PREDATOR REGULATION OF SEDIMENTARY FAUNA IN A SUB-ARCTIC FJORD ECOSYSTEM

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PREDATOR REGULATION OF SEDIMENTARY FAUNA IN A SUB-ARCTIC FJORD ECOSYSTEM

by

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Abstract

Historical changes in predator composition in the Newfoundland ecosystem as a result of over-fishing have resulted in a switch from a cod-dominated system to one with abundant decapod crustaceans. In order to understand the consequences of this switch to benthic ecosystems, it is critical to evaluate how epifaunal crustaceans regulate sedimentary communities. An array of exploratory and experimental studies was undertaken in Bonne Bay, a sub-arctic Newfoundland fjord, in order to document predator and prey spatial variation and community responses to predator manipulation.

The distribution of snow crab and at least one shrimp species in the main arms of Bonne Bay fjord were found to be related to planktonic larval supply, particularly, late larval stages. The distribution of infaunal prey varied in parallel with predator patterns and, as shown by detailed analysis of the dominant taxon (polychaetes), was related to habitat quality and distribution. Sandy and muddy habitats supported different infaunal communities, and species that occupied a variety of substrates were more broadly distributed inside the fjord and the region. Field exclusion and inclusion experiments carried out in the two main arms of the fjord were complemented with laboratory experiments using the main predators of the fjord: snow crab (*Chionoecetes opilio*), rock crab (*Cancer irroratus*) and toad crab (*Hyas* spp). Results suggest that i) crustacean predation regulates benthic composition, density, and sometimes diversity, ii) predator effects vary spatially, iii) the same infaunal species were important in describing predator exclusion treatments both in the field and in the laboratory experiments, and iv) snow crab and rock crab are the predators that have the strongest effects on infaunal communities. Given that both predators are targeted by the fishery, these results also suggest that the potential impacts of fishing may be even broader than expected through cascading effects on infauna. Finally, the effects of predation on benthic infauna were examined using surrogates or taxonomic categories coarser than species. Although results obtained with data at the family level resemble those with data at the species level, the lack of generality in surrogate performance suggests a cautious use of surrogates in experimental and biodiversity studies.

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Statement of co-authorship

The author of this thesis designed experiments and sampling, participate in the collection of all the data, analyzed and wrote all the subsequent manuscripts. Dr Paul VR Snelgrove made a substantial contribution to the elaboration of ideas, experiment design, sampling design, and provided editorial review of all the chapters. Dr Snelgrove is the second author of all the manuscripts included in the thesis.

CHAPTER 1

OVERVIEW: BIODIVERSITY REGULATION AND SPATIAL SCALE

1.1 PREFACE

As patterns of biodiversity change from one spatial scale to another, processes that regulate or control those patterns may also change. In order to provide a general context for the study of predators and sedimentary communities, a brief review of the regulation of biodiversity at the global, regional (10'-100's km), and local scales (m-10's km) is developed below. Then, this overview focuses on the spatial variation in diversity that is seen at the scale of bays or fjords such as Bonne Bay, and the role that predation may play at that scale. The organization and objectives of Chapters 2-7 are then summarized. Although in some ecological contexts the term "regulation" holds a density-dependence connotation, in this overview and the remaining Chapters of the thesis, "regulation", "control" or "structuring", are all used interchangeably.

1.2 BIODIVERSITY FROM GLOBAL TO LOCAL

1.2.1 Patterns of biodiversity at the global scale

Large-scale patterns, particularly latitudinal gradients in biodiversity, constitute "the major unexplained pattern in natural history" (RE Ricklefs, quoted by Lewin 1989).

Latitudinal diversity gradients have been documented for coastal gastropods and bivalves (Roy et al 1994; 1998; 2000), deep-sea bivalves, gastropods, and isopods (Rex et al. 1993; 1997), deep-sea nematodes (Lambshead et al. 2000), and foraminiferans (Culver & Buzas 2000). These diversity gradients have been related to two other major latitudinal gradients: productivity (Huston 1999; Rosenzweig & Abramski 1993), and effective evolutionary time, or energy-related speciation rates in contemporary terminology (Rhode 1999; Sepkoski 1999). Unfortunately, the evidence supporting both hypotheses has been questioned on the grounds of restricted sampling effort (Gray 1994; 1997), and the consistency of both hypotheses has been undermined by increasing evidence of groups that i) do not exhibit latitudinal gradients or ii) exhibit patterns that differ from an equator-pole gradient (Rhode 1992; Rutherford 1999; Clarke & Lidgard 2000).

The lack of stronger evidence for large-scale gradients results from the variation detected at the nested (regional) scales. Lambshead et al. (2000) argued that large-scale patterns in the North Atlantic should be interpreted with caution, given that at least six different basins (with their own age and geological history), can be found in the area. Biogeography and history, therefore, play a fundamental role at the regional scale (Fraser & Currie 1996; Myers 1997; Sepkoski 1999; Culver & Buzas 2000).

1.2.2 Patterns of biodiversity at the regional scale

Limited transfer of energy from producers to consumers may play a critical role in the regulation of biodiversity at the regional scale. The length of trophic webs is related to productivity (Pimm 1982), in a so-called "bottom-up" process that has been reported in pelagic systems, coral reefs, rocky shores, and estuaries (Angel 1997; Lapointe 1997; Menge et al. 1997), but that has not been well documented in sedimentary habitats (Posey et al. 1999). The relationship between productivity and biodiversity at the regional scale is not linear, because diversity increases and then decreases with increasing productivity in a characteristic "hump-shaped" curve (Wright et al. 1993). Unfortunately, there are no consistent hypotheses to explain this relationship, particularly, the latter (decreasing) phase, from any of the ecosystems where it has been tested (Rosenzweig & Abramski 1993; see Hall et al. 2000 for an example on sedimentary habitats). Moreover, strong variations in temporal and spatial levels of primary productivity (Schoener 1989) that may occur at any level of productivity, suggest that other factors are influential at this scale. A more general hypothesis was proposed by Huston (1979) by linking intermediate levels of productivity and disturbance with higher biological diversity. The predictions of that hypothesis, however, remain largely untested in shallow-water sedimentary habitats, though broad-scale patterns have been linked to Huston's hypothesis in deep-sea systems (Rex 1983).

Supply-side ecology, which is a natural extension of bottom-up regulation, is one paradigm that can link regional and local scales of biodiversity (Roughgarden et al. 1988; Underwood & Fairweather 1989), The idea of a pool of larvae distributed among local "nested" communities can be easily related to a "pool of species", supplying food webs in which higher productivity results in new trophic components (Jenkins et al. 1992).

Supply-side oceanographic processes are related to the transport or loss of propagules, the regional dynamics of primary productivity, large-scale events such as ENSO, and the biological interactions that shape the diversity of local communities (Connolly & Roughgarden 1998, Estes & Duggins 1995, Robles 1997; Duke et al. 1998; Wotton et al. 1999). These linkages have generated debate about the scale (regional or local) of the factors that ultimately regulate biodiversity (e.g. Caley & Schluter 1997). In a scenario where regional diversity increases linearly, local diversity should either increase (i.e. regional factors prevail), or instead asymptote (i.e. saturation; local factors prevail). An explicit test of these predictions supported the latter pattern for butterfly fish diversity (Findley & Findley 2001). However, similar studies are currently lacking for other types of communities and organisms, including those from soft-sediments.

1.2.3 Patterns of biodiversity at the local scale

Physical factors and biological (top-down) interactions are the most relevant determining relative abundance and therefore, at a very local scale, biodiversity. Although the role of waves, desiccation, and other physical factors is more evident on intertidal rocky shores (Paine & Levin 1981), parallel examples may be found in unconsolidated sediments of sandy beaches ("swash exclusion hypothesis" McArdle & McLachlan 1992), estuaries (e.g. salinity gradients; Day et al. 1989), and marine subtidal bottoms elsewhere (e.g. redox gradients and flow dynamics, see reviews by Nowell & Jumars 1984; Watling 1991; Hall 1994; Snelgrove & Butman 1994). In addition to the limits imposed by physical factors, predation (top-down control), and competition have been shown to play strong regulatory roles in many different habitats (e.g. Menge 2000 for an example from rocky shores). Because marine food webs tend to be simpler than their terrestrial counterparts (Strong 1992), reduced trophic redundancy has been invoked to explain strong top-down regulation.

Predation may alternatively be seen as a form of "biological" disturbance, and a form of the Intermediate Disturbance Hypothesis (IDH; Connell 1978; Sousa 1979). This hypothesis has been invoked for rocky shores (Connell 1978), coral reefs (Aronson & Pretch 1995), cobble beaches (Sousa 1979), and salt marshes (Bertness & Ellison 1987). However, in unstructured sedimentary habitats, where competition does not appear to play a strong role, the applicability of the IDH is less clear (Huxman et al. 2000; but see Austen et al. 1998 for an exception in meiofauna). Thus, predation alone clearly outweighs competition as the main biological process regulating soft-sediment fauna (Schneider 1978; Peterson 1979; Wilson 1991; Lenihan & Micheli 2001). Predator-mediated sediment disturbance (e.g. Brenchley 1981; Thrush 1999) creates a mosaic of patches akin to those generated by predators such as sea stars or carnivorous marine snails in rocky walls (Paine 1994). However, compared to bare rock patches, predator mediated pits in soft-sediments are rarely fully defaunated, and recolonization takes place quickly by active immigration of adults and passive immigration of settlers / recruits (Frid & Townsend 1989; Commito et al 1995). Disturbance, as a local creator or supporter of higher diversity applies to hard bottoms but not to sedimentary bottoms (Woodin 1981).

1.3 PREDATORS AND PREY

1.3.1 Local variation of predators and prey

Predator and prey distribution are regulated by an array of factors acting at dissimilar spatial scales, either locally or regionally, and over different stages of the life cycle (Gaines & Lafferty 1995). Distribution of young predatory crustaceans has been related to a combination of pre- and post-settlement factors. Recruitment of lobsters, for example, has been linked to availability of shallow cobble habitats (m scale), mainly at the lower reach of embayments (10 km's scale), in western but not eastern Maine (100 km scale; Palma et al. 1999). At smaller scales, the abundance of juveniles is regulated primarily by post-settlement predation and cannibalism (e.g. Eggleston & Armstrong 1995; Etherington & Eggleston 2000). At large scales, however, the supply of larvae and settlers that initially establishes benthic crustacean populations is regulated primarily by currents and circulation patterns (Hobbs et al. 1992; Cobb et al. 1999).

The large-scale effects of circulation patterns have parallels with large-scale fishing disturbances that affect the adult fraction of populations such as lobsters, crab and shrimp. Selective and non-selective fishery by-catch can account for reduction and even depletion of entire stocks (cf. Agardi 2000; Jackson et al. 2001). In the North Atlantic, particularly in coastal Newfoundland, depletion and collapse of cod stocks have triggered an increase in the abundance of and commercial exploitation of crab and shrimp (Lilly 2000; Bundy 2001; Schiermeier 2002). Although the literature has repeatedly focused on the consequences of these changes on local fishery resources (e.g. Fahrig, et al. 1993), an ecosystem approach incorporating the indirect effects on bottom communities is lacking.

1.3.2 Local community regulation

There is an extensive body of literature on the scale at which bottom-up and top-down factors operate on individual populations of predators or prey. However, studies to disentangle the factors that regulate interacting communities of predators and preys are lacking. The elusive interplay of bottom-up (productivity, larval supply) and top-down (predation) factors restricts the predictive power of most hypotheses in studies on the role of predation in local sedimentary habitats (Thrush 1999). For instance, studies of crab predation on individual clam species suggest that predation will be more effective in habitats with low, rather than high, food availability (Seitz & Lipcius 2001). Other studies suggest that predator efficiency will change with sediment or habitat type (Micheli 1997; Seitz et al. 2001). Yet other studies suggest that predation effects on benthic species will depend strongly on predator diversity and aggregation (Schneider 1992; Davis et al. 2003), factors that also change at the local scale.

1.3.3 Setting the stage: the Bonne Bay system

Bonne Bay is a sub-arctic fjord located on the west coast of Newfoundland (Fig. 1.1). The Bay borders Gros Morne National Park along much of is perimeter, and with the exception of a handful of small communities such as Norris Point, it is bordered by boreal forest. The fjord is comprised of two main arms: East Arm, a deep (up to 230 m) inner basin, and South Arm, a shallower outer basin (up to 55 m deep) open to the waters of the Gulf of St. Lawrence (Fig. 1.1). East and South Arms are partly separated by a shallow sill (~12 m deep) at the mouth of East Arm.

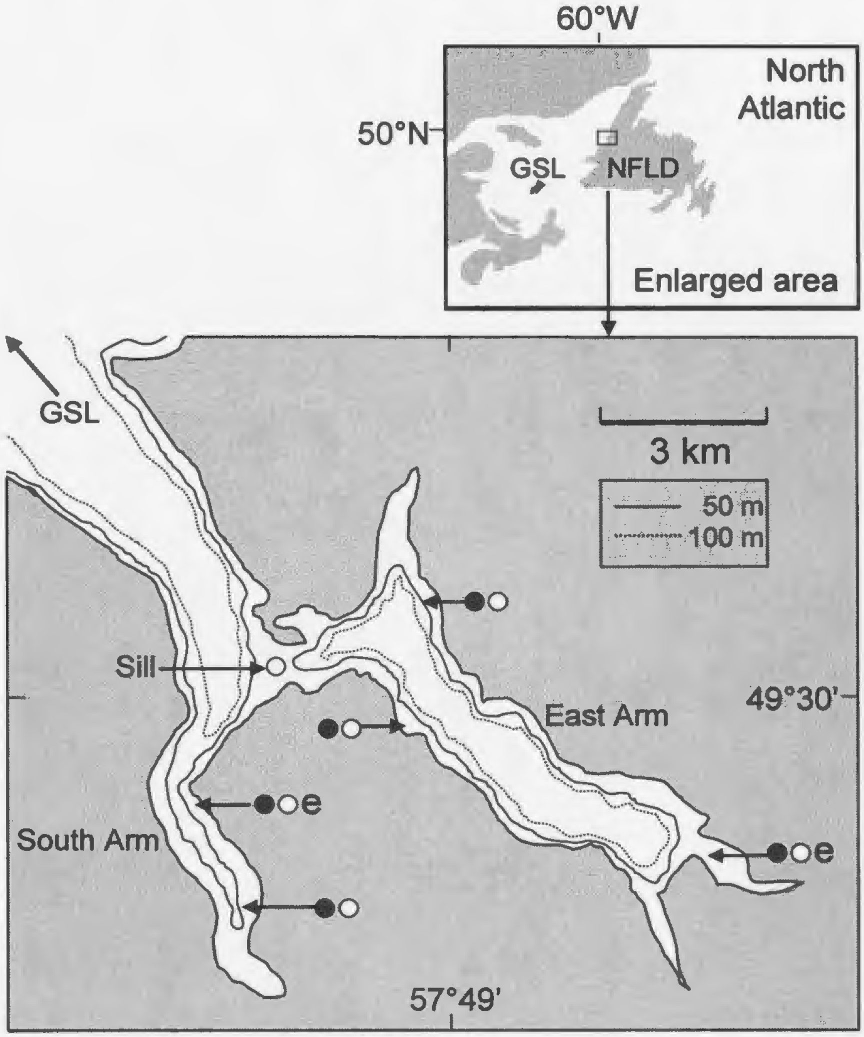

Fig. 1.1 Location, main areas, and bathymetry (50 and 100 m deep iso-lines) of the Bonne Bay fjord, Western Newfoundland. South and East Arms as well as the shallow sill separating both Arms are also indicated. Filled symbols indicate stations where benthic and epibenthic organisms were collected. Open symbols indicate stations where meroplankton samples were collected. Stations Identified by "e" symbols correspond to those where experimental manipulations were conducted. GLS: Gulf of St. Lawrence.

Currents and circulation in some of the main areas of the fjord have been described by Gilbert & Pettigrew (1993). Circulation between South and East Arms is strongly related to tidal exchange (de Young, Pers. Comm.), although several other factors may influence transport of suspended sediments, propagules, and planktonic forms (e.g., freshwater discharge, wind intensity and direction, freezing and melting of surface waters; cf. Ennis 1983; Stein 1988). Significant freshwater inflow occurs at Deer Brook and Lomond River in East Arm and several smaller brooks in South Arm Deep water basins (>50 m deep; Fig. 1.1) in both Arms are surrounded by shallower exposed bedrock and sedimentary deposits (10-30 m deep) located in protected coves and arms (see figures and local data summarized in Chapter 3). South-East Arm, Norris Cove, and Deer Arm are representative of East Arm embayments. Small Cove and Mike's Cove are representative of South Arm embayments.

Biological studies on epibenthic predators or benthic (infaunal) communities in the fjord are restricted to lists of invertebrates (Rivard & Bowen 1971; Hooper 1975), and communities from selected locations (Wieczorek 1991; Wieczorek & Hooper 1995). Seasonal (spring-summer) migrations to shallower areas have been described for predators that typically occur at greater depths (Hooper 1996; Ennis et al. 1990). Studies on their life history are restricted to snow crab (Conan et al. 1996; Comeau et al. 1998, 1999), although several other studies have focused on this species, rock crab and pandalid shrimp in the Gulf of St. Lawrence (eg. Brêthes et al. 1987; Hudon & Lamarche 1989; Simard et al. 1990; Ouellet & Lefaibre 1994; Sainte-Marie & Gibert 1998).

1.3.4 Predators and preys: scope and scale of interest

The study of predation requires exploratory and experimental studies that encompass a representative range of spatial variation. In this thesis, exploratory studies focused on the distribution of predators and a representative group of infauna (polychaetes), whereas experiments focused on the role of predation in structuring benthic communities (see chapters overview below). The scope of the survey conducted to describe predator distribution and the field exclusion experiments conducted to evaluate their influence can be visualized using a temporal-spatial diagram (Table 1.1; Fig. 1.2).

Table 1.1 Minimum spatial scale (A_0), minimum temporal scale (T_0), spatial range (A) and temporal range (T) of the survey of predatory crab and shrimp and the sampling of two exclusion experiments.

Study	level	unit	A_0 (m^2)	A (m^2)	T_0 (sec)	T (sec)
Survey	trap	1	0.2400	1964.0	180	86400
	site	6	1.4400	20000.0	1080	86400
	bay	30	7.2000	2000000.0	5400	604800
Experiments	core	1	0.0039	--------	60	--------
	sample	2	0.0077	0.8	120	300
	cage	2	0.0077	19.6	240	600
	site	10	0.0770	20000.0	1200	86400
	bay	20	0.1540	2000000.0	2400	259200

A general scale of interest has also been defined for this study (Fig. 1.2). The spatial scale of interest is defined as a shallow (20-50 m) ~500 m fringe of coastal sedimentary bottoms around Newfoundland, Labrador, the Gulf of St. Lawrence and the southern sub-arctic littoral (roughly ~10,000-20,000 km of coast, and thus ~5-10 x$10^9$$m^2$). This scale represents the main overlap in distributions of the major Bonne Bay predators and prey, although the distribution of most species extends far beyond this depth and range (cf. Williams 1984; Pocklington et al. 1987; Squires 1996).

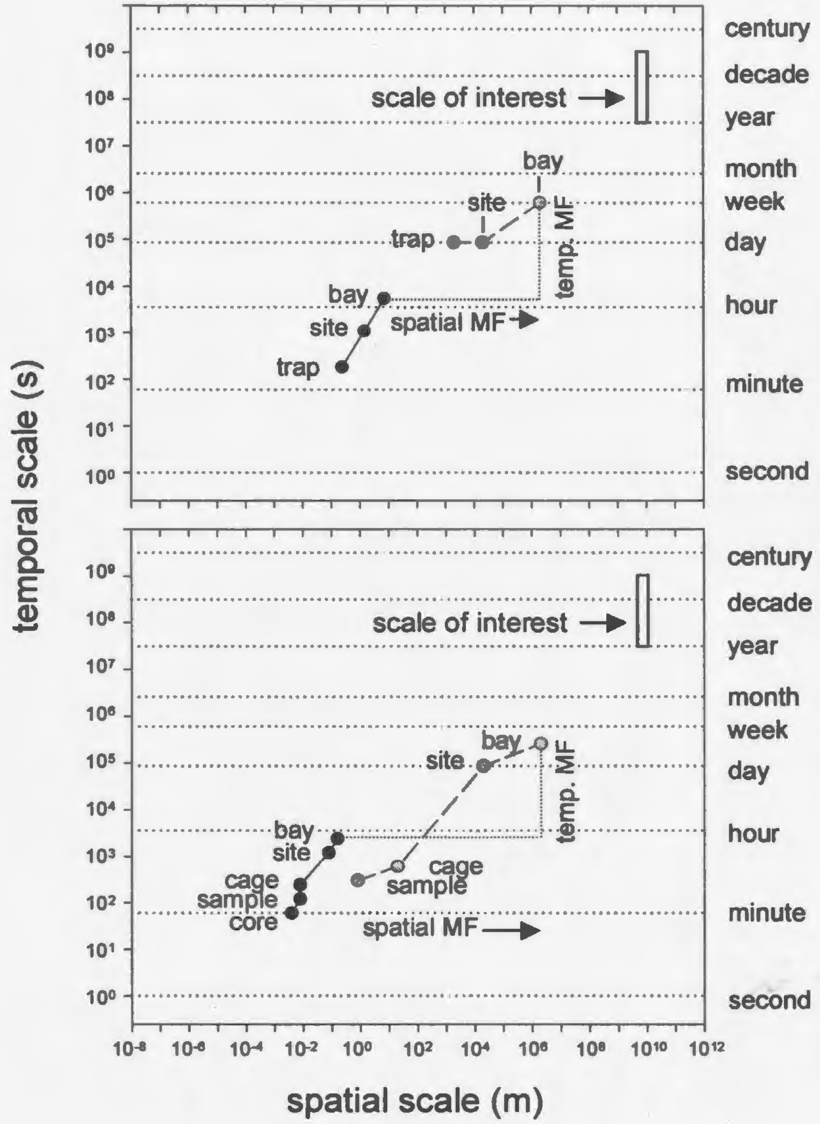

Figure 1.2 Spatial/ temporal scope for the sampling of crab and shrimp carried out in five sites (top plot) and for the exclusion experiments carried out in two sites of Bonne Bay (bottom plot). Direct measurements (filled circles linked by solid lines) and targets of inference (gray circles connected by dashed lines), in addition to spatial and temporal magnification factors are shown. The scale of interest is also plotted at the top right corner (see details in the text and the corresponding chapters).

The temporal scale of interest corresponds to a period of 1-30 years. One year is the minimal temporal range required to characterize monthly or seasonal variation in adult distribution and recruitment. Thirty years is a period that encompasses the major changes in the fishery with respect to cod and subsequently snow crab, shrimp and indirectly several other Bonne Bay predators (Mallet & Landsburg 1996; Paul et al. 2001). The spatial and temporal scales delineated here constitute the framework by which the thesis is organized as outlined below.

1.4 GENERAL OBJECTIVES AND CHAPTERS

The main objective of this thesis is to relate spatial variation in predators with their role in structuring sedimentary communities at the scale of a sub-arctic fjord. The following five Chapters use exploratory and experimental approaches (cf. Eberhardt & Thomas 1991) to address the main questions involved in this relationship.

Chapter 2 focuses on the predators, and explores density and distribution of the main predatory crustaceans (crabs and shrimps) found in the fjord and evaluates the extent to which that distribution relates to larval supply. Are areas of the fjord that support high densities of a given predator also areas where larvae are most abundant? Or instead, are densities set by post- rather than pre-settlement processes?

Chapter 3 focuses on the prey, and explores the distribution and identification of a representative subset of species (polychaetes) of the macrobenthos of Bonne Bay. The main part of this chapter explores the association of polychaetes with different sedimentary habitats inside the fjord and in the region encompassing Newfoundland, Labrador, and the Gulf of St. Lawrence.

