for sea star and scallop size classes. Sample size is shown in parenthesis.

Sea star Size	Scallop Size	Probability of capture	Probability of consumption
Small & Small-medium	Small	0.00 ± 0.00 (8)	-
Small & Small-medium	Medium	0.00 ± 0.00 (8)	-
Small & Small-medium	Large	0.00 ± 0.00 (8)	-
Medium	Small	0.19 ± 0.07 (3)	0.17 ± 0.17 (3)
Medium	Medium	0.02 ± 0.02 (3)	1.00 (1)
Medium	Large	0.00 ± 0.00 (3)	-
Large	Small	0.20 ± 0.08 (3)	0.09 ± 0.06 (3)
Large	Medium	0.04 ± 0.03 (3)	0.67 ± 0.17 (2)
Large	Large	0.00 ± 0.00 (3)	-

Table 2.7. Results of G-tests comparing the total number of scallops consumed in each scallop size class for different predator size classes in the multiple prey size experiment (observed frequencies, Sea star Experiment 2.3 and Crab Experiment 2.3) to the expected frequencies computed from the total number of scallops consumed in each scallop size class for similar predator size classes in the single prey size experiment (Sea star Experiment 2.2 and Crab Experiment 2.2). Degrees of freedom = 2. See Table 2.1 for predator and scallop size classes.

Predator type and size	Scallop size	Observed frequencies (Multiple prey size experiment)	Expected frequencies (Single prey size experiment)	*G*	*P*
Sea star-medium	small	25	26.9	2.0	>0.05
	medium	5	2.6		
	large	1	1.5		
	total	31	31.0		
Sea star-large	small	26	26.7	0.3	>0.05
	medium	18	16.3		
	large	6	7.0		
	total	50	50.0		

Table 2.7 continued.

Predator type and size	Scallop size	Observed frequencies (Multiple prey size experiment)	Expected frequencies (Single prey size experiment)	*G*	*P*
Crab-small	small	12	29.0	140.5	<0.001
	medium	25	58.1		
	large	62	11.9		
	total	99	99.0		
Crab-medium-small	small	7	58.2	137.7	<0.001
	medium	56	74.0		
	large	128	58.8		
	total	191	191.0		
Crab-large	small	2	0.9	140.4	<0.001
	medium	47			
	large	161	77.7		
	total	210	210.0		

Encounter rates observed in single prey size Experiment 2.2 were not significantly correlated with consumption rates of medium and large sea stars in the multiple prey size experiment (*r*=0.27, df=4, *P*>0.05), indicating that encounter rate was not important in determining prey selectivities. Only predation rates observed in the multiple prey size experiment (rather than in the single prey size experiment) were employed in the correlation analyses, since preference can only be assessed if a predator is given a choice of prey types. Encounter rates were measured only in the single prey size experiment since they were unaffected by the presence of alternative prey types. The probability of capture in both the single prey size and multiple prey size experiments was positively correlated with consumption rate (*r*=0.86 and 0.92, respectively, df=4, *P*<0.05), indicating that the probability of capture was important in determining prey selection. The probability of consumption measured in the multiple prey size experiment was negatively correlated with consumption rate (*r*=-0.97, df=2, *P*<0.05), indicating that sea stars may actively reject small scallops. Only the probabilities of consumption measured in the multiple prey size experiment were employed in the correlation analysis since the probability of consumption was considered to be an active component and since it did not differ from 1 in the single prey size experiment.

EXPERIMENTS WITH CRABS

Behavioural observations

Upon the approach of a crab, juvenile scallops occasionally assumed the "ready-to-swim" position as described for experiments with sea stars. Scallops either closed their valves (passive escape) or swam or jumped away (active escape) upon contact with the crab. Occasionally, scallops would swim away before contact with an approaching crab. These swims were considered avoidances, and were not included in the encounter rate. More often, however, scallops simply partially or completely closed their valves to the approaching crab. A passive escape occurred if a crab, going through the probing motions, squatted over an encountered scallop and failed to pick up the closed scallop before walking away.

Crabs opened scallops usually by crushing the hinge or the whole shell with the chelae, as described by Elner and Jamieson (1979). Occasionally, crabs feeding on medium scallops rotated the scallop while biting at the edges with the mouthparts. After biting through the hinge, the claws were used to separate the valves bound by the adductor muscle only. Two other opening techniques were specific to particular crab and scallop size combinations. Small crabs (<65 mm) often opened large scallops by chipping at the shell edge with the chelae, until the chelae tips could be inserted between the valves, and then by pulling the valves apart (see also Elner and Jamieson 1979, Moody and Steneck 1993). Medium crabs (70-85 mm) picked up small scallops with their chelae and manipulated and grinded them with their mouthparts.

Eating involved tearing flesh with the chelae and mouthparts after cracking open the shell. Occasionally, for >80 mm crabs offered medium scallops, only the mouthparts were used to remove flesh from the shell.

Single prey size experiments

In Experiment 2.1, consumption rates of medium and large juvenile scallops by crabs were significantly greater than consumption rates of small scallops, and small crabs consumed significantly more scallops than medium and large crabs (Table 2.8, Fig. 2.7a). In Experiment 2.2, all crab sizes consumed significantly more medium scallops than large or small scallops (Table 2.9, Fig. 2.7a). Crab size did not significantly affect consumption rates in Experiment 2.2, most likely due to the crab size classes differing from those in Experiment 2.1. In both Experiments 2.1 and 2.2 however, consumption rates of small scallops by large (>95 mm) crabs and of medium scallops by very large (>110 mm) crabs were negligible.

Table 2.8. ANOVA and SNK test results for consumption rate (no. scallops predator^{-1} d^{-1}) (log transformed data) and standardized energy consumption rate (J g^{-1} d^{-1}) in Crab Experiment 2.1. S=small, M=medium and L=large. See Table 2.1 for crab and juvenile scallop size classes.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Consumption rate	crab size	2	2.981	8.71	0.008	scallop sizes pooled: $\underline{\text{M L}}$ S
	scallop size	2	2.248	6.57	0.017	crab sizes pooled: S $\underline{\text{M L}}$
	interaction	4	1.037	3.03	0.077	
	error	9	0.342			
Energy	crab size	2	83492	17.15	0.001	small scallops: $\underline{\text{M L S}}$ medium scallops: $\underline{\text{L M S}}$ large scallops: $\underline{\text{M L}}$ S
	scallop size	2	96966	19.92	0.000	small crabs: S M L medium crabs: $\underline{\text{S M L}}$ large crabs: $\underline{\text{S M L}}$
	interaction	4	32297	6.63	0.009	
	error	9	4868			

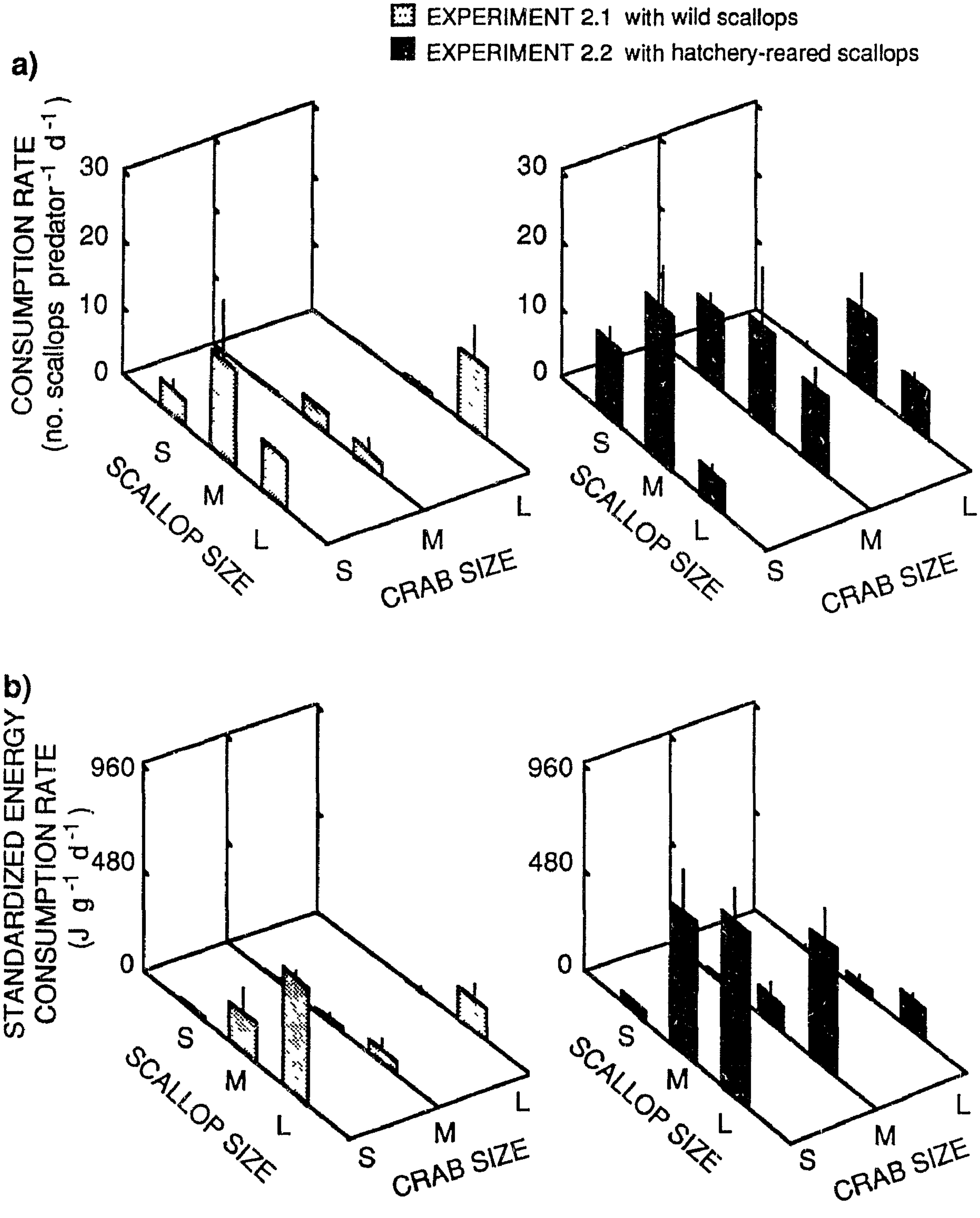


Fig. 2.7. Mean a) consumption rate and b) standardized energy consumption rate (± SE) for each crab-scallop size combination in single prey size Crab Experiment 2.1 and 2.2. See Table 2.1 for crab and scallop size classes.

Table 2.9. ANOVA and SNK test results for consumption rate (no. scallops predator^{-1} d^{-1}) and standardized energy consumption rate (J g^{-1} d^{-1}) in Crab Experiment 2.2. S=small, M=medium and L=large. See Table 2.1 for crab and juvenile scallop size classes.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Consumption rate	crab size	2	123.0	2.89	0.082	
	scallop size	2	220.3	5.18	0.017	crab sizes pooled: $\underline{\text{S L}}$ M
	interaction	4	68.0	1.60	0.218	
	error	18	42.6			
Energy	crab size	2	440667	15.97	0.000	small scallops: $\underline{\text{L M S}}$
						medium scallops: $\underline{\text{L M}}$ S
						large scallops: L $\underline{\text{M S}}$
	scallop size	2	534865	19.37	0.000	small crabs: S $\underline{\text{M L}}$
						medium crabs: $\underline{\text{S M}}$ L
						large crabs: $\underline{\text{S M L}}$
	interaction	4	114470	4.15	0.015	
	error	18	27584			

Standardized energy consumption rate was greatest for small crabs offered large juvenile scallops, resulting in a significant interaction between crab and scallop size in both Experiments 2.1 and 2.2 (Tables 2.8 and 2.9, Fig. 2.7b).

In Experiment 2.2, crabs spent less than 11% of their time searching for scallops (Fig. 2.8a), typically in short bursts of ~1 min or less. Crab size did not significantly affect the percentage of time spent searching (Table 2.10, Fig. 2.8a). However, crabs offered medium scallops spent significantly more time searching than crabs offered large or small scallops. Prey handling times increased with scallop size and decreased with crab size (Fig. 2.9). The percentage of time spent handling prey was significantly greater for small and medium crabs than for large crabs, and was significantly greater for crabs offered medium or large scallops than for crabs offered small scallops (Table 2.10, Fig. 2.8a). Profitability increased with scallop size (Fig. 2.9). Profitability was higher for large crabs than for smaller crabs because of lower handling times. Rejection times were 0.6 ± 0.1 min (mean ± SE, n=14) for all crab and scallop size classes combined.

Crabs had significantly lower encounter rates with small scallops than with medium or large scallops in Experiment 2.2 (Table 2.10, Fig. 2.8b). Observed encounter rates did not differ significantly from those calculated with equation 2.1 ($-1.5<t<1.6$, df=1 or 2, $P>0.05$) (Fig. 2.8b). The probability of capture upon encounter was usually high (>0.13) (Table 2.11, Fig. 2.8b), except for large crabs offered small scallops. Large crabs were not observed to capture small scallops. In Experiment 2.2, the probability of capture was significantly greater for medium scallops than for small or large scallops and was higher for small crabs than for large crabs (Table 2.10). Because of low foraging times and encounter rates of crabs offered small scallops, there were too few observations of captures and, therefore, the small scallop size class was omitted from the analysis of the probability of consumption upon capture. The probability of consumption was not significantly affected

Table 2.10. ANOVA and SNK, T', or GT2 test results for searching time (%), handling time (proportion) (arcsine-square root transformed data), encounter rate (no. scallops h^{-1}), probability of capture, and probability of consumption in Crab Experiment 2.2. S=small, M=medium and L=large. See Table 2.1 for crab and juvenile scallop size classes.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Searching time	crab size	2	16.92	1.81	0.192	
	scallop size	2	39.39	4.22	0.031	crab sizes pooled: S L M
	interaction	4	20.94	2.24	0.105	
	error	18	9.34			
Handling time	crab size	2	0.066	5.41	0.015	scallop sizes pooled: L M S
	scallop size	2	0.074	6.01	0.010	crab sizes pooled: S L M
	interaction	4	0.017	1.36	0.287	
	error	18	0.012			
Encounter rate	crab size	2	777.2	2.08	0.157	
	scallop size	2	2499.5	6.69	0.008	crab sizes pooled: S M L
	interaction	4	252.7	0.68	0.618	
	error	16	373.4			

Table 2.10 continued.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Capture probability	crab size	2	0.317	5.73	0.016	scallop sizes pooled: L M S
	scallop size	2	0.290	5.23	0.022	crab sizes pooled: L S M
	interaction	4	0.096	1.73	0.204	
	error	13	0.055			
Consumption probability	crab size	2	0.065	0.72	0.509	
	scallop size	1	0.233	2.60	0.138	
	interaction	2	0.028	0.31	0.741	
	error	10	0.090			

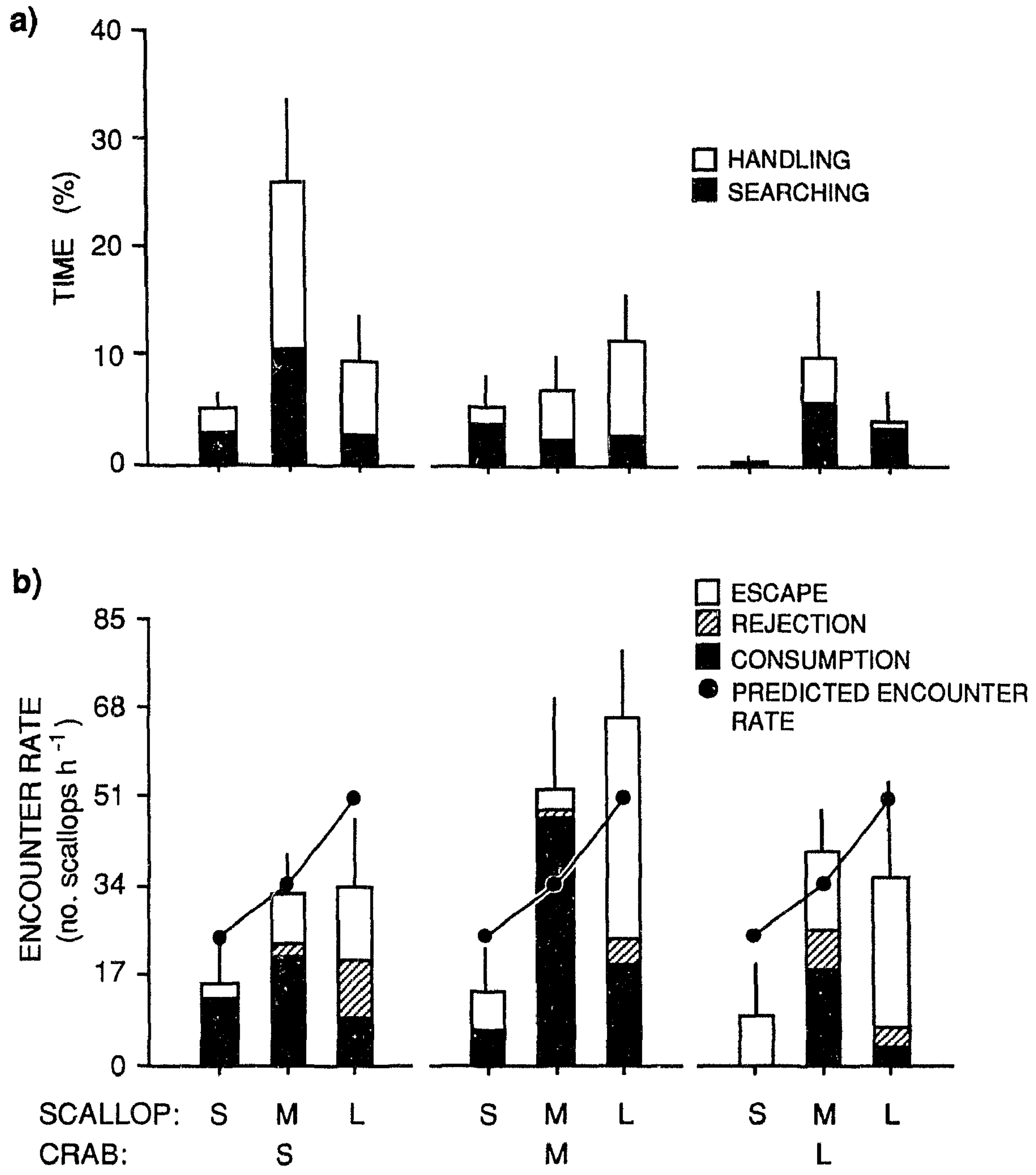


Fig. 2.8. Behaviours observed in each crab-scallop size combination in the single prey size Crab Experiment 2.2. a) Crab foraging time (% foraging time = % searching time + % handling time. b) Observed encounter rates (bars), different outcomes of encounter (different shadings), and predicted encounter rates (line) based on body area in contact with the bottom and movement velocity of crabs and scallops. Mean shown for all variates; error bars = SE for % foraging time in a and for observed encounter rate in b. See Table 2.1 for crab and scallop size classes. Observation time = 250 min aquarium^{-1}.

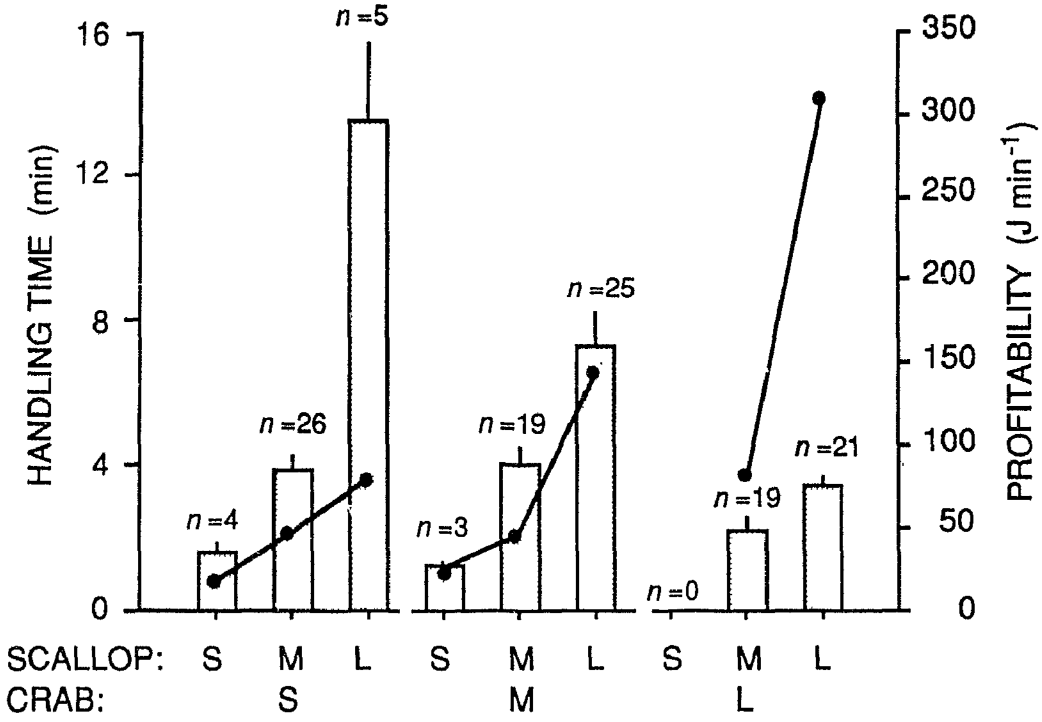


Fig. 2.9. Mean prey handling time (± SE) (bars) and profitability (line) in different crab-scallop size combinations. The number of observations (*n*) is indicated. Profitability was calculated as the energy obtained from the mean scallop size of a size class divided by mean handling time. Scallop size classes were small=5-8.5, medium=10-15 and large=20-25 mm SH. Crab size classes were small=45-58, medium=70-89 and large=100-110 mm CW. Water temperature range: 7.3-12.0°C.

Table 2.11. Probability of capture and of consumption (mean ± SE) in Crab Experiment 2.2. See Table 2.1 for crab and juvenile scallop size classes. Sample size is shown in parenthesis.

Crab Size	Scallop Size	Probability of capture		Probability of consumption	
Small	Small	0.83 ± 0.14	(2)	1.00 ± 0.00	(2)
Small	Medium	0.67 ± 0.05	(3)	0.89 ± 0.07	(3)
Small	Large	0.60 ± 0.22	(3)	0.53 ± 0.29	(3)
Medium	Small	0.45 ± 0.04	(2)	1.00 ± 0.00	(2)
Medium	Medium	0.88 ± 0.13	(3)	0.93 ± 0.07	(3)
Medium	Large	0.36 ± 0.02	(3)	0.83 ± 0.17	(2)
Large	Small	0.00	(1)	-	
Large	Medium	0.61 ± 0.20	(3)	0.83 ± 0.17	(3)
Large	Large	0.13 ± 0.10	(2)	0.50	(1)

by crab or scallop size (Table 2.10) and did not differ significantly from 1 ($-1.6<t<0$, df=1 or 2, $P>0.05$) (Table 2.11). No trend was observed in the proportion of passive or active escapes to total escapes with crab or scallop size. Passive escapes occurred 57.9 ± 41.1% (mean ± SD) of total escapes, for all crab and scallop sizes combined.

Behavioural observations between crabs and hatchery-reared scallops in Experiment 2.2 (refer to Table 2.10) did not differ from those between crabs and wild-collected scallops in Experiment 2.1 ($-2.0<t<0.9$, df=2 or 3, $P>0.05$)

Multiple prey size experiment

When given a choice, crabs of all size classes showed similar trends in consumption rate. Large juvenile scallops were consumed in greater number than small or medium scallops (Fig. 2.10). Small scallops were consumed infrequently. The probability of capture increased with scallop size (Table 2.12). The probability of consumption did not differ significantly from 1 (t=1, df=7 or 8, P>0.05).

The numbers of small, medium and large scallops consumed in the multiple prey size experiment (Experiment 2.3) differed significantly from the expected numbers calculated from the single prey size experiment (Experiment 2.2) (Table 2.7), indicating that crabs actively selected scallops when given a choice. Although the multiple prey size and single prey size experiments were conducted at different temperatures (Table 2.1), this should not confound comparisons since subsequent experiments with crabs showed no significant difference in consumption rates between 3° and 8°C (Chapter 3).

Encounter rate in single prey size Experiment 2.2 was positively correlated with consumption rate of small, medium-small and large crabs in the multiple prey size experiment (r=0.68, df=7, P<0.05), indicating that encounter rate was important in determining prey selectivities. The probability of capture observed in the single prey size experiment was not significantly correlated with consumption rate (r=-0.30, df=7, P>0.05). However, the probability of capture observed in the multiple prey size experiment was positively correlated with consumption rate (r=0.86, df=4, P<0.05). These contrasting results indicate that the availability of alternative prey types influences the probability of capture. The probability of consumption observed in the multiple prey size experiment was not significantly correlated with consumption rate (r=0.42, df=2, P>0.05), indicating that it was unimportant in determining selectivities.