Chapter 4 examines predator regulation, and tests the role of predation in structuring macrofaunal communities in the two main arms of the bay. Field exclusion and inclusion experiments are the basis of this study, in parallel with laboratory experiments using sediments and communities from the same (two) areas, and snow crab, the most abundant predator of the bay.

Chapter 5 also examines predator regulation, but in this case evaluating the specific roles of each of three main predators in the bay: snow crab, rock crab, and toad crab. This study is based on several laboratory experiments that test the community effects of each predator, and a field experiment carried out in the same locale from which sediments and communities used in the laboratory experiments were originally collected.

Chapter 6 tests the utility of species surrogates in studies on biodiversity. Specifically, this study uses predation as a natural source of disturbance to test whether taxonomic levels coarser than species (family, order, class) with or without data transformation can be used reliably to assess biodiversity responses in sedimentary infauna.

Chapter 7 summarizes the main conclusions of each chapter and proposes future research directions.

1.4.1 Status of submission and publication of manuscripts

Chapters 3, 4, and 5 are currently accepted for publication (in press) in Polar Biology, Oecologia, and Marine Ecology Progress Series, respectively. Chapters 2 and 6 have been submitted to Journal of Marine Research and Journal of Experimental Marine Biology and Ecology, respectively.

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CHAPTER 2

SPATIAL LINKAGES BETWEEN DECAPOD PLANKTONIC AND BENTHIC ADULTS STAGES IN A NEWFOUNDLAND FJORDIC SYSTEM

2.1 PREFACE

This chapter examines the composition, relative abundance, and distribution of benthic (adults and juveniles) and planktonic (larval) stages of the main predatory crustaceans, and focuses on spatial patterns at the scale of the fjord in order to evaluate whether adult distribution relates to larval supply. Indirectly, this chapter evaluates the relative influence of pre- versus post-settlement processes in determining subsequent spatial patterns of predator distribution.

2.2 ABSTRACT

The relative importance of predatory decapod crustaceans in sedimentary communities depends on spatial variability in their abundance and composition. At the scale of a fjord, such spatial patterns are likely related to sill mediated larval supply. This study examines larval and adult distributions of the main predatory decapod crustaceans at six representative sites in a sub-arctic Newfoundland fjord during three consecutive summers. Multivariate analysis and non-parametric comparisons of potential links

between larval abundance and composition and adult distribution suggest that a shallow sill separating inner and outer portions of the fjord results in differences in larval supply that correspond to adult abundances for at least two of the five species analyzed here. Specifically, adult snow crab and toad crab inhabited areas outside the fjord sill whereas adult pandalid and crangonid shrimp were the dominant epifaunal predator inside the sill. Although larval abundance was not clearly related to adult distribution when all zoeal stages were considered, correspondence between larval and adult patterns emerged when only later stages (zoeae ≥ II) were included in the multivariate analyses. Non-parametric comparisons that removed seasonal variation supported this result, indicating significant differences between inner and outer populations for the corresponding species and stages. These results suggest that larval supply may play a critical role in establishing spatial patterns for some species of epifaunal crustaceans in this fjord system.

2.3 INTRODUCTION

Predatory crustaceans such as crab and shrimp are well known to play important roles in structuring soft-sediment communities (Thrush 1999; Lenihan & Micheli 2001). The study of decapod spatial dynamics is therefore a critical component in models of benthic regulation (Clark et al. 1999; Davis et al. 2003). Several seminal studies have demonstrated the importance of pre- and post-settlement factors in regulating predator populations and related prey communities at a regional scale (Connolly & Roughgarden 1998; Menge 2000). For instance, these studies have shown that the strength and nature of biological interactions changes as a result of geographical variation in the supply of larvae, settlers, and /or recruits (Underwood & Fairweather 1989; Robles 1997). At large spatial (e.g. 10's of kilometers) and temporal (e.g. year to year variation) scales, the link between the numbers or biomass of adult populations and pre-settlement factors such as larval supply or settlement is likely strong (Wainwright & Armstrong 1993; Epifanio & Garvine 2001). However, the link between adult abundance and larval supply over time periods of weeks and spatial scales of kilometers is less clear.

Most predatory crab and shrimp are highly mobile organisms that hatch and release larval forms able to remain in the water column from days to months (e.g. Felder et al 1985; Moloney et al. 1994). Both facts suggest that a close link between larval and adult patterns for these species is unlikely (Todd 1998; Robinson & Tully 2000). Studies attempting to link larvae and adult distribution have traditionally focused on the much closer relationship between larval supply and megalopae or settler abundance, or instead, between settler or recruit success and adult abundance (cf. Eggleston et al. 1998; Etherington & Eggleston 2000; Mokness & Wennhage 2001). Studies have rarely attempted to relate larval supply and adult distribution directly, despite the fact that adult distribution must link to larval supply at some scale. Nonetheless, linkages in patterns may be obscured by post-settlement processes. The geography or 'seascape' that characterizes fjord basins (Sköld et al. 2003) introduces a scenario where larval and adult spatial patterns of crab and shrimp could be linked to a much greater degree than for open coastline environments.

The retention of masses of cold, deep water in inner portions of fjords is thought to reduce dispersal of planktonic and meroplanktonic species (Gagnon & Lacroix 1983; Lewis & Thomas 1986; Bergstrom 1991). Shallow sills influence the hydrography of the fjord by creating barriers to the exchange between adult populations inside and outside the fjord basin (Larsen 1997; Holte & Gulliksen 1998). Larval dispersal is therefore reduced substantially and although this partial isolation is unlikely to result in genetic differentiation at the scale of a fjord (but see Sköld et al. 2003), patterns of abundance and distribution will likely be influenced by this limited exchange. Stronger links between larval supply and adult patterns can therefore be expected.

Decapod crustaceans that dominate coastal areas of the North Atlantic (e.g. snow crab, rock crab, several shrimp species) typically hatch and release larvae that remain in the water column from May to September (e.g. Locke & Corey 1988; Robichaud et al. 1989; Locke 2002). Variable abundances of these and other crab and shrimp species are found irregularly distributed in inner and outer areas of bays and fjords of the Maritimes, and Newfoundland and Labrador (Locke & Corey 1988; Squires 1996, 2000). Variable numbers of snow crab and shrimp in sub-arctic fjords such as Bonne Bay, Newfoundland have been sporadically reported in the literature (Hooper 1996; Wieczoreck & Hooper 1995) but have not been studied in relation to specific physical or biological factors. Whether larval supply to different areas contributes to differences in adult distribution or whether larvae greatly facilitate dispersal across potential barriers such as shallow sills are both questions that so far have not been addressed. This study analyzes the spatial structure of meroplanktonic larvae collected during a three-year summer survey in the inner and outer arms of Bonne Bay, Newfoundland and evaluates whether spatial patterns in larval stages correspond to spatial patterns observed in benthic adults and juveniles. In order to evaluate the degree of interchange of larvae in and out of the main portions of the fjord, the surveys also included intensive sampling of the shallow sill (~12 m deep) that separates inner and outer basins.

2.4 MATERIALS AND METHODS

2.4.1 Study area

Bonne Bay fjord is located on the west coast of Newfoundland (Fig. 2.1) and comprises two main arms: South Arm (~49°30N, 57°54'W), a shallow basin (up to 55 m deep) opens to the Gulf of St. Lawrence, and East Arm (~49°30'N, 57°49'W), a deeper inner basin (up to 230 m) partly separated from South Arm by a shallow sill (~12 m deep). Data on hydrology and circulation (Gilbert & Pettigrew 1993) as well as sediment types and macrobenthic species composition (Wieczoreck & Hooper 1995; Quijón & Snelgrove, in press) from several areas of the fjord have been reported previously (see Chapter 1). Five stations were sampled to estimate larval and adult abundance, including two sites in South Arm (Small Cove and Mike's Cove) and three in East Arm (Deer Arm, Norris Cove, and South East Arm). An additional station was located at the sill (meroplankton sampling only) in order to document the abundance and potential exchange of larvae between South and East Arm.

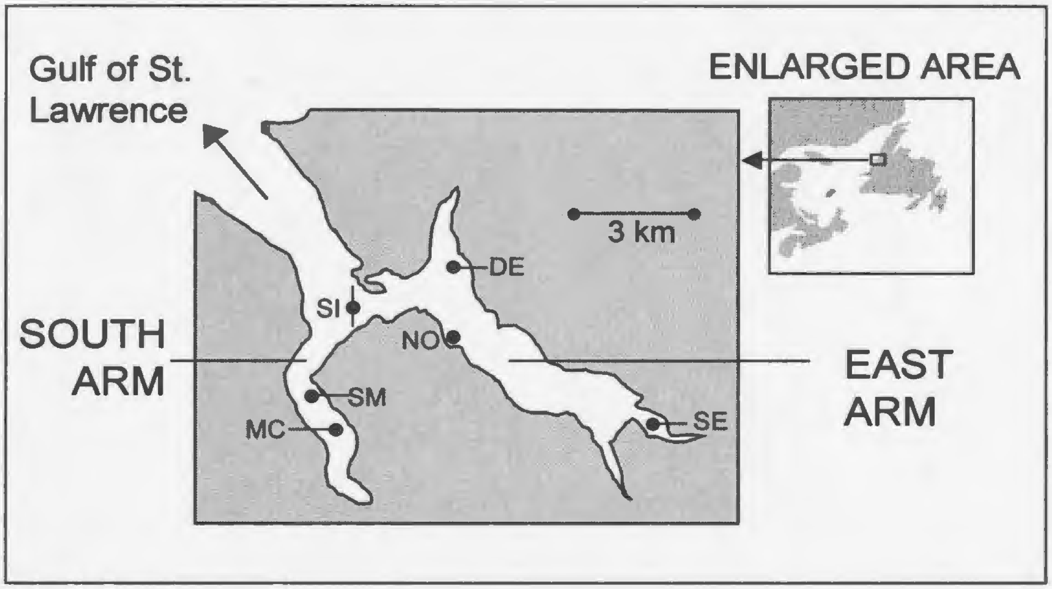

Figure 2.1 Map of Bonne Bay fjord and location of sampling sites in East Arm (SE= South-East Arm; NO= Norris Cove; DE= Deer Arm) and South Arm (MI= Mike's Cove; SM= Small Cove). The location of the sill (SI) is also indicated.

2.4.2 Crab and shrimp distribution

Relative abundance of crabs and shrimp were estimated by deploying bottom traps (~40 x 30 x 60 cm) fitted with 1 cm mesh and baited with mackerel, during the summers of 1999, 2000 and 2001 (see Table 2.1 for number of deployments). Traps were deployed at 35-50 m deep for 1-2 days (data standardized as crab$\cdot$ trap^{-1}day^{-1}) at approximately two-week intervals. Specimens collected were identified and counted and, in most cases, immediately returned to the water unharmed. Baited traps do not provide absolute abundance estimates, and this approach yields only relative comparisons between the two sites. The abundance of juvenile shrimp, which are too small to be effectively sampled by the baited traps, was also estimated using passive traps (Yund et al. 1991) composed of PVC tubes 7.5 cm in external diameter and 91 cm in length (~1:12 aspect ratio) projected vertically from the bottom. Traps (n=3-4 per site) were fastened to cement bases on the seafloor and deployed at 30-50 m deep for periods of 2-4 weeks (data were standardized to shrimp · $trap^{-1}$ $month^{-1}$) (see Table 1 for number of deployments per season). In order to retain and preserve organisms entering the traps, the bottom of each tube was filled with a salt-formalin solution as described by Yund et al. (1991). For unknown reasons, juveniles but not late larval stages (megalopae) were collected in these traps.

Table 2.1 Seasonal sampling effort for bottom and plankton organisms in South-East Arm (SE), Norris Cove (NO), Deer Arm (DE), Mike's Cove (MC), and Small Cove (SM). For the benthos, numbers of trap deployments (estimations of adults) are followed by number of cylindrical trap deployments (estimations of juvenile shrimp) in parentheses. For plankton tows, the number of surface sampling is followed by number of bottom sampling in parentheses.

Sampling	Season	SE	NO	DE	MC	SM
Benthos (traps)	1999	6 (1)	5 (1)	5 (1)	5 (1)	7 (1)
	2000	4 (6)	12 (4)	6 (7)	7 (5)	7 (5)
	2001	2 (1)	1 (1)	2 (2)	2 (1)	2 (1)
Plankton	1999	5 (5)	5 (5)	5 (5)	5 (5)	5 (5)
	2000	5 (2)	5 (2)	5 (2)	5 (1)	4 (2)
	2001	4 (3)	4 (3)	4 (3)	4 (3)	4 (3)

2.4.3 Larvae collection and analysis

Larval sampling was carried out using a 0.3 mm mesh net (1 m diameter opening ring, 3 m length) fitted with a flow meter to estimate filtered volume. Five-minute tows were conducted approximately bi-weekly at the surface (~0-5 m depth) and less frequently near bottom (~3-10 m above bottom; estimated using depth sounder; see Table 1). Samples were preserved in a 5% sea-water and formalin solution, prior to transfer to 70% ethanol. Larvae were identified and enumerated to the lowest possible taxonomic level, based on descriptions by Haynes (1981; 1985), Corey (1981), Roff et al. (1984), Squires (1993; 1996), and Davidson & Chin (1991).

2.4.4 Data analysis

Comparisons of crab and shrimp catches and frequencies among sites were not possible because deployments were not simultaneous and there was high catch variability (within and among traps, sites, and summers). In the case of larvae, annual and seasonal variation of species concentrations per unit time were estimated, and then averaged summer mean densities for all samples from each site for each year. Larval numbers were standardized to larvae $\cdot 100\ m^{-3}$. Among-site comparisons of larvae were constrained by field logistics that limited within-date replication (n=2) at each site, particularly for bottom samples. This problem was exacerbated by strong within and among season variation. In order to discriminate spatial patterns from the strong temporal variation, a two-way ANOVA design including date, area, and their interaction was used. The model for this analysis was $y = \mu + \text{date} + \text{area} + \text{date} \times \text{area} + \varepsilon$, where y refers to each response variable, μ is a mean constant, date refers to the 14 larval sampling dates, and area denotes the geographic location based on site clustering in the multivariate analysis (see PCA-H below). As expected, strong deviations from ANOVA assumptions required the re-estimation of P-values using randomization (500 iterations with replacement). For each comparison, randomization was used to assess the significance of F-values associated with date, area, and the interaction between area and date.

Similar analyses were carried out with a subset of data including seasonal peaks or supply pulses only (*sensu* Paula et al. 2001). Seasonal peaks were identified as those dates when two conditions were met: i) high diversity of larvae (simultaneous occurrence of all or most species) and ii) relatively high concentrations. Analyses of this subset of data (July 2nd 1999, July 4th 2000, and July 16th 2001) included N=3 samples per site (total N=15). These dates are also considered representative of seasonal peaks, based on previous reports of high concentrations of larvae of shrimp, snow crab, rock crab, and toad crab for this region (Lanteigne 1985; Ouellet et al. 1994; Comeau et al. 1991). In order to separate the contribution of late larval stages from the overwhelming abundance of the first zoea of most species, a parallel analysis was carried out that included only zoea stages ≥ II and megalopae. Analyses of total and late stages were performed with the complete and the (seasonal peak) subset of data.

For multivariate analyses Chord Normalized Expected Species Shared (CNESS) was used as a similarity index; this index estimates the number of species shared between two samples based on a random draw of m individuals (cf. Trueblood et al. 1994). The CNESS dissimilarity sample x species matrix also clustered samples based on un-weighted pair-group mean average sorting. The program COMPAH 90 (E.D. Gallagher, U. Massachusetts, Boston) was used for this analysis. In order to detect the relative contribution of different species and stages, random draws of m=25 and 10 were used, respectively (cf. Grassle and Smith 1976). A two-dimensional metric scaling of CNESS distances among samples was produced from a Principal Component Analysis of hypergeometric probabilities (hereafter PCA-H) and a CNESS sample x species matrix transformed to a normalized hypergeometric probability matrix (H). Gabriel Euclidean Distance Biplots (Gabriel 1971) were used to identify species and stages particularly important in determining the variability of CNESS among samples, and thus, driving community composition. Groupings based on the cluster and PCA-H analyses were compared with the two-way ANOVA randomization described above. As in the previous analyses, these spatial comparisons used total concentrations (all stages included) and late stages (zoeae ≥ II) as response variables.

2.5 RESULTS

2.5.1 Adult and juvenile abundance

Four decapod species dominated average summer abundances of most sites (Fig. 2.2). Snow crab (*Chionoecetes opilio* Fabricius) dominated baited trap samples from Small Cove (0.46-1.67crabs • trap^{-1}day^{-1}) and was found in lower abundance at other sites. Pandalid shrimp (*Pandalus montagui* Fabricius) dominated baited trap samples from South-East Arm (0.57-2.29 shrimp • trap^{-1}day^{-1}), and were also present, though in lower abundance, at the other inner sites (Norris Cove and Deer Arm); they were almost completely absent from sites outside East Arm (Mike's Cove and Small Cove).

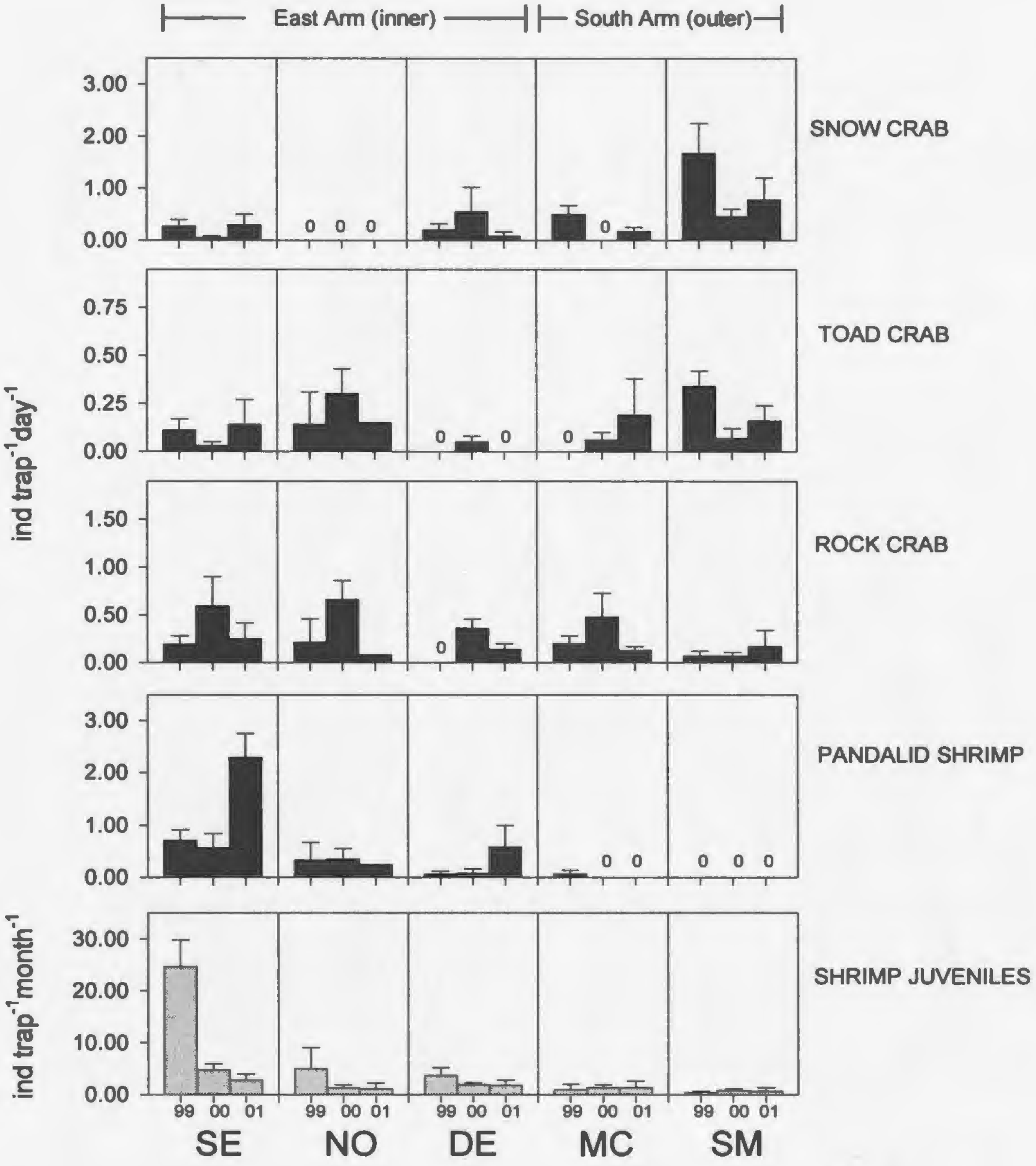

Figure 2.2 Total abundance (mean + 1 s.e.), integrated over the entire sampling period, of juvenile and adult crabs and shrimp collected in bottom traps at the five sampling sites: South East Arm (SE), Norris Cove (NO), Deer Arm (DE), Mike's Cove (MC), and Small Cove (SM). Gray bars in the bottom panel represent average summer abundance of juvenile shrimp collected in cylindrical traps (see Methods).

Numbers of toad crab (*Hyas* spp.) and rock crab (*Cancer irroratus* Say) were lower than for snow crab and shrimp, and were more uniformly distributed among the 5 bottom sites.

The highest numbers of toad crab were recorded at Small Cove and Norris Cove (up to 0.34 and 0.30 crab • $trap^{-1}day^{-1}$, respectively) whereas the highest numbers of rock crab were found in Norris Cove and South East Arm (up to 0.66 and 0.59 crab • $trap^{-1}day^{-1}$, respectively). Highest numbers of juvenile shrimp, as estimated by cylindrical traps, were detected in South East Arm (2.78-24.67 shrimp • $trap^{-1}month^{-1}$), and numbers gradually decreased from inner to outer sites (Fig. 2.2 bottom panel).

2.5.2 Larvae abundance

Two zoeal stages of snow crab and toad crab, and 3-5 zoeal stages of rock crab, pandalid shrimp, crangonid shrimp (*Crangon septemspinosa* Say) and two additional species (hermit crab *Pagurus* sp., and a shrimp *Sabinea* sp.) were collected in net samples. Megalopae were also collected in net samples, but all were either toad crab or rock crab. Data on larval abundance and distribution of the five dominant species is summarized in Figs. 2.3 and 2.4. Larvae were more diverse and generally more abundant in early to mid July for all years (arrows in Fig. 2.3). Crab larvae were generally more abundant in surface waters whereas shrimp larvae were either found primarily in near-bottom samples (pandalid shrimp) or were equally abundant in bottom and surface (crangonid shrimp). Snow crab larvae were far more abundant and comprised more late stages (zoea II) in Small Cove (1.23-9.25 larvae • 100 m^{-3}) than at any other site. Toad crab larvae were more abundant in Mike's Cove and Small Cove (up to 19.51 and 5.94 larvae •100 m^{-3}, respectively) where late stages (≥ zoea II) of this species were also found (Fig. 2.4).