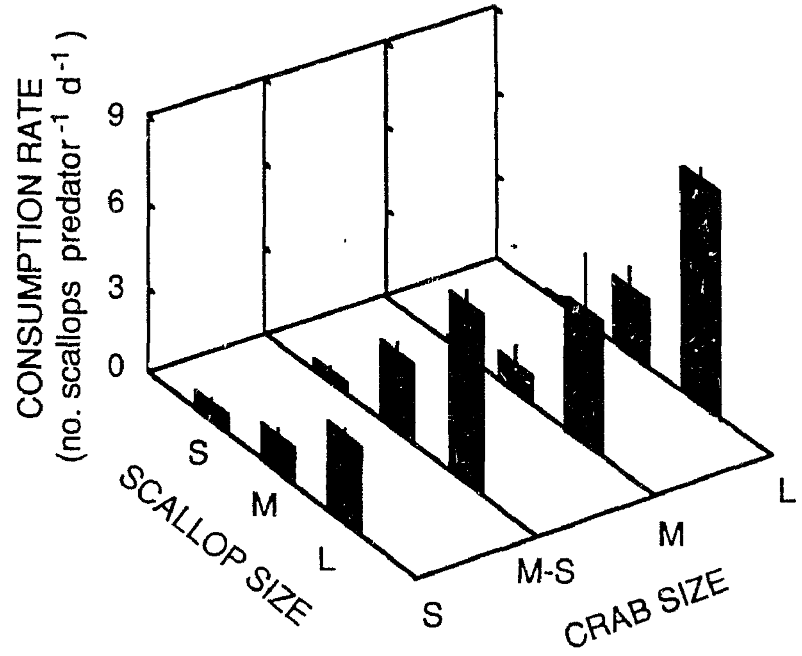


Fig. 2.10. Mean consumption rates (± SE) in multiple prey size Crab Experiment 2.3. See Table 2.1 for crab and scallop size classes.

Table 2.12. Probability of capture and of consumption (mean ± SE) in Crab Experiment 2.3. All crab size classes are combined. See Table 2.1 for scallop size classes. Sample size is shown in parenthesis.

Scallop Size	Probability of capture		Probability of consumption	
Small	0.13 ± 0.13	(8)	1.00	(1)
Medium	0.31 ± 0.06	(8)	0.96 ± 0.04	(8)
Large	0.59 ± 0.10	(10)	0.99 ± 0.01	(9)

Discussion

Sea stars (*Asterias vulgaris*) and rock crabs (*Cancer irroratus*) both showed preferences for particular size classes of juvenile sea scallops. Sea stars preferred small scallops whereas crabs preferred large scallops when given a choice in prey size. The apparent preferences were attributable to specific components of predation rate, including encounter rate between predator and prey, probability of capture upon encounter, and probability of consumption upon capture.

Preference for small scallops by sea stars was determined by passive selection resulting from differential prey vulnerabilities. The primary component underlying the selection of small scallops was the probability of capture upon encounter, even though it was <0.20. It was significantly higher for small scallops than for medium and large scallops and correlated positively with consumption rates in the multiple prey size experiment. In other words, small scallops experienced higher predation rates because they had less powerful escape responses than larger ones (*e.g.*, swimming distances were shorter, retractions occurred less often). The vulnerability of different scallop size classes was not related to encounter rate, as encounter rates measured in the single prey size experiment were similar for all sea star-scallop size combinations. These encounter rates did not differ significantly from encounter rates calculated on the basis of body sizes and movement velocities (equation 2.1). In the single prey size experiment, probability of consumption upon capture did not differ significantly from 1, presumably because alternative prey types were not available. In the multiple prey size experiment, probability of consumption decreased with decreasing scallop size, suggesting that it is an active component. Nonetheless, active selection played only a minor role in determining observed prey selectivities since the frequencies of each scallop size class consumed in the multiple prey size experiment were similar to the frequencies calculated from the single prey size experiment (Table 2.7). Based on profitability calculations, all sea stars should preferentially attack larger scallops over small scallops when given a choice (Fig. 2.5).

Although sea stars did reject small scallops more often, active choice for larger scallops was obscured by the low probabilities of capture. Consequently, any factor affecting the active escape response of scallops (and, hence, the probability of capture) would probably dramatically affect predation rate by sea stars. For example, Dickie and Medcof (1963) suggested that rapid changes in water temperature may debilitate sea scallops, making them more vulnerable to slow-moving predators such as sea stars.

Prey size selection by rock crabs was more complex, and appeared to be due to a combination of passive and active selection. In single prey size experiments, medium scallops were generally consumed in greatest number by crabs. However, in the multiple prey size experiment, large scallops were preferred. Observed encounter rates (measured in the single prey size experiment and, therefore, unaffected by the presence of alternative prey types) were important in determining prey selection as indicated by the positive correlation with predation rates observed in the multiple prey size experiment. These encounter rates did not differ significantly from encounter rates calculated on the basis of body sizes and movement velocities (equation 2.1). The low consumption rate of small scallops most likely resulted from low encounter rates with crabs. However, observed encounter rates did not differ significantly between medium and large scallops in the single prey size experiment and, therefore, passive selection due to differing encounter rates could only partially explain the observed selection of prey.

In theory, passive components should be similar in single prey size and multiple prey size experiments and active components should show differential effects in the multiple prey size experiment only. The probability of capture upon encounter was assumed to be a passive component of prey selection. However, scallops often closed their valves upon encounter with crabs, and therefore, the probability of capture upon encounter was not limited by the attributes of the prey, except perhaps when scallops were too small relative to crab size to be effectively grasped. The probability of capture varied differently in single prey size and multiple prey size experiments, such that the probability of capture in the single prey size experiment was not significantly correlated with consumption rate in the multiple prey size experiment, while the probability of capture in the multiple prey size experiment was positively correlated with consumption rate. These results suggest that the probability of capture may be better considered as a product of active and passive sub-components. In other words, the probability of capture may depend on the probability of a crab actively deciding to seize (*i.e.*, attack) a contacted scallop, the probability of a scallop successfully jumping or swimming away, and the probability of the crab successfully grasping a scallop.

The probability of consumption upon capture did not show any significant trend in the single prey size experiment (which was expected) or in the multiple prey size experiment (which was unexpected). It has been suggested that non-visual predators require a brief manipulatory period to assess their prey (Hughes 1979, 1980a, Jubb *et al.* 1983). More specifically, Jubb *et al.* (1983) hypothesized two mechanisms for active prey selection in the crab *Carcinus maenas*: the prey evaluation and the relative stimulus hypotheses. In the prey evaluation hypothesis, crabs gauge bivalves during a brief manipulatory period (termed recognition time) and reject small bivalves on the basis of size and large bivalves on the basis of strength (resistance to crushing). In the relative stimulus hypothesis, retention or rejection of bivalve prey grasped in the chelae depend on the strength of the chelae stimulus relative to stimuli simultaneously received by the walking legs touching other bivalves. Based on these hypotheses, the probability of consumption upon capture was expected to be the active predation component and was expected to reflect profitabilities in the multiple prey size experiment. Prey size refuges were not observed within the scallop size range used in my experiments: once captured, scallops closed their valves and were totally vulnerable to crabs which could quickly crush the shell. Profitability calculations showed that rock crabs should preferentially attack large scallops over smaller scallops (Fig. 2.9). Indeed, active selection was indicated by crabs selecting large scallops more often than expected when given a choice than when not given a choice (Table 2.7). Nonetheless, my study showed that the probability of consumption upon capture was not important in determining prey selection by crabs. Active prey selection may be dependent on other elements in the predation cycle. For example, the probability of attack upon encounter, which occurs post encounter and prior to prey capture, has been suggested to be the active component for predators such as fish, salamanders and aquatic insects (Allan *et al.* 1987, O'Brien 1987, Osenberg and Mittelbach 1989, Peckarsky and Penton 1989, Sih and Moore 1990, Litvak and Leggett 1992). My study, however, was not able to measure the probability of attack separately. The probability of attack was most likely incorporated in the measure of the probability of capture upon encounter (as discussed above).

The different results with medium and large scallops (in terms of the prey size class consumed in greatest number) in the single prey size and multiple prey size experiments with crabs may be explained by the interaction of active selection (probability of attack or probability of consumption) and satiation. The consumption rate of large scallops (mean ± SE: 5.5 ± 2.1 scallops d^{-1}) observed for crabs (all sizes combined) in the multiple prey size experiment was within the range recorded in the single prey size experiment (7.0 ± 3.3 scallops d^{-1}). In the single prey size experiments, crabs offered large scallops quickly reached satiation whereas those offered medium scallops did so more gradually. Crabs offered medium scallops, therefore, searched more and consumed more scallops (Fig. 2.7a and 2.8a). In the multiple prey size experiment, crabs consumed large scallops first, reached satiation and did not eat as many medium scallops (Fig. 2.10).

Given that the probabilities of capture and consumption by crabs can be high, encounter rate with prey would probably be the major determinant of crab predation on scallops in nature. Only fairly large sea scallops may be invulnerable to crab attack, either by being powerful swimmers and therefore hard to capture (>50 mm SH; Dadswell and Weihs 1990) or by being difficult to open (>70 mm SH; Elner and Jamieson 1979). In nature, crabs may increase encounter rates by locating and following prey odour plumes in smooth-turbulent water flows. However, in rough-turbulent flows, odour plumes are difficult to locate and follow, and crab search patterns become more circuitous (Zimmer-Faust 1989, Weissburg and Zimmer-Faust 1993).

Juanes (1992) reviewed decapod-mollusc interactions and found that decapods generally preferred small bivalves over large ones. By contrast, my study with juvenile scallops showed that rock crabs preferred the largest scallop size offered. Elner and Jamieson (1979) found that very large (>120 mm) rock crabs offered 20-70 mm sea scallops preferred 40-50 mm scallops. Scallops are soft shell bivalves when compared to other bivalves (*e.g.*, oysters, clams, mussels). Their swimming abilities require light weight rather than shell toughness (Vermeij 1987). As a result, relatively large sizes of scallops, compared to hard shell bivalves, are vulnerable to decapod predation.

Sih and Moore (1990) suggested that active selection is more likely to occur with non-mobile prey, since the behaviour of mobile prey often determines consumption rates. This is consistent with the results of my study: crabs exhibited active selection with scallops which often closed their valves upon encounter and remained immobile, whereas sea stars did not show active selection with scallops which often actively escaped upon encounter. Other studies have demonstrated that prey escape responses can similarly influence the probability of capture and, hence, predation rate: *e.g.*, sea urchins (*Strongylocentrotus purpuratus* and *S. franciscanus*) and gastropods (*Calliostoma ligatum* and *Tegula pulligo*) attacked by sea stars (*Pycnopodia helianthoides* and *Pisaster giganteus*, respectively) (Moitoza and Phillips 1979, Harrold 1982), and copepods attacked by planktivorous fish (Drenner *et al.* 1978, Cooper *et al.* 1985).

Sea scallops displayed mobile and non-mobile escape responses with both sea stars and crabs. The non-mobile response, however, was different with crabs than with sea stars. Upon contact with a crab, a scallop often closed its valves and passively escaped, providing the crab did not pick it up. Before and upon contact with a sea star, a scallop always assumed the ready-to-swim position. Non-swimming/jumping escapes from sea stars occurred when contact with the tentacles of scallops caused sea stars to retract their arm and move away. Retractions occurred more frequently with larger scallops and with smaller sea stars (Fig. 2.4b). Non-predatory sea stars (*Henricia sanguinolenta*) show a similar response and moonsnails (*Lunatia heros*) retract their mantle edge upon contacting sea scallops (personal observation). Scallop tentacles may produce a chemical deterrent which causes retractions. Ultrastructural studies of sea scallop tentacles by Moir (1977) showed concentrations of secretory granules in the sensory cell complex. Owen and McCrae (1979) described gland cells associated with the sensory cell complex in the tentacles of file shells (*Lima hians*), which are closely-related to scallops. The gland cells contain a sticky acrid substance that is emitted when tentacles are autotomized.

The different escape behaviours exhibited by scallops with sea stars and crabs may be due to the use of different modalities in detecting predators. Scallops are known to discriminate between predatory sea star or gastropod species and non-predatory species (LeComte 1952, Thomas and Gruffydd 1971, Ordzie and Garofalo 1980). Predatory sea stars emit saponins (steroid glycosides) to which scallops and other prey species react vigorously (Feder 1972, Mackie and Grant 1974, Stephens 1978a, b, Stephens and Boyle 1978, Sloan 1980a, Harvey *et al.* 1987). Scallops may detect slow moving predators like sea stars by distance chemoreception, and then respond by extending sensory tentacles to monitor the situation in the ready-to-swim position. Fast moving predators such as crabs or fish may be detected visually and scallops may respond by closing their valves or by actively escaping before or upon contact. Caddy (1968) observed that sea scallops detected and escaped from a diver at distances of 15-91 cm.

Two other studies have looked at predation rate of sea scallops by sea stars and rock crabs. Chiasson (in Dickie and Medcof 1963) offered 100 sea scallops of "various sizes" to 71 sea stars (*Asterias vulgaris*) and recorded a consumption rate of 0.02 scallops predator^{-1} d^{-1}, which is at the low end of the consumption rates measured in my study. Elner and Jamieson (1979) found that very large rock crabs (120-130 mm) offered 40-50 mm sea scallops consumed about 6 scallops predator^{-1} d^{-1}. This is similar to the consumption rate of large juvenile scallops (20-25 mm) by all size classes of rock crabs measured in my single prey size experiments (about 7 scallops predator^{-1} d^{-1}). Since scallops were confined to aquaria and did not always realize the full potential of their active escape, these predation rates may be overestimates.

Sea stars and crabs can have a significant negative impact on natural and seeded bivalve populations (MacKenzie 1970, Virnstein 1977, Morgan *et al.* 1980, Flagg and Malouf 1983, Boulding and Hay 1984, Peterson 1990, Minchin 1991, Hatcher *et al.* In press a). My study indicates that crabs have the ability to decimate a juvenile scallop population much more quickly than do sea stars. Predation rates on juvenile scallops (size classes combined) in the laboratory experiments were five times higher for crabs (10 scallops predator^{-1} d^{-1}) than for sea stars (2 scallops predator^{-1} d^{-1}) (Table 2.13). The higher predation rates by crabs are due to higher rates of foraging movement (which increase encounter rates), higher probabilities of capture, and lower handling times.

Table 2.13. Means ± SE of predation rate and various behaviours of sea stars (80-150 mm diameter) and rock crabs (45-110 mm CW) preying on juvenile sea scallops (5-25 mm SH) in the single prey size experiments (Sea star Experiment 2.2 and Crab Experiment 2.2). Predator and scallop size classes are combined.

Behaviour	Units	Sea stars	Crabs
Predation rate	no. scallops d^{-1}	1.9 ± 1.6	10.4 ± 6.3
Searching time	%	19.9 ± 6.2	4.0 ± 2.8
Handling time	%	6.6 ± 4.8	4.9 ± 4.9
Handling time	min	74.3 ± 28.1	4.6 ± 4.1
Encounter rate	no. scallops h^{-1}	16.6 ± 3.3	33.4 ± 18.7
Probability of capture		0.04 ± 0.04	0.50 ± 0.30
Probability of consumption		0.76 ± 0.30	0.82 ± 0.20

CHAPTER 3: Temperature effects on predation of juvenile sea scallops by sea stars and crabs.

Introduction

For marine invertebrates, variations in water temperature has profound effects on metabolic rate, locomotory activity, and general physiological performance (Newell and Branch 1980, Cossins and Bowler 1987). Predation can be viewed as a series of sequential behaviours (location, attack, capture and ingestion of prey) (O'Brien 1979, 1987), each of which is dependent on physiological functions and therefore influenced by temperature. Based on this series of sequential behaviours (termed predation cycle), predation rate can be analyzed in terms of three components: encounter rate, probability of capture upon encounter, and probability of consumption upon capture (Cooper *et al.* 1985, Osenberg and Mittelbach 1989, Pennings 1990, Chapter 2). For the marine benthos, predation rates have rarely been examined in this way, and the effect of temperature on the components has not been directly investigated. Within the 'normal' temperature range of an animal, physiological processes generally increase with temperature (Newell and Branch 1980, Cossins and Bowler 1987). However, since a specific component of predation rate may be dependent on more than one physiological process affecting the predator and/or the prey, that component may not always increase with temperature. For example, the probability of capture upon encounter may appear to be independent of temperature because of offsetting increases with temperature in both the rate of attack by the predator and the rate of escape by the prey. The rapidity of change in temperature within the sublethal range also affects physiological processes (Newell and Branch 1980, Cossins and Bowler 1987). Upon a rapid temperature change, animals exhibit an acute response, in which rate functions are directly affected by temperature. Upon longer exposure to a temperature change, animals may exhibit an acclimated response, in which compensatory changes in rate functions occur.

Sea scallops (*Placopecten magellanicus*) range from North Carolina to Newfoundland (Posgay 1957, Brand 1991). Although considered a cold-water species, sea scallops along the coast of Nova Scotia experience a seasonal temperature range from -1 to +18°C (Petrie and Jordan 1993). Recently, there has been increased interest in seeding coastal environments with wild-collected and/or hatchery-reared juvenile sea scallops to establish or augment populations (*i.e.*, bottom culture) (Dupouy 1983, Tremblay 1988, Picard 1992, Hatcher *et al.* In press a). However, predation on juvenile scallops particularly by sea stars and crabs may limit bottom culture (Naidu and Cahill 1986, Hatcher *et al.* In press a). Predators affect both survival and dispersal of scallops, since scallops swim to escape predators (Peterson *et al.* 1982, Dadswell and Weihs 1990, Manuel and Dadswell 1991). As temperature may regulate both predator activity and scallop escape responses, understanding the effect of water temperature on these processes has implications for aquaculture (*e.g.*, timing of bottom seeding) and predator-prey interactions in general.

The objective of this study was to determine the effect of seawater temperature on interactions between juvenile sea scallops and two invertebrate predators, the sea star *Asterias vulgaris* and the rock crab *Cancer irroratus* . Both *A. vulgaris* and *C. irroratus* have been observed to be important predators of sea scallops in the laboratory and in the field (Table 1.1). Predation rates by sea stars and crabs on juvenile scallops were measured at different water temperatures in laboratory experiments. To determine underlying behavioural mechanisms, predation rates were analyzed in terms of three components: encounter rate, probability of capture upon encounter, and probability of consumption upon capture. Predator foraging activity, measured as the percentage of time that predators spend searching for prey, predator movement velocity when searching, and prey handling time, was also quantified. Since animals often cease to feed immediately after a temperature change (Laudien 1973), I examined acclimated responses.

Materials and Methods

EXPERIMENTAL DESIGN

Three experiments examining the effect of water temperature on predation of juvenile scallops were conducted (Table 3.1), two with sea stars (summer 1990 and spring 1992) and one with crabs (winter 1992). To test the effect of temperature on predator-prey interactions, 15 scallops were offered to one predator in replicate 54 L glass aquaria at three different temperatures (Table 3.1). One control aquarium with 15 scallops and without a predator was run concurrently at each water temperature to measure non-predatory mortality. Aquaria were placed in two wooden trays which were considered separate blocks (upper and lower). In the first experiment with sea stars, each temperature treatment had 3 replicate aquaria per block. In the second experiment with sea stars and the experiment with crabs, each temperature treatment originally had 4 replicate aquaria per block. However, replicates in which predators consumed ≤ 1 prey item during a 2-wk acclimation period, died (1 sea star) or acted abnormally (1 crab could not right itself after falling on its back) were not included in the analyses. To balance the experimental design to 3 replicate aquaria per block, remaining temperature-block treatment combinations had one replicate randomly removed. Scallop and predator sizes used were those which had demonstrated high predation rates in previous experiments (Chapter 2) (Table 3.1). To provide shelter for crabs, a black plastic sheet over one end of the aquarium was used to shade 25% of the bottom area. Aquaria were monitored twice daily (at the beginning and end of the light period) to record the number of scallops consumed and to replace them. Consumption rate of individual predators was averaged over the duration (in days) of the experiment.

Sea stars (*Asterias vulgaris*) and rock crabs (*Cancer irroratus*) were collected from either Halifax Harbour or Lunenburg Bay, Nova Scotia. Prior to experiments, predators were held in 140 L tanks with flowing ambient seawater for approximately 20 wk and fed mussels (*Mytilus edulis*). Crabs were held singly in plexiglass compartments (30 cm width, 30 cm length, 25 cm height) within the tanks to prevent cannibalism. Only male crabs were

Table 3.1. Description of three laboratory experiments conducted on interactions between juvenile scallops (*Placopecten magellanicus*) and predatory sea stars (*Asterias vulgaris*) and crabs (*Cancer irroratus*) at three water temperatures. Scallops were obtained from collectors (wild) or from a hatchery as indicated. Scallop size was measured as shell height. Predator size was measured as diameter for sea stars and carapace width for crabs.

Experiment	Predator	Months and year	Mean (± SD) water temperature (°C)	Duration of experiment (d)	Scallop source	Scallop size (mm)	Predator size (mm)
3.1	Sea star	July-Aug. 1990	6.4 ± 0.3 11.3 ± 0.3 15.7 ± 0.2	6	Wild	5.0-8.5	80-100
3.2	Sea star	April-May 1992	3.6 ± 0.2 8.2 ± 0.2 14.7 ± 0.2	15	Hatchery	5.0-9.5	80-100
3.3	Crab	Feb.-March 1992	3.0 ± 0.1 8.1 ± 0.1 14.5 ± 0.1	9	Hatchery	19.0-23.0	80-98

used to avoid potential, confounding sex-related variation. For the first experiment with sea stars, juvenile sea scallops (*Placopecten magellanicus*) were obtained from the commercial supplier (Chapter 2). For the second experiment with sea stars and the experiment with crabs, scallops were obtained from the experimental hatchery. Prior to experiments, scallops were held in tanks with flowing seawater for 1-10 wk and continually drip-fed cultured algae (Chapter 2).

In the first experiment with sea stars, scallops and sea stars were kept in separate holding tanks and acclimated to the different experimental temperatures for 5 d. Ambient seawater temperature was used as the intermediate experimental temperature. During this period, sea stars were starved and scallops were drip-fed as described above.

In the second experiment with sea stars and the experiment with crabs, predators were placed singly in aquaria and scallops were placed in three holding tanks. Ambient seawater temperature was used as the low experimental temperature. The temperature of the water for intermediate and high temperature treatments was increased daily by increments of ≤2°C during the first week and then maintained at the appropriate temperature during the second week of acclimation. During this 14-d acclimation period, predators were fed mussels and monitored daily to maintain mussel availability. Scallops were continually drip-fed as described above. Sea stars were then starved for 48 h and crabs for 24 h to standardize hunger levels before adding scallops to experimental aquaria.

The seawater was sandbed filtered to 50 μm, and the flow to each aquarium regulated at 400-500 ml min^{-1}. Salinity was 31.00 ± 0.34$^{o}/_{oo}$ (mean ± SD) for all experiments combined. Water temperature was regulated using the chilling and heating facilities of the Aquatron of Dalhousie University. Water temperature was measured twice daily and averaged over the duration of each experiment (Table 3.1). The light:dark regime was 12:12 h. In the first experiment with sea stars, the upper and lower blocks were exposed to different light intensities (~11000 and ~25 lux, respectively). In the subsequent experiments, a plastic cover was used to shade the upper block to provide similar light conditions (mean ± SE for all aquaria: 35 ± 4 lux).

BEHAVIOURAL MEASURES

To determine the mechanisms underlying observed predation rates, predator and prey behaviours were quantified. In all experiments, visual sampling of predator and prey behaviours by an experimenter was continuous for 20-30 min intervals at randomly chosen times. Total observation periods by an experimenter were 500, 330 and 230 min aquarium $^{-1}$ for the first and second experiments with sea stars and the experiment with crabs, respectively. In the second experiment with sea stars and the experiment with crabs, randomly chosen aquaria also were monitored by time-lapse video recording (RCA TC2011N camera and Panasonic AG-6010 video cassette recorder) for 24 h periods. Six replicate aquaria per temperature in the second sea star experiment and three replicate aquaria in the crab experiment were monitored by video. For night time observation, a red light (60 Watt white lightbulb with safelight filter Kodak 11 or 40 Watt red lightbulb), to which marine invertebrates appear insensitive, was used (Yoshida *et al.* 1984, Cronin 1988, Lythgoe 1988).

Predator and scallop behaviours were defined in Chapter 2. Measurements based on the behavioural observations included: 1) encounter rate between predators and scallops (*i.e.*, number of encounters/searching time), 2) probability of capture upon encounter (*i.e.*, (number of rejections + consumptions)/number of encounters), 3) probability of consumption upon capture (*i.e.*, number of consumptions/(number of rejections + consumptions), 4) percent time predators spent searching for scallops (*i.e.*, searching time/observation time x 100), 5) predator movement velocity when searching, 6) percent time predators spent handling scallops (*i.e.*, handling time/observation time x 100), 7) prey handling time of individual predators, and for sea star experiments only, 8) ratio of scallop active escapes to total escapes (*i.e.*, (number of swims + jumps)/(number of swims + jumps

+ retractions)), 9) proportion of active escapes resulting in swims (*i.e.*, number of swims/(number of swims + jumps)), and 10) proportion of active escapes resulting in collision with aquarium walls (*i.e.*, number of collisions/(number of swims + jumps)). The time budget of predators and individual prey handling times were obtained from both experimenter and video observation. Encounter behaviours were obtained from experimenter observation and predator movement velocities were obtained from video observation.

STATISTICAL ANALYSIS

The experiments were analysed using two-way, fixed factor analyses of variance (ANOVA) with temperature and block as factors. The assumption of homogeneity of variance was tested using Cochran's test. When heteroscedasticity was significant, the dependent variable was transformed using logarithms, square root or arcsine of square roots as most appropriate. Blocks were pooled when the block effect was non-significant at P=0.25 (Underwood 1981), and the data were reanalysed using one-way ANOVA. Non-predatory mortality in the controls was zero. Therefore, the controls were not included in the statistical analysis. Post hoc comparisons of means (at the 0.05 significance level) were done with Student-Newman-Keul's test when sample sizes were equal or with the T' or GT2 method (Sokal and Rohlf 1981) when sample sizes were unequal. Probabilities of consumption were statistically compared to 1 using the two-tailed t-test.

Regressions of the logarithm of rate on temperature were done to calculate Q_{10} values and assess the agreement of the data with the Q_{10} relationship (Cossins and Bowler 1987).

Results

EXPERIMENTS WITH SEA STARS

The consumption rate of small juvenile scallops by sea stars generally increased with water temperature. In the first experiment, there was a significant interaction between temperature and blocks: in the lower block, consumption rate did not differ significantly with temperature, whereas, in the upper block, consumption rate was significantly higher at 16°C than at 6° and 11°C (Table 3.2, Fig. 3.1a). In the second experiment, the block effect was not significant ($P>0.25$). Consumption rate was significantly higher at 15°C than at 4° and 8°C (Table 3.3, Fig. 3.2a), and the Q_{10} value over the whole temperature range was 6.9 ($r^2=0.348$, df=1, 15, $P<0.05$).

Sea stars spent up to 60% of their time foraging (searching and handling) for scallops. In the first experiment, there was a significant interaction between temperature and blocks in the percentage of time sea stars spent searching for and handling scallops (Table 3.2). In the lower block, percentages of time spent searching and handling were not significantly affected by temperature. In the upper block, percentage time spent searching increased significantly with each temperature level, and percentage time spent handling was significantly higher at 16°C than at 6° and 11°C (Table 3.2, Fig. 3.1b). In the second experiment, the percentage of time spent searching was marginally non-significant ($P=0.066$) based on experimenter observation (Table 3.3, Fig. 3.2b), but was significantly higher at 8° and 16°C than at 4°C based on 24 h video observation (Table 3.4, Fig. 3.3a). Temperature did not significantly affect the percentage of time spent handling in the second experiment (Tables 3.3 and 3.4, Fig. 3.2b and 3.3a). Percentage of time spent handling is dependent on both consumption rate and individual prey handling time. Prey handling time decreased significantly with increasing temperature (Table 3.4, Fig. 3.3c) and the inverse, *i.e.*, the rate of prey handling, had a Q_{10} of 2.8 ($r^2=0.944$, df=1, 13, $P<0.001$).

Table 3.2. Sea star-scallop interactions in Experiment 3.1. ANOVA and SNK or GT2 test results for consumption rate (no. scallops predator^{-1} d^{-1}), searching time (%), handling time (%), encounter rate (no. scallops h^{-1}), probability of capture (square root transformed data), probability of consumption, proportion of active escapes to total escapes, proportion of active escapes resulting in swims (arcsine square root transformed data), and proportion of active escapes resulting in collisions with aquarium walls. B1 = upper block and B2 = lower block. Blocks were pooled when *P*>0.25. Temperatures were 6°, 11° and 16°C. For the post hoc comparisons, treatment levels sharing a common underline did not differ significantly.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Consumption rate	temperature	2	17.96	3.51	0.063	B1: $\underline{6\ \ 11}\ \ 16$
						B2: $\underline{16\ \ 6\ \ 11}$
	block	1	1.08	0.21	0.655	6°C: $\underline{\text{B1 B2}}$
						11°C: $\underline{\text{B1 B2}}$
						16°C: B2 B1
	interaction	2	38.59	7.54	0.008	
	error	12	5.12			

Table 3.2 continued.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Searching time	temperature	2	689	8.25	0.006	B1: 6 11 16
						B2: 16 6 11
	block	1	212	2.53	0.137	6°C: B1 B2
						11°C: B1 B2
						16°C: B2 B1
	interaction	2	737	8.83	0.004	
	error	12	84			
Handling time	temperature	2	72.9	0.83	0.459	B1: 6 11 16
						B2: 16 11 6
	block	1	14.2	0.16	0.695	6°C: B1 B2
						11°C: B1 B2
						16°C: B2 B1
	interaction	2	405.5	4.63	0.032	
	error	12	87.6			

Table 3.2 continued.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Encounter rate	temperature	2	182	5.80	0.017	6 11 16
	error	12	31			
Capture probability	temperature	2	0.475	30.30	0.000	16 11 6
	error	12	0.016			
Consumption probability	temperature	2	0.262	2.02	0.178	
	error	11	0.130			
Active escapes	temperature	2	0.0044	0.98	0.406	
	error	11	0.0044			

Table 3.2 continued.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Swims	temperature	2	975	2.26	0.167	
	block	1	1372	3.18	0.112	
	interaction	2	568	1.32	0.321	
	error	8	432			
Collisions	temperature	2	0.0217	0.50	0.619	
	error	11	0.0433			

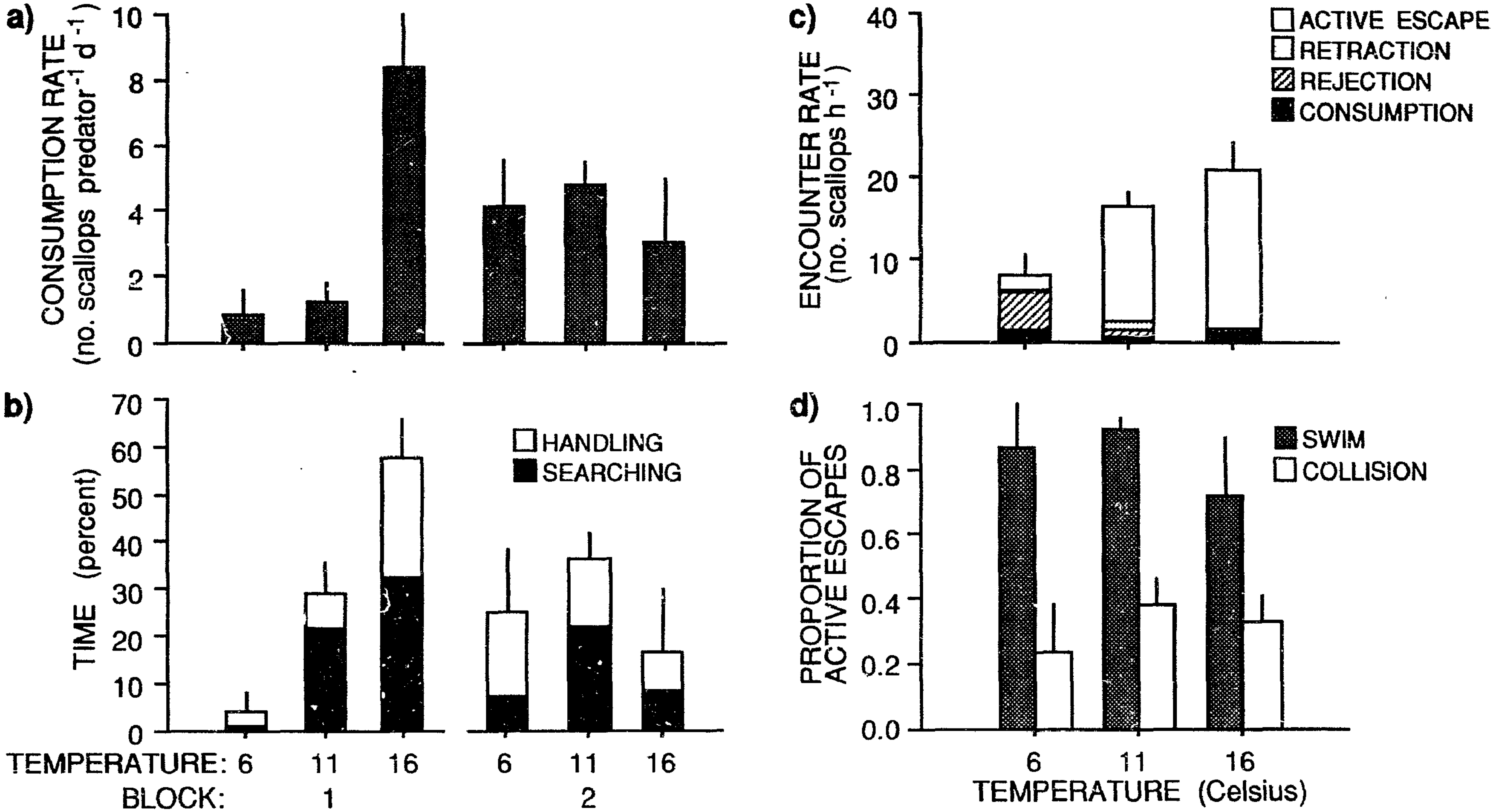


Fig. 3.1. Sea star-scallop interactions in Experiment 3.1. a) Consumption rate and b) foraging time budget (foraging = searching + handling) of sea stars for each temperature-block combination. c) Encounter rate and types of encounter between sea stars and scallops, and d) proportion of active escapes in which scallops swam (active escapes = swims + jumps) and in which scallops collided with aquarium walls for each temperature treatment (blocks were pooled). Observation time in b, c and d = 500 min aquarium^{-1}. Mean shown for all variates; error bars = SE (for foraging time in b and for encounter rate in c).

Table 3.3. Sea star-scallop interactions in Experiment 3.2. ANOVA and SNK test results for consumption rate (no. scallops predator^{-1} d^{-1}), searching time (%), handling time (%), encounter rate (no. scallops h^{-1}), probability of capture (log transformed data), probability of consumption, proportion of active escapes to total escapes (arcsine square root transformed data), proportion of active escapes resulting in swims (arcsine square root transformed data), and proportion of active escapes resulting in collisions with aquarium walls (arcsine square root transformed data). B1 = upper block and B2 = lower block. Blocks were pooled when P>0.25. Temperatures were 4°, 8° and 15°C.

Dependent variable	Sources of variation	df	MS	F	P	Post hoc mean comparisons (listed in increasing magnitude)
Consumption rate	temperature	2	89.1	16.22	0.000	4 8 15
	error	15	5.5			
Searching time	temperature	2	749	3.28	0.066	
	error	15	228			
Handling time	temperature	2	301	1.85	0.200	
	block	1	861	5.29	0.040	temperatures pooled: B2 B1
	interaction	2	33	0.21	0.818	
	error	12	163			

Table 3.3 continued.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Encounter rate	temperature	2	833	27.73	0.000	4 8 15
	error	15	30			
Capture probability	temperature	2	26.2	7.87	0.005	4 8 15
	error	15	3.3			
Consumption probability	temperature	2	0.093	4.20	0.072	
	error	6	0.022			
Active escapes	temperature	2	913	4.93	0.023	8 4 15
	error	15	185			
Swims	temperature	2	779	1.93	0.180	
	error	15	404			
Collisions	temperature	2	1098	2.69	0.101	
	error	15	409			

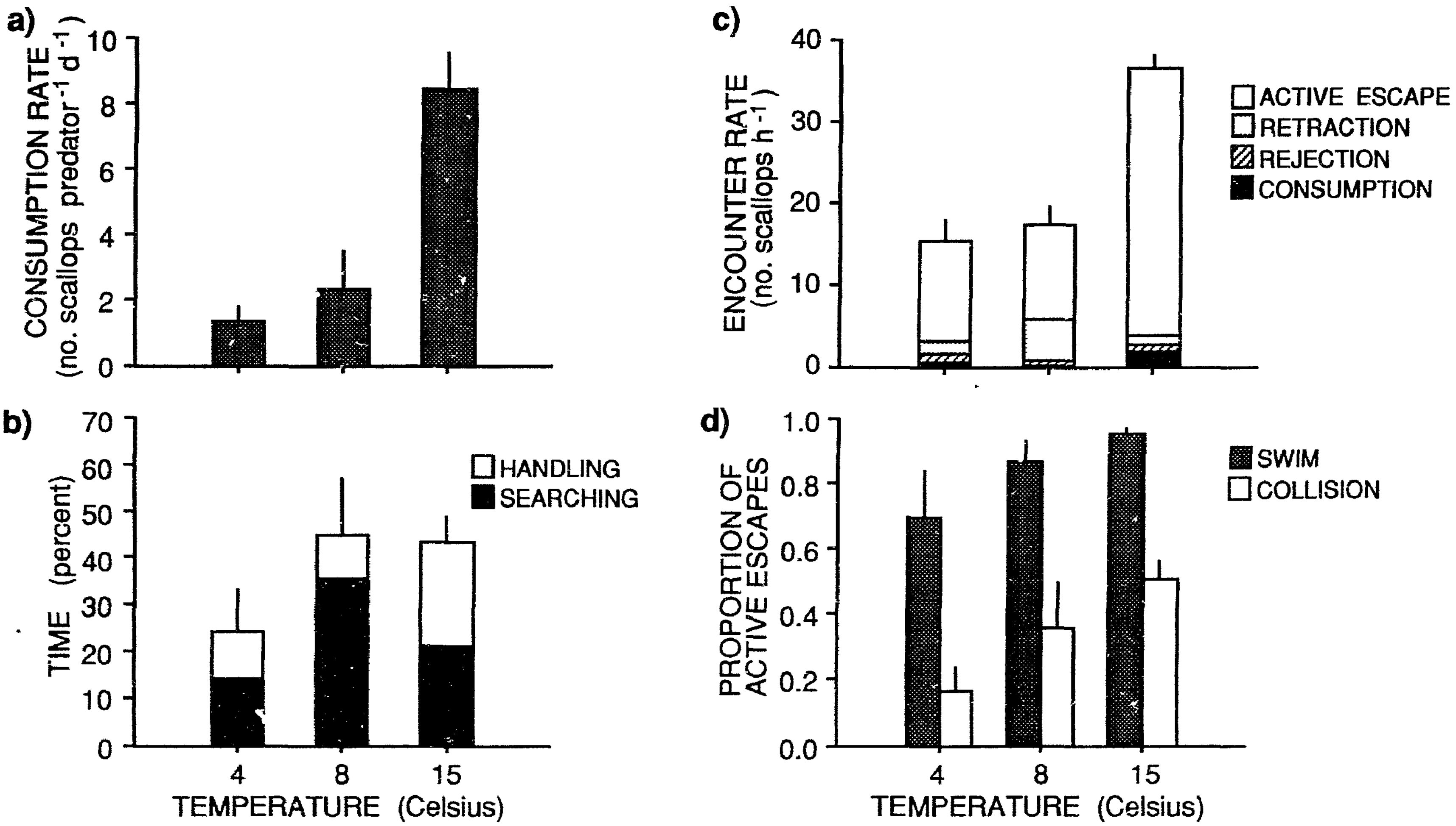


Fig. 3.2. Sea star-scallop interactions in Experiment 3.2. a) Consumption rate per sea star, b) foraging time budget (foraging = searching + handling) of sea stars, c) encounter rate and types of encounter between sea stars and scallops, and d) proportion of active escapes in which scallops swam (active escapes = swims + jumps) and in which scallops collided with aquarium walls for each temperature treatment (blocks were pooled). Observation time in b, c and d = 330 min aquarium^{-1}. Mean shown for all variates; error bars = SE (for foraging time in b and for encounter rate in c).

Table 3.4. Sea star-scallop interactions in Experiment 2.2. ANOVA and SNK, T' or GT2 test results for active and non-foraging time (%), searching time (%), handling time (%), sea star movement velocity when searching (cm min^{-1}) (log transformed data) and prey handling time (min) (log transformed data) during 24 h video observations. Blocks were pooled when $P>0.25$. Temperatures were 4°, 8° and 15°C.

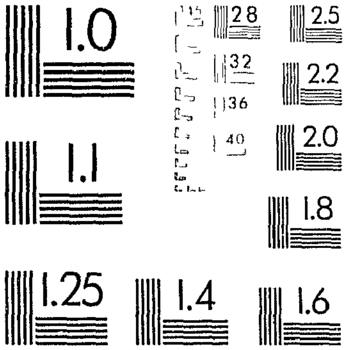
Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Active & non-foraging	temperature	2	103	0.68	0.521	
	error	15	152			
Searching time	temperature	2	648	5.18	0.024	4 8 15
	block	1	187	1.50	0.245	
	interaction	2	83	0.66	0.534	
	error	12	125			
Handling time	temperature	2	342	2.32	0.141	
	block	1	235	1.59	0.231	
	interaction	2	27	0.18	0.837	
	error	12	148			

Table 3.4 continued.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Movement velocity	temperature	2	0.591	58.69	0.000	4 8 15
	error	14	0.010			
Prey handling time	temperature	2	0.308	117.77	0.000	15 8 4
	error	12	0.003			

2 OF/DE 2

PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT



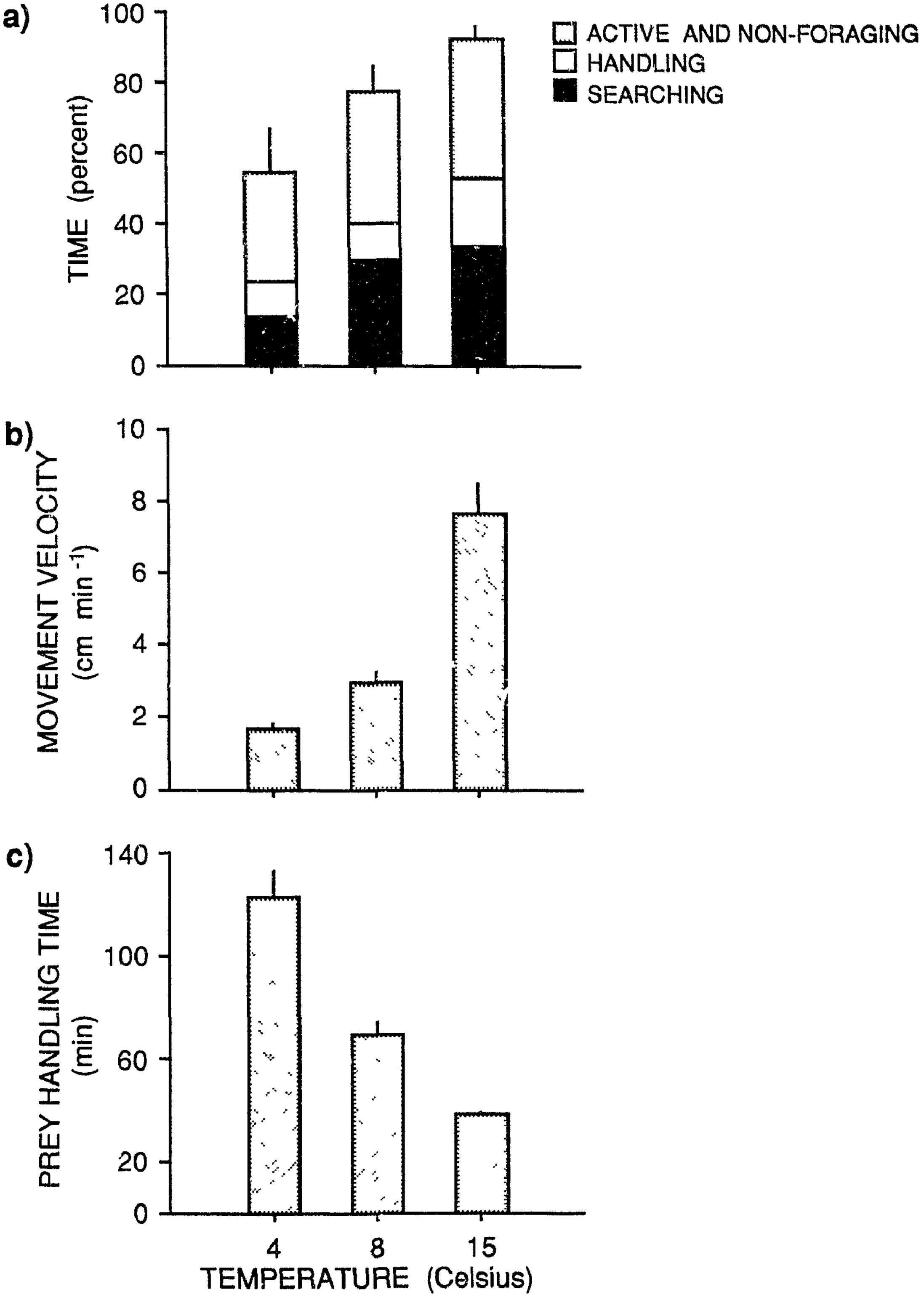


Fig. 3.3. Sea star-scallop interactions in Experiment 3.2. a) Time budget, b) searching movement velocity, and c) prey handling time of sea stars for each temperature treatment in 24 h video observations (blocks were pooled). Mean shown for all variates; error bars = SE (for total active time in a).

The block effect was non-significant for the various encounter behaviours in the two sea star experiments ($P>0.25$). In both experiments, encounter rate was significantly greater at the high temperature than at the two lower temperatures (Tables 3.2 and 3.3, Fig. 3.1c and 3.2c). The Q_{10} values for encounter rate were 2.7 ($r^2=0.465$, df=1, 13, $P<0.01$) and 2.4 ($r^2=0.629$, df=1, 16, $P<0.001$) in the first and second experiments, respectively. The significant increase in sea star movement velocity when searching with temperature (Table 3.4, Fig. 3.3b; $Q_{10}=3.8$, $r^2=0.889$, df=1, 15, $P<0.001$) most likely explained the observed increase in encounter rate. The probability of capture upon encounter was ≤ 0.1, except at 6°C in the first experiment (Table 3.5, Fig 3.1c and 3.2c). In the first experiment, the probability of capture did not differ significantly at 11° and 16°C, but was significantly higher at 6°C (Table 3.2). In contrast, in the second experiment, the probability of capture was significantly higher at 15°C than at 4° and 8°C (Table 3.3). The probability of consumption upon capture was not affected by temperature in either experiments (Table 3.2 and 3.3) and did not differ significantly from 1 ($0>t>-2.6$, df=1, 3 or 5, $P>0.05$), except at 11°C in the first experiment ($t=-3.6$, df=5, $P<0.05$) (Table 3.5).

In the first experiment, temperature did not affect the proportion of active escapes to total escapes (Table 3.2, Fig. 3.1c). In the second experiment, however, scallops actively escaped from sea stars proportionally more often at 15°C than at 4° and 8°C (Table 3.3, Fig. 3.2c). Active escape was usually by swimming rather than jumping (Fig. 3.1d and 3.2d) and temperature did not affect this pattern (Table 3.2 and 3.3). Less than 50% of active escapes resulted in collisions with aquarium walls (Fig. 3.1d and 3.2d). Collisions did not differently affect predation at each temperature (Table 3.2 and 3.3).

Table 3.5. Probability of capture and of consumption (mean ± SE) for different temperature treatments in the first and second sea star experiments. Sample size is shown in parenthesis.

Experiment	Temperature (°C)	Capture Probability	Consumption Probability
3.1	6	0.66 ± 0.12 (4)	0.43 ± 0.22 (4)
	11	0.09 ± 0.02 (6)	0.46 ± 0.15 (6)
	16	0.05 ± 0.02 (5)	0.88 ± 0.13 (4)
3.2	4	0.05 ± 0.05 (6)	0.50 (1)
	8	0.01 ± 0.01 (6)	1.00 ± 0.00 (2)
	15	0.06 ± 0.01 (6)	0.93 ± 0.07 (6)

EXPERIMENT WITH CRABS

Consumption rate of large juvenile scallops by crabs was significantly higher at 15°C than at 3° and 8°C (Table 3.6, Fig. 3.4a). The Q_{10} value over the whole temperature range was 2.1 ($r^2=0.701$, df=1, 16, $P<0.001$).