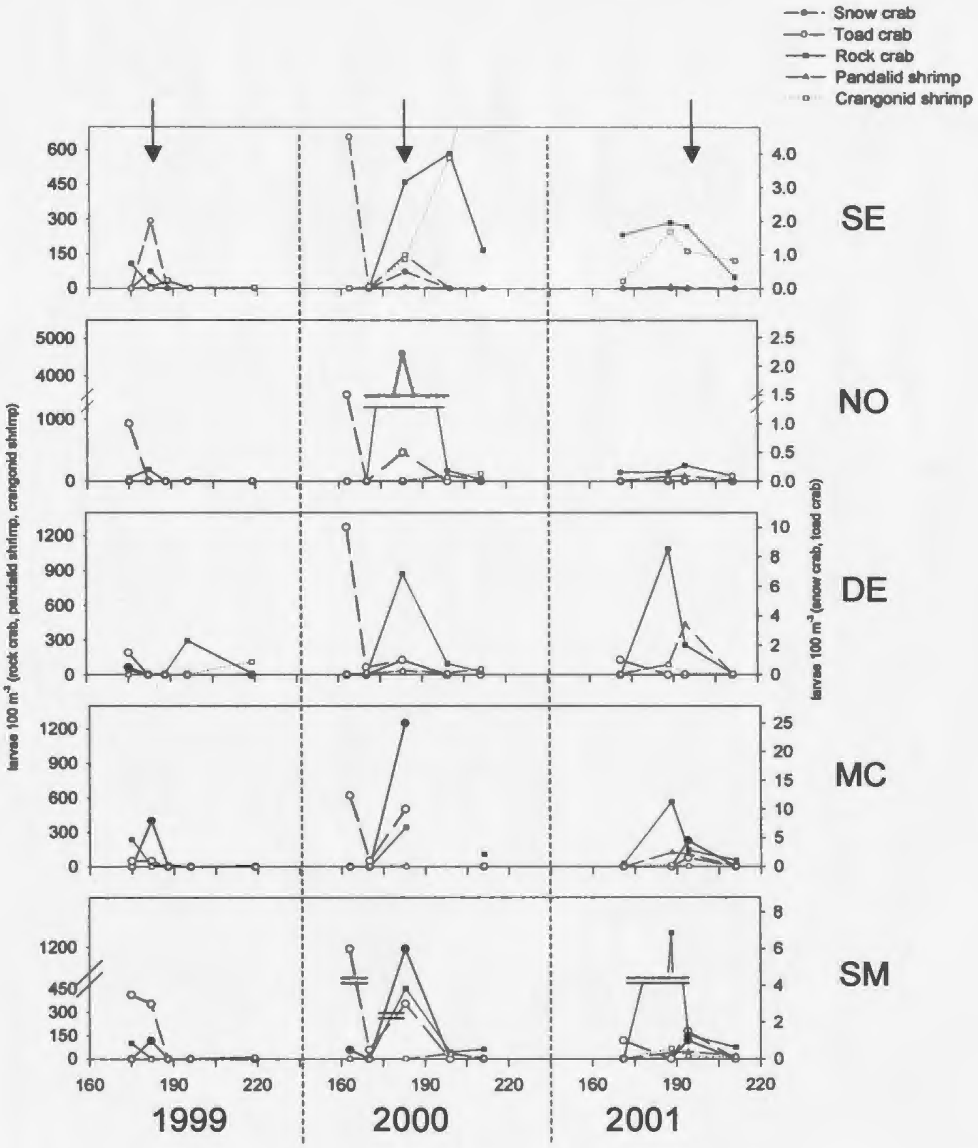

Fig. 2.3 Total concentrations of larvae (mean per 100m^3) during the summer seasons of 1999-2001 in South-East Arm (SE), Norris Cove (NO), Deer Arm (DE), Mike's Cove (MC), and Small Cove SM). Numbers on the x-axis correspond to correlative days for each year. Timing of seasonal peaks in diversity and density are indicated by arrows (see text).

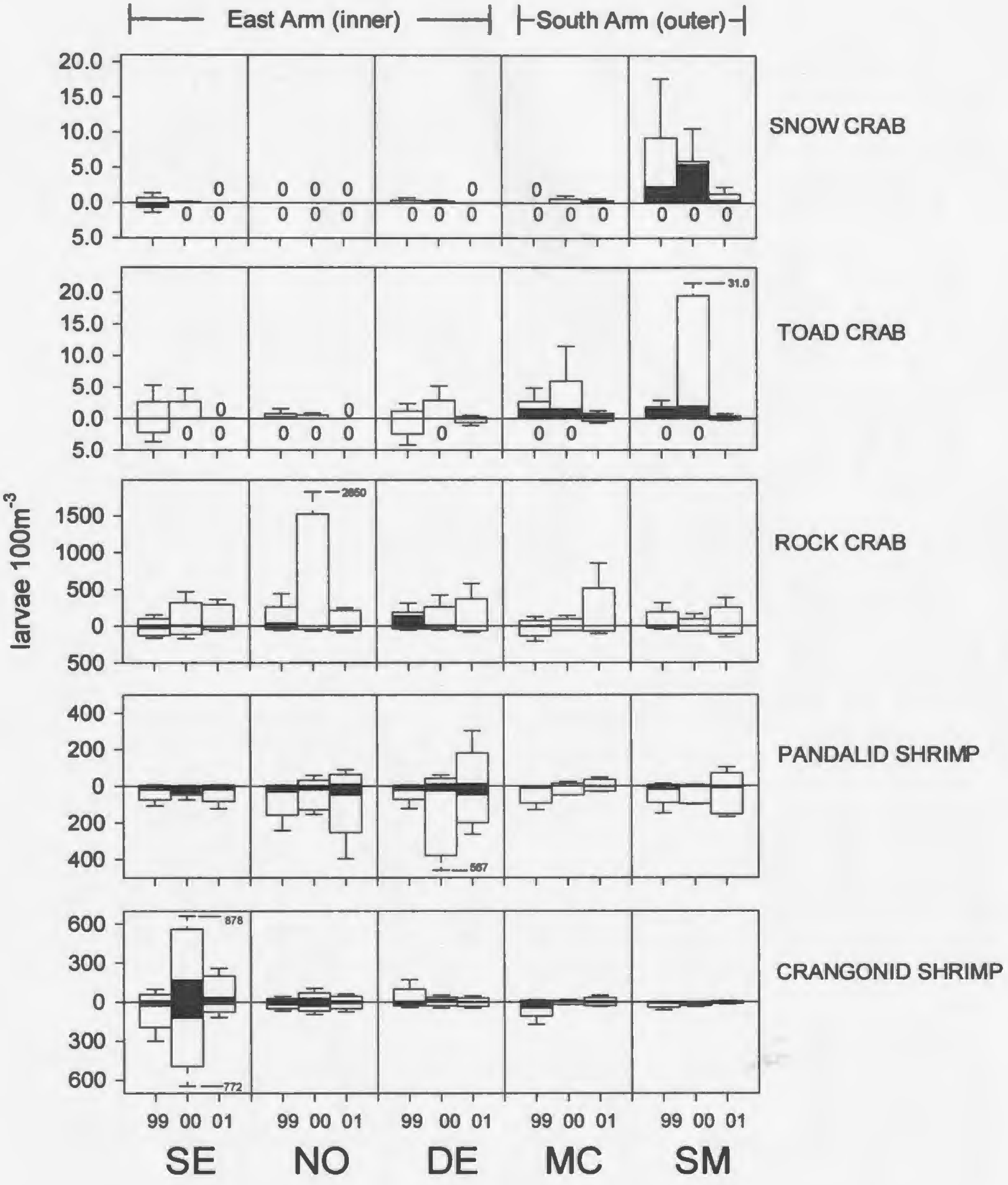

Figure 2.4 Mean summer abundance of crustacean larvae (+ 1 s.e.) collected in South-East Arm (SE), Norris Cove (NO), Deer Arm (DE), Mike's Cove (MC), and Small Cove (SM). Open bars represent total concentrations whereas black bars represent the corresponding proportion of late zoeal stages (including megalopae; see text). Values plotted above zero in each panel represent abundance in surface samples whereas values below zero represent abundance in bottom samples.

Rock crab and pandalid shrimp larvae were more abundant in bottom waters of Norris Cove and Deer Arm (up to 253 and 380 larvae • 100 m^{-3}, respectively), although their total concentrations were more uniformly distributed among the other sites than was observed for snow crab and rock crab larvae. Late stages of both species were more frequent and abundant in the inner fjord (South-East Arm, Norris Cove, Deer Arm) than in the outer sites (Mike's Cove, Small Cove). Crangonid shrimp larvae were far more abundant in South-East Arm (59-560 larvae • 100 m^{-3}), where the highest numbers of late stages were also detected (Fig. 2.4).

2.5.3 Larvae abundance at the sill

Abundance of larvae collected at the sill showed no clear pattern with respect to tidal period (Figure 2.5). No snow crab larvae were found in any of the 23 samples collected from the sill during the three summers of sampling. Larvae of toad crab (zoeae I) were found in low numbers and only on four occasions during flood tide (1.26-6.02 larvae • 100 m^{-3}). Larvae of rock crab, pandalid and crangonid shrimp were collected during ebb and flood tides in relatively similar frequencies, and concentrations ranged from tens to thousands of larvae • 100 m^{-3} (cf. Fig. 2.5). The proportion of late stage larvae (dark symbols) was zero for snow crab and toad crab, and less than 25% in most of the samples analyzed for rock crab, pandalid and crangonid shrimp.

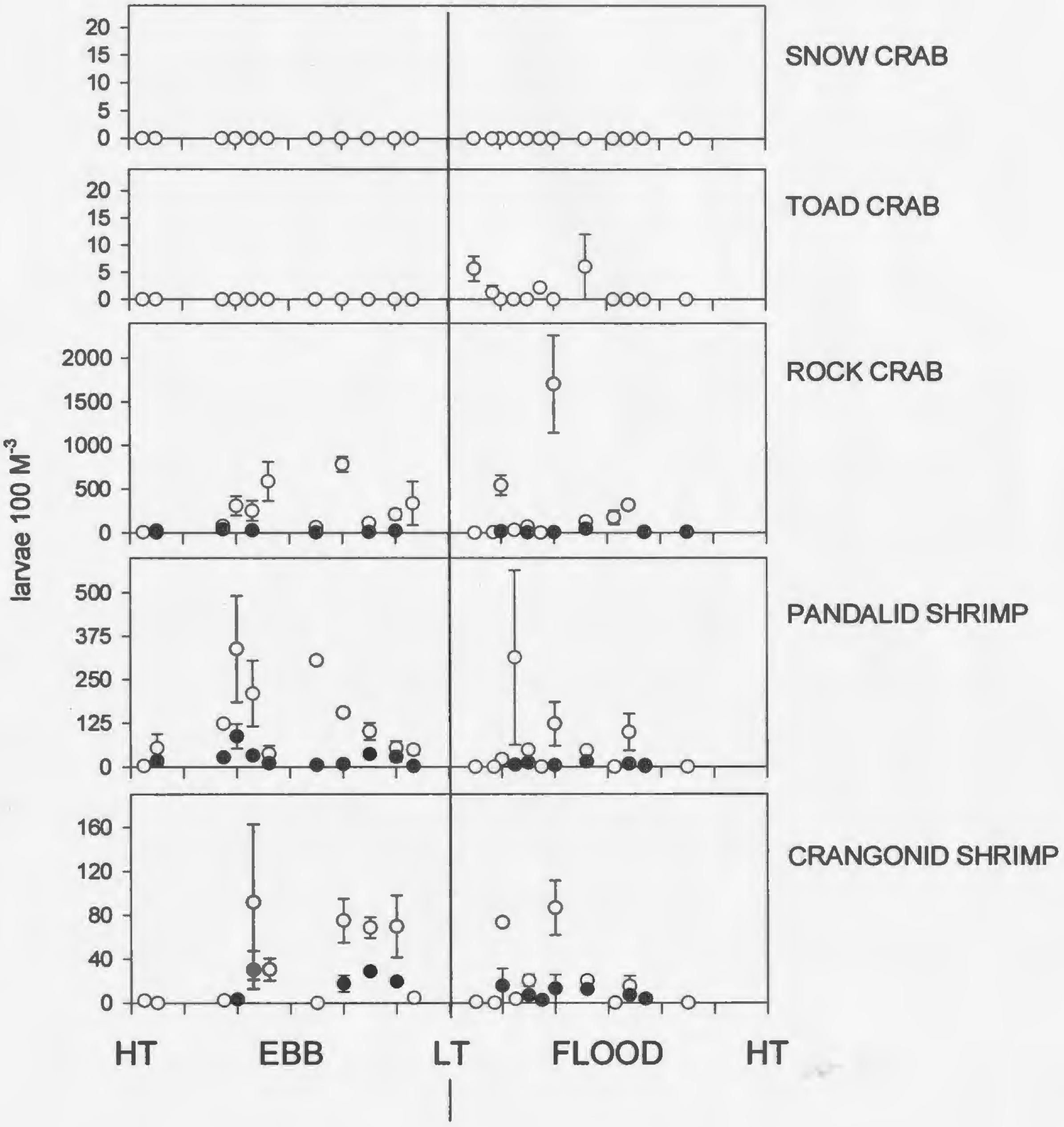

Figure 2.5 Larval abundance (mean +/- s.e.) at the sill during ebb (out of East Arm) and flood (into East Arm) tides. Samples from the three summer seasons have been plotted together in relation to tidal phase. Open circles represent total concentrations (all stages included) and black circles represent the corresponding proportion of late stages (including megalopae).

2.5.4 Community structure

The spatial structure of the meroplankton community (all larvae and stages included) during peak seasonal abundance is summarized in Figure 2.6. Together, the first two Principal Components of the analysis explained 59% of the variation when early and late larval stages were included (top plot). Although the PCA-H separated samples from South East Arm ($SE_{2000-2001}$), most of the samples from the remaining sites and seasons were intermixed in a second major group. Gabriel biplots identified early stages (zoeae I) of rock crab and pandalid shrimp, as the two main taxa associated with the mixture of stations. Crangonid larvae I and II were the most important taxa in describing South-East Arm stations (Fig. 2.6).

In the PCA-H analysis of late stages only (i.e. restricting the analysis to zoeae ≥ II and megalopae) the first two principal components explained 51% of the data variation (Fig. 2.6 bottom plot). Two main groups of samples separated along the first axis: those from the inner (East Arm) fjord (South-East Arm, Norris Cove, and Deer Arm) including the sill, and those from the outer (South Arm) portion of the bay (Mike's Cove and Small Cove). In the outer group, the two subgroups that formed were based on year rather than geographic site (2001 and 1999-2000), whereas for the inner group, samples did not group clearly by sampling year or site. Gabriel biplots identified pandalid and crangonid larvae II as the main drivers of community structure; these stages were strongly associated with samples collected from the inner fjord (including the sill). Biplots also identified the second zoeae of snow crab, toad crab, and *Sabinea* sp. shrimp as the most important taxa in outer bay samples (see Fig. 2.3 for comparisons of relative abundance).

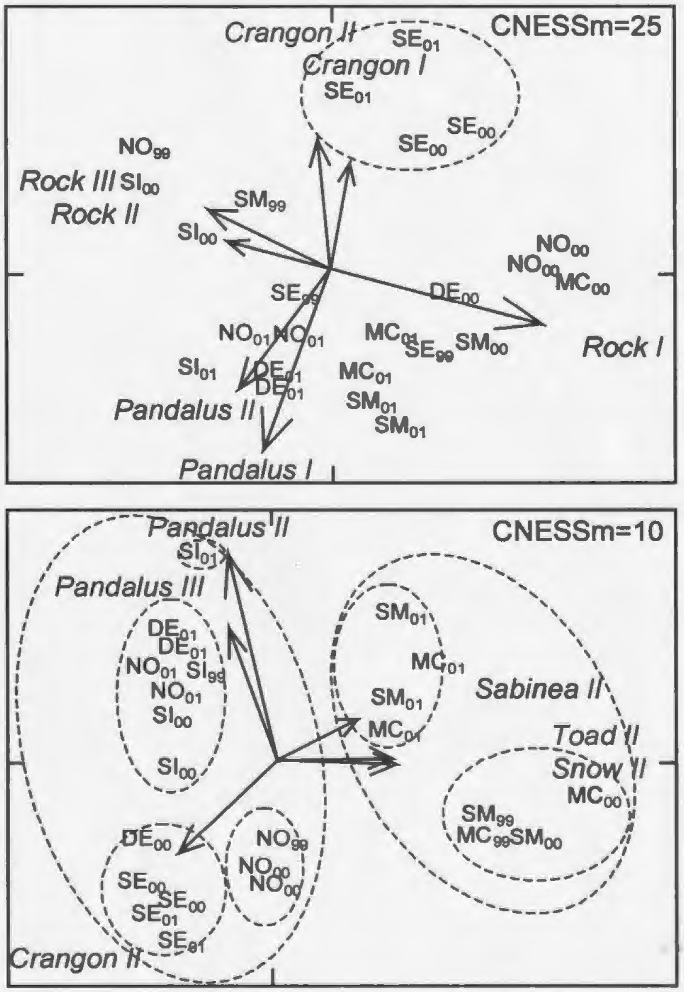

Figure 2.6 Metric scaling plot using PCA-H of CNESS dissimilarity for larval samples collected during the seasonal peak in abundance. Dashed lined identify major groupings identified by cluster analysis. Top: data analyzed with all zoeal and megalopal stages. Bottom: analysis based only on zoeal stages ≥ II and megalopae. Letters indicate sampling location: South-East Arm (SE), Norris Cove (NO), Deer Arm (DE), Mike's Cove (MC), and Small Cove (SM). Subscripts denote year (1999-2001). Arrows are Gabriel Biplot vectors that identify species and stages that contribute the most to between- sample differences.

Results from comparisons of the two main groups generated by the cluster and PCA-H analyses (inner versus outer sites) are summarized in Table 2.2. When all data were used in the comparison (N=42 and 28 for inner and outer areas, respectively), significant differences were detected for total number of larvae of four taxa: snow crab, toad crab, crangonid shrimp, and *Sabinea* (P=0.000 – 0.036). The same species exhibited significant "inner-outer" differences when the abundances of their corresponding late stages were compared (P=0.000 –0.014; Table 2.2). Although significant interactions between site and date were detected in the comparisons of snow crab, toad crab, and *Sabinea* sp., within-year analyses carried out separately showed that the spatial differences (inner-outer) were consistently significant (P<0.05; cf. Fig. 2.4).

Comparisons carried out with the seasonal peak data subset (n=15 and 8 for inner and outer areas, respectively), showed similar results with the exception of crangonid shrimp (P>0.05 for spatial comparisons). The total abundance of larvae of snow crab, toad crab, *Sabinea* sp., and *Pagurus* sp. varied significantly between the main areas of the bay (P=0.012 – 0.020). A comparison of the abundance of late larval stages again showed significant differences between inner and outer portions of the bay for the same taxa (P= 0.004 – 0.036) (Table 2.2; Fig. 2.3).

Table 2.2 Results of the two-way ANOVAs comparing the main groups of samples generated by the cluster and PCA-H analyses: inner and outer groups. Analyses were carried out using all data (N=42 and 28 for samples from Inner and outer areas, respectively; 13, 1, 13, and 42 degrees of freedom), and a subset that included seasonal peak data only (N=15 and 8 samples from the same areas; 2, 1, 2, and 9 degrees of freedom). Factors include Date (14 sampling), Area (inner vs. outer) and their interaction. Response variables are total number of larvae (All) and late stages only (zoeae ≥ II). P-values estimated by randomization (500 iterations). SV= Source of variation.

Data	Zoeae	SV	Response variables													
			Snow crab		Toad crab		Rock crab		*Pandalus* sp.		*Crangon* sp.		*Pagurus* sp.		*Sabinea* sp.	
			F	P	F	P	F	P	F	P	F	P	F	P	F	P
Full data	All	Date	4.38	0.000	10.32	0.000	1.48	0.166	2.14	0.032	0.92	0.542	2.49	0.013	3.37	0.001
		Area	9.44	0.000	5.61	0.024	0.82	0.416	0.49	0.574	5.06	0.026	1.08	0.340	5.11	0.036
		DxA	3.75	0.004	0.99	0.490	0.85	0.584	0.34	0.972	0.73	0.698	1.15	0.332	1.54	0.136
	≥ II	Date	3.50	0.001	4.70	0.000	1.00	0.467	1.84	0.068	1.26	0.276	4.04	0.000	5.33	0.000
		Area	5.80	0.010	24.65	0.000	2.75	0.116	2.18	0.152	6.27	0.014	1.17	0.308	7.86	0.010
		DxA	3.50	0.008	4.52	0.002	0.68	0.752	0.80	0.660	0.95	0.500	1.99	0.056	4.76	0.002
Seasonal Peak	All	Date	1.78	0.223	3.34	0.082	1.60	0.253	1.95	0.198	0.70	0.520	1.06	0.384	3.71	0.067
		Area	8.13	0.018	9.63	0.012	1.06	0.396	0.41	0.818	2.04	0.122	3.55	0.070	5.60	0.020
		DxA	2.14	0.174	1.85	0.210	0.77	0.478	0.31	0.690	0.49	0.552	0.85	0.380	0.98	0.352
	≥ II	Date	1.87	0.210	1.83	0.215	0.26	0.773	2.61	0.128	0.87	0.452	1.50	0.274	1.28	0.324
		Area	5.18	0.036	14.98	0.004	2.03	0.180	1.24	0.300	1.84	0.150	1.85	0.154	12.63	0.008
		DxA	2.80	0.112	2.75	0.114	0.12	0.804	1.10	0.388	0.50	0.604	0.87	0.426	2.12	0.156

2.6 DISCUSSION

2.6.1 Adult abundance and larval supply

Differences in spatial distributions in Bonne Bay were evident for larval and adult snow crab and shrimp. Three related factors may explain the higher numbers of snow crab in Small Cove: the higher larval supply observed in this study, the higher surface productivity of the South and Outer Arms (relatively low C:N ratios; Quijón & Snelgrove, in prep), and the adjacent larger population in the outermost part of the fjord (Comeau et al. 1991; Conan et al. 1996). More productive waters could result in higher concentrations of sinking phytoplankton that have been linked to larval release in snow crab (Starr et al. 1994) and likely in toad crab (Harms & Seeger 1989). Higher productivity outside of the East Arm also supports denser assemblages of the benthic prey consumed by this species (Wieckzorek & Hooper 1995; Quijón & Snelgrove in press).

In contrast, pandalid shrimp were far more abundant in the inner than in the outer portion of the bay, a result at least partially related to elevated abundance of larvae and juvenile shrimp. Although crangonid shrimp have been previously reported from Bonne Bay (Hooper 1975) the traps used here did not succeed in collecting adults of this species, probably because of inappropriate sampling (cf. Squires et al. 1996). However, the high larval abundance recorded in South-East Arm, suggest that this estuarine species (Lazzari 2002; Grabe 2003) is primarily distributed in the innermost portion of the bay where there is significant freshwater input. This finding is similar to results from the Bay of Fundy where crangonid larvae were found concentrated in the innermost part of the bay (Locke & Corey 1988), although no correspondence with adult distribution was found.

In comparison with snow crab, toad crab and rock crab are species with shallower distribution, and therefore have the capacity to move across the sill as larvae, juveniles, or adults (cf. Johns 1981; Squires 1996). Although there are differences in larval numbers and particularly in the distribution of advanced larval stages, larval supply probably does not dictate the adult distribution of toad crab and rock crab (Hudon & Fradette 1993). Post-settlement factors may also explain differences in recruitment and adult abundance of toad and rock crab, particularly post-settler predation by crangonid shrimp (Olmi & Lipcius 1991).

2.6.2 Meroplankton at the sill

Remarkably, meroplanktonic larvae that were more abundant in the outer part of the bay (snow crab and toad crab) were largely absent from samples collected at the sill. Densities of snow crab larvae are typically low in comparison to rock crab (cf. Starr et al. 1994; Conan et al. 1996; Hudon & Fradette 1993). However, the absence of snow crab larvae in 23 replicate sampling trips using the same method that documented larvae at other sampling sites suggests that snow crab zoeae do not occur in proximity to the sill. Thus, tidal exchange, the dominant short-term transport process in shallow-sill fjords (Brookins & Epifanio 1985; Lewis & Thomas 1986) including Bonne Bay (B. de Young pers. comm.) does not transport larvae into East Arm. This may indicate unidirectional transport of early stages out of Bonne Bay towards the Gulf of St. Lawrence ("flushing out of zoeae" *sensu* Comeau et al. 1991). Similar early emigration processes have been widely reported for other species of vertebrates and invertebrates (Melville-Smith et al. 1983; Christy & Morgan 1998), however, no conclusive evidence on the timing of larval emigration and immigration with respect to Bonne Bay is currently available.