Crabs spent <12% of their time foraging (Fig. 3.4b and 3.5a). Crabs were generally more active and tended to spend more time searching for scallops at 15°C than at 3° and 8°C (Fig. 3.4b and 3.5a). However, these trends were not significant because of high variability between crabs (Table 3.6 and 3.7). The percentage of time crabs spent handling scallops was also not significantly affected by temperature. Individual prey handling time, however, decreased significantly with increasing temperature (Table 3.7, Fig. 3.5c) and the rate of prey handling had a Q_{10} of 2.3 ($r^2=0.562$, df=1, 14, $P<0.001$).

Crabs had high encounter rates with scallops (Fig. 3.4c). The probability of capture upon encounter was also high (>0.3) (Table 3.8, Fig. 3.4c). The probability of consumption upon capture did not differ significantly from 1 ($-0.9>t>-2.5$, df=2-4, $P>0.05$). However, temperature did not appear to significantly affect any of the predation rate components (Table 3.6). The Q_{10} value for encounter rate was 1.5 ($r^2=0.033$, df=1, 12, $P>0.05$). Crab movement velocity when searching tended to increase with temperature ($Q_{10}=1.7$, $r^2=0.397$, df= 1, 5, $P>0.05$), but this trend was not significant (Table 3.7, Fig. 3.5b), most likely because low replication resulted in low power ($\phi=1$, df=2,4, power=0.2). Passive escapes occurred in 36 ± 10% (mean ± SE) of total escapes for all temperatures combined.

Table 3.6. Crab-scallop interactions in Experiment 3.3. ANOVA and SNK test results for consumption rate (no. scallops predator^{-1} d^{-1}), searching time (%), handling time (%), encounter rate (no. scallops h^{-1}) (log transformed data), probability of capture, and probability of consumption in the crab experiment. B1 = upper block and B2 = lower block. Blocks were pooled when P>0.25. Temperatures were 3°, 8° and 15°C.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Consumption rate	temperature	2	90.4	14.62	0.000	$\underline{3\ 8}\ 15$
	error	15	6.2			
Searching time	temperature	2	2.73	1.21	0.325	
	error	15	2.25			
Handling time	temperature	2	13.5	0.89	0.430	
	error	15	15.1			
Encounter rate	temperature	2	0.095	0.41	0.674	
	error	11	0.232			

Table 3.6 continued.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Capture probability	temperature	2	0.027	0.48	0.635	
	block	1	0.300	5.38	0.049	temperatures pooled: B2 B1
	interaction	1	0.039	0.70	0.523	
	error	8	0.056			
Consumption probability	temperature	2	0.237	3.98	0.058	
	error	9	0.060			

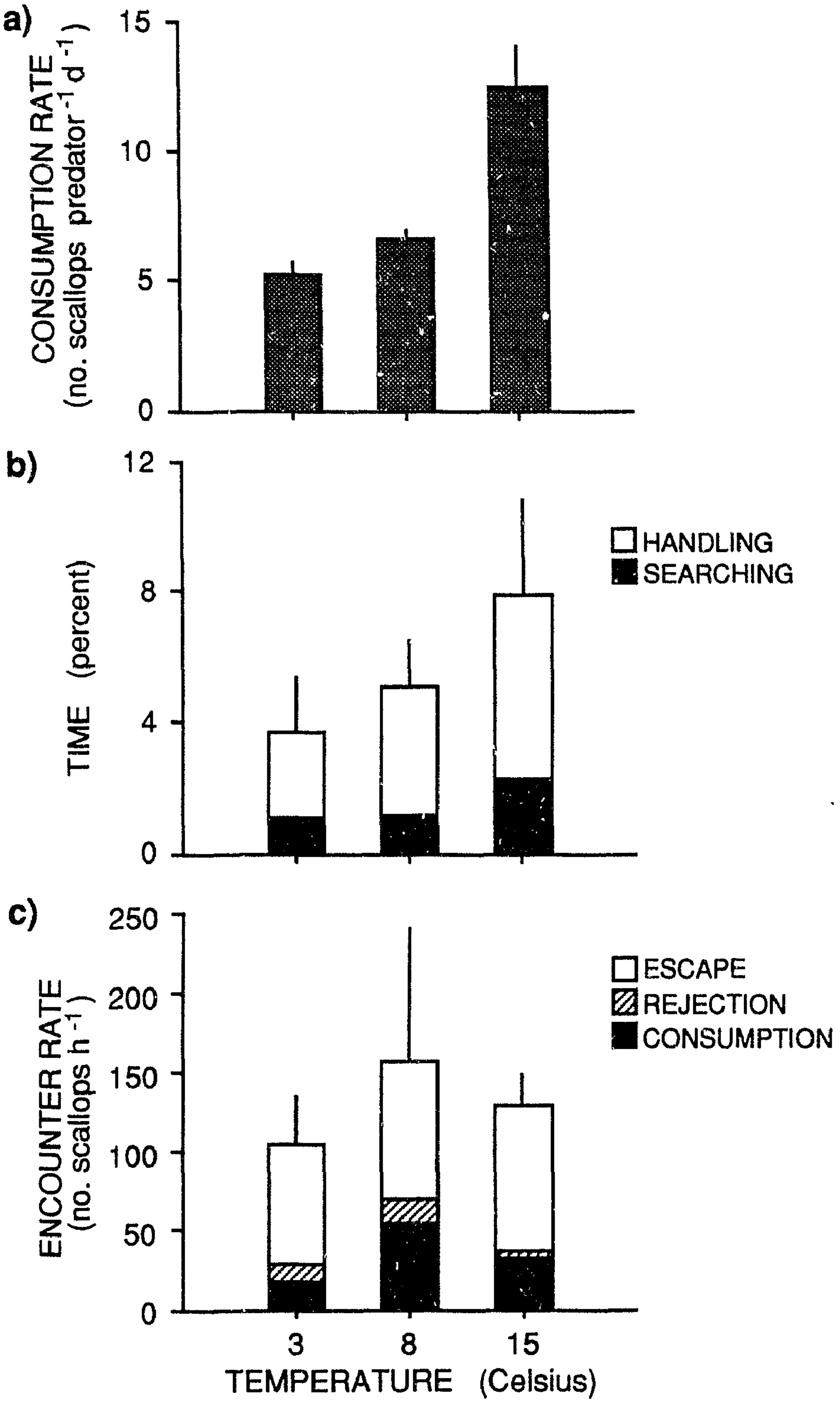


Fig. 3.4. Crab-scallop interactions in Experiment 3.3. a) Consumption rate per crab, b) foraging time (foraging = searching + handling) of crabs, and c) encounter rate and types of encounter between crabs and scallops for each temperature treatment (blocks were pooled). Observation time in b and c = 230 min aquarium^{-1}. Mean shown for all variates; error bars = SE (for foraging time in b and for encounter rate in c).

Table 3.7. Crab-scallop interactions in Experiment 3.3. ANOVA results for active and non-foraging time (proportion) (arcsine square root transformed data), searching time (%) (log transformed data), handling time (%) (log transformed data), and crab movement velocity when searching (cm min^{-1}) during 24 h video observations in the crab experiment. ANOVA and T' test results for prey handling time (min) are also presented (data was obtained from video and experimenter observation). Temperatures were 3°, 8° and 15°C.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Active & non-foraging	temperature	2	303	1.78	0.248	
	error	6	170			
Searching time	temperature	2	0.274	0.78	0.499	
	error	6	0.351			
Handling time	temperature	2	1.20	0.67	0.546	
	error	6	1.79			
Movement velocity	temperature	2	426	2.02	0.247	
	error	4	211			
Prey handling time	temperature	2	55.0	7.47	0.007	15 8 3
	error	13	7.4			

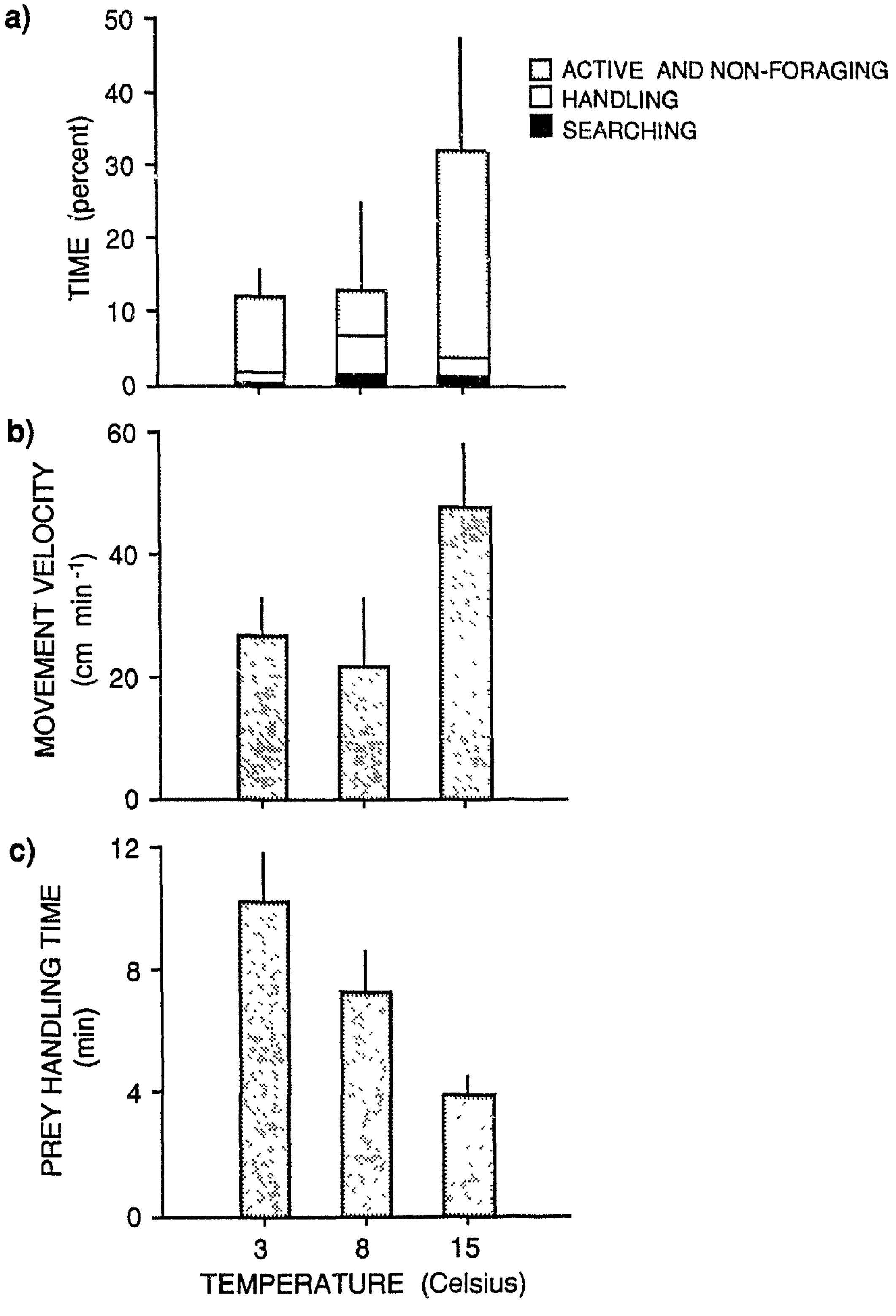


Fig. 3.5. Crab-scallop interactions in Experiment 3.3. a) Time budget and b) searching movement velocity of crabs for each temperature treatment in 24 h video observations, and c) prey handling time of crabs in experimenter and video observations of the experiment. Mean shown for all variates; error bars = SE (for total active time in a).

Table 3.8. Probability of capture and of consumption (mean ± SE) for different temperature treatments in the crab experiment. Sample size is shown in parenthesis.

Temperature (°C)	Capture Probability	Consumption Probability
3	0.34 ± 0.13 (4)	0.44 ± 0.22 (3)
8	0.48 ± 0.16 (5)	0.88 ± 0.13 (4)
15	0.30 ± 0.07 (5)	0.92 ± 0.05 (5)

Discussion

Predation rate on juvenile sea scallops by sea stars (*Asterias vulgaris*) and crabs (*Cancer irroratus*) generally increased with temperature, more so for sea stars than for crabs. Since the relationship between rate functions and temperature tends to be logarithmic, it is not surprising that there were significant differences in predation rates between the higher and two lower temperatures, but not between the two lower temperatures for both sea stars and crabs. Analysis of predation rate in terms of component behaviours allows one to determine the mechanisms that underlie observed patterns of predation as well as identify the components most affected by temperature.

In the second experiment with sea stars, the increase in predation rate with temperature resulted in a Q_{10} of 6.9 (for 4-15°C), which is greater than that previously observed in other sea star-bivalve interactions (*e.g.*, Q_{10}=1.7 (5-20°C) for *Asterias forbesi* preying on *Crassostrea virginica* (calculated from MacKenzie 1969) and Q_{10}=2.8 (17-27°C) for *Luidia clathrata* preying on *Donax variablis* (calculated from Watts and Lawrence 1990)). This increase in predation rate with temperature reflected increased metabolic demand and foraging activity of sea stars, as evidenced by increased time spent searching, increased movement velocities of searching sea stars (Q_{10}=3.8) resulting in higher encounter rates (Q_{10}=2.4), and increased rate of prey handling (Q_{10}=2.8). However, the high Q_{10} value of predation rate suggests that increased sea star activity only partly explains the increased consumption rate. In most sea star-bivalve interactions, the prey are sessile and sea star predation rates are not limited by the probability of capture upon encounter. In the sea star-scallop interaction, however, the probability of capture upon encounter is also dependent on the ability of scallops to escape, which increases with temperature. Scallops appeared more liable to swim or jump away from sea stars at higher temperatures, as indicated by the significant increase with temperature in the proportion of active escapes to total escapes. In bay scallops (*Argopecten irradians*), response time after contact from predatory sea stars and gastropods has been shown to be significantly shorter at 20°C than at 12°C (Ordzie and Garofalo 1980). Furthermore, an increase in valve clapping rate with increasing temperature has been measured for both *Placopecten magellanicus* (Manuel and Dadswell 1991) and *A. irradians* (Olson and Marsh 1993). In my second experiment with sea stars, the ability of sea stars to capture scallops appeared to increase more with temperature than did the ability of scallops to escape, as indicated by a small but significant increase in the probability of capture upon encounter at 15°C compared to that at 4° and 8°C. Hence, the large increase in predation rate by sea stars was due to both increased foraging activity of sea stars and decreased escape effectiveness of scallops with increasing temperature.

The probability of consumption upon capture depends upon prey size (a prey item may be too small or large to handle) and/or on active predator choice (a predator may choose to accept or reject a captured prey item) (Hughes 1980a, Chapter 2). In the experiments described in this chapter, a preferred size class of juvenile scallops was offered to the predators based on results of previous experiments (Chapter 2), to maximize predation rates. Therefore, the probability of sea stars consuming captured scallops was generally not significantly different from 1 and was independent of temperature.

In the first experiment with sea stars, the pre-experimental acclimation procedure to the different temperature levels had a shorter duration and a more abrupt temperature increment than in the second experiment. Sea stars in the first experiment may not have been adequately acclimated to the experimental temperature, and, consequently, exhibited greater individual variability in the percentage of time spent searching for scallops, resulting in significant interactions between temperature and blocks. The escape response of scallops also was affected. Scallops acclimate more readily to increases than to decreases in temperature (Dickie 1958, Dickie and Medcof 1963). The effect of the limited acclimation time was apparent in the high probability of capture upon encounter (>0.6) at the low temperature in the first experiment (Fig. 3.1c). Unstressed scallops usually have a probability of capture by sea stars of <0.2 (Chapter 2). In nature, temperature fluctuations within the sublethal temperature range have been suggested to cause temporary debility in scallops, rendering them more vulnerable to slow-moving predators such as sea stars (*Asterias vulgaris*) and moonsnails (*Lunatia heros*) (Dickie and Medcof 1963). The results of my first experiment with sea stars emphasize the importance of the condition of scallops in determining the outcome of sea star-scallop interactions.

In the crab experiment, the increase in predation rate with temperature resulted in a Q_{10} of 2.1 (for 3-15°C), which is similar to that observed in most other crab-bivalve interactions (*e.g.*, $Q_{10}=1.9$ (10-24°C) and $Q_{10}=2.6$ (10-17°C) for *Carcinus maenas* preying on *Mytilus edulis* (calculated from Wallace (1973) and Elner (1980), respectively), and $Q_{10}=3.2$ (10-24°C) for *Panopeus herbstii* preying on *Mercenaria mercenaria* (calculated from Whetstone and Eversole 1981); an exception being $Q_{10}=5\text{-}6$ (6-15°C) for *C. maenas* preying on *Cerastoderma edule* (Sanchez-Salazar *et al.* 1987)). This increase in predation rate with a Q_{10} within the expected range of 2-3 may result more from changes in crab behaviour than from changes in scallop behaviour. Increased crab activity was indicated by the significant decrease in prey handling time with increased temperature ($Q_{10}=2.3$). Shorter prey handling times were also observed at higher temperatures in the crab *Liocarcinus puber* preying on the crab *C. maenas* (ap Rheinallt and Hughes 1985). Most other crab behaviours recorded in my study showed an increasing trend with temperature, although differences between treatments were non-significant. Since crabs spent less than 3% of their time searching for scallops, foraging bouts could easily have been missed in the behavioural sampling, resulting in high variability between individual crabs. One way to counter this problem would have been to sample behaviours more frequently. Nonetheless, the observed trends suggest that, with increasing temperature, crabs increased time spent searching and movement velocity which would tend to increase encounter rate with scallops. However, given that encounter rate is also dependent on prey density (Holling 1966), high consumption rates by crabs on scallops at 15°C, coupled with the short foraging times, may have decreased the prey density quickly enough to offset an observed increase in encounter rate. Increased movement velocities with temperature have been observed in other crab species (*Chionoecetes opilio* (Foyle *et al.* 1989), *C. maenas* (Carter and Fraser 1991)). Eggleston (1990) attributed increased encounter rates between blue crabs (*Callinectes sapidus*) and juvenile oysters (*Crassostrea virginica*) between 13°C and 27°C to increased motility in crabs.

Predation rate on scallops by crabs were not limited by the probability of capture upon encounter: scallops often closed their valves upon encounter and, hence, the probability of capture was high (>0.2) (Chapter 2). Since a single prey type within the preferred size range was offered to crabs, the probability of consumption upon capture was was high (~1). Both probabilities of capture and of consumption appeared to be temperature independent, supporting the conclusion that the increase in predation rate by crabs with temperature was due to changes in the behaviour of crabs (*i.e.*, activity level) and not to changes in the behaviour of scallops.

Sea star and crab predators have both been shown to be important agents of mortality that limit production in cultured and natural bivalve populations (MacKenzie 1970, Virnstein 1977, Morgan *et al.* 1980, Flagg and Malouf 1983, Boulding and Hay 1984, Peterson 1990, Minchin 1991, Hatcher *et al.* In press a). My study with juvenile sea scallops indicates that temperature has a greater effect on predation rate by sea stars than by crabs, and that this difference can be related to underlying behavioural mechanisms. Increased predator foraging activity with temperature explained most of the increased predation rate by crabs and part of that by sea stars. Decreased effectiveness of scallops' escape response with increasing temperature also accounted for increased predation rate by sea stars. Since the probability of sea stars capturing scallops is an important component determining predation rate, any factor affecting scallop escape responses such as temperature shock will greatly affect the outcome of sea star-scallop interactions. The results of this study have implications for bottom culture of sea scallops, since seeding juvenile scallops on the sea bed during a period of cold water temperature may increase their probability of survival. The low temperature and consequent reduction in predator activity may allow time for juvenile scallops to grow, albeit at a slower rate (Dadswell and Parsons 1991, Kleinman 1994), to a size at which they are less vulnerable to sea star predation once the water warms. However, since crabs have relatively high predation rates on scallops even at low temperatures, this procedure may be less successful in a crab dominated than in a sea star dominated environment.

CHAPTER 4: Procedural effects and the analysis of prey tethering experiments: predation of juvenile scallops by crabs and sea stars.

Introduction

Manipulative field experiments have played a major role in demonstrating the importance of biological interactions such as predation and competition in regulating population dynamics and community structure in marine benthic environments (Connell 1975, Dayton and Oliver 1980, Peterson 1982, Watanabe 1984, Witman 1985). Many experimental studies have used physical barriers, such as caging or tethering, to control densities or movement of animals (Virnstein 1977, Vadas *et al.* 1986, Heck and Wilson 1987, Aronson 1989, Prescott 1990, Pohle *et al.* 1991, Scheibling and Hamm 1991, Ambrose and Irlandi 1992, Witman and Sebens 1992). However, it is generally conceded that these procedures may have artifactual effects which should be controlled or assessed (for caging studies, see Dayton and Oliver 1980, Hall *et al.* 1990). Studies involving tethering of prey usually attempt to determine the relative intensity of predation in different situations rather than measure actual predation rates. The advantages of the tethering procedure are that tethered animals can be individually identified and monitored through time, and that the cause of mortality of the individuals can often be determined from the remains. However, the relative importance of different predators on mortality cannot be assessed if tethering affects these predators differently. It is often assumed that if a prey species does not rely on active escape, but on passive escape or crypsis, then the bias introduced by tethering should be minimal. However, this assumption has never been examined experimentally (see Peterson and Black 1994), although Barshaw and Able (1990) demonstrated that tethering of juvenile lobsters (*Homarus americanus*) affects their burrowing behaviour, a possible escape mechanism from certain predators.

Predation of juvenile sea scallops (*Placopecten magellanicus*), particularly by crabs and sea stars, appears to be important in limiting population size of this commercially important bivalve species in Atlantic Canada and Northeastern USA (Naidu *et al.* 1989, Hatcher *et al.* In press a). To examine predation rate and the biological and physical variables that influence it (*e.g.*, prey size, prey and predator density, temperature, habitat), scallops were tethered in field experiments (Chapter 5). In this study, I examine the effect of tethering scallops on predation rates by crabs and sea stars in laboratory experiments and identify underlying behavioural mechanisms. In addition, I present a method of analysing tethering experiments which circumvents some potential disadvantages of the tethering procedure.

Materials and Methods

In July-August 1993, two laboratory experiments were conducted in 90 x 60 x 50 cm (length x width x height) flow-through seawater tanks to assess the effect of tethering scallops on predation by 1) the rock crab *Cancer irroratus* and 2) the sea star *Asterias vulgaris*. Both species have been observed to be major predators of juvenile sea scallops in the laboratory and the field (Chapter 1). Individual predators were offered 15 scallops in each of two treatments: tethered or free-ranging prey. Based on the laboratory experiments examining size-selective predation in Chapter 2, predators were offered their preferred scallop prey size: large juvenile scallops (mean ± SD: 24.7 ± 1.8 mm shell height (SH)) in the crab experiment and small scallops (10.3 ± 1.5 mm SH) in the sea star experiment. There were three replicate tanks for each treatment in a completely randomized design. Two control tanks, one with 15 tethered scallops and the other with 15 free-ranging scallops, but without a predator, were run concurrently to monitor mortality due to causes other than predation. Non-predatory mortality was negligible in both experiments (one free scallop died in the crab experiment). The duration of the experiment was 5 d and 7 d for crabs and sea stars, respectively. Experimental tanks were monitored daily in the morning and just before sunset to record the number of scallops consumed and to replace consumed scallops. Predation rate (or consumption rate) was calculated for each predator as the total number of scallops consumed by the particular predator during the experiment divided by the duration (in days) of the experiment.

Rock crabs (*Cancer irroratus*; 86 ± 7 mm carapace width (CW)) were collected from East Point Gut, Lunenburg Bay, Nova Scotia, and sea stars (*Asterias vulgaris*; 100 ± 12 mm diameter) from Mill Cove, St. Margaret's Bay, Nova Scotia. Prior to experiments, predators were held in tanks for 3-4 wk and fed mussels (*Mytilus edulis*). Before initiation of experiments, predators were starved for 24 h. Only male crabs were used to avoid potential confounding sex-related variation. Juvenile scallops were obtained from the commercial supplier (Chapter 2). Prior to experiments, scallops were held in 140 L tanks with flowing ambient seawater for 1-2 wk. Prior to and during experiments, scallops were continually drip-fed to maintain ~$1x10^4$ cells ml^{-1} of cultured algae (*T-Isochrysis galbana* or *Thalassiosira pseudonana*). Ambient seawater was sandbed-filtered to 50 μm, and the flow to each experimental tank regulated at 900 ± 200 ml min^{-1} (mean ± SD). Water temperature measured twice daily was 10.7 ± 0.8°C and 13.9 ± 0.4°C over the duration of the crab and sea star experiments, respectively. Salinity averaged 30.4 ± 0.2 ppt during this study. Lighting was by overhead fluorescent lights and natural light through windows. The natural light:dark regime was maintained in both experiments.

The tethering procedure was similar to that used in field experiments (Hatcher *et al.* In press a, Chapter 5). A small area of the upper valve of a scallop was cleaned with a cotton swab and acetone (care was taken not to exposed the scallop's mantle edge to acetone) and dried with an airjet. One end of a 20-25 cm-long monofilament line (Berkley Trilene XL, 8 lb) was glued to this valve using cyanoacrylate glue, and other end was tied to a stainless steel stake (12 cm length, 0.5 cm diameter) with a numbered tag (used to anchor and individually identify tethered scallops in the field). The effective tether length was 17 ± 1 cm (mean ± SD) after gluing and tying. A preliminary laboratory experiment with varying tether lengths (5, 10, 15 cm) showed that predation rates on scallops by sea stars decreased ~30% from 5 to 10 cm tether lengths and but were similar between 10 and 15 cm tether lengths. Scallops were tethered and held in a separate tank at least 24 h before being placed on the bottom of the experimental tanks. To maintain a similar bottom type in the treatment with either free or tethered scallops, stakes were also placed in the tanks with free scallops.

To identify the mechanisms underlying observed predation rates, predators and scallops were observed for 20-30 min periods at randomly chosen times. Total observation times were 420 and 510 min tank^{-1} for the crab and sea star experiments, respectively. Measurements based on these behavioural observations are as described in Chapter 2. Predation rates and other measurements of behaviour were compared between treatments (free and tethered scallops), and the probability of consumption was compared to 1, using two-tailed t-tests, after verifying for homogeneity of variance using Cochran's test. Heteroscedasticity was significant in one case only (sea star predation rate), and log-transformation was successful in homogenizing the variance.

Results

The consumption rate of tethered scallops by crabs (*Cancer irroratus*) did not differ significantly from that of free scallops (t=1.87, df=4, P>0.10, Fig. 4.1a), although the analysis could only detect large differences between treatments (δ=1.4, power=0.3). The percentages time that crabs spent searching for and handling scallops was very low (Fig. 4.1b) and not significantly affected by tethering (t=1.28 and 1.13, respectively, df=4, P>0.20). Encounter rates between crabs and scallops were high (Fig. 4.1c) and also not significantly affected by tethering (t=0.66, df=4, P>0.50). The probability of capture upon encounter was similar for free scallops (mean ± SE: 0.56 ± 0.15) and tethered scallops

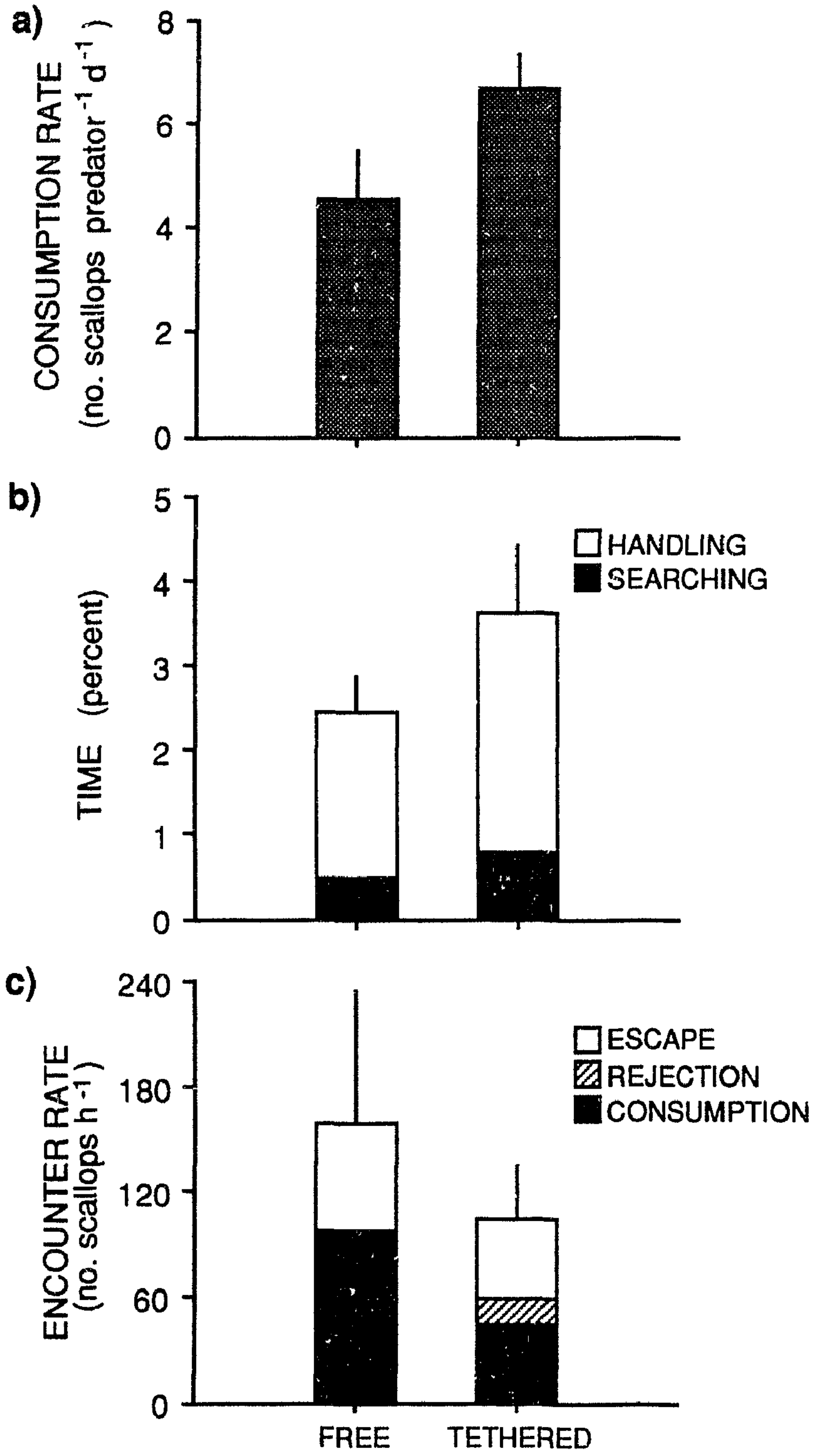


Fig. 4.1. Laboratory scallop tethering experiment conducted with crab predators. a) Consumption rate per crab, b) percent foraging time (% foraging time = % searching time + % handling time) of crabs, and c) encounter rate between crabs and scallops (different outcomes of encounter have different shadings). Crabs were offered either free or tethered scallops. Observation time in b and c = 420 min tank^{-1}. Mean shown for all variates; error bars = SE (for foraging time in b and for encounter rate in c).

(0.64 ± 0.18) ($t=0.37$, df=4, $P>0.50$). The probability of consumption upon capture did not differ significantly from 1 for either group (free scallops: 1.00 ± 0.00; tethered scallops: 0.77 ± 0.15, $t=-1.60$, df=2, $P>0.20$). Although rejection of free scallops by crabs was not observed in this study, it has been observed in previous studies (Chapters 2 and 3). Active escapes from crabs occurred 52 ± 20% of total escapes for tethered and free scallops combined.

Sea stars (*Asterias vulgaris*) consumed 16.7 times more tethered scallops than free scallops ($t=3.77$, df=4, $P<0.05$, Fig. 4.2a). The percentage time that sea stars spent searching for scallops was not significantly affected by tethering ($t=0.52$, df=4, $P>0.50$, Fig. 4.2b). However, sea stars offered tethered scallops tended to spend more time handling scallops (which included extraoral digestion) than those offered free scallops ($t=2.77$, df=4, $P=0.05$), due to the higher consumption rate on tethered scallops. Encounter rate between sea stars and scallops was not significantly affected by tethering ($t=0.16$, df=4, $P>0.50$, Fig. 4.2c). However, the probability of capture upon encounter was 13.1 times lower for free scallops (0.016 ± 0.009) than for tethered scallops (0.209 ± 0.052) ($t=3.65$, df=4, $P<0.05$). The probability of consumption upon capture was similar for free scallops (0.75 ± 0.25, no captures were observed for one sea star) and tethered scallops (0.82 ± 0.10) ($t=0.32$, df=3, $P>0.50$), and did not differ significantly from 1 ($-1.8<t<-1$, df=1 or 2, $P>0.20$). Most encounters resulted in active escapes (Fig. 4.2c). Retractions from scallops by sea stars accounted for only 13% total escapes. The ratio of active escapes to total escapes was not significantly affected by tethering ($t=0.05$, df=4, $P>0.90$). Scallops tended to actively escape from sea stars by jumping more often than swimming (Fig. 4.2d). The proportion of active escapes by swimming tended to be greater for tethered scallops than for free scallops, although the difference was marginally non-significant ($t=2.57$, df=4, $P=0.06$). Collisions with tank walls occurred in <25% of active escapes (Fig. 4.2d) and this was not significantly affected by tethering ($t=0.67$, df=4, $P>0.50$). Tethered scallops reached the end of their tether in 53 ± 7% of active escapes (Fig. 4.2d).

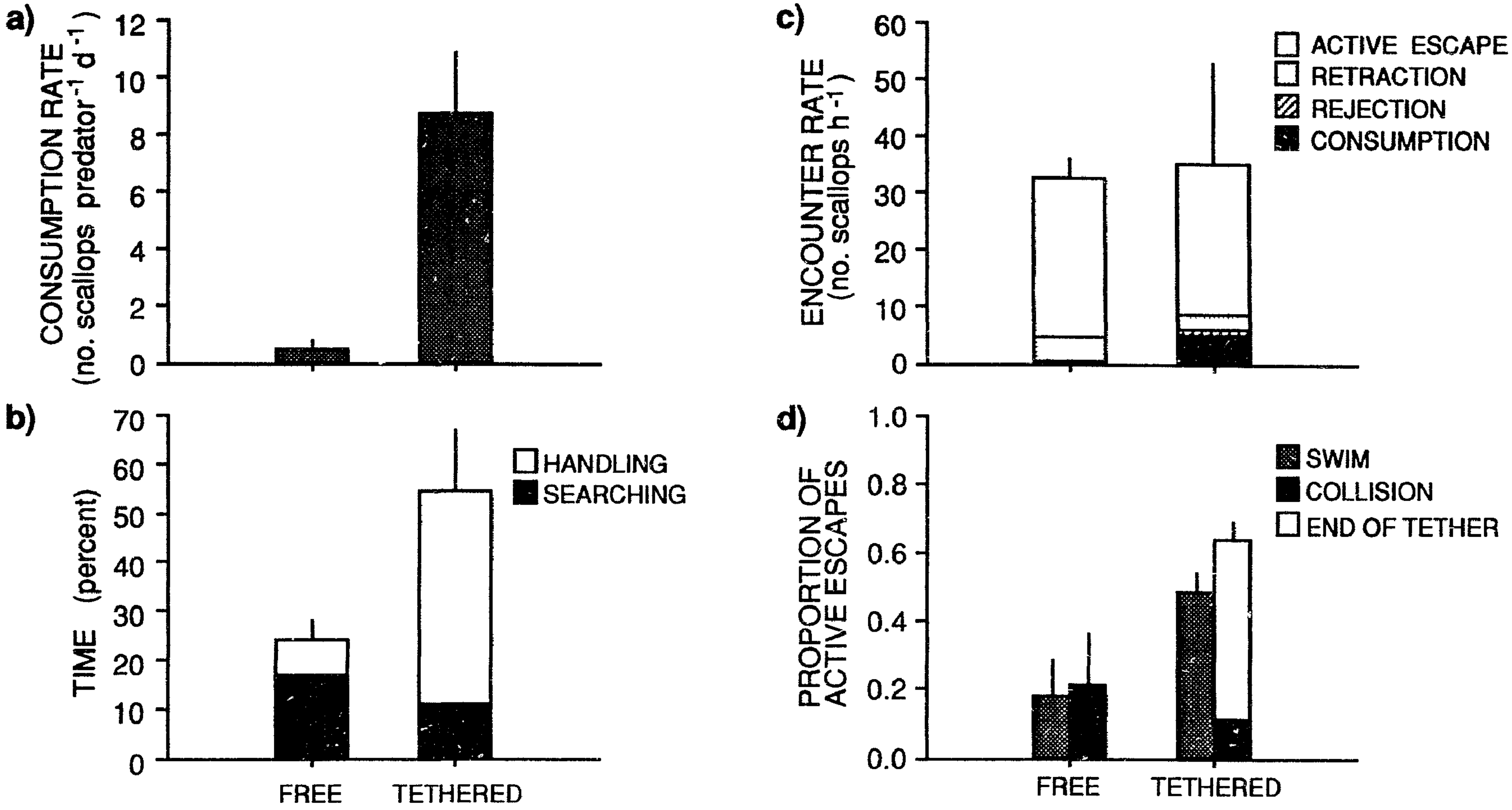


Fig. 4.2. Laboratory scallop tethering experiment conducted with sea star predators (*Asterias vulgaris*). a) Consumption rate per sea star, b) percent foraging time (% foraging time = % searching time + % handling time) of sea stars, c) encounter rate between sea stars and scallops (different outcomes of encounter have different shadings), and d) proportion of active escapes in which scallops swam (active escapes = swims + jumps) and in which scallops collided with the tank walls or reached the end of their tether. Sea stars were offered either free or tethered scallops. Observation time in b, c and d = 510 min tank^{-1}. Mean shown for all variates; error bars = SE (for foraging time in b and for encounter rate in c).

Discussion

Tethering had a much greater effect on scallop mortality due to sea star predation than that due to crab predation. The reason for this difference lies in the behavioural mechanisms underlying predation rate (O'Brien 1987, Osenberg and Mittelbach 1989, Chapter 2). In crab-scallop interactions, encounter rate appears to be a major determinant of predation rate (Chapter 2). Once encountered, juvenile scallops often close their valves, and are likely to be captured and consumed by crabs. Since tethering did not significantly affect encounter rate between scallops and crabs, it did not significantly affect predation rate by crabs.

In sea star-scallop interactions, the probability of capture upon encounter, rather than encounter rate, is a major determinant of predation rate, since scallops readily escape from sea stars by swimming or jumping (Chapter 2). In this study, the probability of sea stars capturing free scallops was very low (<0.1) and similar to that observed in previous studies (Chapters 2 and 3). The probability of sea stars capturing tethered scallops was much higher, since the tether limited active escape. Thus, the higher predation rate by sea stars on tethered than on free scallops reflected the increase in the probability of capture.

This study shows that tethering can have differential effects on predation rates by different predators. Unless a reliable adjustment coefficient is used, it would be difficult to assess the relative importance of crab and sea star predation on scallop mortality in the field. For most field tethering experiments, which usually consist of deploying tethered animals and retrieving them after a few hours or days, frequencies or proportions of animals alive or dead at the end of the experiment are analyzed using contingency tables or analyses of variance (Heck and Thoman 1981, Watanabe 1984, Heck and Wilson 1987, Aronson 1989, Prescott 1990, Wilson *et al.* 1990, Heck and Hambrook 1991, Pohle *et al.* 1991). If the proportion of animals alive is monitored over time, then the proportion surviving at each sampling time is not independent, and a repeated measures analysis of variance (with time as the repeated factor) may be used (Minchinton 1989, Crowder and Hand 1990), or the survival curves may be characterized and statistically compared (*e.g.*, Witman and Sebens 1992). Either all of the causes of mortality are combined in these analyses or certain causes are excluded. If all causes of mortality are combined, then the measure of predation intensity may be biased due to differential effects of tethering on different causes of mortality. If some causes of mortality are excluded from analysis, then useful information is lost. For example, some tethered animals may be alive and under observation for part of the experiment and then disappear without leaving any clues as to whether they were preyed upon or detached from their tether. The knowledge that these animals were alive for part of the experiment is useful information that is often excluded from analysis. Alternatively, if tethered animals are monitored regularly, individual survival times can be used rather than the proportion of total animals alive at each sampling time (*e.g.*, Minello 1993). Such data can be examined through survival analysis (Lawless 1982, Muenchow 1986). Survival analysis allows separate examination, without excluding data (through a procedure termed "censoring"), of competing causes of mortality (*e.g.*, crab and sea star predation). Such an analysis would not assess the relative importance of different causes of mortality of tethered animals, but would allow one to assess the effect of covariates (*e.g.*, size, predator and prey density, temperature, habitat) measured during the individual lifetimes on each cause of mortality. In the next chapter, survival analysis is used to assess the effect of environmental factors on scallop mortality due to crab and sea star predation in the field.

CHAPTER 5: Survival analysis of tethered juvenile sea scallops in field experiments: effects of predators, scallop size and density, site and season.

Introduction

The juvenile stage of marine bivalves is generally considered to be the most vulnerable phase of their benthic life (Jensen and Jensen 1985, Boghen 1989, Juanes 1992). Increasing interest in fisheries assessment, population enhancement and aquaculture of bivalves has focused attention on predation as an important control of juvenile survival (Peterson 1982, Jubb *et al.* 1983, Lake *et al.* 1987, Sanchez-Salazar *et al.* 1987, Eggleston 1990a, Sponaugle and Lawton 1990, Pohle *et al.* 1991) and of population size (Peterson 1990, Minchin 1991, Hatcher *et al.* In press a). In Eastern Canada, predation on juvenile sea scallops (*Placopecten magellanicus*) limits the success of bottom culture, and crabs (*Cancer irroratus*) and sea stars (*Asterias* spp.) have been shown to be the major predators (Naidu and Cahill 1986, Tremblay 1988, Wildish *et al.* 1988, Picard 1992, Hatcher *et al.* In press a). However, the rate-determining processes affecting predation of scallops by crabs and sea stars in the field have not been elucidated.

Predation rate is influenced by various biological and physical factors. For instance, laboratory experiments demonstrate that prey size and water temperature affect predation rates by crabs and sea stars feeding on scallops (Elner and Jamieson 1979, Lake *et al.* 1987, Chapters 2 and 3). Other laboratory and field experiments show that the rate of crab predation on several species of bivalves increases with prey density (Lipcius and Hines 1986, Eggleston 1990a, Sponaugle and Lawton 1990, Eggleston *et al.* 1992). Density-dependent predation may result from accelerated consumption rates of individual predators (a functional response) and/or enhanced local density of predators (a numerical aggregative response) (Hughes 1980b, Taylor 1984). Field studies also demonstrate that site (which encompasses many biological and physical variables) accounts for much of the variation observed in bivalve survival (Flagg and Malouf 1983, Boghen 1989). However, the relative significance of predation in determining the site effect has rarely been assessed.

In this chapter, I present an analysis of the survival of tethered juvenile sea scallops at three field sites. I examine the interacting effects on predation rate of various biological and physical factors (*e.g.*, prey size and density, predator density, water temperature and site). The experiments include one designed to examine the effect of scallop density on scallop mortality rate at one site, and a series of five other experiments designed to monitor the survival of different size classes of scallops tethered at different sites and seasons, and in different densities of surrounding scallops and predators. Since individual tethered scallops in the latter series of experiments were followed until mortality, the effects on survivorship of explanatory variables measured during the individual lifetimes (*i.e.*, covariates such as size, density, temperature, and site) were examined through survival analysis. Survival analysis (also termed hazard analysis) is a powerful statistical procedure designed for time-to-transition data (*e.g.*, time to failure, time to conception, and other waiting times). It is frequently employed in engineering and clinical studies, but has seldom been exploited in ecological studies (Kalbfleisch and Prentice 1980, Lawless 1982, Muenchow 1986). Through survival analysis, I am able to evaluate the effects of covariates on the distribution of survival times of individual scallops rather than simply measure the proportion of scallops surviving at a given time. Survival analysis is particularly attractive because in addition to indicating the significance of covariates, it allows one to calculate probabilities of survival as a function of the covariates.

Materials and Methods

DESCRIPTION OF SITES

Field experiments using tethered juvenile sea scallops (*Placopecten magellanicus*) were conducted at three sites in Lunenburg Bay, Nova Scotia (Fig. 5.1). Site 1 (Corkum Island Channel, Lat: 44° 20.5' N, Long: 64° 18.9' W) is located in a tidal channel (1 km long, 0.35 km wide), on a mixed substrate (small cobbles, shell fragments and silt) at a depth of 7.5 m at mean low tide. The semi-diurnal tides have an amplitude ranging from 0.7 to 2.1 m for neap and spring tides, respectively, and near-bed tidal currents reach up to 0.60 m s^{-1} along-channel (Hatcher *et al.* In press a). Site 2 (Lat: 44° 20.7' N, Long: 64° 18.8' W) is located in the open bay at the mouth of Corkum Island Channel and is more exposed. Site 2 has a substrate similar to Site 1 and a depth of 8.4 m at mean low tide. The tidal and current regimes at Site 2 are similar to those at Site 1, but the current velocities at Site 2 are lower and more variable. Site 3 (East Point Gut, Lat: 44° 21.1' N, Long: 64° 12.8' W) is located in a narrow channel (1 km long, 25 m wide). The substrate at Site 3 is similar to that at Sites 1 and 2, but with a higher silt fraction and at a depth of 4.8 m at mean low tide. The tidal amplitude at Site 3 ranges from 0.7 to 1.9 m for neap and spring tides, respectively, and the current reaches 0.48 m s^{-1} along-channel (Hatcher *et al.* Unpubl.). All sites have naturally occurring populations of scallops.

FIELD TETHERING EXPERIMENTS

Single factor experiment: effect of scallop density

To examine the effect of scallop density on predation rate, an experiment using tethered scallops was conducted at Site 1 from Sept. 27 to Oct. 5, 1991 (8 d). Sixteen 4 m^2 plots were set up in a 4 x 4 matrix within a 40 m^2 area, each plot separated by 10 m. One of four scallop density treatments (0, 5, 15 and 45 scallops m^{-2}) was randomly allocated to each plot to give four replicates of each treatment in a completely randomized design. In the non-zero density plots, 20 tethered scallops (13-18 mm shell height (SH)) were deployed

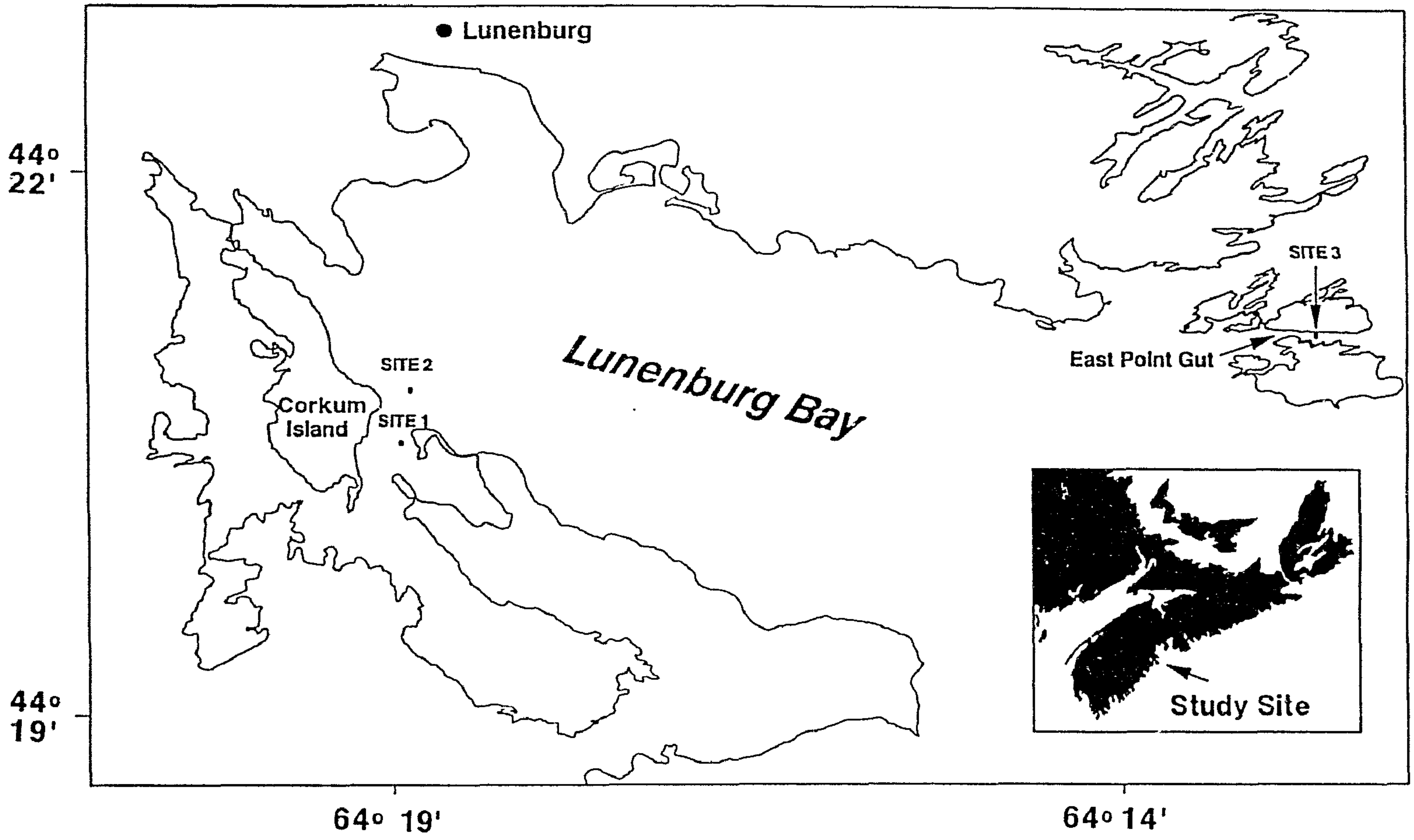


Fig. 5.1. Field sites in Lunenburg Bay, Nova Scotia, Canada, where experiments using tethered scallops (*Placopecten magellanicus*) were conducted.