Although snow crab secondary migration through such a shallow sill is unlikely, interchange with the inner semi-enclosed population may occur with the winter renewal of deep water, associated with enhanced wind forcing and sea intrusion (Hudon & Fradette 1993; Epifanio & Garvine 2001). This phenomenon, which is well described for *Pandalus borealis* (Bergstrom 1991), has not been studied in snow crab, or more closely related species such as *P. montagui* or crangonid shrimp. In comparison, species that exhibited higher larval concentrations in the inner portion of the bay, and apparently resulted in increased settlement, were collected far more frequently at the sill. Unexpectedly, species-related differences in larval numbers on ebb versus flood conditions were not apparent in sill samples, despite the fact that species such as rock crab are not known to display the behavioural mechanisms that have been shown to enhance retention in estuarine habitats for crangonid shrimp (Sandifer 1975; Brookins & Epifanio 1985). For shrimp, larval dispersal alone would suggest more uniformly distributed populations, as was observed for rock crab. However, the gradient in abundance between the inner and outer fjord exhibited by the two species of shrimp suggests that post-settlement factors such as cannibalism or inter-specific predation may be a primary determinant of spatial patterns (Todd 1998; Morgan 2001).

Adult and juvenile shrimp abundances reflect increased settlement in the inner portion of the bay, or higher post-settlement mortality in the outer portion; data reported here are insufficient to differentiate between these possibilities. An additional possibility is that the efficiency of the passive traps is not consistent among sites, as would be predicted if flow conditions differ among sites (Butman 1989). Unfortunately there is no detailed circulation data for the study sites. Logistic restrictions also constrained our sampling to daylight. Although the spatial patterns described here are generally clear, further sampling that incorporates day-night variation is needed in order to fully describe patterns of spatial variation at the scale of the fjord (cf. Garland et al. 2002; Mokness et al. 2003).

2.6.3 Meroplankton community structure

High abundances of first zoeae of rock crab, pandalid shrimp, and even crangonid shrimp swamp any clear pattern in meroplankton. Early stages of these species have been described as among the most abundant in coastal meroplanktic communities of Eastern North America (e.g. Locke & Corey 1988; Wehrtmann 1994). Moreover, an almost simultaneous peak of these early stages suggests a near synchrony in hatching in Bonne Bay (Starr et al. 1994) and at higher latitudes (Atthorsson & Gislason 1991; Locke 2002). However, the earliest larval stage is also less meaningful than later stages in determining subsequent settlement and recruitment patterns, as demonstrated in studies on settlement of crustaceans and other invertebrates in laboratory and in the field (Todd 1998; Snelgrove et al. 1999). This conclusion is supported by the second PCA-H analysis that used only late stages (≥ zoea II) and the non-parametric analyses done with the subset of seasonal peak data. The patterns observed with late stages were clearer and supported a more consistent association between samples collected from related sites or years.

These results link spatial gradients in the meroplankton with those in the benthos, and support the argument that a strong link between pelagic and benthic stages in species with indirect development is more likely for late larval stages, which tend to show a higher degree of correspondence with settlement and post-settlement distribution (e.g. Todd 1998; Etherington & Eggleston 1999). Although the sill may not represent an obstacle to primary and secondary dispersal in most of the species studied here, it may represent an inflexion point (*sensu* Locke & Corey 1988) for the distribution of advanced larval stages. This conclusion is consistent with the argument that the sill may constitute the main topographic feature of fjords that determines community structure both in the water column (Gagnon & Lacroix 1983) and the benthos (Larsen 1997). Future studies that sample post-larvae and first instars (young of the year; cf. Eggleston & Armstrong 1995) at the scale analyzed here may be more effective in linking recruitment and adult distribution. These studies may clarify regulation in benthic adult stages that cannot be explained by variation in larval supply alone, as was the case in this study.

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CHAPTER 3

POLYCHAETE ASSEMBLAGES OF A SUB-ARCTIC NEWFOUNDLAND FJORD: HABITAT, DISTRIBUTION, AND IDENTIFICATION.

3.1 PREFACE

Infaunal organisms constitute the main source of food for predatory crustaceans in Bonne Bay. The study of infaunal communities from this region is far from complete mainly because issues as basic as taxonomy and habitat-related variability have not been examined quantitatively. This Chapter examines a representative subset of the benthic diversity of the fjord (polychaetes), and uses quantitative and qualitative sampling in combination with literature records to explore their distribution at local and regional scales.

3.2 ABSTRACT

This study explores the association of 24 polychaete species with sandy and muddy habitats located in a sub-arctic fjord, and across Atlantic Canada from Labrador, Newfoundland, to the Gulf of St. Lawrence. Key characters used to facilitate species identification are also summarized. Within Bonne Bay, distinctive polychaete assemblages were associated with specific sediment types and polychaete species richness and density were significant predictors of corresponding total (infauna) density

and species richness. Polychaetes were more dense and diverse in sandy sediments, partly because sandy locales were associated with the outer portion of the bay, and therefore were closer to the more productive and diverse Gulf of St. Lawrence region. In general, species that occupied both sediment types were more widely distributed within Bonne Bay and across the region. The biogeography of most species also suggests that the Bonne Bay fauna is transitional between the Labrador and Acadian biogeographic provinces.

3.3 INTRODUCTION

Although marine benthic environments constitute the largest habitat on the planet (~70%), our knowledge of their biodiversity continues to be limited. Invertebrates account for most of the known marine species (Norse 1993; Snelgrove 1998) and are critical in the provision of numerous ecosystem services (Myers 1996; Snelgrove et al. 1997). Unfortunately, undocumented habitat and species loss are ongoing as a result of increasingly widespread human activities (Irish & Norse 1996; Carlton et al. 1999) and research on this issue is lagging (NRC 1995; Roberts & Hawkins 1999). Despite the pressing need for more exploration and research, ecological information as basic as species composition and habitat association remain far from complete, even in shallow, coastal areas (NRC 1995). Among the most abundant and species-rich macrobenthic taxa are the polychaetes (Grassle & Maciolek 1992; Hutchings 1998). The rich diversity of polychaetes is reflected not only in the large numbers of species, but also in families, orders, and functional groups (Giangrande 1997; Hutchings 1998). Not surprisingly, members of this class have colonized almost every habitat in the marine realm, and have been proposed as indicators (Pocklington and Wells 1992; Pearson 1994) and surrogates of overall biodiversity (Olsgard and Somerfield 2000; Olsgard et al. 2003).

It is ironic that despite the success polychaetes have achieved in diversifying and adapting to almost every benthic habitat, they remain virtually absent from most major geographical studies on marine biodiversity (e.g. Briggs 1974; Pocklington & Tremblay 1987). In contrast with some other groups of invertebrates, biogeographic limits are not well established for many polychaete species, mainly because of their presumed wide distribution, not clearly defined endemism, and the frequency of cosmopolitism (Day 1967; Glasby & Alvarez 1999). Two issues account for this apparent discordance with other groups. First, several studies suggest that species originally considered cosmopolitan often comprised two or more sibling (Grassle & Grassle 1976; Knowlton 1993) or misidentified species ("the cosmopolitan syndrome" Williams 1984; Hutchings & Glasby 1991; Dauvin & Thiébault 1994). Second, records of polychaete composition and distribution are permeated by large geographic gaps in benthic studies (Giangrande 2003). Both issues suggest that poorly explored areas remain a primary problem for studying spatial patterns in diversity and the association of polychaete species with particular habitats.

Sub-arctic fjords such as Bonne Bay, Newfoundland (~49°N) are among the many regions where polychaete assemblages are not well described. Although preliminary lists have been published for the area (e.g. Rivard & Bowen 1970; Hooper 1975), our knowledge of local invertebrates in general, and polychaetes in particular, remains fragmentary. More studies are therefore required in order to evaluate the biodiversity of the region, and basic habitat associations. Although sedimentary habitats represent a wide gradient of types and ecotones (e.g. Zajac & Whitlatch 2003) a contrast between highly energetic environments (sandy sediments) and low-energy, depositional conditions (muddy sediments) represents a useful starting point for comparison (Peterson 1991; Reise 2001). This basic approach is used here to describe habitat association and quantify the abundance of 24 representative species of polychaetes. This Chapter also reviews their distribution in the Bonne Bay area, including the two arms of the fjord, the region encompassing Newfoundland, Labrador, and the Gulf of St. Lawrence, and provides a succinct review of key identification characters, using external and internal morphology.

3.4 MATERIALS AND METHODS

3.4.1 Study area and sampling

Bonne Bay is a sub-arctic fjord located in western Newfoundland (Fig. 3.1). The fjord is comprised of two main arms: South Arm (55 m maximum depth), a basin open to the Gulf of St. Lawrence, and East Arm (230 m maximum depth), a semi-enclosed basin separated from the Gulf of St, Lawrence and South Arm by a shallow sill (~12-15 m deep). Sampling of sediments and benthic organisms was carried out in two phases. First, a preliminary survey was conducted in May-June of 1999 at 10 sites (15-30 m deep; 2-3 samples per site) distributed along the two main arms of the bay. Second, in June-August of 1999 a more extensive survey (16 samples per site, 32 samples in total) was completed in two representative habitats: sandy sediments (Small Cove) and muddy sediments (Southeast Arm) (Fig. 3.1).

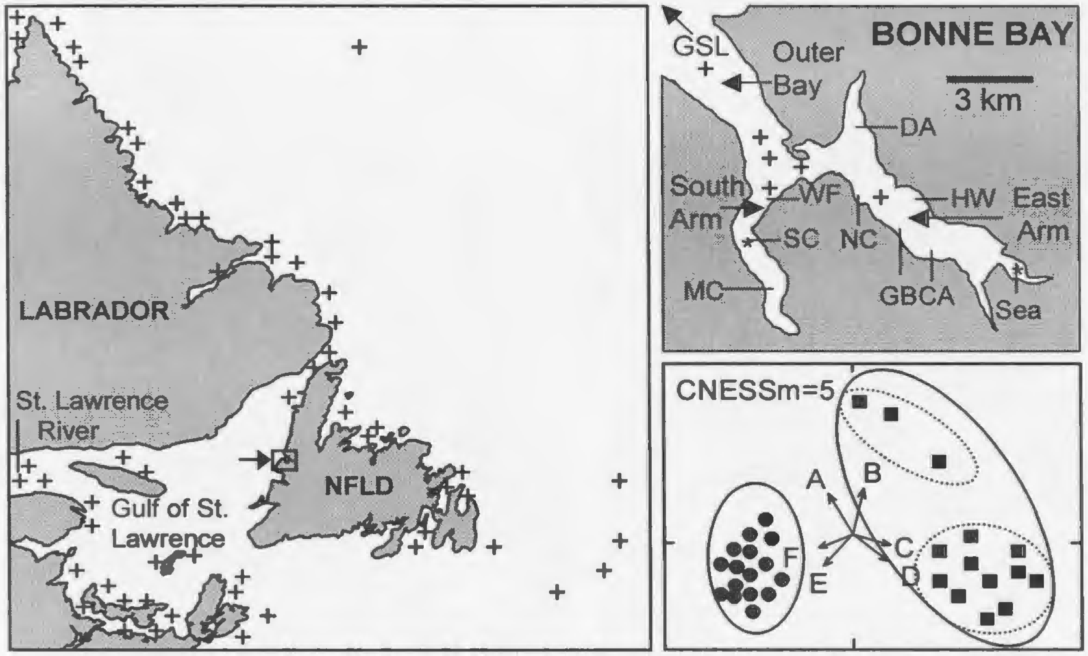

Figure 3.1 Left panel: Newfoundland, Labrador, Gulf of St. Lawrence (GSL), and approximate location of Bonne Bay (arrow), and sampling areas from which records of fauna were available (crosses). Upper right panel: Bonne Bay and location of sites for detailed (*) and preliminary sampling: DA= Deer Arm, NC= Norris Cove, GB= Gravel Beach, HW= Highway Wharf, CA= Camping Area, SEA= South-East Arm, SC= Small Cove, MC= Mike's Cove. Lower right panel: Cluster and PCA-H analysis of communities from muddy (squares) and sandy sediments (circles). Gabriel biplots (arrows) identify the most important species: A= *T. acutus*, B= *E. papillosa*, C= *O. cylindricaudata*, D= *P. praetermissa*, E= *P. steenstrupi*, and F= *P. lyra*.

Samples from both surveys were collected by scuba divers using plastic cores (7 cm diameter) that were inserted ~10 cm into the sediment and then corked at both ends to seal the sample. This method ensured that no organisms were lost during handling or transport of the samples until their processing in the laboratory (see below). Additional samples were collected from these two sites for grain size analysis, which was based on wet sieving for coarser fractions and a Sedigraph 5100 Particle Size Analyzer for finer fractions (Quijón & Snelgrove in press).

3.4.2 Sample processing and identification

Faunal cores were sieved through a 500-μm mesh and preserved in a 10% sea water-formalin solution; they were later transferred to 70% ethanol with Rose Bengal. Macrofaunal organisms were sorted, counted and identified to species level, using stereo and light microscopy. Twenty-four representative species from an array of different clades (*sensu* Rouse & Pleijel 2001) and families were selected for further microscopic examination and photography. Key external and internal (cross sections) morphological characters were photographed and stored using a Sony Hyper HAD Color Video Camera connected to a computer. Pictures were then organized using the Micrografx Picture Publisher 7 software.

3.4.3 Data analysis

The structure of polychaete assemblages was analyzed with Chord Normalized Expected Species Shared (CNESS). This similarity index estimates the number of species shared between two samples based on a random draw of individuals (set here at m=5, see

Trueblood et al. 1994). CNESS dissimilarity was also used to cluster samples based on un-weighted pair-group mean average sorting, using the program COMPAH 90 (E.D. Gallagher, U. Massachusetts, Boston). Groups identified by the cluster analysis were depicted in a two-dimensional metric scaling plot of CNESS distances among samples, generated with a Principal Component Analysis (PCA-H). In addition, Gabriel Euclidean Distance Biplots (Gabriel 1971) identified those species that contributed the most to sample variability, and thus, drove community composition (see details in Ramey & Snelgrove 2003 and Quijón & Snelgrove, in press).

Polychaete total abundance and species richness were estimated and compared between habitats using one-way ANOVAs. The model used in each analysis was $y = \mu + \text{habitat} + \varepsilon$, where y refers to each response variable, μ is a mean constant, habitat refers to sandy or muddy sediments, and ε refers to the error term. Regression analyses were also carried out to test whether abundance and species richness of polychaetes were useful predictors of overall community (all other macrofaunal taxa included) abundance and richness. The model for this analysis was similar to the model described above: $y_{\text{comm parameter}} = \mu + \text{polychaete}_{\text{parameter}} + \varepsilon$, where $y_{\text{comm parameter}}$ and $\text{polychaete}_{\text{parameter}}$ correspond to the community richness or abundance, and polychaete community richness or abundance, respectively, within each corresponding habitat type.

Summaries of distributional patterns within Bonne Bay for the 24 polychaete species were based on the preliminary and detailed surveys described above, and in sampling subsequently carried out at ~20 m deep in sedimentary bottoms of Small Cove during May-September of 2002 (South Arm; Kelly & Snelgrove, in prep). Additional records came from studies conducted in similar habitats by Rivard & Bowen (1970), Hooper (1975), Wieczoreck (1991), and Wieczoreck & Hooper (1995). Polychaete Distribution was also examined at the regional scale (Newfoundland, Labrador, and Gulf of St. Lawrence) by checking occurrences in published studies by Pettibone (1956), Peer (1972), Barrie (1979; 1980), Appy et al. (1980), Bousfield (1981), Pockington (1989), Brunel et al. (1998), Ramey (2001), and unpublished data by Ryan & Thompson (Notre Dame Bay), and Snelgrove (Trinity and Conception Bays, Newfoundland).

3.5 RESULTS

Sediment analyses confirmed that differences in the coarser (sand) and finer fractions (silt and clay; <63μm) of the sediments collected were significantly different between sandy and muddy sites ($P<0.05$). Carbon: Nitrogen ratios were also estimated (15.9 in sandy and 20.6 in muddy sediments) and significant differences detected ($P<0.05$) (see Chapter 4: Table 4.2 or Quijón & Snelgrove, in press, for details on the ANOVA comparisons).

3.5.1 Habitat comparisons

Mean densities and species richness of polychaetes and all macrofaunal taxa at each habitat are summarized in Table 3.1. Polychaetes were at least three times more abundant and two times more diverse in sandy than in muddy sediments ($P<0.001$ in both comparisons). Similar results were detected when all macrofaunal taxa were compared ($P<0.001$). Polychaetes encompassed ~65% of all macrofauna in terms of numbers of species and individuals in sand communities, but only ~30-40% in mud communities. Linear regression analyses using the density of polychaetes to predict density of all macrofaunal taxa resulted in relatively low explanatory levels: $R^2_{adjusted} = 0.38$ (sandy habitat; $P=0.007$), and 0.12 (muddy habitat; $P=0.100$). Results of regressions using polychaete species numbers to predict total infaunal taxa were significant for both habitats, but were clearly higher in muddy sediments ($R^2_{adjusted}$ 0.22; $P=0.038$ for sand, and 0.75; $P<0.001$ for mud; Table 3.1).

Table 3.1 Mean (+95% confidence intervals) densities and species richness in sandy and muddy habitats. Values are based on all macrofaunal taxa or polychaetes only. Results from linear regression analyses testing polychaetes as a surrogate for all macrofaunal taxa are reported for each variable and each habitat.

	Sandy		Muddy	
	All taxa	Polychaetes	All taxa	Polychaetes
Density (ind 38.5 cm^{-2})	54.63 (4.51)	35.56 (3.64)	31.88 (4.07)	10.00 (3.25)
Species (# 38.5 cm^{-2})	19.13 (1.03)	12.5 (0.89)	13.13 (1.71)	5.69 (1.43)
Density $R^2_{adjusted}$ (P_{value})	0.38 (0.007): $d_t=26.0+0.81d_p$		0.12 (0.100): $d_t=26.5+0.54d_p$	
Species $R^2_{adjusted}$ (P_{value})	0.22 (0.038): $s_t=11.6+0.60s_p$		0.75 (0.000): $s_t=7.16+1.05s_p$	

Between-habitat differences were also evident in polychaete community structure (Fig. 3.1, right lower panel). The first two principal components of the PCA-H analysis explained 49% of the variation in species composition and abundance. Although there was greater variability within muddy samples, the clustering and separation of the sand and mud habitats was clear. Six species of polychaetes were identified by the Gabriel biplots (arrows in Fig. 3.1) as drivers of sample variability. *Euchone papillosa*, *Ophelina cylindricaudata*, and *Praxillella praetermissa* were closely associated with muddy sediments, whereas *Prionospio steenstrupi*, and *Paradoneis lyra* were associated with sandy sediments. These results are consistent with patterns in density and frequency of occurrence of these species in each habitat (Table 3.2; Figs. 3.2-3.9).

Table 3.2. List of polychaete species, mean densities (per 38 cm^2), and frequencies of occurrence (presence/absence in all samples collected) per habitat. P values from ANOVAs comparing species densities between habitats are also reported. A "---" symbol indicates cases where the species was lacking in one of the habitats and therefore the statistical comparison was not required.

Taxa	Sand		Mud		ANOVA
	Mean	F (%)	Mean	F (%)	(P)
Ophelina cylindricaudata Hansen 1878	0.00	0.0	1.94	68.8	---
Ophelina acuminata Oersted 1843	0.00	0.0	0.13	6.3	---
Ophelia rullieri Bellan 1975	0.69	25.0	0.00	0.0	---
Petaloproctus tenuis Arwidson 1907	0.00	0.0	0.25	12.5	---
Praxillella praetermissa Malmgren 1865	0.00	0.0	1.81	68.8	---
Mediomastus ambiseta (Hartman 1947)	1.81	68.8	0.13	12.5	0.000
Scoloplos armiger (OF Müller 1776)	0.69	50.0	0.31	18.8	0.213
Lumbrinereis fragilis (OF Müller 1776)	0.06	6.3	0.00	0.0	---
Nothria conchilega (Sars 1835)	0.06	6.3	0.13	12.5	0.559
Glycera capitata Oersted 1843	0.06	6.3	0.00	0.0	---
Goniada maculata Oersted 1843	1.06	68.8	0.81	56.3	0.465
Pholoe tecta Stimpson 1854	1.75	68.8	0.00	0.0	---
Prionospio steenstrupi Malmgren 1867	5.69	100.0	0.25	18.75	0.000
Polydora websteri Hartman 1943	1.13	68.8	0.13	12.5	0.002
Laonice cirrata (Sars 1851)	0.44	31.3	0.00	0.0	---
Trochochaeta multisetosa (Oersted 1844)	0.06	6.3	0.00	0.0	---
Euchone papillosa (Sars 1851)	0.31	31.3	0.94	50.0	0.079
Pectinaria granulata (Linnaeus 1767)	0.06	6.3	0.00	0.0	---
Nephtys ciliata (O.F. Müller 1776)	0.25	18.8	0.06	6.3	0.243
Phyllodoce mucosa Oerstead 1843.	0.44	25.0	0.00	0.0	---
Hartmania moorei Pettibone 1955	1.50	62.5	0.00	0.0	---
Ampharete lindstroemi Malmgren 1867	0.00	0.0	0.19	6.3	---
Lysippe labiata (Malmgen 1866)	0.13	12.5	0.75	56.3	0.011
Terebellides stroemi Sars 1835	0.25	18.8	0.00	0.0	---

In most of the 24 species included in Table 3.2, a given species was either restricted to one habitat type or differences in density between habitats were significant ($P<0.05$). Nine out of twenty four species were collected in both habitats and densities were significantly different ($P<0.05$) in four cases.

3.5.2 Local and regional distribution

Species occurrences at the local (Bonne Bay) and regional scale (Atlantic Canada) are summarized in the top panels of Figs. 3.2-3.9. With the exception of *Ophelia rullieri*, the opheliids have been recorded from several locations in the region (Fig. 3.2). Within Bonne Bay, however, the three species were collected from single sites. Both *Petaloproctus tenuis* and *Mediomastus ambiseta* were relatively limited in their distributions across Atlantic Canada (Fig. 3.3), whereas *Praxillella praetermissa* has been reported from Labrador to the Gulf of St. Lawrence. In contrast, within the fjord *P. praetermissa* was the only species restricted to a single site.

Scoloplos armiger, *Lumbrineris fragilis*, and *Nothria conchilega* are widely distributed in Atlantic Canada, although *L. fragilis* was restricted to sandy sediments of South Arm in Bonne Bay (Fig. 3.4). Broad local and regional occurrences have also been recorded for *Glycera capitata*, *Goniada maculata*, and *Pholoe tecta* (Fig. 3.5). *Prionospio steenstrupi* is broadly distributed throughout Atlantic Canada whereas the two other spionids (*Polydora websteri* and *Laonice cirrata*) have more restricted distributions within and outside Bonne Bay (Fig. 3.6).

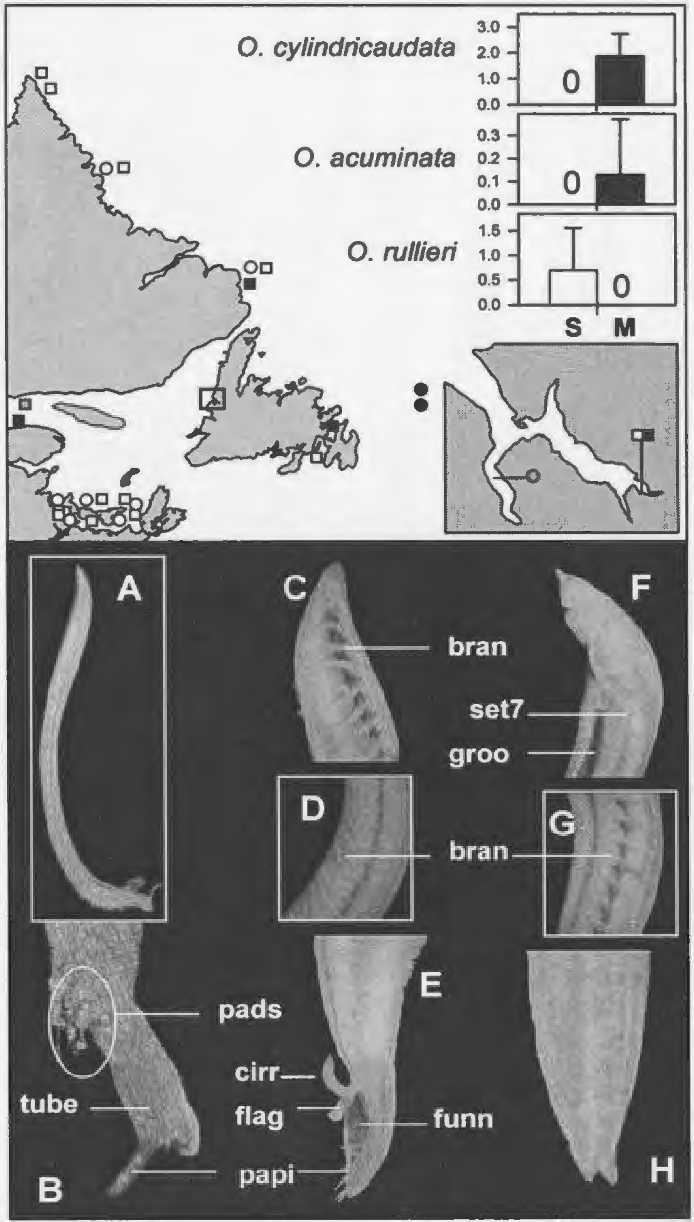

Figure 3.2 Maps: *O. cylindricaudata* (black symbols), *O. acuminata* (white), and *O. rullieri* (gray). Squares and circles are from muddy and sandy sediments, respectively. Graphs are mean densities per 38.5 cm2 (+ 95% CI) in sandy (S, open bars) and muddy sediments (M, filled bars). Identification characters: *O. cylindricaudata,* A) body shape, B) anal tube (tube) with rounded parapodia (pads), and long papilla (papi). *O. acuminata,* C) anterior end with branchiae in firsts setigers, D) middle region, E) anal funnel (funn) with anal cirri (cirr), flagellum (flag), and papillae (papi). *O. rullieri,* F) anterior end with groove (groo) starting at setiger 7 (set7), G) middle region with short branchiae (bran), H) pygidium with rounded papillae (papi).

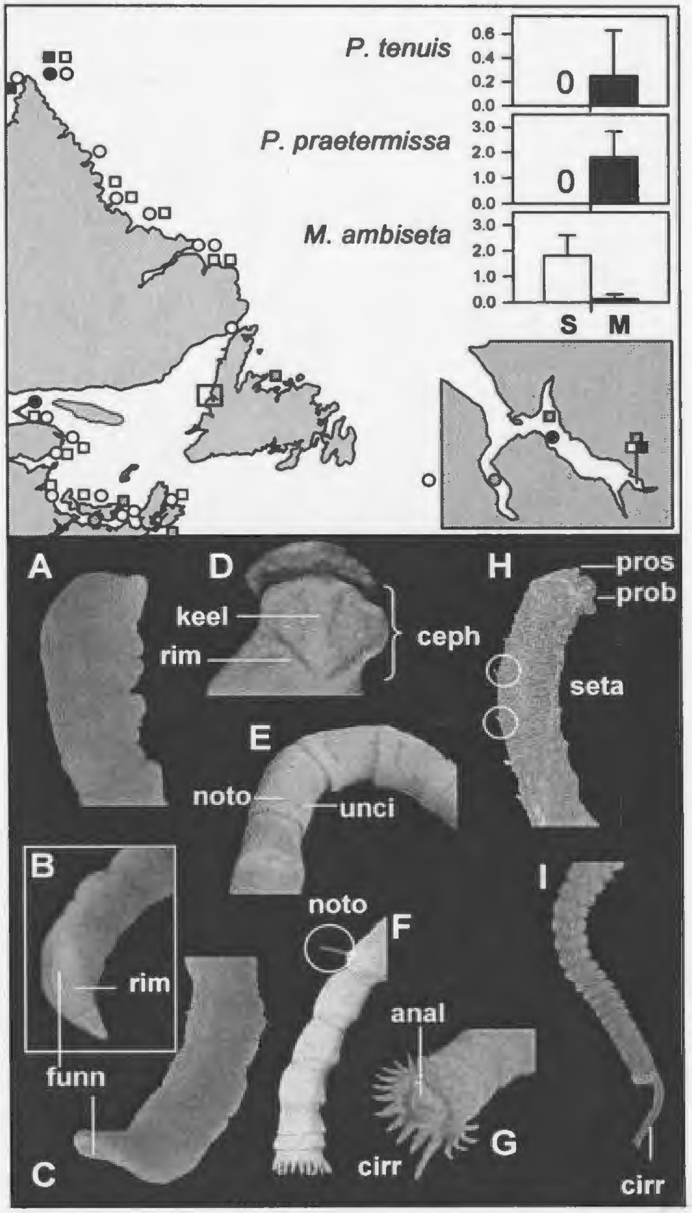

Figure 3.3 Maps: *P. tenuis* (black symbols), *P. praetermissa* (white), and *M. ambiseta* (gray). Other details as in Fig. 2. Identification characters: *P. tenuis,* A) anterior end, B) and C) posterior end and detail of anal funnel (funn) and rim. *P. praetermissa,* D) cephalic plate (ceph) and detail of keel and rim, E) anterior setigers with notosetae (noto) and neuropodial uncini (unci), F) pre-anal achetous segments, and G) anal plate with cirri (cirr). *M. ambiseta,* H) anterior end with prostomium (pros), proboscis (prob) and notosetae (seta), I) anal cirrus (cirr).

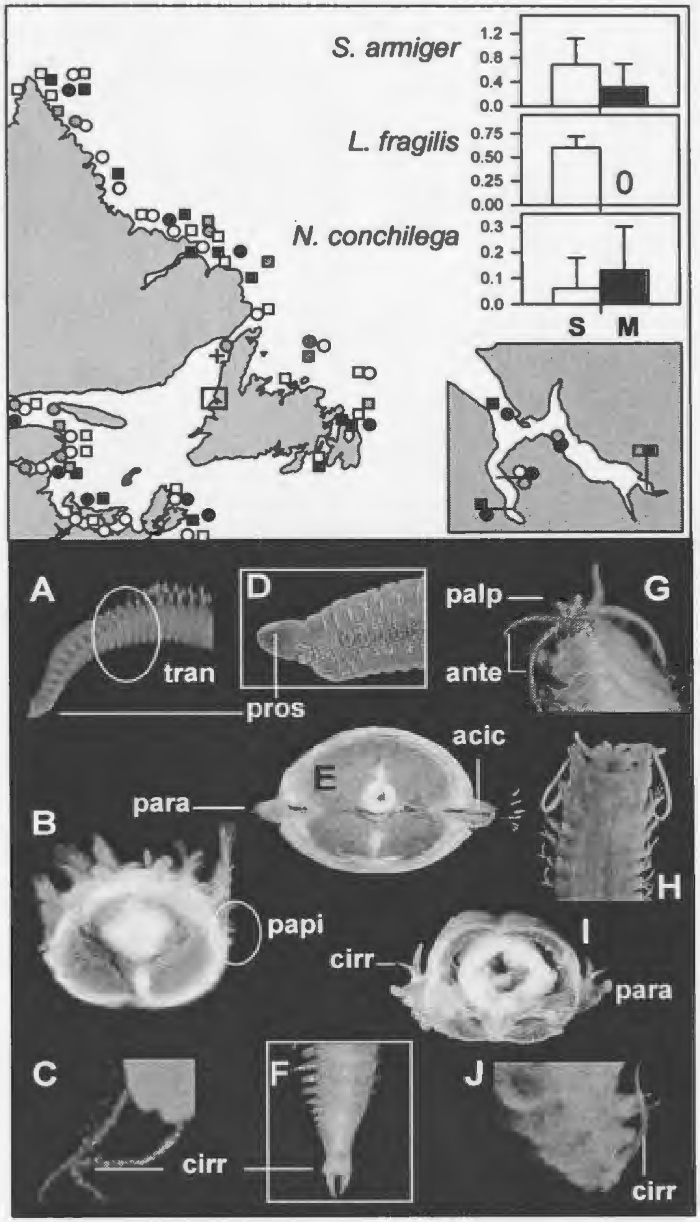

Figure 3.4 Maps: *S. armiger* (black symbols), *L. fragilis* (white), and *N. conchilega* (gray). Other details as in Fig. 2. Identification characters: *S. armiger,* A) anterior and transitional (tran) parapodia, B) cross section (2 segments) with subpodal papillae (papi), C) anal cirri (cirr). *L. fragilis,* D) prostomium (pros), E) cross section of parapodium (para) with black aciculae (acic), F) posterior end and cirri. *N. conchilega,* G) and H) anterior end with palps and antennae (ante), I) cross section with parapodial branchia (para) and cirri (cirr), J) posterior end with anal cirri.

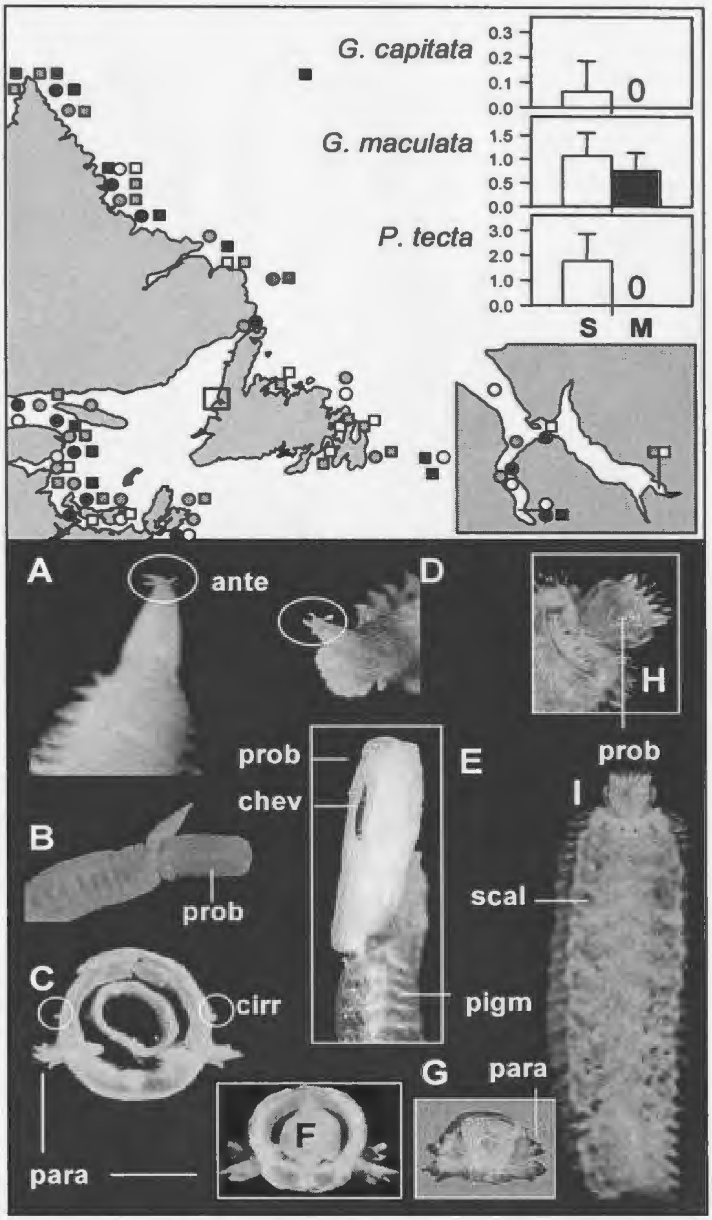

Figure 3.5 Maps: *G. capitata* (black symbols), *G. maculata* (white), and *P. tecta* (gray). Other details as in Fig. 2. Identification characters: *G. capitata,* A) and B) anterior end with antennae (ante) and proboscis (prob), C) parapodial dorsal cirri (cirr). *G. maculata,* D) and E) anterior end with antennae, proboscis (prob) with chevrons (chev), and pigmentation (pigm), F) and G) cross sections of anterior uniramous and posterior biramous parapodia (para). *P. tecta,* H) anterior end showing eyes and everted proboscis (prob), I) dorsal view, cover of scales (scal) and pigmentation.

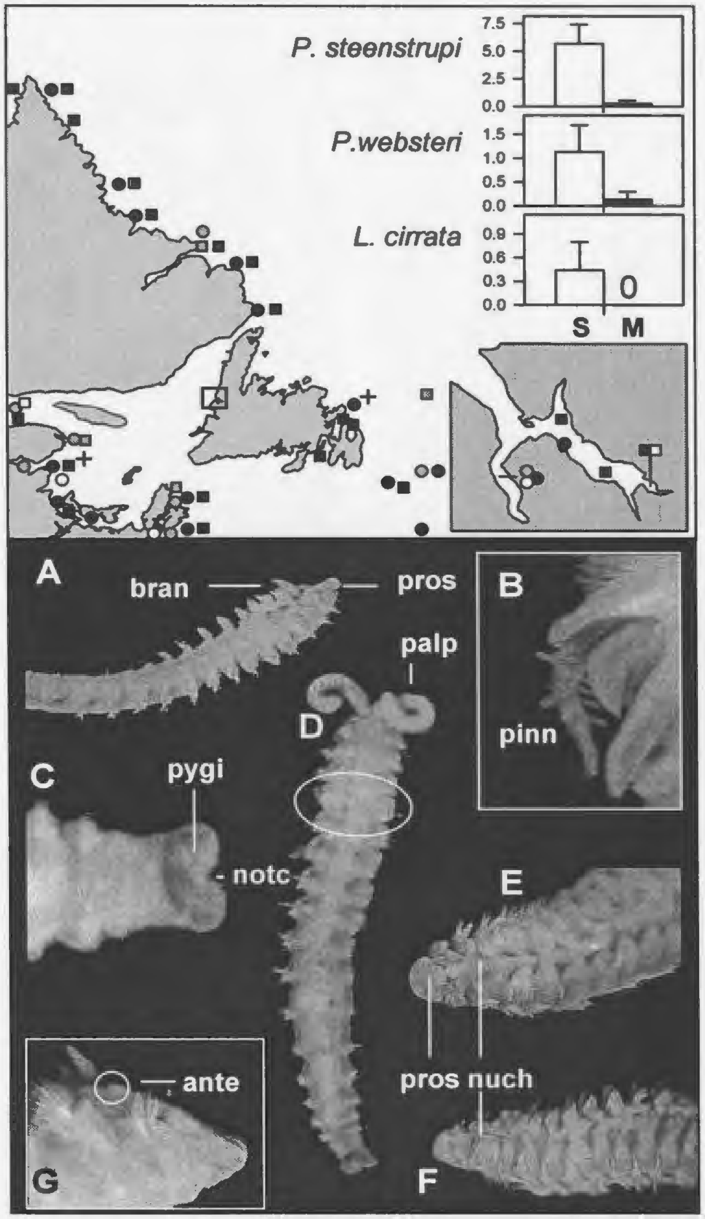

Figure 3.6 Maps: *P. steenstrupi* (black symbols), *P. websteri* (white), and *L. cirrata* (gray). Other details as in Fig. 2. Identification characters: *P. steenstrupi:* A) prostomium (pros) and anterior end with branchiae (bran), B) detail of pinnate branchiae (pinn). *P. websteri*: C) pygidium (pygi) with typical notch (notc), D) dorsal view with 5th modified setiger. *L. cirrata*: E) and F) prostomium (pros) and nuchal organ (nuch), G) lateral view showing the occipital antenna (ante).

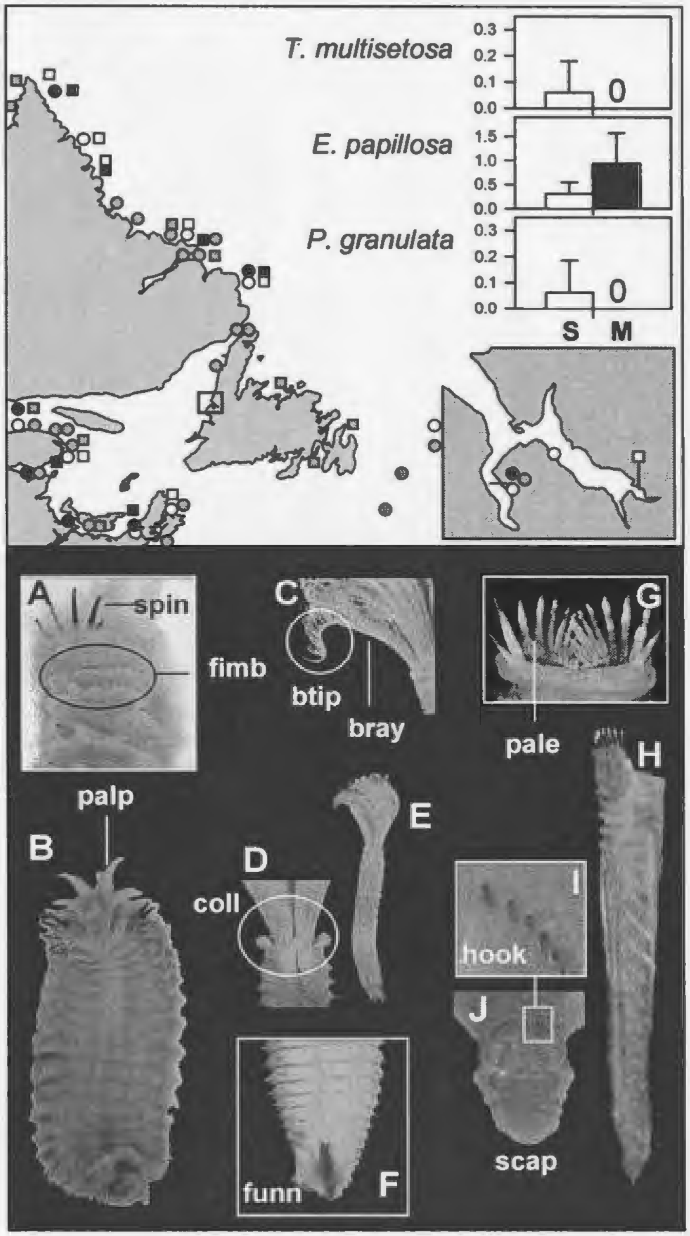

Figure 3.7 Maps: *T. multisetosa* (black symbols), *E. papillosa* (white), and *P. granulata* (gray). Other details as in Fig. 2. Identification characters: *T. multisetosa,* A) anterior end with spines (spin) and fimbriated post-setal noto and neuropodia (fimb), B) ventral view with position of palps (palp). *E. papillosa,* C) branchial ray and tip (bray, btip), D) basal collar (coll) and gap, E) body shape, and F) anal funnel (funn). *P. granulata,* G) anterior end with cephalic paleae (pale), H) lateral view, and I) and J) scaphal hooks and scaphal region.

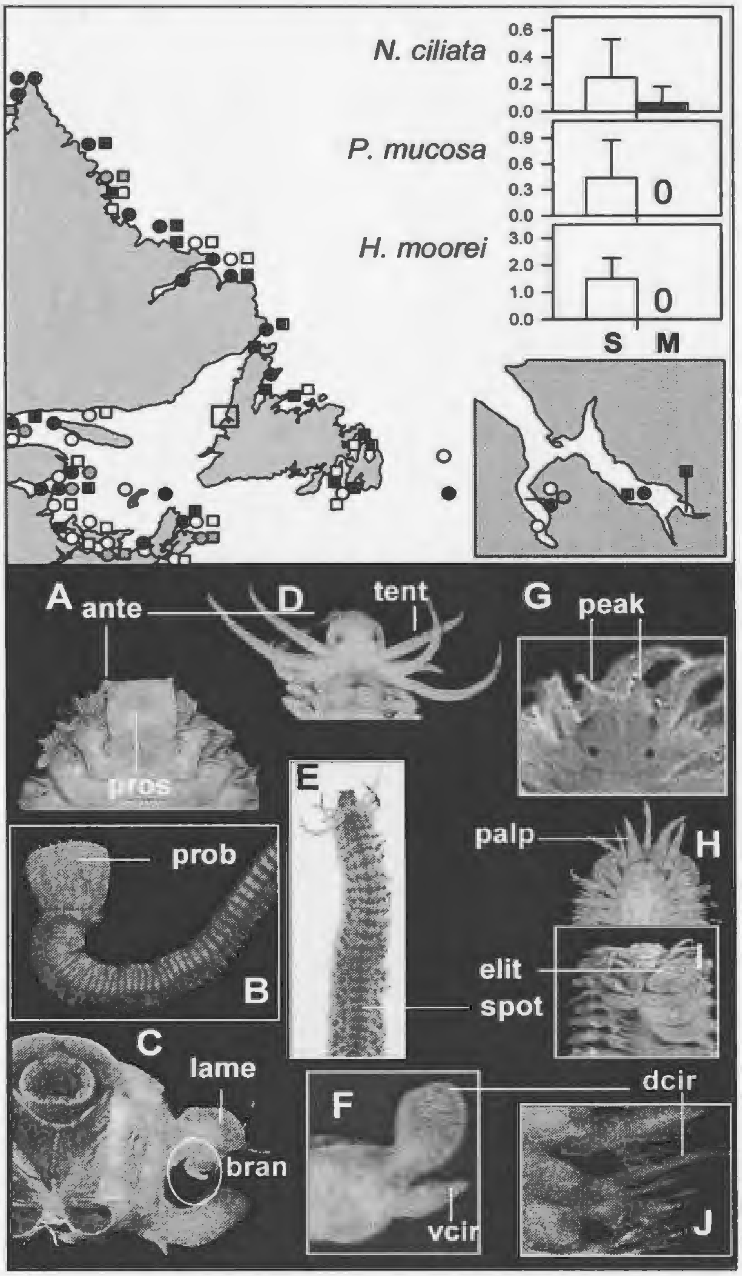

Figure 3.8 Maps: *N. ciliata* (black symbols), *P. mucosa* (white), and *H. moorei* (gray). Other details as in Fig. 2. Identification characters: *N. ciliata:* A) prostomium (pros) and antennae (ante), B) proboscis (prob), C) cross section showing recurved branchia (bran) and posterior lamella (lame). *P. mucosa*: D) Anterior end with antennae (ante) and tentacular cirri (tent), E) dark spots on a dorsal view, F) cross section showing parapodial dorsal and ventral cirri (vcir, vcir). *H. moorei*: G) anterior end with eyes and cephalic peaks, H) ventral view showing palps, I) dorsal view with elitra (elit), J) detail of parapodial dorsal cirri (dcir).