(4 equally spaced rows of 5 scallops) and, in the 15 and 45 scallop m^{-2} treatments, free-living scallops were added to reach the appropriate densities. All plots were monitored daily (between 12:00 and 16:00 h) by SCUBA divers to record the state (alive, dead or missing) of tethered scallops, to replace dead tethered scallops with live ones, and to count the number of crabs and sea stars in the plots. Predators of tethered scallops could be identified by the shell remains at the end of the tether: crabs left shell fragments and sea stars left empty intact valves (termed "cluckers"). Missing scallops (*i.e.*, the stake and tether were intact, but the scallop or shell remains were absent) were "unassigned". The density of live scallops within each plot was estimated daily by quadrat sampling (three quadrats of 0.25 m^2) and free scallops were added or removed to maintain designated treatment densities. Since scallops dispersed during the 24 h interval between sampling times, scallop density in the four density treatments averaged 0.07 ± 0.03, 5.2 ± 0.4, 14.7 ± 0.4, and 36.7 ± 1.2 scallops m^{-2} (± SE, *n*=4), respectively, over the duration of the experiment. Predator density and scallop mortality rate in each plot were calculated as the total number of predators and dead tethered scallops, respectively, recorded during the experiment divided by the duration (in days) of the experiment.

A randomly chosen plot was monitored for 24 h with an underwater camerahead linked to a time-lapse (3 frames 10 s^{-1}) video recorder (Fuhram Diversified Inc.). The infrared-sensitive camerahead was mounted on a scaffolding to give a field of view of 0.34 m^2, and was surrounded by two banks of infrared lights which were triggered on at dusk and off at dawn. During the experiment, two replicate plots in each treatment group were monitored in this way. However, the video system failed on both a 0 and a 5 scallop m^{-2} plot, leaving these treatments with only one plot. The video recordings were used to quantify the number of entrances by predators into the field of view, the movement velocities of these predators (the path of 3 randomly chosen crabs and sea stars per plot was measured and timed), and the average time and cumulative time (*i.e.*, the sum of all time periods over the 24 h time interval) that predators spent within the field of view.

Juvenile scallops were obtained from the commercial supplier (Chapter 2). Prior to experiments, scallops were held in 140 L tanks with flowing ambient seawater for 1 wk and continually drip-fed to maintain ~1×10^4 cells ml^{-1} of cultured algae (a mixture of *T-Isochrysis galbana*, *Thalassiosira pseudonana* and *Chaetoceros mülleri*). Scallops were tethered as described in Chapter 4. Tethered scallops were maintained in the laboratory for 1-2 d before being transported to the field. In the field, surplus tethered and free scallops were held in pearl nets attached to a surface float. Mean (± SD, *n*=9) water temperature was 12.5 ± 2.1°C during the experiment.

Two congeneric species of predatory sea stars (*Asterias vulgaris* and *A. forbesi*) co-occur in Lunenburg Bay where the field experiments were conducted. The two *Asterias* species were combined into a functional group after verifying in a laboratory experiment that their foraging behaviours did not differ (Appendix A).

Multifactor experiments: effect of scallop size, scallop and predator density, site and season

To examine the effect of scallop size, scallop and predator density, site and season (water temperature) on juvenile scallop survival, five tethering experiments (A, B, C, D, and E) were conducted between July 1991 and June 1992 at Sites 2 and 3 (Table 5.1). Thirty tethered scallops, ten from each of three size classes (small=7-12 mm, medium=13-18 mm, and large=23-28 mm SH) were randomly arranged at ~30 cm intervals in a circular array (1.5 m radius). There were 3-4 replicate circular arrays separated by 20-50 m at each site. Tethered scallops were monitored by SCUBA divers daily for the first two days, then weekly for the first month, and monthly thereafter. On each monitoring day, the state of each tethered scallop and the type of shell remains were recorded as described above (Single factor experiment: effect of scallop density). The experiments were terminated when the proportion of dead or missing tethered scallops reached 80-90% of the original number.

As controls for tether loss and mortality due to handling, nine tethered scallops (three from each size class) were concurrently placed in a cage (1 m diameter, 0.5 m high,

Table 5.1. Description of five multifactor experiments measuring survival of tethered juvenile sea scallops (*Placopecten magellanicus*) at Sites 2 and 3, in Lunenburg Bay, Nova Scotia, between June 1991 and June 1992. There were 3-4 tethering arrays at each site. Video sampling was used to estimate densities of free scallops and predators (*Cancer irroratus* and *Asterias* spp.) in a 30-60 m^2 area surrounding each tethering array (except for Experiment A at Site 3, in which density estimates over the entire site (2500 m^2) were used). The video sampling date in parenthesis in Experiment C, Site 3, indicates that scallops densities were obtained by quadrat sampling and predator densities were not available. Densities of free scallops and predators, and water temperature were averaged over the duration of each experiment.

Experiment	Site	Dates of experiment	Duration (d)	Dates of video sampling	Density (m^{-2}) (Mean ± SE)			Temperature (Mean ± SD; °C)
					Scallops	Crabs	Sea stars	
A	2	June 27-July 26/91	29	July 19/91	0.44 ± 0.14	0.02 ± 0.01	1.04 ± 0.37	11.7 ± 1.6
	3	"		Aug. 27/91, entire site	0.10 ± 0.01	0.26 ± 0.03	0.84 ± 0.11	12.1 ± 1.6
B	2	Aug. 1-15/91	14	Aug. 29/91	0.52 ± 0.08	0.04 ± 0.01	1.11 ± 0.13	16.8 ± 1.5
	3	"		Aug. 27/91	0.10 ± 0.01	0.48 ± 0.16	1.33 ± 0.13	16.9 ± 2.0
C	2	Sept. 3-Oct. 1/91	28	Sept. 4 and 9/91	1.99 ± 0.48	0.09 ± 0.03	0.97 ± 0.20	12.6 ± 2.9
	3	Aug. 27-Sept. 5/91	9	(Aug. 28) and Sept. 5/91	2.87 ± 1.15	0.56 ± 0.17	1.00 ± 0.28	12.6 ± 1.1

Table 5.1 continued.

Experiment	Site	Dates of experiment	Duration (d)	Dates of video sampling	Density (m^{-2}) (Mean ± SE)			Temperature (Mean ± SD; °C)
					Scallops	Crabs	Sea stars	
D	2	Nov. 6/91-Jan. 13/92	68	Nov. 6-7/91	0.74 ± 0.07	0.04 ± 0.01	1.41 ± 0.07	6.4 ± 3.0
	3	Nov. 21/91-Jan. 13/92	53	Nov. 22/91	0.20 ± 0.07	0.09 ± 0.02	1.27 ± 0.10	7.7 ± 2.3
E	2	Mar. 19-June 23/92	96	Mar. 20 and 26, Apr. 23, and May 26/92	1.13 ± 0.23	0.03 ± 0.01	0.91 ± 0.18	3.6 ± 3.7
	3	Mar. 4-May 19/92	76	Mar. 6, 17 and 31, and Apr. 15/92	0.14 ± 0.03	0.01 ± 0.01	0.47 ± 0.05	2.8 ± 1.5

15 mm mesh aperture) anchored to the substratum at Site 1 and in a pearl net (35 cm x 35 cm bottom dimensions; 8 mm mesh aperture) suspended 1-2 m above bottom at Sites 2 and 3. The proportion of tether loss for scallops in the cage was minimal (mean ± SD: 0.08 ± 0.04, *n*=5). There was no mortality of tethered scallops in the pearl net during any experiment.

Juvenile scallops were obtained from the commercial supplier or the experimental hatchery (Chapter 2). They were maintained in the laboratory for up to 10 wk prior to an experiment and tethered as described above (Single factor experiment: effect of scallop density).

These tethering experiments were run concurrently with large-scale bottom seeding experiments with similar juvenile scallops (Hatcher *et al.* In press b, Unpubl.). In these seeding experiments, 9-20 thousand scallops were released within a 5000 m^2 area (50 m x 100 m) at Site 2 and a 2500 m^2 area (25 m x 100 m) at Site 3 in late summer 1991 (Sept. 3 at Site 2 and Aug. 27 at Site 3) and late winter 1992 (Mar. 18 at Site 2 and Mar. 5 at Site 3). The density of free scallops, therefore, varied with the seeding schedule, dispersion and mortality of the seeded populations. During the tethering experiments, scallop and predator abundances were sampled by video camera (Sony V801 High-8 videorecorder in an Amphibico housing) in transects (0.5 m wide x 100 m long) running parallel at 2.5 or 5 m intervals within the seeded area (Table 5.1). The densities of free scallops and of their major predators, rock crabs (*Cancer irroratus*) and sea stars (*Asterias vulgaris* and *A. forbesi*), were estimated from the video tapes by averaging the counts of scallops and predators in successive 1 m (0.5 m^2) sections of transects within a 30 m^2 (3 m x 10 m) to 60 m^2 (6 m x 10 m) area surrounding each circular array (*n*=9 to 30 sections) . Two exceptions were: 1) Experiment A at Site 3, in which video estimates of scallop and predator density over the entire site (2500 m^2) were used, and 2) Experiment C at Site 3, in which estimates of scallop density were obtained on Aug. 28, 1991, from quadrat (0.25 m^2) sampling rather than video sampling and estimates of predator density were not available (Table 5.1).

Scallop and predator densities were averaged over all sampling days during each tethering experiment.

Seawater temperature was monitored by various means: 1) by diver's temperature gauge at each sampling time (all sites), 2) min-max thermometers reset at each sampling time (Site 2), 3) hourly logging on an *in situ* current meter (Emerson and Grant In press) stationed 1 km southeast of Site 2, and 4) Ryan recording thermograph (Site 3). Temperature was averaged over the duration of each tethering experiment using the most accurate data available (Table 5.1).

STATISTICAL ANALYSIS

The single factor experiment at Site 1 was analyzed by one-way, fixed factor analysis of variance (ANOVA). The fixed factor was scallop density, and the response variables were: 1) mortality rate of tethered scallops, 2) density of predators, 3) number of entrances of predators into the video field of view, 4) average time that predators spent within view, and 5) cumulative time that predators spent within view. The multifactor experiments (A, B, C, D and E) at Sites 2 and 3 were analyzed by two- or three-factor, repeated measures ANOVA (Winer 1971, Crowder and Hand 1990). The repeated factor was time. The fixed factors were site and scallop size in Experiments A and B, and scallop size in the remaining experiments at each site. The response variable was the proportion of tethered scallops alive. All response variables were found to be homogeneous after using Cochran's test. The assumption of equal covariance in the repeated measures ANOVA was tested using the sphericity test (Crowder and Hand 1990, Dixon 1990). If the data were non-spherical, then the degrees of freedom of the sources of variation with the repeated factor were adjusted using Greenhouse-Geisser estimate ε. Multiple comparisons of means were performed using Student-Newman-Keul's test or Tukey's method (if the number of comparisons was > 4). The error mean squares used in the post hoc tests were calculated as described in Winer (1971).

Since each tethered scallop was numbered in experiments A, B, C, D and E at Sites 2 and 3, time to mortality of individual scallops was known. Survival times were analyzed using Cox Proportional Hazards Model, which allows assessment of the effects of covariates on scallop survival. Covariates used in the survival analysis included scallop size, scallop and predator density (estimated from video transects), water temperature, and site (scallop size and site were categorical variables). The proportional hazards model is given by:

$$h(t|\mathbf{x})=h_0(t)e^{\mathbf{x}\boldsymbol{\beta}},$$

where the hazard function (*i.e.*, instantaneous mortality rate) at time t for a vector of covariates $\mathbf{x}$ (*i.e.*, $h(t|\mathbf{x})$) is equal to the baseline hazard function at time t ($h_0(t)$; *i.e.*, when all covariates=0) multiplied by the exponent of $\mathbf{x}\boldsymbol{\beta}$, where $\mathbf{x}\boldsymbol{\beta}=x_1\beta_1+...+x_p\beta_p$ and β_i's are unknown coefficients (Kalbfleisch and Prentice 1980, Lawless 1982). The proportional hazards model estimates $h_0(t)$ and $\boldsymbol{\beta}$ from the survival times. The hazard function is related to the survival function (*i.e.*, probability of survival) as the negative derivative of the natural logarithm of the survival function. Survival analysis also allows one to use censored observations of individuals which were not observed for the full time to failure; *i.e.*, information is available from these individuals while they are alive and under observation. Scallops which went missing, died of causes other than the cause of interest, or were alive at the end of an experiment were censored. Survival analyses were performed using BMDP (Dixon 1990). The assumption of proportional hazards between different levels of a covariate was checked graphically (Kalbfleisch and Prentice 1980, Dixon 1990). The importance of two-way interactions between all covariates and of each covariate on scallop survival were tested using likelihood ratio tests (Lawless 1982, Dixon 1990). Diagnostic checks were performed and the models were deemed adequate (Lawless 1982).

Results

SINGLE FACTOR EXPERIMENT: EFFECT OF SCALLOP DENSITY

Immediately before the experiment examining the effect of scallop density on predation rate, predator densities did not differ significantly between plots (F=1.00, 1.78, and 0.67, df=3, 12, P>0.20, for *Cancer irroratus*, *Asterias vulgaris* and *A. forbesi*, respectively). After initiation of the experiment, crab predation rate on tethered scallops (as indicated by shell fragments) increased with scallop density (Table 5.2, Fig. 5.2a). Crab density, however, did not differ significantly among scallop density treatments (Table 5.2; Fig. 5.2b). There were no significant differences in sea star predation rate on tethered scallops, as indicated by cluckers, or in sea star density (Table 5.2, Figs. 5.2a and b) among scallop density treatments. There also were no significant differences in the number of tethered scallops with an unassigned mortality among scallop density treatments (Table 5.2; Fig. 5.2a).

Video analysis indicated that the number of crabs (*Cancer irroratus*) or sea stars (*Asterias* spp.) entering the 0.34 m^2 video field of view, and the average time and cumulative time these predators were in view, did not vary significantly with scallop density (for crabs: $0.8<F<2.0$, df=2, 3, P>0.20; for sea stars: $0.07<F<0.12$, df=2, 3, $\underline{P}$>0.50), although the power of the analyses to detect differences was very low due to the low level of replication (ϕ=1, df=2, 3, power=0.2). (Since only one plot was video-monitored in the 0 and 5 scallops m^{-2} treatments, the observations were combined.) Over a 24 h interval, an average of about 8 rock crabs and 11 sea stars were observed entering the field of view (Fig. 5.3a). Crabs spent on average 0.06 h in view (Fig. 5.3b) and moved at a mean velocity (± SE, n=18) of 66.6 ± 19.1 cm min^{-1}. Sea stars spent on average 2.11 h in view and moved at a mean velocity of 1.1 ± 0.1 cm min^{-1}. On average, the cumulative time that crabs and sea stars spent in view during the 24 h interval was 0.5 and 24.2 h, respectively (Fig. 5.3c).

Table 5.2. ANOVA and SNK test results for mortality rate of tethered scallops (no. shell fragments m^{-2} d^{-1}, no. cluckers m^{-2} d^{-1}, and no. unassigned m^{-2} d^{-1}) and predator densities (no. *Cancer irroratus* m^{-2}, and no. *Asterias* spp. m^{-2}) in the single factor experiment at Site 1 in Lunenburg Bay. Scallop density treatments were 5, 15, and 45 scallops m^{-2} for scallop mortality rates, and 0, 5, 15, and 45 scallops m^{-2} for predator densities. For the post hoc comparisons, treatment levels sharing a common underline did not differ significantly.

Dependent variable	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing magnitude)
Shell fragments	scallop density	2	0.457	5.51	0.027	5 15 45
	error	9	0.083			
Cluckers	scallop density	2	0.152	0.38	0.697	
	error	9	0.405			
Unassigned	scallop density	2	0.001	0.27	0.767	
	error	9	0.005			
Cancer irroratus	scallop density	3	0.383	1.31	0.317	
	error	12	0.292			
Asterias spp.	scallop density	3	6.54	1.36	0.301	
	error	12	4.80			

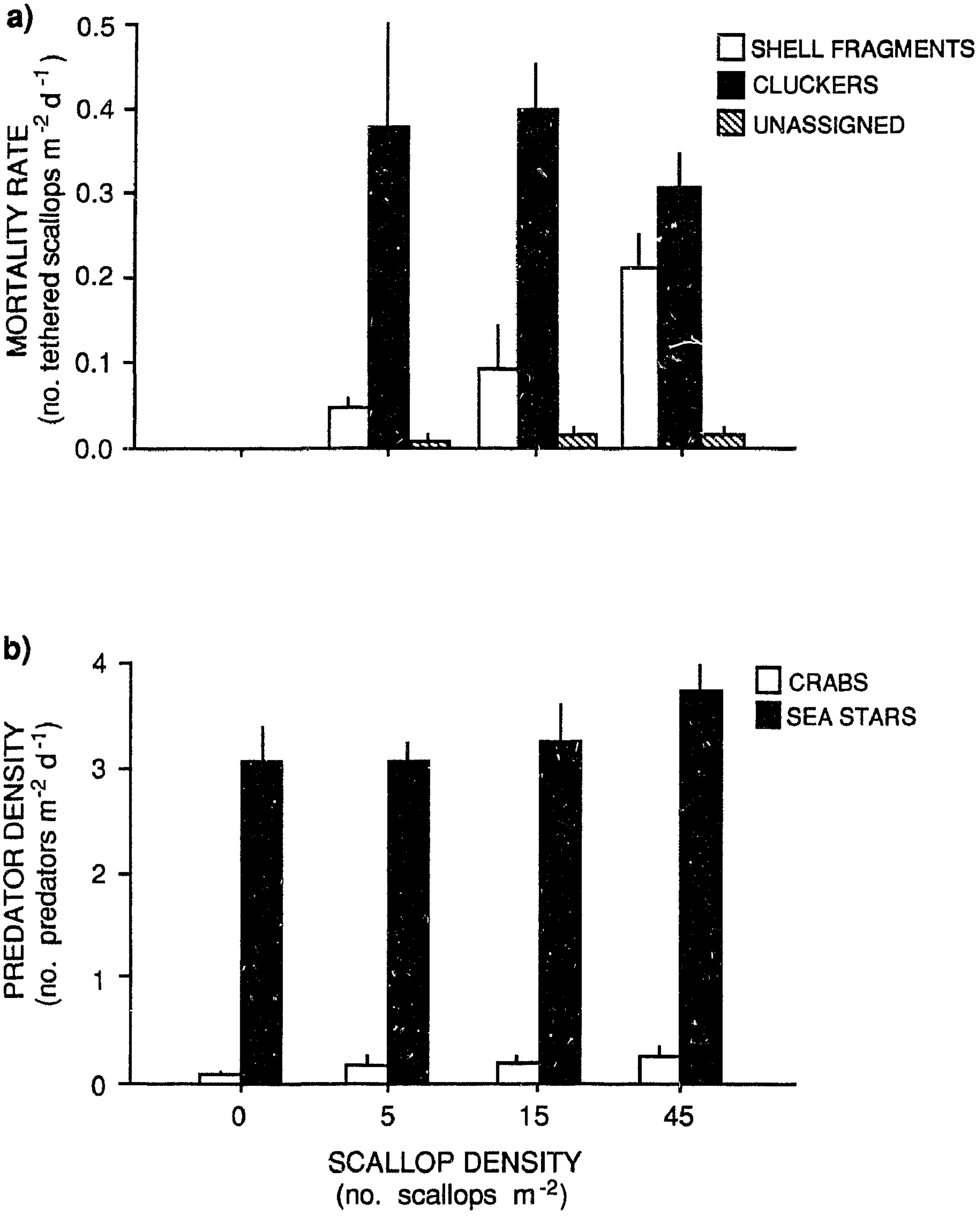


Fig. 5.2. Results of the single factor experiment using tethered scallops at Site 1 in Lunenburg Bay. a) Scallop mortality rate for each type of shell remains, and b) density of each predator, at different scallop densities. Mean ± SE shown for all variates (*n* =4).

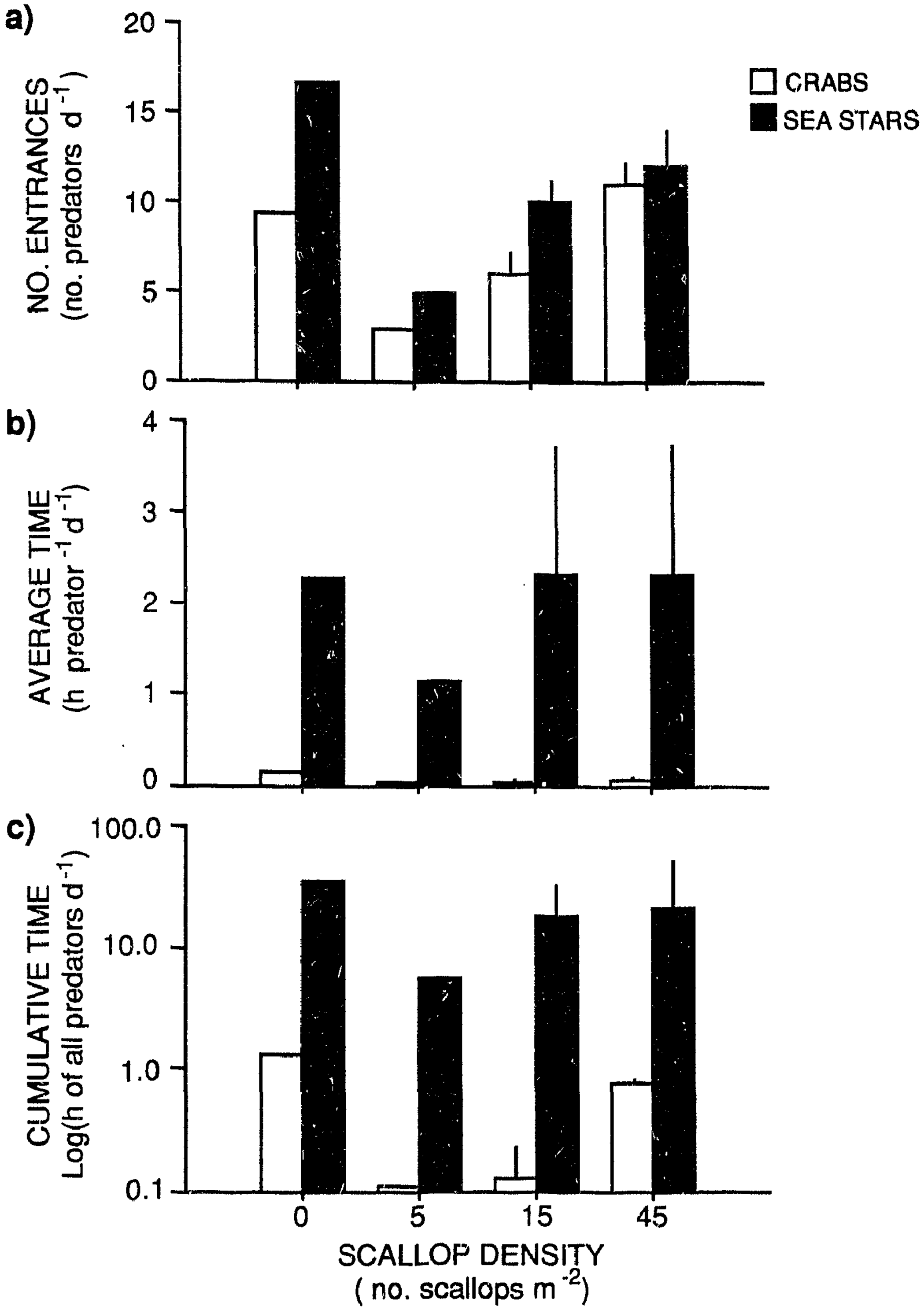


Fig. 5.3. Time-lapse video observations of the single factor experiment at Site 1 in Lunenburg Bay. a) Number of predators observed entering the 0.34 m^{-2} video field of view, and b) average and c) cumulative time predators spent within view at different scallop densities over 24 h. Only one plot was video-monitored in each of the 0 and 5 scallops m^{-2} treatments. Mean ± SE shown for all variates in the 15 and 45 scallops m^{-2} treatments (*n* =2).