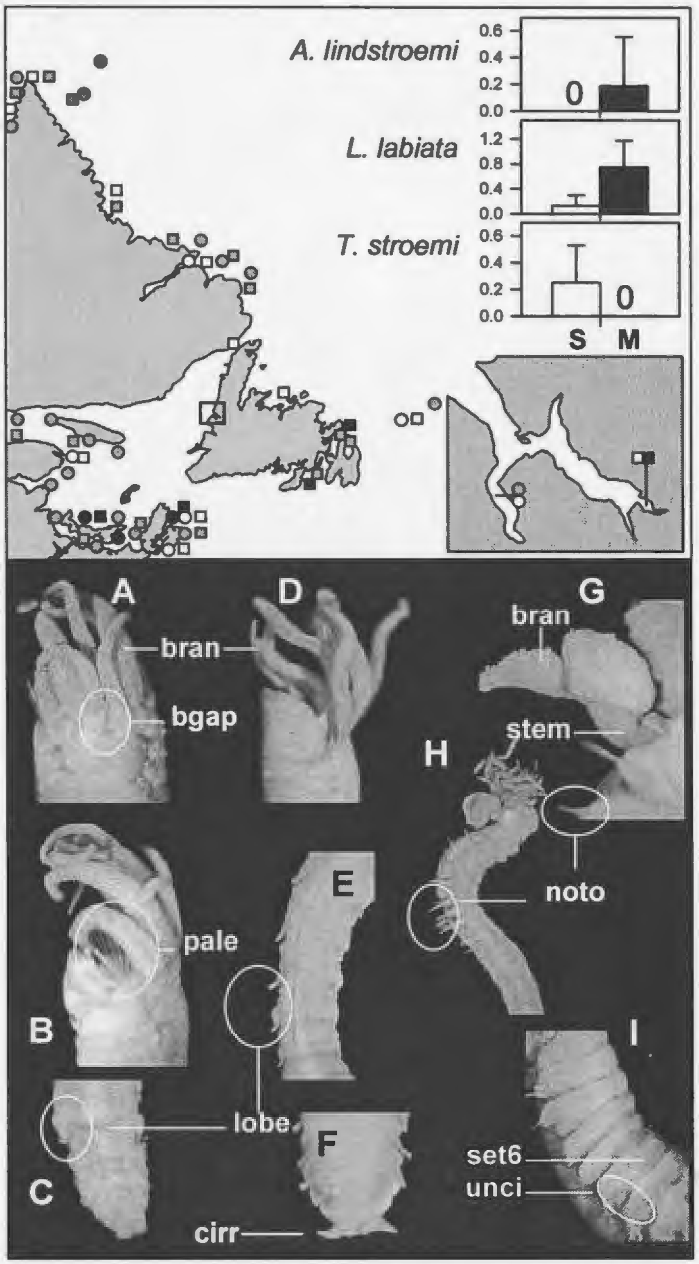

Figure 3.9 Maps: *A. lindstroemi* (black symbols), *L. labiata* (white), and *T. stroemi* (gray). Other details as in Fig. 2. Identification characters: *A. lindstroemi*: A) anterior end with branchial gap (bgap), B) lateral view with paleae (pale), C) abdominal segments with neuropodial lobes (lobe). *L. labiata* D) anterior end, lateral view, E) abdominal segments with neuropodial lobes (lobe), F) anal cirri (cirr). *T. stroemi*: G) anterior end and branchial lobes (bran) and stem, H) notopodial setae (noto), and I) uncini (unci) starting at setiger 6 (set6).

Trochochaeta multisetosa, *Euchone papillosa*, and *Pectinaria granulata* are all broadly distributed regionally, but only *E. papillosa* was collected in more than one area of Bonne Bay (Fig. 3.7). *Hartmania moorei* was restricted to the South Arm of Bonne Bay, and scattered areas of the Gulf of St. Lawrence and Labrador (Fig. 3.8). In contrast, *Nephtys ciliata* and *Phyllodoce mucosa* were more broadly distributed throughout the region. *Ampharete lindstroemi* was restricted to Southeast Arm and the southern Gulf of St. Lawrence (Fig. 3.9). *Lysippe labiata* and *Terebellides stroemi* were more widely distributed throughout Newfoundland and coastal Labrador.

3.5.3 Identification characters

Key characters to identify the 24 polychaetes are displayed in the lower panels of Figures 3.2-3.9. They are provided to facilitate the initial identification of many of the abundant sedimentary polychaetes, but subsequent (confirmatory) work with detailed taxonomic keys is recommended.

3.6 DISCUSSION

The results of this Chapter suggest that species associated with more than one type of sedimentary habitat (9 out of 24 species in this study) are more broadly distributed within the fjord and across the region. In contrast, species associated with a single sediment type were less widely distributed, although no cases of strict association with either sediment type were found in the examination across the region. The association of species with one or more sediment types is the result of multiple rather than single causal factors (see reviews by Gray 1974; Snelgrove & Butman 1994). These factors likely include dispersal strategies, food availability, interactions with benthic and epibenthic fauna, and physical disturbance (rewieved by Josefson 1985; Olafsson et al. 1994; Lenihan & Micheli 2001).

3.6.1 Habitat and local distribution

Polychaetes accounted for most of the diversity and abundance of the infauna communities at the sandy site, but were less numerically important at the muddy site. Cumaceans (mainly *Lamphros fuscata*) and amphipods (*Bathymedon obtusifrons*) were found in high numbers in the muddy sediments (Quijón & Snelgrove in press) and explain why polychaete density is a poor predictor of overall macrofaunal diversity. These results suggest limitations in the use of polychaetes as surrogates for biodiversity (cf. Olsgard et al. 2003) when contrasting habitats are included. Although hydrodynamic conditions in the muddy site were presumably more calm and stable (Nowell & Jumars 1984), density and diversity of polychaetes (and complete communities) were higher in the sandy habitat. This pattern suggests that an array of factors other than just hydrodynamics contributes to polychaete diversity, despite the relatively high proportion of polychaete species that are deposit feeders (cf. Fauchald & Jumars 1979) and would therefore be expected to occur in higher diversity in mud environments. Differences in food availability (as shown by C:N ratios) likely contribute to habitat differences in diversity and abundance. Quality and presumably quantity of organic matter were better in the sandy habitat (lower C:N ratio, $P<0.05$; Blackburn et al. 1996), a result likely related to higher surface productivity in South Arm (R. Hooper, pers comm). The muddy site was located in an inner arm near a river inflow, which represents an area where accumulation of refractory debris with low nutritional value is more likely (Klitgaard-Kristensen & Buhl-Mortensen 1999).

Those species distributed in more than one sediment type habitat belong to an array of feeding guilds including surface and sub-surface deposit feeders (e.g. *Scoloplos armiger* and *Prionospio steenstrupi*, respectively; Fauchald & Jumars 1979; Josefson 1986), suspension feeders (e.g. *Euchone papillosa*; Fauchald & Jumars 1979), and predatory worms (e.g. *Nephtys ciliata* and *Goniada maculata*, Josefson 1986). Such a diversity of feeding guilds suggests that there are a variety of shallow sedimentary deposits suitable for species to occupy within the fjord (cf. Armonies & Reise 2003), or simply a higher dispersal potential (*sensu* Bhaud 1998) to colonize areas of contrasting hydrodynamics. Physical contrasts are typically observed between inner and outer areas of fjords and are accentuated by the presence of shallow sills like the one in Bonne Bay (~15 m deep). Sills significantly influence the flux and distribution of organic matter (Aure & Stigebrandt 1989), and therefore the distribution of benthic organisms (Buhl-Mortensen 1996; Holte & Gulliksen 1998).

3.6.2 From local to regional distribution

Given the contrast between habitats inside and outside fjords, species that occur in both the inner and outer arms of Bonne Bay are more likely to be broadly distributed regionally. Several species collected here (e.g. *Scoloplos armiger*, *Laonice cirrata*) have been documented from an array of habitats from offshore to inner fjord habitats in northern latitudes (Holte 1998; Holte & Gulliksen 1998, Oug 2000). Instead, species such as *Terebellides stroemi* have been collected from narrower distributional ranges along Norwegian fjords (Hutchings and Peart 2000). At the geographical scale reviewed here, most species occurred along the Labrador coast and the northern coast of Nova Scotia. Although absence of a given species may simply reflect insufficient sampling effort (Briggs 1974), the polychaete assemblage of the fjord reflects its association with the Gulf of St. Lawrence, a transitional system between the Labrador and Acadian provinces (Brunel et al. 1998). As many as 505 and 498 invertebrate species from the Labrador and Acadian provinces, respectively, occur in the Gulf of St. Lawrence (Brunel et al. 1998). Moreover, the Gulf of St. Lawrence should harbor most of the 123 species of polychaetes shared by those two provinces (Pettibone 1956; Pocklington & Tremblay 1987).

Biogeographic limits in the Western North Atlantic have been reviewed and debated for decades (e.g. Briggs 1974; Steele 1975; Longhurst 1998). Based on affinity and species overlaps, several authors have proposed to merge the fauna from the Arctic and Labrador in a large "Arctic" province, and the Acadian and Virginian faunas in a "Boreal" province (see review by Pocklington & Tremblay 1987). Remarkably, the distinction between Labrador (Arctic) and Acadian (Boreal) provinces has not been questioned, and most authors agree on a boundary located between 44° and 52°N (Briggs 1974; Pocklington & Tremblay 1987). This reinforces the argument that the fauna of Bonne

Bay is transitional and therefore representative, at least in terms of species composition, of a large portion of the Western North Atlantic.

3.6.3 Polychaete identification

Taxonomy represents a challenge not only because the high proportion of un-described species, but also because of confusion over the taxonomy of those already described (Hutchings 1998). Although the specimens analyzed match the available descriptions (Pettibone 1963; Banse & Hobson 1974; Fauchald 1977; Appy et al. 1980; Hobson and Banse 1981; Light 1978; Blake et al. 1995), several cases are under scrutiny, and thus, require a note of caution. Younger stages of *Scoloplos armiger* have been frequently confused with *S. acutus* (Verrill, 1873), and *Pholoe tecta* synonymized with *P. minuta* (Fabricius, 1780) (Pocklington 1989). Although some authors use *Pholoe (minuta) tecta* (eg. Rouse & Pleijel 2001), the most frequently used name (*P. tecta*) should prevail (K. Fauchald, pers comm). In a few other cases, the debate focuses on the use and change of names: Some authors use *Onuphis* instead of *Nothria conchilega* (e.g. Banse & Hobson 1974), *Praxilla* instead *of Praxillella praetermissa* (eg. Fauchald 1977) or *Cisterna* instead of *Pectinaria granulata* (Appy et al. 1980). Further studies are required in order to clarify the taxonomy of these and several other groups of polychaetes (e.g. *Polydora*; Manchenko & Radashevsky 1998; *Phöloe*, Petersen 1998; *Terebellides*, Hutchings and Peart 2000; *Euchone*, Cochrane 2000; *Prionospio*, Sigvaldadóttir 2002). Given their abundance and species richness, polychaetes are essential for future research on benthic biodiversity. That research would help to alleviate the biases generated by the geographical gaps that still exist, particularly at high latitudes of the North Atlantic. This research should also re- valuate taxonomy as a central discipline for the study of biodiversity (Maurer 2000; Giangrande 2003), and the ecological processes that affect and regulate biodiversity.

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CHAPTER 4

PREDATION REGULATION OF SEDIMENTARY INFAUNA: POTENTIAL EFFECTS OF A FISHERY-INDUCED SWITCH IN PREDATORS IN A NEWFOUNDLAND SUB-ARCTIC FJORD

4.1 PREFACE

The predator spatial patterns and prey habitat-related variability explored in Chapters 2 and 3, respectively, set the stage for the experimental examination of predator regulation that is the basis of this Chapter. Field exclusion and inclusion experiments, in parallel with laboratory experiments, are used to evaluate the influence of crustacean predators on an array of benthic community response variables. This chapter also places crustacean decapods into a broader context that relates to historical changes in their abundance as a result of the Newfoundland fishery, and potential changes occurring in infaunal communities.

4.2 ABSTRACT

The collapse of the cod fishery in Newfoundland has coincided with marked increases in abundances of snow crab, pandalid shrimp, and other crustaceans that prey on sedimentary infauna. A three- year sampling program in Bonne Bay, Newfoundland

indicates differences in composition and number of these predators in the two main arms of the fjord that coincides with strong differences in benthic community structure. To test whether predation pressure contributes to the observed patterns in sedimentary fauna, exclusion field experiments with full and partial cages were deployed in both arms at 30-m depth and sampled along with ambient sediments at 0, 4, and 8 week periods.

Predation significantly influenced species composition, abundance and, in some cases, diversity. The most striking changes included increases in the polychaetes *Pholoe tecta* and *Ophelina cylindricaudata* in exclusions relative to controls, and corresponding declines in the polychaete *Paradoneis lyra* and the cumacean *Lamphros fuscata*. In laboratory experiments, fresh non-disturbed sediment cores from each experimental area were either protected or exposed to snow crab, the most abundant predator in the bay. A snow crab inclusion experiment was also carried out in the field, using cages similar to those used for exclusions. Both types of experiments detected between-site differences and a predator effect that was very similar to that documented in exclusion experiments. Thus, despite differences in the scales associated with each type of experiment, our results suggest that crab predation is a significant structuring force in Newfoundland sedimentary communities. Given the historical changes that have occurred in predator composition as a result of over-fishing, it is hypothesized that broad-scale community changes may be taking place in North Atlantic benthic ecosystems.

4.3 INTRODUCTION

Among the most pervasive effects of fisheries is the alteration of food webs through removal or alteration of top predators (e.g. Botsford et al. 1997; Pauly et al. 1998; Jackson et al. 2001), and the potential establishment of alternate states that favor different predator fields. In coastal Newfoundland, overfishing led to a complete collapse of all cod stocks (Hutchings 1996; Myers et al. 1996), with an associated increase in primarily benthic predators such as snow crab and shrimp (Koeller 2000; Worm & Myers 2003). The collapse of cod, a natural predator of snow crab and shrimp, may represent a predator release that has resulted in increased numbers of both crustacean species (Lilly 2000; Bundy 2001). This switch in top predators is expected to have significant ramifications for benthic infauna, given that snow crab and shrimp, in contrast with adult cod, are primarily benthic feeders (Brêthes et al. 1984; Bergström 2000). Few studies have examined cascading effects of ecosystem alteration in the marine realm, but there is evidence that top-down effects may be more important than bottom-up effects (Jennings & Kaiser 1998; Micheli 1999). Thus, the rapid increase in shrimp and crab in coastal Newfoundland over the last decade may have cascading effects for sedimentary systems.

Numerous benthic predators including blue crab reach their northern distribution limit near Cape Cod (Williams 1984), and it has been suggested that predation plays a lesser role in benthic communities located farther north in the western Atlantic (Woodin 1976). Nonetheless, increasingly large numbers of northern-native species (rock crab, Jonah crab, snow crab, pandalid shrimp, mud shrimp) and invasive species (e.g. green crab in Nova Scotia and New England) suggest otherwise (Hudon & Lamarche 1989; Jamieson 2002). Predation is thought to play a key role in marine sedimentary systems in part because of the lack of clear evidence for competitive exclusion (Peterson 1979; Wilson 1991; Woodin 1999). Although some effects of predation have been demonstrated (see Olafsson et al. 1994; Lenihan & Micheli 2001), numerous experimental studies have found no consistent regulatory role (Thrush 1999). Explanations for the absence of a clear effect include prey mobility and exchange that mask predation losses (Frid 1989; Englund 1997; Cooper et al. 1990), prey recruitment outpacing post-settlement consumption (Thrush 1999), time limitation and habitat accessibility to predators (Kneib 1997; Webb & Kneib 2004), landscape structure (Webb & Kneib 2004), and indirect interactions counterbalancing negative effects of epibenthic predators (Commito & Ambrose 1985; Kneib 1991). Variation in predator density, mobility, and feeding rates also hinder our capacity to detect predation effects (Clark et al. 1999; Seitz et al. 2001).

Detection of predation is challenging. Field manipulations have significant limitations (Hulberg & Oliver 1980; Peterson & Black 1994) but remain the best tool for testing predator effects (Hall et al. 1990). Nonetheless, cage experiments alone may not suffice if they are restricted to a single site (Fernandes et al. 1999) or are not combined with surveys and/or other types of manipulations (Thrush et al. 1997 and references therein). Combined field and laboratory experiments have proven to be the most informative experimental approach because they examine different scales, have different strengths, and may potentially complement each other (Wiens 2001). This combined approach was used to study the role of predation in Bonne Bay, a Newfoundland sub-arctic fjord in the northwest Atlantic. Preliminary observations from inner and outer areas of the bay indicated strong differences in benthic community structure, and in the number and composition of epibenthic predators (Hooper & Wieczoreck 1995). The fact that infaunal organisms, particularly polychaetes, constitute the main part of crab and shrimp diets (Squires & Dawe 2003; Scarrat & Lowe 1972; Bergstrom 2000) suggests that increased predation pressure from these species may play a key regulatory role for benthic community structure.

This hypothesis was tested by deploying cage exclusion experiments and an inclusion experiment in the two main arms of the fjord, and by using sediments (with intact infauna) from those sites to carry out parallel laboratory predation experiments. Bonne Bay also offers a unique opportunity to study these interactions because an abundant guild of crab and shrimp, which typically occur at greater depths, congregate in sedimentary habitats that are accessible by divers during the spring-summer season (Hooper 1996; Ennis et al. 1990), Additional studies have focused on predator life histories in the bay (snow crab: Comeau et al. 1998, 1999; Conan et. al. 1996), and in the Gulf of St. Lawrence (snow crab: Brêthes 1987; Sainte-Marie & Gibert 1998; pandalid shrimp: Ouellet & Lefaibre 1994; Ouellet et al. 1995; Simard et al 1990; Rock crab: Hudon & Lamarche 1989). Based on these preliminary observations, we hypothesize that there are strong epifaunal predatory influences on infaunal abundance, diversity and dominance.

4.4 MATERIALS AND METHODS

4.4.1 Study area

Bonne Bay fjord is located in Western Newfoundland (Fig. 4.1) comprises two main arms. East Arm is a deep (up to 230 m) inner basin that is partly separated from the outer bay by a shallow sill (~12 m deep), whereas South Arm is a shallower basin (up to 55 m deep) that is fully open to the adjacent Gulf of St. Lawrence. Study sites for crab abundance estimates and experiments were established in each of these main arms. Currents and circulation in some areas of the bay have been described by Gilbert & Pettigrew (1993). Detailed studies of benthic communities are lacking except for lists of invertebrates (Rivard & Bowen 1971; Hooper 1975), and selected communities (Wieczorek & Hooper 1995).

4.4.2 Predator distribution

Relative abundance of epibenthic predators were estimated with baited traps (~40x30x60 cm, ~1 cm net) that were deployed during the summer seasons of 1999 to 2001. Traps were deployed at 35-50 m deep for 1-2 days (data standardized as crab • $\text{trap}^{-1}\text{day}^{-1}$) every 2-3 weeks. Direct comparison of catch numbers and frequencies was not possible because deployments were not simultaneous and catch rates were highly variable (within and among traps, sites, and summers). Instead, summer averages were calculated by using catches per sampling period as replicates. Baited traps do not provide absolute density estimates, and this approach yields only relative density comparisons between the two sites.

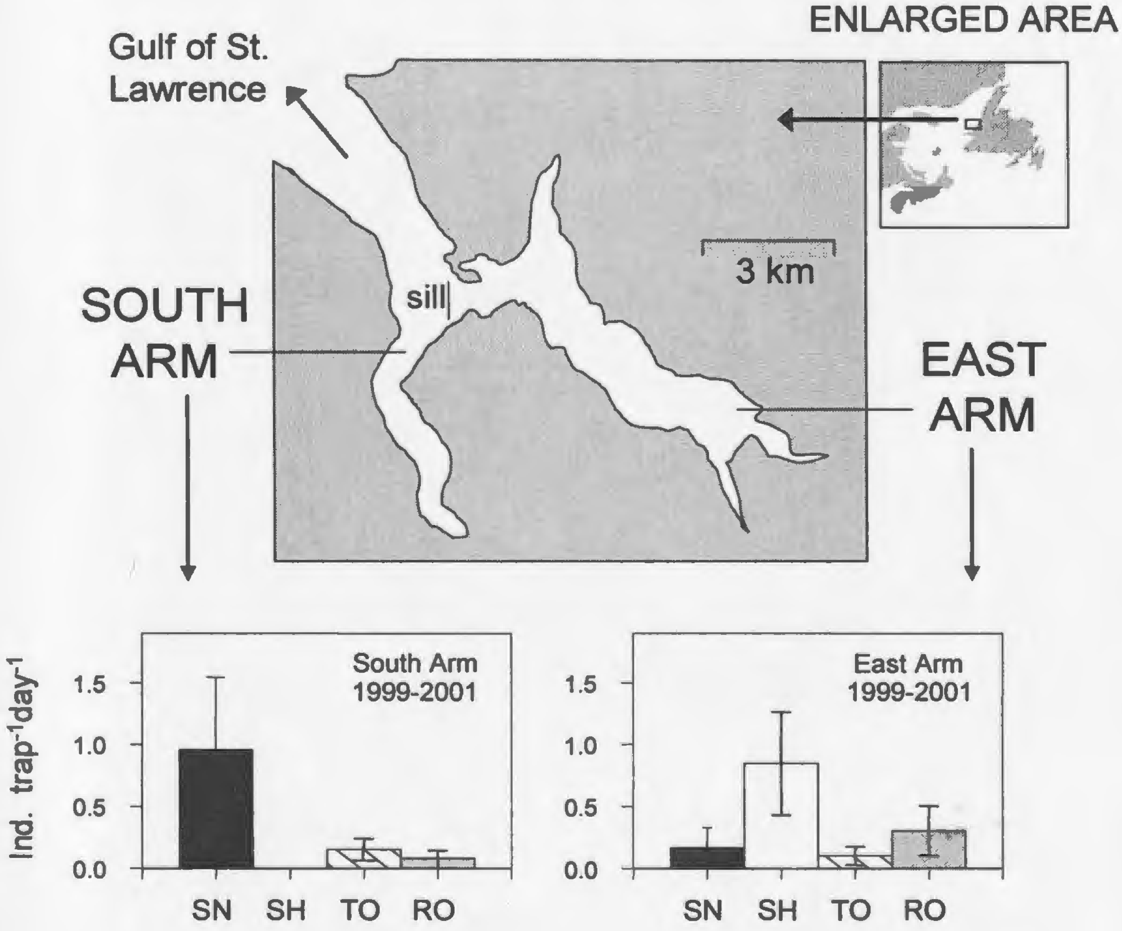

Figure 4.1 Map of Bonne Bay, with the location of South and East Arms where predator sampling and manipulative experiments were conducted. Lower panels indicate mean summer abundances (+/- 95% confidence intervals) of the main epibenthic predators at each site during 1999-2001. SN: Snow crab, SH: Shrimp, TO: Toad crab, RO: Rock crab.

4.4.3 Field exclusion experiments

Two exclusion experiments were deployed at ~30-m depth in South and East Arms (Fig. 4.1). Each experiment included three treatments and four replicates that were haphazardly interspersed; treatments included full cages or “exclusions”, partial cages or “artifact treatments”, and ambient undisturbed sediments or “controls”. Cages (1-m diameter x 15 cm high, pushed 3 cm into sediments) were circular in shape to minimize erosion / deposition of sediments in different areas of the cages. Cages were anchored to the bottom by four ~4 cm long “legs” extended from the main frame into the sediment. Plastic 1x1 cm mesh covered partial (50% of top and side) and full cages.

Infaunal organisms were sampled with tube cores (7 cm diameter; 10 cm deep; 2 cores per sample) that were collected by scuba divers. Initial sampling (two sets of four samples) took place on June 25th 1999, immediately prior to deployment of full and partial cages. These samples were used for comparison with ambient sediments and cages sampled after 4 and 8 wk (see BACI design below). Sampling was never repeated within a given caged or ambient location, because cages were removed immediately after sampling. This approach minimized potential disturbance effects and created statistical independence in evaluating predation after 4 and 8 weeks. Coincident with the 8-wk samples, additional sediment cores were collected from all treatments in order to study grain size distribution and CHN content. These analyses allowed us to evaluate potential sediment-related artifacts associated with caging treatments.