MULTIFACTOR EXPERIMENTS: EFFECT OF SCALLOP SIZE, SCALLOP AND PREDATOR DENSITY, SITE AND SEASON

In tethering experiments in the summer of 1991 (A and B), before Sites 2 and 3 were seeded with juvenile scallops, large tethered scallops had a higher survivorship than small and medium scallops (Table 5.3, Figs. 5.4a and 5.5a). Shell remains indicated that most of the predation of all size classes was by sea stars (Figs. 5.4b and 5.5b). However in experiments in late summer (C), after increasing scallop density at Sites 2 and 3 through seeding, there were no longer any size-related differences in scallop survivorship (Table 5.3, Figs. 5.4a and 5.5a), and shell remains indicated that crabs were the more important predators particularly for the large size class of scallops (Figs. 5.4b and 5.5b). In experiments in late fall and winter (D), there also were no size-related differences in scallop survivorship (Table 5.3), but scallop survival time increased (Figs. 5.4a and 5.5a). Crabs continued to be a major cause of mortality among the large size class of scallops (Figs. 5.4b and 5.5b). In the final set of experiments (E), after reseeding both sites in late winter, scallop survival time remained high, and large scallops tended to have a higher survivorship than smaller scallops at Site 2 but not at Site 3 (Table 5.3, Figs. 5.4a and 5.5a). Scallops at Site 3 generally experienced more crab predation than those at Site 2 (Figs. 5.4b and 5.5b). A significant Size x Time interaction on the proportion of scallops surviving was observed in experiments A and E (Table 5.3).

Table 5.3. Repeated measures ANOVA and SNK or Tukey's test results for tethered scallops of different sizes surviving over time in the multifactor experiments at Sites 2 and 3. Experiments A and B were each conducted at Sites 2 and 3 at the same time; therefore, the factor 'site' was included in the analysis of these experiments. The remaining experiments were conducted at Sites 2 and 3 at different times, and, therefore, were analyzed separately for each site. T1 to 9 are consecutive monitoring times; S = small, M = medium, and L = large.

Experiment	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing order)
A, both sites	site	1	0.006	0.04	0.837	
	size	2	1.033	7.69	0.007	T1: M S L
						T2: S M L
						T3: S M L
						T4: S M L
						T5: S M L
						T6: S M L
	site x size	2	0.084	0.63	0.552	
	$\text{error}_{\text{between}}$	12	0.134			
(ε=0.491)[a]	time	$5\varepsilon^a$	1 303	111.49	<0.001	small scallops: T6 T5 T4 T3 T2 T1
						medium scallops: T6 T5 T4 T3 T2 T1
						large scallops: T6 T5 T4 T3 T2 T1
	site x time	5ε	0.008	0.66	0.554	
	size x time	10ε	0.059	5.01	0.002	
	site x size x time	10ε	0.010	0.89	0.497	
	$\text{error}_{\text{within}}$	60ε	0.012			

Table 5.3 continued.

Experiment	Sources of variation	df	MS	F	P	Post hoc mean comparisons (listed in increasing order)
B, both sites	site	1	0.007	0.18	0.678	for each time: Site 2 Site 3
	size	2	0.374	9.97	0.003	time intervals pooled: S M L
	site x size	2	0.029	0.77	0.484	
	error$_{\text{between}}$	12	0.038			
	time	3	1.281	170.83	<0.001	Site 2: T4 T3 T2 T1 Site 3: T4 T3 T2 T1
	site x time	3	0.023	3.03	0.042	
	size x time	6	0.017	2.30	0.056	
	site x size x time	6	0.004	0.49	0.809	
	error$_{\text{within}}$	36	0.008			
C, Site 2	size	2	0.039	0.68	0.533	
	error$_{\text{between}}$	9	0.057			
(ε=0.388)	time	5ε	1.726	127.09	<0.001	T6 T5 T4 T3 T2 T1
	size x time	10ε	0.003	0.24	0.908	
	error$_{\text{within}}$	45ε	0.014			

Table 5.3 continued.

Experiment	Sources of variation	df	MS	F	P	Post hoc mean comparisons (listed in increasing order)
C, Site 3	size	2	0.067	1.16	0.375	
	error$_{between}$	6	0.058			
	time	2	0.829	62.19	<0.001	T3 T2 T1
	size x time	4	0.004	0.28	0.887	
	error$_{within}$	12	0.013			
D, Site 2	size	2	0.081	0.81	0.487	
	error$_{between}$	6	0.100			
(ε=0.368)	time	6ε	0.404	37.56	<0.001	T7 T6 T5 T4 T3 T2 T1
	size x time	12ε	0.010	0.93	0.484	
	error$_{within}$	36ε	0.011			
D, Site 3	size	2	0.079	1.73	0.256	
	error$_{between}$	6	0.046			
	time	4	0.834	101.18	<0.001	T5 T4 T3 T2 T1
	size x time	8	0.010	1.21	0.336	
	error$_{within}$	24	0.008			

Table 5.3 continued.

Experiment	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing order)
E, Site 2	size	2	0.368	6.01	0.037	T1: S M L T2: S M L T3: S M L T4: S M L T5: S M L T6: S M L
	error$_{between}$	6	0.061			
	time	5	1.020	120.60	<0.001	small scallops: T6 T5 T4 T3 T2 T1 medium scallops: T6 T5 T4 T3 T2 T1 large scallops: T6 T5 T4 T3 T2 T1
	size x time	10	0.021	2.51	0.025	
	error$_{within}$	30	0.008			

Table 5.3 continued.

Experiment	Sources of variation	df	MS	*F*	*P*	Post hoc mean comparisons (listed in increasing order)
E, Site 3	size	2	0.070	0.63	0.565	
	$\text{error}_{\text{between}}$	6	0.111			
(ε=0.402)	time	8ε	0.993	105.17	<0.001	T9 T8 T7 T6 T5 T4 T3 T2 T1
	size x time	16ε	0.018	1.93	0.126	
	$\text{error}_{\text{within}}$	48ε	0.009			

[a] When the data were non-spherical, the degrees of freedom of the sources of variation with the repeated factor were adjusted using Greenhouse-Geisser estimate ε, a measure of deviation from sphericity.

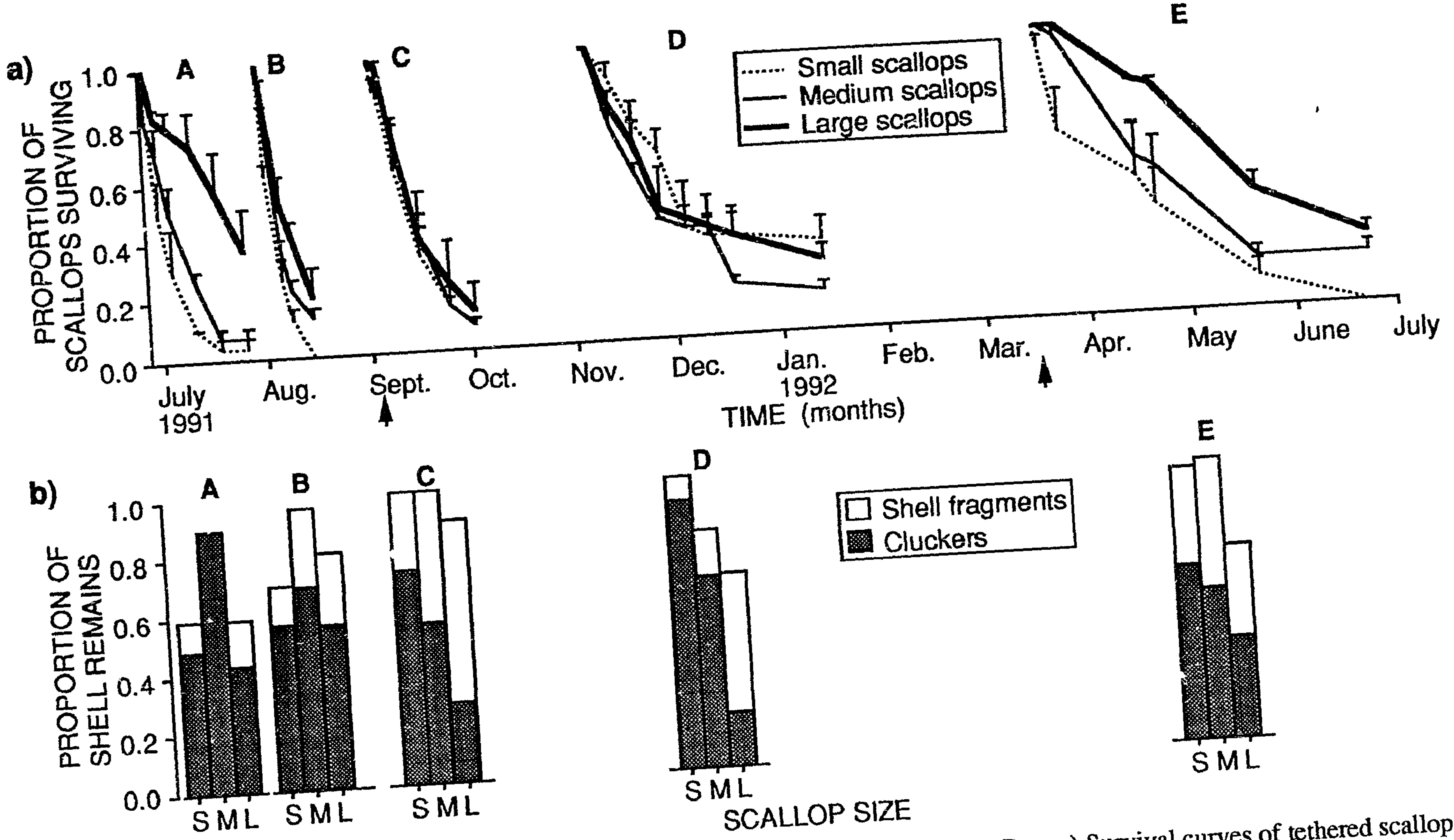


Fig. 5.4. Results of five multifactor experiments (A, B, C, D, E) at Site 2 in Lunenburg Bay. a) Survival curves of tethered scallops for each size class, averaged over 3 or 4 arrays (error bars = SE). b) Proportion of the different types of shell remains in each scallop size class (S=small, M=medium, L=large) at the end of the experiments. The remainder represents scallops with an unassigned cause of mortality. Arrows indicate dates at which the site was seeded with juvenile scallops.

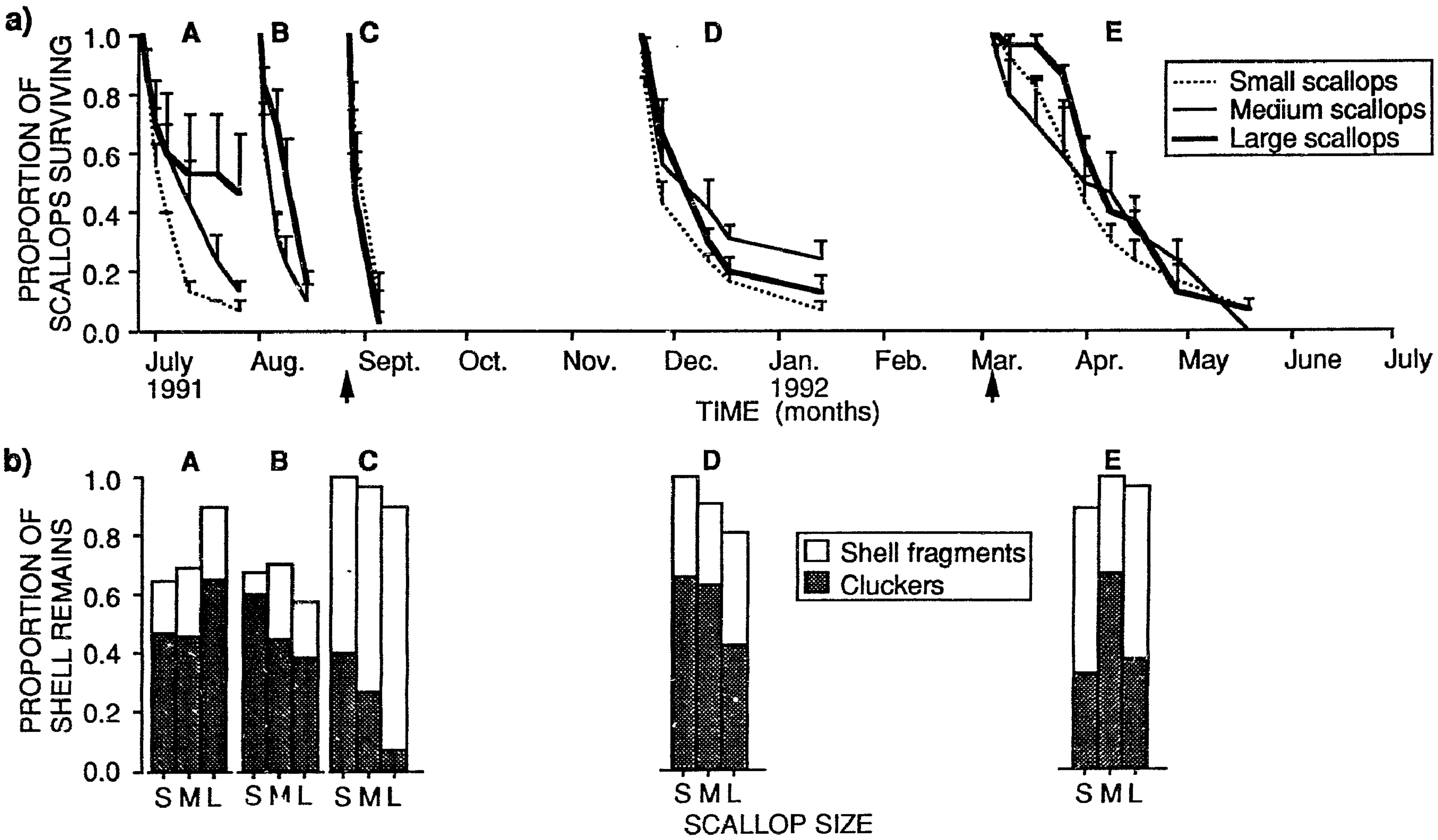


Fig. 5.5. Results of five multifactor experiments (A, B, C, D, E) at Site 3 in Lunenburg Bay. a) Survival curves of tethered scallops for each size class, averaged over 3 arrays (error bars = SE). b) Proportion of the different types of shell remains in each scallop size class (S=small, M=medium, L=large) at the end of the experiments. The remainder represents scallops with an unassigned cause of mortality. Arrows indicate dates at which the site was seeded with juvenile scallops.

Tables 5.4 and 5.5 give the results of the Cox Proportional Hazards Analysis of scallop survival times in all experiments (A, B, C, D, E) combined, and the models (Model 1 and Model 2) quantify the relationship between survivorship and a set of explanatory variables (scallop size, site, density of surrounding scallops, density of predators, and/or water temperature (a seasonal variable) (see Table 5.1)). Crab and sea star predation were competing causes of scallop mortality. Since laboratory experiments indicated that the tethering procedure affected crab predation and sea star predation differently (Chapter 4), scallop survival times were analysed separately for crab-specific mortality (while censoring sea star-specific mortality; Table 5.4) and sea star-specific mortality (while censoring crab-specific mortality; Table 5.5). This procedure assumes that the removal of one cause of mortality simply reduces the hazard function for that cause to zero and leaves the hazard for the other cause unchanged.

For crab-specific mortality of scallops (proportion of observations censored = 0.71, number of cases = 930), Model 1 includes all covariates except non-significant two-way interaction terms, and Model 2 only includes the significant covariates (Table 5.4). The global χ^2 of both Model 1 and Model 2 was significant, indicating that at least one of the included covariates significantly affected the instantaneous mortality rate. Excluding the non-significant covariates of Model 1 from Model 2 did not greatly change the coefficients of the covariates of Model 2. A positive coefficient of a covariate indicates that the instantaneous mortality rate increases (*i.e.*, survival decreases) with increasing value of the covariate; a negative coefficient indicates the reverse. The hazard function ($h(t)$) of scallops due to crab predation is calculated, using Model 2 (Table 5.4) for example, as $h_0(t)\exp(0.121\text{Temperature} + 1.994\text{Site} - 0.130\text{Temperature} \times \text{Site} + 0.480\text{Scallop density} + 1.077\text{Crab density})$; and the survival function is equal to the exponent of the negative integral of the hazard function. In the analysis of scallop mortality attributed to crab predation, there was a significant interaction between site and temperature (Table 5.4): at Site 2, the probability of survival of scallops was highest at low temperature and decreased with increasing temperature (Fig. 5.6); at Site 3, the probability of survival was similar for different temperatures. All other two-way interactions did not significantly affect scallop mortality (Likelihood ratio χ^2=16.71 when comparing a model including all interactions to Model 1 in Table 5.4, df=13, *P*>0.05). Although the instantaneous mortality rate increased with scallop size (Size1 compares medium scallops to small ones, Size2 compares large scallops to small ones, and the effect of small size on survival is incorporated in the baseline hazard), scallop size did not have a significant effect on crab predation (Table 5.4, Model 1). Scallop density had a highly significant effect on crab predation: the instantaneous mortality rate of scallops increased with scallop density (Table 5.4, Model 2, and Figs. 5.6a and b). Crab density had a marginally significant effect on crab predation: the instantaneous mortality rate increased with crab density (Table 5.4, Model 2).

For the sea star-specific mortality of scallops (proportion of observations censored = 0.56, number of cases = 930), Model 1 includes all main (*i.e.*, non-interaction) covariates; Model 2 only includes the temperature and scallop size covariates (Table 5.5). The global χ^2 of both Model 1 and Model 2 was significant, indicating that at least one of the included covariates significantly affected the instantaneous mortality rate. None of the two-way interactions were significant (Likelihood ratio χ^2=19.56 when comparing a model including all interactions to Model 1 of Table 5.5, df=14, *P*>0.05). Site, scallop density and sea star density also did not significantly affect sea star predation (Table 5.5, Model 1). Temperature had a highly significant effect on sea star predation: the instantaneous mortality rate of scallops increased with temperature (Table 5.5, Model 2, Fig. 5.7). Scallop size also affected sea star predation: the instantaneous mortality rate of medium scallops did not differ significantly that of small scallops (Size1), but large scallops had a significantly lower instantaneous mortality rate than small scallops (Size2) (Table 5.5, Model 2, Fig. 5.7).

Table 5.4. Cox Proportional Hazards Analysis of scallop mortality due to crab predation in the multifactor experiments at Sites 2 and 3 in Lunenburg Bay. Model 1 quantifies the relationship between scallop mortality and all covariates except the non-significant two-way interaction terms. Model 2 includes only the significant covariates. The coefficient and its standard error are shown for each covariate within each model. To test the significance of a covariate, the log likelihood of a submodel that excludes that particular covariate is statistically (χ^2) compared to the log likelihood of the full model (Model 1 or Model 2; listed on bottom line). The likelihood ratio test is defined as -2(log likelihood of submodel - log likelihood of full model). This test was done for each covariate within Model 1 and Model 2; some covariates were combined into groups to lower the experimentwise error rate. Statistical results for Temperature and Site are not shown because of the significant Temperature-Site interaction term.

Model 1						Model 2					
Covariate	Coefficient (SE)	Log Likelihood of submodel that excludes covariate	Likelihood ratio χ^2	df	*P*	Covariate	Coefficient (SE)	Log Likelihood of submodel that excludes covariate	Likelihood ratio χ^2	df	*P*
Temperature	0.121 (0.024)					Temperature	0.121 (0.024)				
Site[a]	2.005 (0.321)					Site[a]	1.994 (0.321)				
Temp x Site	-0.131 (0.034)	-1591.90	15.29	1	<0.001	Temp x Site	-0.130 (0.034)	-1592.25	15.07	1	<0.001
Scallop density	0.484 (0.073)	-1604.55	40.58	1	<0.001	Scallop density	0.480 (0.073)	-1604.77	40.11	1	<0.001

Table 5.4 continued.

Model 1						Model 2					
Covariate	Coefficient (SE)	Log Likelihood of submodel that excludes covariate	Likelihood ratio χ^2	df	*P*	Covariate	Coefficient (SE)	Log Likelihood of submodel that excludes covariate	Likelihood ratio χ^2	df	*P*
Crab density	1.085 (0.513)	-1586.54	4.57	1	0.032	Crab density	1.077 (0.512)	-1586.97	4.52	1	0.034
Size1[a]	0.062 (0.158)	-1584.71	0.91	2	0.634						
Size2[a]	0.142 (0.151)										
		Log Likelihood of model	Global χ^2	df	*P*			Log Likelihood of model	Global χ^2	df	*P*
Full model		-1584.26	194.77	7	<0.001	Full model		-1584.71	194.01	5	<0.001

[a] Site, Size1 and Size2 are catergorical variables, where site 2 is defined as Site=0 and site 3 as Site=1, and small scallops are defined as Size1=0, Size2=0, medium scallops as Size1=1, Size2=0, and large scallops as Size1=0, Size2=1.

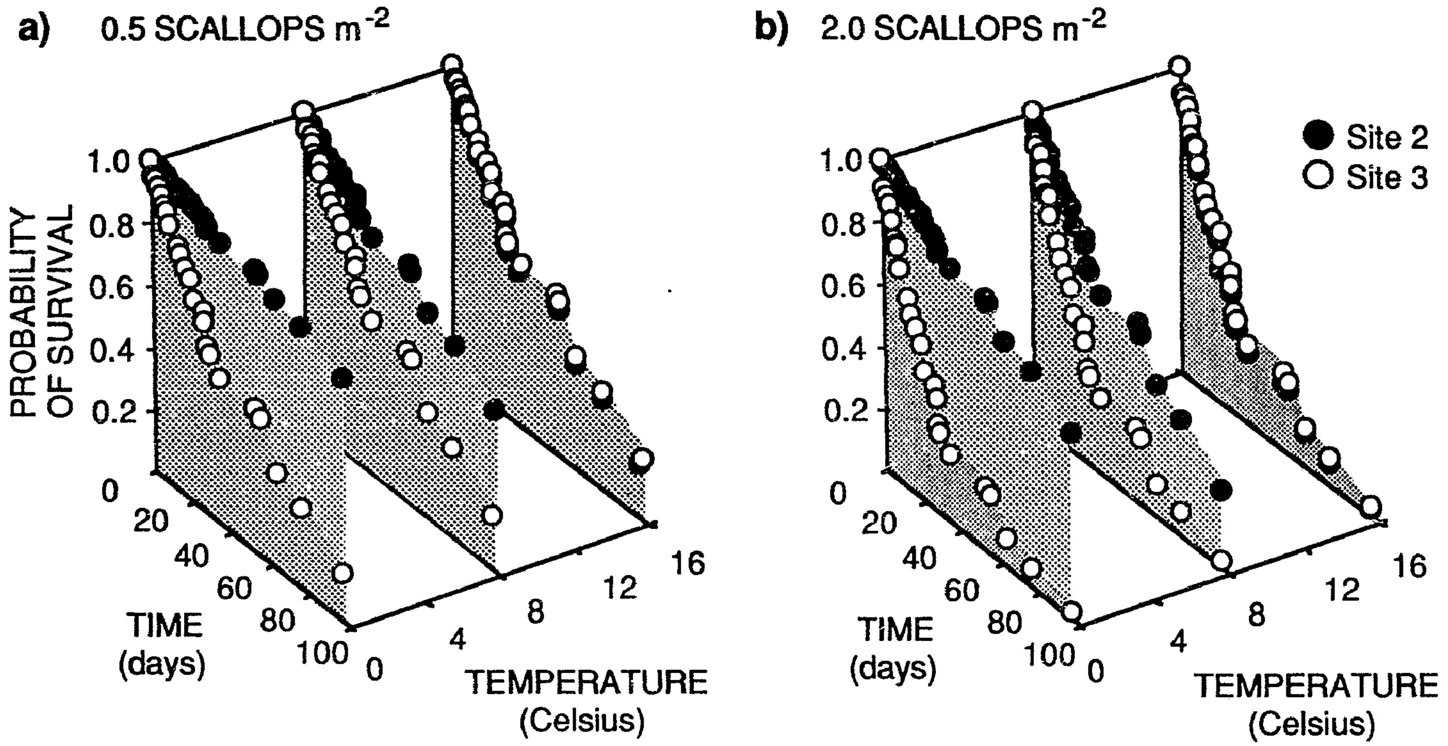


Fig. 5.6. Simulated survival curves of tethered sea scallops for mortality attributed to crab predation at Sites 2 and 3, and at different water temperatures and scallop densities (calculated using Model 2 of the crab predation survival analysis; Table 5.4). The temperatures of 0°, 8° and 16°C were chosen to show scallop survivorship over the temperature range in the field. The scallop densities were chosen to reflect the approximate densities at the sites before seeding (*i.e.*, a) 0.5 scallops m^{-2}) and after seeding (*i.e.*, b) 2.0 scallops m^{-2}). A crab density of 0.1 animals m^{-2} was used. The longest scallops survival time observed was 96 d.