4.4.4 Laboratory and inclusion experiments

Two laboratory experiments were conducted in June 2000 to evaluate the potential impact of snow crab predation on benthic organisms under controlled conditions. A series of flow-through tanks (1°C) at the Bonne Bay Field Station were supplied with cold water pumped from depths where cores were collected. Within these tanks, freshly-collected sediment cores with intact infauna were exposed to snow crab feeding. Sediment cores (7-cm diameter, ~10 cm depth) were obtained by divers from each experimental site (South and East Arms). Cores were taken carefully to avoid physical disturbance and were transported to the laboratory in coolers to minimize stress to infauna, thus maximizing the likelihood that core treatments would be representative of natural communities.

Six sediment cores were placed in each tank (three tanks per experiment) and a plastic plate was used to create a false bottom so that the plastic core tube was flush with the plate. Sediment inside the cores was gently extruded so that it was also flush with the acrylic plate, creating a smooth transition between sediments, core tube, and plastic plate. Sediments (and infauna) were acclimated to these conditions for 24 hours prior to initiation of experiments. One snow crab (male, 60-75 mm carapace length) was added to each tank with open access to three of the cores (controls). The other three cores in the tank were protected with plastic mesh, thus excluding predators. Exposed and protected treatments were randomly distributed within each tank. Experiments lasted for 96 hours, after which snow crabs were removed, tanks were carefully drained, and sediment cores were collected and processed (see below).

In order to provide a linkage between field exclusion experiments and laboratory manipulations, full cages (N=4) similar to those used for exclusion experiments were used in the field to confine snow crabs (1 crab per cage) for 96 h. After that crabs were released and samples were collected from cages and ambient sediments as described above for exclusion experiments. Inclusion experiments were initiated in both arms of the bay during June 1999 but weather constraints made recovery of samples from South Arm impossible. Thus, only results from East Arm are reported here.

4.4.5 Sample processing and analysis

Cores of sediments from field and laboratory experiments were processed through a 500 μm sieve and preserved in a 10% sea water- formalin solution, prior to transfer to 70% ethanol with Rose Bengal to facilitate sorting and identification. Macrofaunal organisms were enumerated and identified to the lowest taxonomic level possible, which was usually species. Samples for grain size analysis were pre-treated with a 1:1 water: peroxide solution and heated to 300°C to remove organic matter. They were then disaggregated by re-suspension with 0.1% Calgon solution, and passed through sieves to separate fractions of >350, >250, >177, >125, >88, and >62.5 μm by wet sieving. Finer fractions were sub-sampled (50 ml) and analyzed with a Sedigraph 5100 Particle Size Analyzer. Based on grain settling velocity the Sedigraph separated >53, >44, >37, >31,

>15, >7.8, >3.9, >2.0, >0.98, and >0.49 μm fractions. Each fraction was then expressed as percentage of total dry weight, and pooled into categories based on the Wentworth scale (Folk 1980): fine + very fine sand (>62.5 μm), silt (>3.9 μm), and clay (<3.9 μm). Additional sediment samples were processed with a CHN analyzer (Perkin Elmer Model 2400) to estimate C and N as a function of sediment dry weight. C:N ratios (an estimator of food quality for deposit feeders; Blackburn et al. 1996) were also calculated.

4.4.6 Data analysis

Patterns in benthic community structure were studied using Chord Normalized Expected Species Shared (CNESS). This similarity index estimates the number of species shared between two samples based on a random draw of m=10 individuals (cf. Trueblood et al. 1994) that makes the index sensitive enough to detect the contribution of rare as well as abundant species (Grassle & Smith 1976). The CNESS dissimilarity sample x species matrix was also used to cluster samples based on un-weighted pair-group mean average sorting. The program COMPAH 90 (E.D. Gallagher, U. Massachusetts, Boston) was used for this analysis. The CNESS sample by species matrix was then transformed to a normalized hypergeometric probability matrix (H), which was used in a Principal Components Analysis of hypergeometric probabilities (hereafter called PCA-H) to produce a two-dimensional metric scaling of CNESS distances among samples. Gabriel Euclidean Distance Biplots (Gabriel 1971) identified the species most important for among sample variation, and thus, driving community composition.

Four community response variables were calculated: total density and number of species per sample (77 cm^2), Shannon-Wiener Diversity ($H' = -\sum pi \log_e(p_i)$; with p_i= density of i species / total density), and Evenness ($J' = H'/H'max$; with $H'max = \log_e S$). Selection of indices was based on their widespread use in the literature (H'), sensitivity to rare species and independence from species richness (J'), and discriminant ability (H') (Magurran 1988; Smith & Wilson 1996). Statistical comparisons were all carried out with ANOVAs. For the field exclusion experiments, a "before-after, control-impact" (BACI) design was used. In this factorial design, the evidence for an impact (predation effect) appears as a significant time by treatment interaction (Green 1979). The model for this ANOVA was $y = \mu + \text{time} + \text{treatment} + \text{time x treatment} + \varepsilon$, where y refers to each response variable, μ is a mean constant, time refers to the "before-after" comparison (0-4wk or 0-8 wk), treatment refers to the "impact" comparison (control versus predator exclusion), and ε refers to the error term. Because logistic restrictions, artifact treatments were available only for the 8-week period, and therefore, artifact data were analyzed separately using the model $y = \mu + \text{site} + \text{treatment} + \text{site x treatment} + \varepsilon$. In this model, site is South or East Arm, treatment is control or artifact, and ε is the error term.

The model for the laboratory experiments was $y = \mu + \text{tank} + \text{treatment} + \varepsilon$, where tank refers to replicate tanks 1-3, and treatment refers to control (exposed to crab predation) versus exclusion. The model for the inclusion experiment was $y = \mu + \text{treatment} + \varepsilon$, where treatment refers to crab inclusion versus ambient sediments. All variables, with the exception of "tank" (laboratory experiments) were treated as fixed factors. ANOVA assumptions were tested in each analysis, and in those few cases where the data did not fit the assumptions data were $\log_e$ transformed (Sokal & Rohlf 1994).

4.5 RESULTS

4.5.1 Predator abundance

Four species of decapods dominated average summer abundances of epibenthic predators (Fig. 4.1). Snow crab (*Chionoecetes opilio*, South Arm mean = 0.96 crabs • $trap^{-1}day^{-1}$) and pandalid shrimp (*Pandalus montagui*, East Arm mean = 0.85 shrimp • $trap^{-1}day^{-1}$) dominated the two study sites respectively. Snow crabs were almost 5 times less abundant in East Arm (0.21 crab • $trap^{-1}$ day^{-1}), whereas shrimp were absent from South Arm. Toad crabs (*Hyas* sp.) were less abundant but similar in density between sites (0.15 and 0.10 crabs • $trap^{-1}day^{-1}$). Rock crab (*Cancer irroratus*) abundances were 0.08 and 0.30 crab • $trap^{-1}$ day^{-1} at South and East Arms. Although the traps were efficient in trapping predatory fishes, they were far less abundant and frequent, in comparison to crustacean predators.

4.5.2 Ambient communities and predator exclusion experiments

Overall, abundances in ambient sediments from South Arm were significantly higher than East Arm ($P<0.05$; Fig. 4.2). The three most abundant species from South Arm (the clam *Astarte* sp. and the polychaetes *Paradoneis lyra* and *Prionospio steenstrupii*) were all significantly more abundant than in East Arm ($P<0.05$) for each time period. The cumacean *Lamphros fuscata* was consistently more abundant at East Arm than in South Arm (P<0.05), however, the two next most abundant species from East Arm (the bivalve *Thyasira flexuosa* and the amphipod *Bathymedon obstusifrons*), were generally not significantly different from corresponding densities in South Arm (Fig. 4.2).

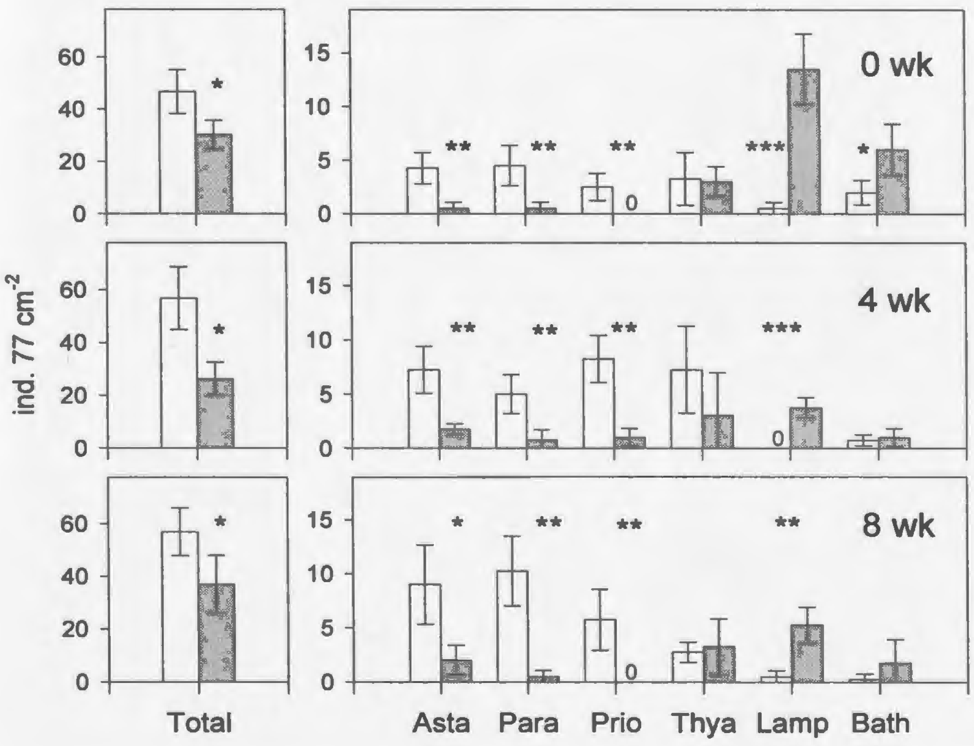

Figure 4.2 Mean total densities and most abundant infaunal taxa (+/- 95% confidence intervals) in ambient (control) sediments from South (open bars) and East Arms (shaded bars) at 0,4, and 8 week periods corresponding to field experiments. Asta = *Astarte* sp., Para = *Paradoneis lyra*, Prio = *Prionospio steenstrupi*, Thya = *Thyasira flexuosa*, Lamp = *Lamphros fuscata*, Bath = *Bathymedon obstusifrons*. Asterisks indicate significant differences in between areas comparisons. *: P<0.05, **: P<0.01, ***: P<0.001.

Exclusion experiments carried out in both arms of the bay are summarized in Fig. 4.3. Together, the first two Principal Components of the analysis explained 44% of the data variation. As was apparent in the clustering analysis, the PCA-H clearly separated South from East Arm communities (PCA1), and predator exclusions from ambient and partial cages treatments (PCA2). At both sites, sampling period (4th versus 8th week) had no clear effect on patterns in the PCA-H plot.

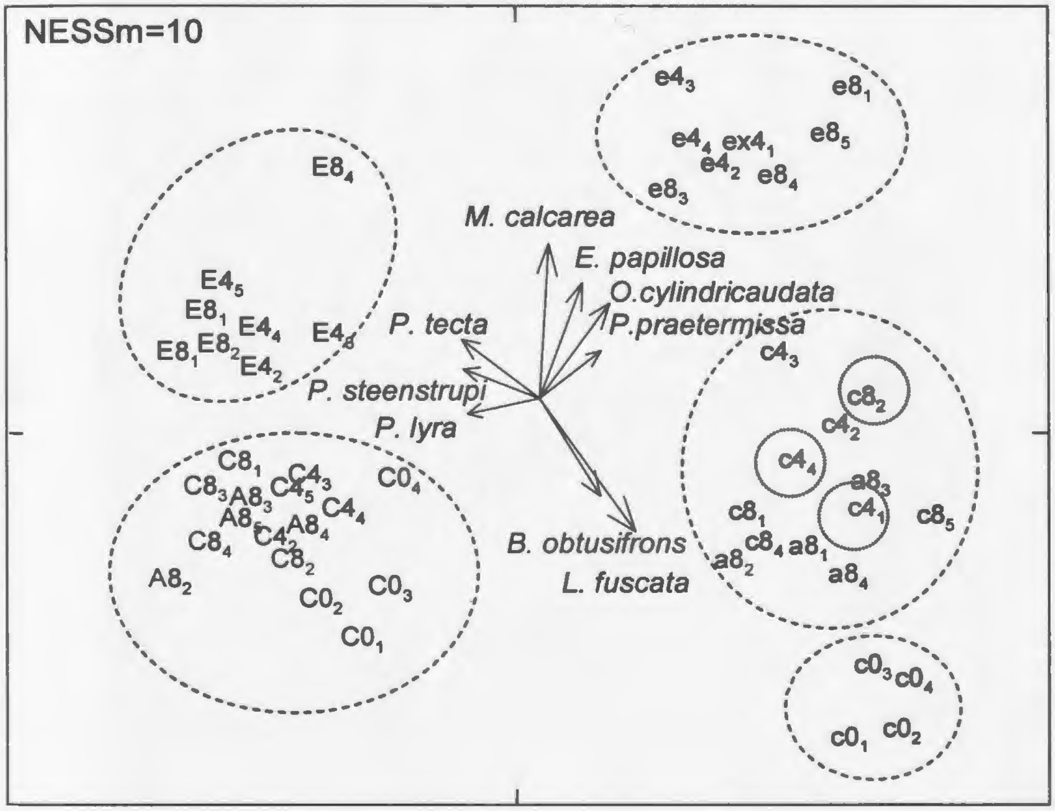

Figure 4.3 Cluster and metric scaling plot of treatments and ambient samples using PCA-H of CNESS similarities. South Arm (upper case) and East Arm (lower case) treatments are indicated as follows: C, c= control, E, e= exclusion, A, a =artifact. Numbers indicate sampling periods (0, 4, or 8 wk) and subscript numbers replicates (1-4). Vectors represent Gabriel biplots that identify species that explain the most variability among samples.

Gabriel biplots identified two polychaetes, *Pholoe tecta* and *Prionospio steenstrupi,* as the most important in protected sediments in South Arm (Fig. 4.3). Three other polychaetes, *Ophelina cylindricaudata*, *Euchone papillosa*, and *Praxillella praetermissa,* were important in exclusion treatments in East Arm. The polychaete *Paradoneis lyra* was important in describing ambient and partial cage sediments in South Arm, whereas the cumacean *Lamphros fuscata* and the amphipod *Bathymedon obtusifrons* were important in those from East Arm. Species densities (Fig. 4.4) were consistent with the biplots (Fig. 4.3). For example, *P. tecta* was abundant in exclusion treatments, whereas *L. fuscata* was more abundant in controls (P<0.001). Densities of *O. cylindricaudata* and *P. lyra* were also consistent with the biplots, though differences were not significant.

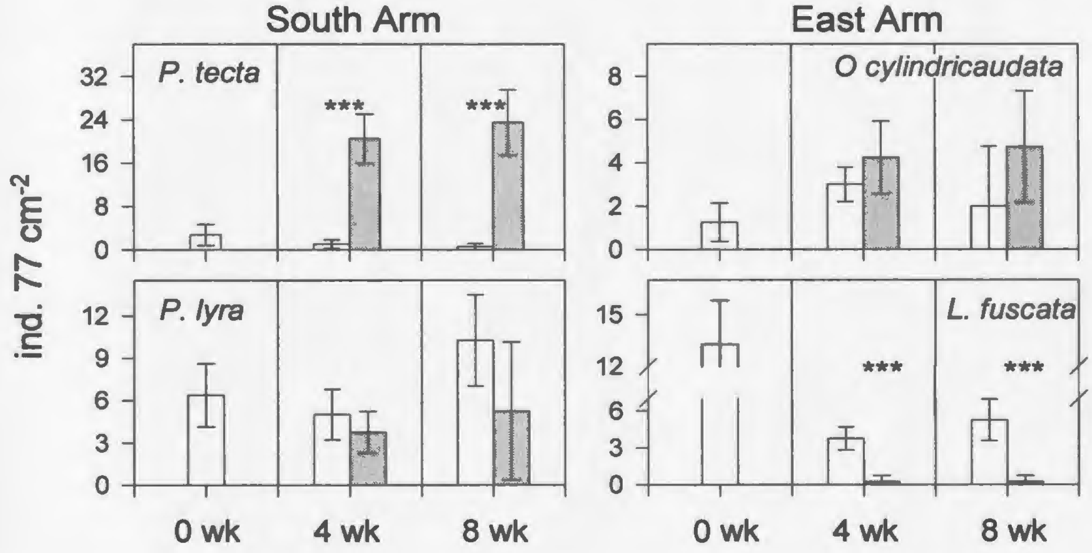

Figure 4.4 Mean densities (+/- 95% confidence intervals) of species that explain most of the between-sample variation between controls (ambient sediments, open bars) and exclusion treatments (shaded bars) in Figure 4.3.

Predation effects (i.e. significant time x treatment interactions) on density and evenness were detected after 4 and 8 weeks in South Arm (Table 4.1). Similar effects were detected on density, number of species, and diversity after 4 wk at East Arm but these effects did not persist to the 8th wk (Table 4.1). A control-exclusion comparison at each sampling date (Fig. 4.5) indicates that the exclusion of predators increased the density and reduced evenness (South Arm), whereas species richness and Shannon diversity were not significantly affected. In East Arm, exclusion of predators significantly increased density, species richness and Shannon diversity but did not affect evenness (Fig. 4.5). Sedimentary and faunal response variables were used to test for potential artifacts (Table 4.2). In all cases, site was the only significant factor, indicating no measurable caging effects on sediment composition or community structure.

Table 4.1 Predation effects on community response variables. Values are Sum of Squares (SS) from two-way ANOVAs (BACI design, see text). Factors include Time (before-after; 0-4 and 0-8 wk), Treatment (control-exclusion) and their interaction. Asterisks indicate significance associated with each SS. *: P<0.05, **: P<0.01, ***: P<0.001.

	Source	df	N	S	H'	J'
South Arm	Time	1	885.06**	2.25	0.0728	0.0133**
0-4 wk	Treatment	1	95.06	0.25	0.0169	0.0026
	Interaction	1	1040.06**	2.25	0.0748	0.0048*
	Error	12	946.25	65.00	0.2842	0.0088
South Arm	Time	1	1139.06**	7.56	0.1561	0.0302**
0-8 wk	Treatment	1	175.56	7.56	0.0184	0.0074*
	Interaction	1	1278.06**	0.56	0.0779	0.0108*
	Error	12	1147.75	86.25	0.4970	0.0165
East Arm	Time	1	10.56	203.06***	2.9451***	0.1036***
0-4 wk	Treatment	1	126.56	14.06	0.0092	0.0008
	Interaction	1	351.56**	45.56**	0.2424**	0.0015
	Error	12	444.25	48.25	0.2659	0.0235
East Arm	Time	1	162.56	156.25***	2.3846***	0.0853***
0-8 wk	Treatment	1	0.56	1.00	0.0305	0.0015
	Interaction	1	45.56	4.00	0.0491	0.0007
	Error	12	738.75	64.50	0.2093	0.0175

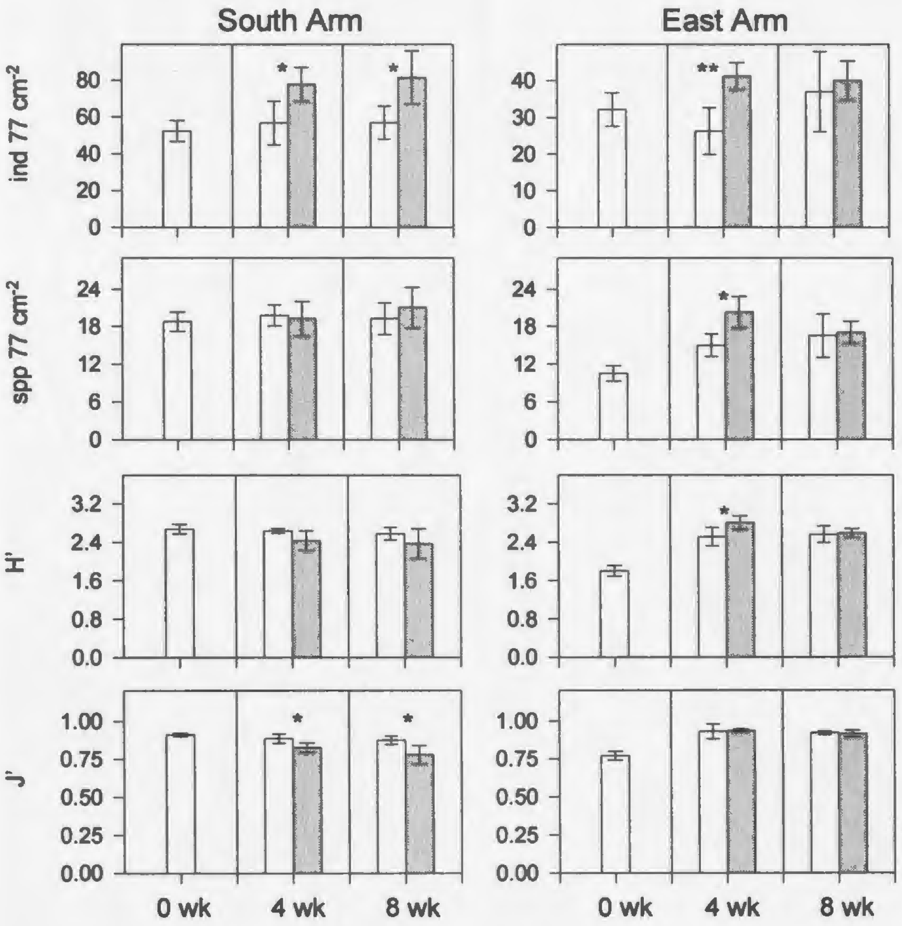

Figure 4.5 Mean values (+/- 95% confidence intervals) for community response variables estimated from control (open bars) and exclusion (solid bars) treatments. Mean values are based on four replicates except at the beginning of the experiments (week 0; n=8) when two sets of 4 samples were averaged and plotted as a single open bar. Asterisks indicate significant differences between treatments at each period. *: P<0.05; **: P<0.01.

Table 4.2 Artifact effects on sedimentary and community response variables. Values are Sums of Squares (SS) from two-way ANOVAs. Factors include Site (South vs. East), Treatment (Control vs. Artifact), and their interaction. *: P<0.05, **: P<0.01; ***: P<0.001.

Sedimentary variables	df	Fine Sand	Silt	Clay	C : N
Site	1	406.51***	350.43*	302.71*	84.08*
Treatment	1	2.73	116.97	9.89	0.84
Site x Treatment	1	1.06	19.35	19.48	1.44
Error	12	142.3	471.24	99.83	18.32

Table 4.2 (Continuation)

Community variables	df	N	S	H'	J'
Site	1	1444.0**	5.06	0.008	0.007**
Treatment	1	1.0	7.56	0.074	0.002
Site x Treatment	1	4.0	10.56	0.014	~ 0.000
Error	12	1376	158.75	0.445	0.005

4.5.3 Laboratory and inclusion experiments

The use of snow crab as a predator in laboratory experiments yielded similar results to those observed in the field experiments (Fig. 4.6). The first two principal components of the laboratory experiments explained 50 and 45% of the variation in South and East Arm, respectively. Irrespective of the source of the sediments (South or East Arms), cores exposed to predators were distinct from predator exclusion treatments (Fig. 4.6, top and middle panels). The polychaete *P. tecta* and the bivalve *Macoma calcarea* were important in describing exclusion treatments for South Arm, whereas the polychaetes *O. cylindricaudata* and *E. papillosa* were important in exclusions for East Arm. *Mediomastus ambiseta* and *E. papillosa* (South Arm) and *Aricidea nolani* (East Arm) were important to control treatments. In the field inclusion experiment (Fig. 4.6, bottom panel), the first two components explained 54% of the variation, and clearly separated inclusion from ambient sediments. *E. papillosa*, *Yoldia* sp., and *Tharyx acutus* were important species in the inclusion treatment, whereas *Lamphros fuscata* was the most important species in ambient sediments. In general, densities of most of the representative species identified by the Gabriel biplots were significantly different between treatments (see Fig. 4.6 and Fig. 4.7).