Table 5.5. Cox Proportional Hazards Analysis of scallop mortality due to sea star predation in the multifactor experiments at Sites 2 and 3 in Lunenburg Bay. Model 1 quantifies the relationship between scallop mortality and all covariates. Model 2 includes only the temperature and scallop size covariates. The coefficient and its standard error are shown for each covariate within each model. To test the significance of a covariate, the log likelihood of a submodel that excludes that particular covariate is statistically (χ^2) compared to the log likelihood of the full model (Model 1 or Model 2; listed on bottom line). The likelihood ratio test is defined as -2(log likelihood of submodel - log likelihood of full model). This test was done for each covariate within Model 1 and Model 2; some covariates were combined into groups to lower the experimentwise error rate.

Model 1						Model 2					
Covariate	Coefficient (SE)	Log Likelihood of submodel that excludes covariate	Likelihood ratio χ^2	df	*P*	Covariate	Coefficient (SE)	Log Likelihood of submodel that excludes covariate	Likelihood ratio χ^2	df	*P*
Temperature	0.149 (0.014)	-2428.12	127.96	1	<0.001	Temperature	0.149 (0.013)	-2434.54	140.18	1	<0.001
Size1[a]	-0.166 (0.112)	-2399.94	71.59	2	<0.001	Size1[a]	-0.165 (0.112)	-2365.54	2.17	1	0.141
Size2[a]	-1.034 (0.135)					Size2[a]	-1.034 (0.135)	-2395.83	62.75	1	<0.001

Table 5.5 continued.

Model 1						Model 2					
Covariate	Coefficient (SE)	Log Likelihood of submodel that excludes covariate	Likelihood ratio χ^2	df	*P*	Covariate	Coefficient (SE)	Log Likelihood of submodel that excludes covariate	Likelihood ratio χ^2	df	*P*
Site[a]	0.077 (0.111)	-2364.45	0.62	3	0.891						
Scallop density	-0.003 (0.061)										
Sea star density	-0.008 (0.161)										
		Log Likelihood of model	Global χ^2	df	*P*			Log Likelihood of model	Global χ^2	df	*P*
Full model		-2364.14	191.54	6	<0.001	Full model		-2364.45	189.85	3	<0.001

[a] Site, Size1 and Size2 are catergorical variables, where site 2 is defined as Site=0 and site 3 as Site=1, and small scallops are defined as Size1=0, Size2=0, medium scallops as Size1=1, Size2=0, and large scallops as Size1=0, Size2=1.

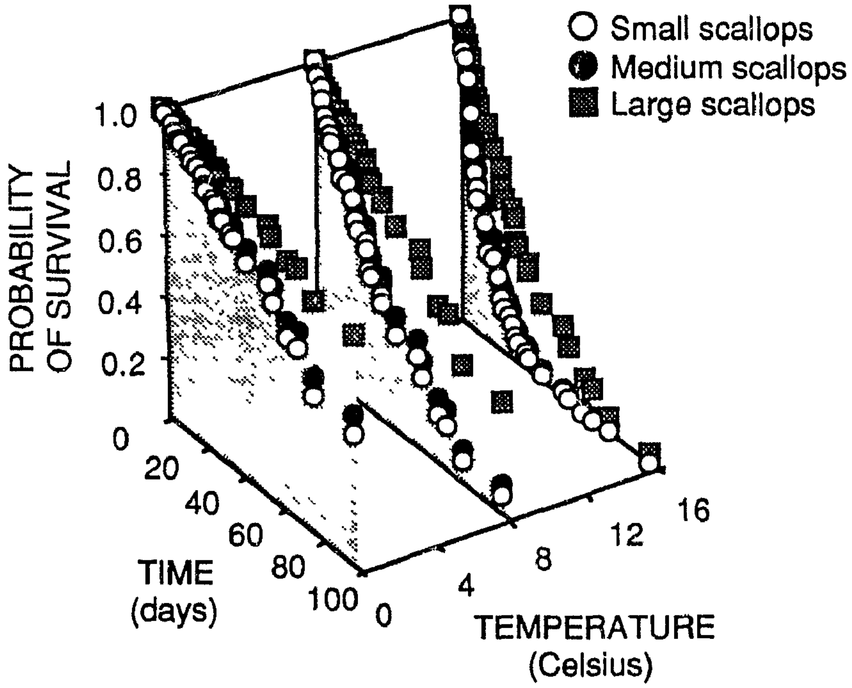


Fig. 5.7. Simulated survival curves of different size classes of tethered sea scallops for mortality attributed to sea star predation at different water temperatures (calculated using Model 2 of the sea star predation survival analysis; Table 5.5). The temperatures of 0°, 8° and 16°C were chosen to show scallops survivorship over the temperature range in the field. The longest scallops survival time observed was 96 d.

Discussion

Through survival analysis, I have examined the interacting effects of biological and physical factors (*i.e.*, scallop size, water temperature, site, scallop density and predator density) on the two major causes of mortality in juvenile sea scallops (*Placopecten magellanicus*) in natural habitats: predation by crabs (*Cancer irroratus*) and sea stars (*Asterias* spp.).

Prey size is generally considered an important variable affecting prey vulnerability to predators (Osenberg and Mittelbach 1989, Palmer 1990, Juanes 1992, Chapter 2). However, survival analysis indicated that scallop size had little effect on scallop mortality due to crab predation in my experiments (Table 5.4, Fig. 5.6). The result contrasts with previous laboratory experiments (Chapter 2) which demonstrated that crabs consumed greater numbers of large juvenile scallops (20-25 mm shell height (SH)) than small or medium scallops (5-9 mm and 10-15 mm SH), due to higher encounter rates of crabs with large scallops than with small ones, and active selection for larger scallops over medium-size ones. In the field experiments, crabs generally consumed more large scallops than smaller ones (Figs. 5.4 and 5.5). Although this trend was apparent in the coefficients of the instantaneous mortality rate for size, it was not significant in the survival analysis (Table 5.4). The apparent discrepancy between field and laboratory results may be due to the large size range of crabs in the field (20-120 mm carapace width (CW); Hatcher *et al.* Unpubl.) compared to that used in the laboratory experiments (45-110 mm CW, Chapter 2). Although predator and prey size were not matched in the field experiments, smaller crabs probably consumed greater numbers of small scallops than large ones in the field, while larger crabs probably consumed mainly large scallops. This may explain the overall non-significant effect of scallop size in my analysis. Elner and Jamieson (1979) observed that large crabs (90-130 mm CW) were able to open sea scallops up to 70 mm SH. Other scallop species appear to attain a size refuge from crab predation only around adult size (Lake *et al.* 1987, Minchin 1991, Pohle *et al.* 1991).

Analysis of scallop survival times indicated that scallop size was an important variable affecting scallop mortality due to sea star predation (Table 5.5, Fig. 5.7): the large size class experienced significantly lower mortality due to sea stars than the small and medium size classes of scallops. This result is consistent with laboratory experiments (Chapter 2) which showed that smaller scallops had a less effective escape response to sea star attack than larger scallops and, therefore, had a higher probability of being captured. Scallops exhibit two types of escapes from sea stars: active escapes in which scallops swim or jump away from sea stars and retractions in which sea stars retract after contacting scallop tentacles, possibly due to a chemical deterrent (Moir 1977, Chapter 2). Although active escapes would be affected by tethering (Chapter 4), retractions would not. Retractions occurred more often with large scallops than with small ones (Chapter 2). Therefore, even when tethered, large scallops may have a lower probability of being captured than smaller scallops, resulting in lower mortality rates from sea stars in the field.

Water temperature is an important variable affecting predation rate and general physiological performance of marine invertebrates (Wallace 1973, Newell and Branch 1980, Cossins and Bowler 1987, Watts and Lawrence 1990). The effect of temperature on scallop mortality due to crab predation in the field experiments differed between sites (Table 5.4, Fig. 5.6). At Site 2, the instantaneous mortality rate increased with temperature with a Q_{10} of 3, which is close to the relationship between temperature and crab predation rate observed in laboratory experiments ($Q_{10} = 2$; Chapter 3). At Site 3, the instantaneous mortality rate was independent of temperature ($Q_{10} = 1$). The site variable encompasses many aspects particular to a site, including topography, substratum, and predator densities. Site 3 is surrounded by rocky shores; this availability of shelter adjacent to the study site may explain the generally higher crab densities there than at Site 2 (Table 5.1) (see also Auster and Malatesta 1991), and may have contributed to the site effect. The temperature dependence of crab predation may be reduced at high crab densities or during periods when crabs increase consumption rate in response to increases in prey density.

Water temperature had a strong effect on sea star predation on scallops in the field, which was consistent between sites (Table 5.5, Fig. 5.7). The instantaneous mortality rate increased with temperature with a Q_{10} of 4. Laboratory experiments have also shown a marked effect of temperature on sea star predation rates ($Q_{10} = 7$; Chapter 3), due to increased sea star foraging activity (searching time, movement velocity, encounter rate) and decreased scallop escape effectiveness with increasing temperature. Lower movement velocities of sea stars in the field (1 cm min^{-1} at 12°C) compared to those observed in laboratory experiments (3 and 7 cm min^{-1} at 8° and 15°C, respectively; Chapter 3) may be due to availability of alternative prey and low predator searching times. This may explain the smaller effect of temperature on sea star predation rates in the field experiments than in the previous laboratory experiments. Also, the temperature variable in the multifactor experiments was confounded by other seasonal variables (*e.g.*, physiological state of the animals) which may have contributed to the differences in the apparent temperature effects on sea star and crab predation between field and laboratory experiments.

Short-term increases in prey mortality rates with increases in prey density may result from a functional response and/or a numerical aggregative response of the predator (Hughes 1980b, Taylor 1984). Analysis of scallop survival times indicated that scallop density was an important variable affecting scallop mortality due to crab predation in the field (Table 5.4, Fig. 5.6). In the single factor experiment at Site 1, crabs displayed a functional response to increasing scallop densities since crab-specific mortality rates of scallops increased with scallop densities, but crab density did not (Fig. 5.2). This functional response was attributed to high movement velocity and short prey handling time of crabs, and to the relative importance of encounter rate in determining their predation rate on scallops (Chapters 2 and 3). Functional responses have also been observed in other crab-bivalve interactions (Boulding and Hay 1984, Lipcius and Hines 1986, Eggleston 1990a, b, c, Sponaugle and Lawton 1990, Eggleston *et al.* 1992). The survival analysis also indicated that crab density had an effect on mortality rates of scallops at Sites 2 and 3 (Table 5.4).

This result may be due to the generally higher density of crabs at Site 3 than at Site 2, rather than to an actual increase in crab density after seeding the sites (*i.e.*, aggregative response). In a total of five seeding trials at Sites 1, 2 and 3, crab density did not increase or increased slightly after seeding (Hatcher *et al.* In press a, b).

Survival analysis indicated that scallop density was not an important factor affecting scallop mortality from sea star predation in the field (Table 5.5). This observation is supported by the results of the single factor experiment at Site 1, which showed that the sea star-specific mortality rate of tethered scallops was independent of scallop density (Fig. 5.2). Sea star consumption rate may be limited by high prey handling times and slow movement velocities (Jangoux 1982, Chapters 2 and 3). This may explain the lack of a functional response by sea stars to increased prey densities. As well, sea stars did not have an aggregative response to increased scallop densities in the single factor experiment at Site 1. In the analysis of survival times of tethered scallops at Sites 2 and 3, sea star density was not significant in affecting scallop mortality (Table 5.5), which may reflect the fact that sea star density did not vary much within and between sites over time (Table 5.1). In the scallop seeding experiment at Site 1, sea star density did not increase significantly after the release of ten thousand juvenile scallops at a density of about 250 m^{-2} (Hatcher *et al.* In press a). In contrast, Volkov *et al.* (1983) observed sea stars (*Distolasterias nipon*) to aggregate and follow patches of released scallops (*Patinopecten yessoensis*). Density-dependent effects on predation appear to be species-specific.

The results of my field tethering experiments have important implications for the bottom culture of sea scallops. The probability of capture by sea stars is low, since scallops have an effective escape response against sea stars. To minimize predation by sea stars, large (≥25 mm SH) juvenile scallops should be used in bottom culture, although, they remain vulnerable to crab predation. Predation by crabs may be reduced by lowering encounter rates, either by seeding scallops at low densities or by lowering crab densities through predator removal procedures. Moreover, seeding scallops at low temperature lowers predation rates, particularly by sea stars, and should increase the success of bottom culture. Finally, survival analysis of tethered prey provides an informative measure of predation intensity, which can be used to assess potential bottom culture sites and predator control tactics.

CHAPTER 6: General Discussion

This thesis elucidates the effects of various biological and physical factors on predation of juvenile sea scallops (*Placopecten magellanicus*) by two major predators, sea stars (*Asterias* spp.) and crabs (*Cancer irroratus*). The research is important because it focuses on a critical life history stage of a commercially important species, develops approaches and principles which can be applied in other predator-prey systems, and extends certain aspects of predation theory.

Throughout this thesis, I have analysed predation rate in terms of components of the predation cycle (Chapters 2, 3, and 4, Appendix A). This approach is time-consuming, but rewarding since underlying mechanisms can be identified. The determining mechanisms tend to be species-specific, as evidenced by contrasting interactions between scallops and their two major predators, sea stars and crabs, but the approach is not. With the component approach, the effect of experimental procedures (*e.g.*, tethering) on a particular predator-prey interaction can be assessed (Chapter 3). In addition, such an approach allows one to measure the relative importance of active predator choice and prey vulnerability in determining prey selection, two relevant concepts in the literature on predation (Chapter 2).

The prey choice model of optimal foraging theory was used as a framework to examine active selection by predators, *i.e.*, to determine which prey type a predator should choose to maximize its rate of energy intake (Chapter 2). This study shows that predation rates and prey selection do not always depend on a predator making a choice. They may instead be restricted by encounter rates, prey escape responses, or an inability to handle a prey item (Osenberg and Mittelbach 1989, Chapter 2). Some researchers are attempting to incorporate these restrictions into the calculation of profitability to be able to continue comparing profitability to the diet curve (*i.e.*, predation rates on different prey types) (Sih and Moore 1990). If the component approach is employed, one can simply compare profitability to active components rather than to predation rate, which is a product of both active and passive components.

In my analysis of predation experiments in the field, survival analysis was used to determine the significance on survivorship of covariates (key biological and environmental factors) measured during individual lifetimes (Chapter 5). More generally, survival analysis can be used to model any dynamics of populations which involve waiting times in a multivariate environment (Muenchow 1986, Caswell and John 1992). Its use extends from simple procedures such as characterizing survival curves and setting up life history tables, to more complex procedures such as determining the effect of time-dependent covariates on a time-to-response variable (Lawless 1982, Dixon 1990). Although survival analysis is frequently used in engineering and clinical studies (Crowley and Hu 1977, Kalbfleisch and Prentice 1980, Lawless 1982), and recently in human ecology studies (John 1988, Jones 1988), it has been underutilized in other areas of ecology. This thesis illustrates the effective use of survival analysis to better understand ecological processes that influence predation.

The results of my laboratory and field experiments have important implications for the bottom culture of sea scallops. The probability of capture by sea star upon encounter with scallops is low, since scallops have an effective escape response against attack by sea stars. If the efficacy of their escape response is diminished due to small size, physical hindrance (*e.g.*, tethering), or stress (*e.g.*, handling by aquaculturists, temperature shock), the probability of capture by sea star increases. Therefore, in order to minimize predation by sea stars, unstressed, large juvenile scallops should be used in bottom culture. However, large juveniles are vulnerable to crab predation, since their probability of capture and consumption by crabs is high. Predation by crabs may be reduced by lowering encounter rates, either by seeding scallops at low densities or by lowering crab densities by predator eradication measures (*e.g.*, Spencer 1991). Seeding scallops at low temperature (to which they must be acclimated) lowers predation rates by sea stars, and generally by crabs, and should increase scallop survival in bottom culture. These predation-reducing strategies may also interact with the dispersion of scallops because scallop swimming is temperature dependent (Carsen 1994), large scallops are more efficient swimmers than smaller ones (Dadswell and Weihs 1990), and attack by predators is a primary trigger of swimming (Peterson *et al.* 1982, Carsen 1994). Therefore, these strategies may indirectly affect predation rate through changes in scallop density.

A logical follow-on from this thesis is further investigation of density-dependent effects acting on crab-scallop interactions. For example, it is important to determine and quantify the type of functional response that rock crabs exhibit to changes in scallop densities. Researchers studying blue crabs (*Callinectes sapidus*) feeding on bivalves have modelled the change in consumption rate with the change in prey density, and have observed that, at a certain prey density, the bivalves attain a refuge from crab predation (Lipcius and Hines 1986, Eggleston 1990a, b, c, Eggleston *et al.* 1992). Understanding this relationship between rock crabs and sea scallops would be important in the design of bottom seeding operations.

This thesis, through the use of behavioural component analysis and survival analysis, has provided a first step towards modelling scallop survival in Lunenburg Bay, Nova Scotia. However, further work is needed to develop a robust, individual-based model for describing and predicting scallop survival dynamics (DeAngelis and Gross 1992). Such a model would contribute to a more detailed understanding of interrelationships between factors affecting predator-prey interactions in the marine benthos, particularly since it would focus on the mechanisms operating at the level of the individual. It would also have an applied use for enhancing production in invertebrate aquaculture and fisheries.

APPENDIX A: Effect of sea star species (*Asterias vulgaris* and *A. forbesi*) on predation of juvenile sea scallops.

Two congeneric species of sea stars (*Asterias vulgaris* and *A. forbesi*) co-occur in Lunenburg Bay, Nova Scotia, Canada. In November 1991, I compared the effect of each sea star species on predation of juvenile scallops in a laboratory experiment. Fifteen small scallops (7.9 ± 0.6 mm SH) were offered to individual sea stars (96 ± 0.5 mm diameter) in 54 L glass aquaria for 10 d. There were 4 replicates within a sea star species in a completely randomized design. Two control aquaria with 15 scallops and without a predator were run concurrently to monitor non-predatory mortality, but none occurred.

Sea stars were collected from Lunenburg Bay and held in tanks for 5 wk. Scallops were obtained from the experimental hatchery (Chapter 2) and held in tanks for 2 wk. Pre-experimental conditions, experimental setup and monitoring, and behavioural sampling were as described in Chapter 2. Total observation period for behavioural sampling was 220 min aquarium^{-1}. Seawater flow to each aquarium was regulated at 400-500 ml min^{-1}. Water temperature and salinity over the duration of the experiment were 12.3 ± 0.5°C and 30.0 ± 0.1$^{0}/_{00}$ (mean ± SD), respectively.

Consumption rate of small scallops did not differ significantly between *Asterias vulgaris* and *A. forbesi* (t=1.08, df=6, P>0.05; Fig. A.1a). The percentage of time that sea stars spent searching for and handling scallops were not significantly affected by sea star species (t=0.74 and 0.41, respectively, df=6, P>0.05; Fig. A.1b). Encounter rate between sea star and scallop also was not significantly affected by sea star species (t=0.74, df=5, P>0.05; Fig. A.1c). The probability of capture upon encounter was similar for both *A. vulgaris* (0.07 ± 0.03) and *A. forbesi* (0.07 ± 0.04) (t=0.09, df=5, P>0.05). The probability of consumption upon capture did not differ significantly from 1 for both *A. vulgaris* (0.67 ± 0.33; t=-1, df=3, P>0.05) and *A. forbesi* (1.00 ± 0.00). Most encounters between sea stars and scallops resulted in scallops escaping. The ratio of active escapes to

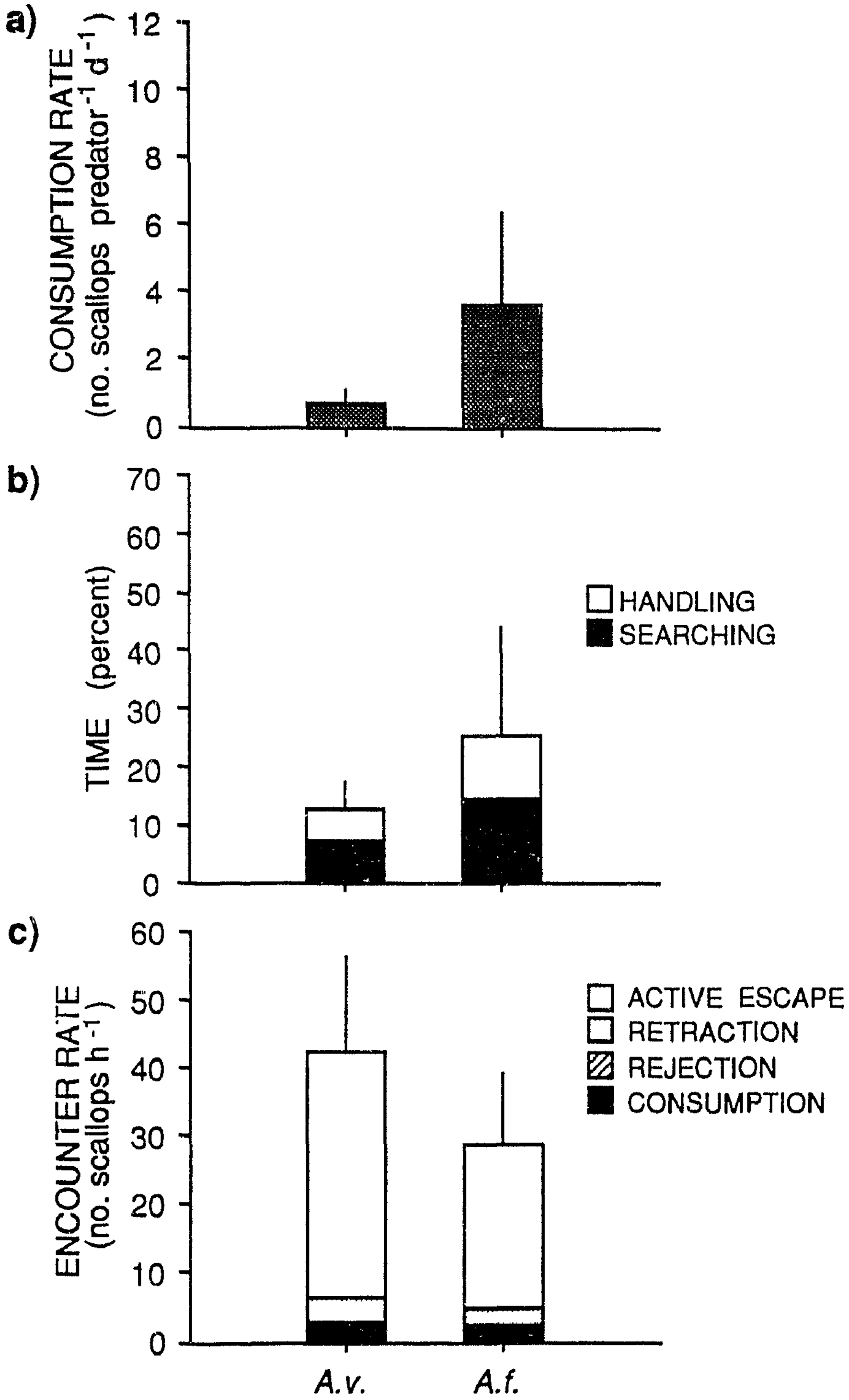


Fig. A.1. Laboratory predation experiment conducted with two species of sea stars (*Asterias vulgaris* (*A.v.*) and *A. forbesi* (*A.f.*)) preying on juvenile sea scallops. a) Consumption rate per sea star, b) percent foraging time (% foraging time = % searching time + % handling time) of sea stars, and c) encounter rate between sea stars and scallops (different outcomes of encounter have different shadings). Observation time in b and c = 220 min aquarium^{-1}. Mean shown for all variates; error bars = SE (for foraging time in b and for encounter rate in c).

total escapes was high and did not differ significantly between *A. vulgaris* (0.87 ± 0.10) and *A. forbesi* (0.82 ± 0.16) (*t*=0.22, df=5, *P*>0.05; Fig. A.1c). The proportions of active escapes resulting in swims and in collisions with aquarium walls were 0.73 ± 0.14 and 0.39 ± 0.13, respectively, for both sea star species combined.

The foraging rates and behaviours of the two co-occuring sea star species (*Asterias vulgaris* and *A. forbesi*) in Lunenburg Bay did not differ significantly and were similar to those observed for *A. vulgaris* in Chapters 2 and 3. Based on the results of this experiment the two sea star species can be combined into a functional group.

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