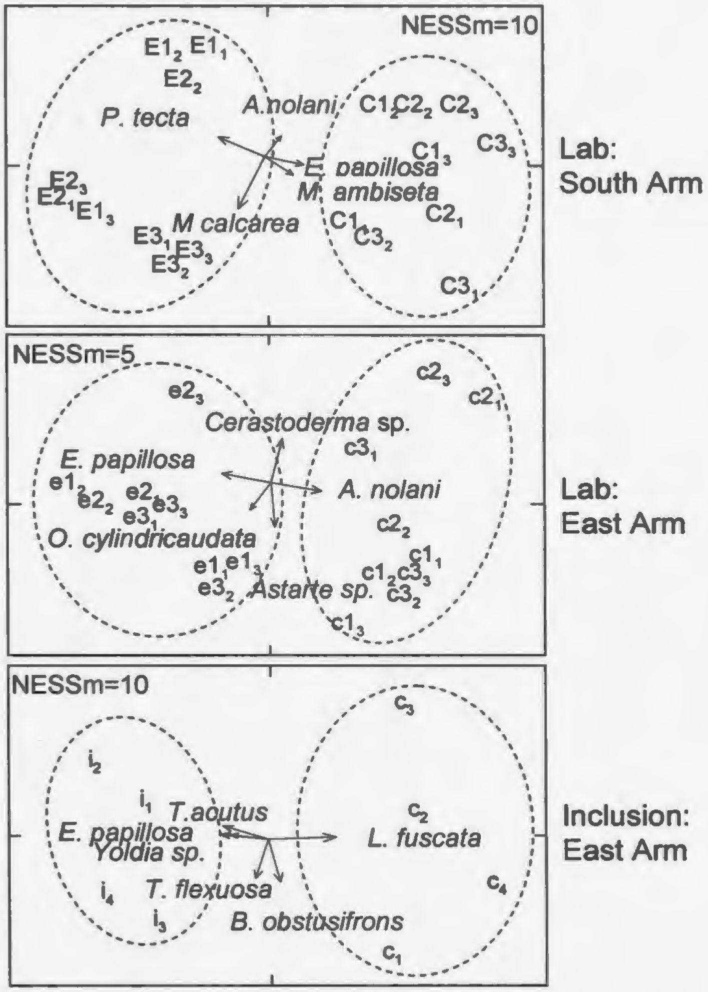

Figure 4.6 Cluster and metric scaling plot of samples collected in laboratory snow crab feeding experiments carried out with sediments (communities) from South and East Arms, and from a field inclusion experiment carried out in East Arm (see text). As in Fig. 4.3 treatments are represented by letters (i: crab inclusion), whereas numbers refer to tanks (1-3) and subscribed numbers to replicates (1-3).

In terms of community variables, results from the laboratory and the inclusion experiments were similar to those in exclusion experiments. In general, site (South or East Arm) explained most of the significant differences in variables ($P<0.05$ for all variables, Table 4.3) but treatment (predator exclusion versus exposed) also had significant effects on density and evenness ($P<0.05$).

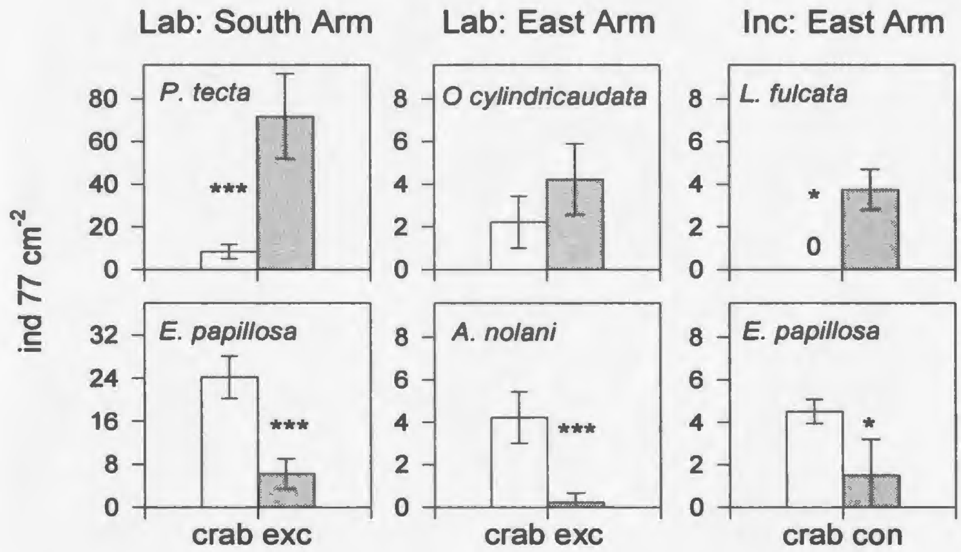

Figure 4.7 Mean densities (+/- 95% confidence intervals) of species that explain most of the between-sample variation between control (crab; open bars) and exclusion (exc; solid bars) treatments in laboratory experiments, and between inclusion (crab) and ambient (con) treatments in the inclusion experiment (see Fig. 4.6).

Table 4.3 Snow crab predation effects on community response variables in laboratory and in the inclusion experiment. Values are Sums of Squares (SS) from three-way and one-way ANOVAs, respectively. In laboratory experiments, factors include Site (from South–East), Tank, and Treatment (Exposed to crab vs. Exclusion). In the inclusion experiment treatment refers to inclusion (crab) versus ambient sediments. Asterisks indicate significant effects associated with each SS. *: P<0.05; **: P<0.01; ***: P<0.001.

Experiment	Source	df	N	S	H	J
Laboratory	Site	1	41877***	1080.21***	3.218***	0.192***
	Tank	2	399	1.47	0.255	0.021
	Treatment	1	1039*	15.05	0.004	0.031**
	Error	30	4577	124.61	2.065	0.099
Field Inclusion	Treatment	1	84.5	24.5*	0.141*	~0.000
	Error	6	147.5	15.5	0.146	0.008

Because site effects were significant, data were re-analyzed separately for each site. For South Arm, snow crab significantly reduced density (N), and increased evenness (J')

(P<0.05), but did not affect species richness or Shannon diversity. For East Arm, snow crab reduced total density and increased species richness and Shannon diversity (H') (P<0.05), but had no effect on evenness (P>0.05) (Fig. 4.8). The results of the inclusion experiment were very similar to the laboratory experiment: confined snow crabs reduced significantly the number of species and diversity (P<0.05), but did not significantly reduce the total density or modify evenness (P>0.05).

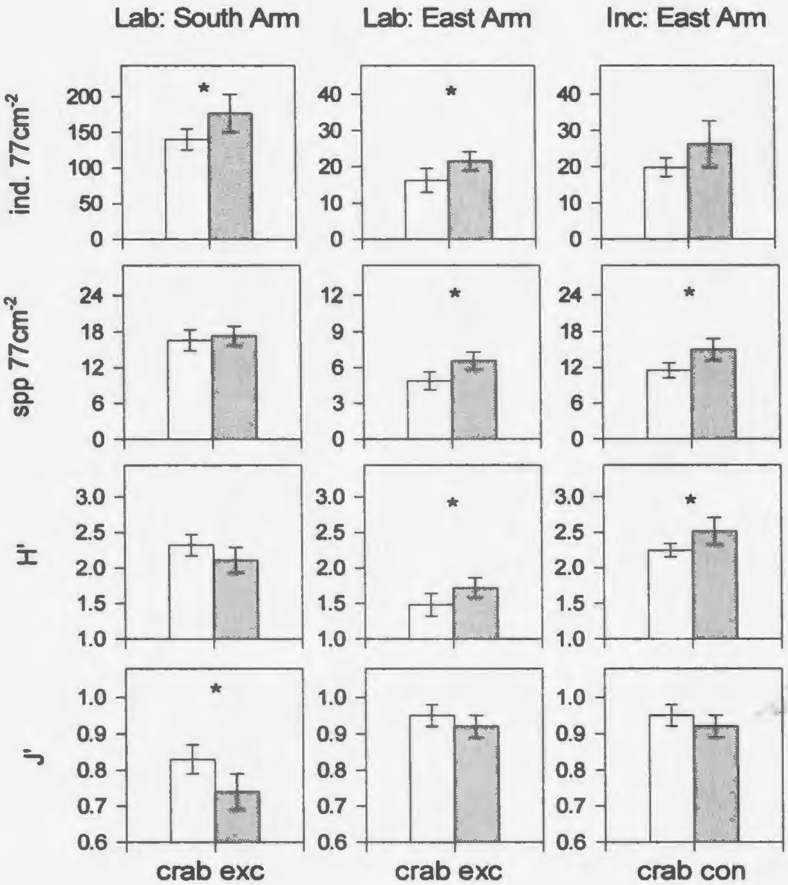

Figure 4.8 Mean values (+/- 95% confidence intervals) for community response variables in control (crab; open bars) and exclusion (exc; solid bars) treatments in the laboratory experiments, and from inclusion (crab) and ambient (con) sediments in the field inclusion experiment. Asterisks indicate significant differences in two way ANOVAs. *: P<0.05.

4.6 DISCUSSION

Overall, the results of this Chapter indicate that predation contributes significantly to patterns of infaunal composition and abundance in Bonne Bay. This conclusion is based on laboratory and field experiments that were consistent in their findings despite their obvious differences in scale (Wiens 2001; Kemp et al. 2001). Predatory fishes may also account for the effects detected in the field exclusion experiments (cf. Ólaffson et al. 1994). However, the strong similarity between the results of these experiments and those conducted in the laboratory using crustaceans only suggest that fish effects are either less important or largely similar to those resulting from crustacean predators. Among-site differences reflect spatial variation that cannot be fully understood with manipulative experiments that are limited to a single site (Fernandes et al. 1999) and exemplify the need for including more than one spatial/ temporal scale in our experiments (Schneider 2001; Thrush et al. 1997).

4.6.1 Predation effects on composition

Two groups of species were expected to benefit most from the exclusion of predators: sedentary polychaetes or clams unable to escape by emigration or burial (Roberts et al. 1989), and infaunal predatory species (Commito & Ambrose 1985). In the experiments, sedentary polychaetes such as the maldanid *P. praetermissa*, the sabellid *Euchone papillosa*, and the ampheretid *Lyssipe labiata*, were nearly twice as abundant in exclusion treatments than in ambient sediments in East Arm. Similarly, *Mediomastus ambiseta*, a subsurface dweller species, was twice more abundant in exclusion than in ambient sediments in South Arm. The clams *Yoldia* sp. and *Macoma calcarea* also benefited from the refuge created by exclusion treatments. *Yoldia* sp. was two times and *M. calcarea* five times more abundant in East and South Arm exclusion treatments, respectively. These results are consistent with data on predator stomach contents. Clams and sedentary polychaetes are important dietary components of snow crab populations from Bonne Bay (Wieckzoreck & Hooper 1995), Gulf of St. Lawrence (Powles 1968), and Eastern Newfoundland (Squires & Dawe 2003).

Pholoe tecta is a member of a predatory guild that is believed to generate trophic complexity in soft-sediment communities (Ambrose 1984; Commito and Ambrose 1985; Posey & Hines 1991). Predatory infauna is expected to aggregate in exclusion treatments to take advantage not only of the refuge from top predators but also the enhanced infaunal prey beneath cages (Kneib 1988; 1991). In South Arm *P. tecta* was five times more abundant in exclusion treatments than in ambient sediments. Similarly, *Phyllodoce mucosa,* the only other abundant predatory species (>1% of total) was ~twice as abundant in exclusion treatments than in ambient sediments. Species able to escape crab predation were expected to dominate ambient sediments. The cumacean *Lamphros fuscata*, the amphipod *Bathymedon obtusifrons*, and the polychaete *Paradoneis lyra*, are all highly mobile species that were indeed more abundant in ambient sediments than in exclusion treatments. Two notable exceptions were the clam *Astarte* sp., and the polychaete *Ophelina cylindricaudata*; neither species differed significantly between ambient and exclusion treatments. However, there is also no evidence to indicate that these species are important in the diets of snow crab (Lefevre and Brêthes 1989), rock crab (Hudon and Lamarche 1989), pandalid shrimp (Bergström 2000), or toad crab (Squires 1996).

4.6.2 Predation effects on community variables

The exclusion of predators produced an increase in total abundance in both sites over four weeks but the increase persisted through 8 weeks only in South Arm. Predation effects are "strong" when a 100% of density increase is detected in exclusion versus ambient sediments (Olafsson et al. 1994). This strong an effect is clearly not the case in Bonne Bay, where field and laboratory experiments show that predation influence is moderate and varies among sites. Spatial differences in predation influence and persistence may be related to predator foraging rates (Micheli 1997; Seitz et al. 2001) and predator composition (Quijón & Snelgrove, in press). On the one hand, snow crab were nearly five times more abundant in South Arm, suggesting that their foraging in this area may be much more frequent than in East Arm (resembling 'press and pulse' forms of disturbance, *sensu* Bender et al. 1984). On the other hand, predation effects on species richness that were detected only in East Arm may be related to higher density of rock crab relative to South Arm. In laboratory conditions, rock crab is at least four times more effective than snow crab in reducing species richness (Quijón & Snelgrove, in press). These differences are consistent with feeding rates reported for both species (Himmelman & Steele 1971; Drummond-Davis et al. 1982; Thompson & Hawryluk 1989).

The influence of rock crab on species richness also explains differences in diversity (H'), but not necessarily in evenness and dominance. Predation may indirectly increase the evenness when predators are non-selective foragers, i.e., when they primarily target the most abundant prey (Schneider 1978). This seems to be the case in South Arm, where the reduction in density by predation tends to equalize numbers per species (both in the field and in the laboratory). Most of the literature suggests that these four predators are primarily generalists (Squires & Dawe 2003; Bergström 2000; Scarrat & Lowe 1972), despite some degree of prey selectivity by snow crab (Wieczoreck & Hooper 1995). In East Arm, the reduction of density by predation (in field and laboratory experiments) resulted in the loss of species without changes in evenness. This pattern suggests that equalization of individuals among species is more likely in communities where abundance and species richness are comparatively high, as it was the case in South Arm, but not in East Arm.

4.6.3 Artifact effects

Cage artifacts are a recurrent concern in predation studies (Olafsson et al. 1994; McGuinness 1997). It is impossible to completely eliminate cage influences on sediments, prey, or predators, but it is possible to evaluate and minimize caging effects. The round shape of the cages effectively eliminated variable deposition within the cage interior because no visual evidence of sediment erosion or deposition was detected, nor were significant changes in sediment parameters observed. Although separate analysis of East Arm data indicated an increase in silt content in the cages, we believe that the effect was not meaningful for overall sediment quality; no other grain size fraction changed significantly, nor did the C/N ratio, our closest surrogate of food quality for deposit feeders (Blackburn et al. 1996). More importantly, no community responses to partial cages were detected. It was impossible to test for artifact effects during the first half of the experiment (0-4 wk), but caging effects tend to be cumulative over time (Hindell et al. 2001) and therefore, if present, should have been apparent in partial cages after 8 weeks of exclusion.

4.6.4 Implications for marine conservation

The collapse of cod, a species that was once extraordinarily abundant in coastal Newfoundland, has lead to an explosion in shrimp, snow crab (Worm & Myers 2003) and presumably, other crustaceans. Given that adult cod is not primarily an infaunal predator, and the clear effects that crab predators have on benthic infauna, it is reasonable to expect that the structure of Newfoundland infaunal communities may have changed in the last few decades with the replacement of cod by a trophic guild that feeds primarily on infauna. The results indicate that crabs modify benthic composition and abundance, and in more depauperate sedimentary habitats, also reduce diversity. As in other systems affected by long-term overfishing (Jackson 2001), the elimination of cod may have established an alternate stable state. The existence of these states has been debated for decades (Connell & Sousa 1983; Peterson 1984; Petraitis & Latham 1999; van de Koppel 2001), though rarely have they been described in relation to over-fishing. Alternate systems in fisheries ecosystems have often been assumed to be unstable, in that they revert back to the previous state with the cessation of the disturbance (fishery) that created them. There are exceptions (Barkai & Branch 1988), however, and situations such as the Newfoundland ecosystem where cod have failed to recover even 10 years after a fishing moratorium was declared. Irrespective of whether or not an 'alternate state' applies to the Newfoundland ecosystem, it is clear that the consequences of cod collapse have been far more severe than anticipated and, as these results suggest, may have been paralleled by a fundamental change in the structure of benthic communities.

Ironically, fishing pressure now focuses on three of the four crab predators studied here. The exploitation of rock crab (Mallet & Landsburg 1996), and at a much larger scale, snow crab (Paul et al. 2002), and pandalid shrimp (Bergström 2000), grew partly as a consequence of the cod collapse and subsequent moratorium (Bundy 2001; Schiermeier 2002). The results indicate a clear influence of these predators on key aspects of the structure of benthic communities. It follows that the decimation of these predators will have indirect consequences on the bottom component of the ecosystems they currently structure. Cascading effects, as a result of fishery exerted at the top of the trophic web (Agardi 2000), have been proposed for systems dominated by fish predators. There is no reason to assume that similar cascading effects are not playing a role in benthic communities of the North Atlantic, a problem that remains largely unknown to date. If over fishing leads to the collapse of crab stocks, as some data are beginning to suggest (Bundy 2001), additional shifts in sedimentary communities may be expected.

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CHAPTER 5

DIFFERENTIAL REGULATORY ROLES OF CRUSTACEAN PREDATORS IN A SUB-ARCTIC, SOFT-SEDIMENT SYSTEM

5.1 PREFACE

Chapter 4 examined predation as a general process regulating benthic community structure. That study is expanded in this Chapter by evaluating the individual roles of the dominant epifaunal crustacean predators of the bay on composition, density and species richness of the infauna. This study relies on several laboratory experiments and a field experiment carried out in the same locale from which sediments and infauna used in the laboratory experiments were collected.

5.2 ABSTRACT

The role of predation in structuring soft-sediment communities varies as a function of the number and composition of predators that co-occur in a given habitat. In Bonne Bay, Newfoundland, contrasting abundances in different areas of the bay may contribute to different regulatory roles of predators on infauna. To test this hypothesis, results from a field exclusion experiment were compared with five laboratory experiments that measured the individual effects of the main predators of the bay: snow crab, rock crab, and toad crab. In the field experiment, the exclusion of predators generated clear differences in infaunal composition, with two species (the polychaete *Pholoe tecta* and the clam *Macoma calcarea*) showing prominent increases to the exclusion treatment. Predator exclusion also resulted in a significant increase in density, but only a modest increase in infaunal diversity. In the laboratory, fresh, undisturbed sediment cores were paired with cores protected by mesh and exposed to each crab species in order to test for their potential effects on infaunal communities. Results indicated that snow crab and rock crab had clear effects on composition and, as was the case with the field experiment, the infaunal species *P. tecta* and *M. calcarea* were prominent components in prey responses to the exclusion of both predatory crabs. These predators also reduced total infaunal density but only rock crab significantly reduced species richness. In contrast, toad crab effects were not significant. Because snow crab and rock crab are both targeted by commercial fisheries in Atlantic Canada, these results suggest that changes associated with crab fishery removal may have multiple indirect effects on infaunal communities.

5.3 INTRODUCTION

Two general conclusions have emerged from studies on predation in soft-sediment communities: exclusion of predators tends to enhance total infaunal density, but density increases do not result in competitive exclusion of some species (Peterson 1979, Wilson 1991; Ólaffson et al. 1994; Lenihan & Micheli 2001). These conclusions have often been used to predict changes in benthic communities as a consequence of natural or artificial variation in numbers of predators (Hall et al. 1990). Although predation at the local scale often produces a change in prey communities (Seitz & Lipcius 2001), this prediction may not be sufficiently specific or informative (Hilborn & Mangel 1997). Our inability to accurately predict the outcome of exclusion experiments (Thrush 1999) is related to the web of indirect interactions among infaunal species (Ambrose 1984, Posey & Hines 1991; Kneib 1988; 1991), and to the natural variability of predators co-occurring in a given area (Hines et al. 1990; Davis et al. 2003). Different predators likely have different prey preferences, rates of predation (Davis et al. 2003), and degrees of sediment/ habitat alteration (Palomo et al. 2003). Regardless, most experimental studies trying to identify individual predator roles remain focused on a single predator species (Sih et al. 1998).

Studies on the role of predatory crustaceans at boreal and sub-arctic latitudes (>35°N) have lagged in the use of experimental approaches (Beal et al. 2001), particularly in sedimentary habitats as deep as 30 m. Literature describing predation effects on benthic communities has largely been restricted to correlative studies and stomach content analyses (Scarrat & Lowe 1972; Hudon & Lamarche 1989; Lefevre & Brêthes 1991; Stehlik 1993). A notable exception is the work on individual predator-prey interactions, particularly on rock crab (*Cancer irroratus*). This work has shown that rock crab feeding rates exhibit a broad range of variation that depends on site, temperature, and season, and also depends on type, size, behavior, density, and even odor plumes of prey (Elner & Jamieson 1979; Drummond-Davis et al. 1982; Barbeau & Scheibling 1994a,b; Salierno et al. 2003). If such variation occurs at the population level, at least the same degree of variation should be expected in comparing the predation effects of different crab species. For instance, based on feeding rates alone, the potential effects of rock crab are clearly different from those of snow crab (*Chionoecetes opilio*), and toad crab (*Hyas* spp) (Thompson & Hawryluk 1989; Nadeau & Cliche 1998).

The guild of predatory crustaceans that dominates the Maritimes to the Eastern sub-arctic comprises snow crab, rock crab, toad crab, pandalid shrimp (*Pandalus borealis*, *P. montagui*), and crangonid shrimp (*Crangon septemspinosa*) among others (cf. Squires 1996). Several members of this guild have increased in commercial importance and apparently in numbers and distribution over the last two decades (Mallet & Landsburg 1996; Bundy 2001). For instance, increasing landings of snow crab have paralleled an increase in numbers and distribution on the Scotian and Newfoundland shelves since the late 80's (Tremblay et al. 1994; Sainte-Marie 1997). Similar increases are also apparent in the Gulf of St. Lawrence and other sub-regions, but the lack of long-term data-sets precludes the description of more conclusive trends in this and other less studied species. Correlative studies have started to link these historical changes in crustacean populations to temperature regime shifts (cf. Gilbert et al. 1996; Colbourne et al. 2002), reduced cannibalism and increased recruitment (eg. in snow crab, Dutil et al. 1997; Lovrich & Sainte-Marie 1997), the collapse or reduction of cod (*Gadus morhua*) and other major predators on large decapods (eg. Robichaud et al. 1991; Worm & Myers 2003), and the interaction of these factors. Snow crab and other decapod crustaceans feed primarily on bottom dwelling organisms such as polychaetes, clams, and peracarid crustaceans

(Scarrat & Lowe 1972; Brêthes et al. 1984; Stehlik 1993; Squires & Dawe 2003). Since cod and other major predators are largely pelagic, the current dominance of decapod crustaceans suggests that the western North Atlantic shelf ecosystem has experienced a switch in predator regimes from primarily pelagic to bottom feeding predators. Irrespective of the relative contribution of cod and other major predators to the spatial-temporal patterns exhibited by decapod crustaceans, this switch may have cascading effects on benthic community structure (Quijón & Snelgrove in press).

In order to evaluate the generality of this hypothesis, studies are needed in order to examine the individual effects of different predators. Such studies could clarify the multiple influences of incipient small-scale fisheries targeting some species (e.g. rock crab and toad crab) and a large-scale fishery targeting others (e.g. snow crab) (cf. Mallet & Landsburg 1996; Sainte-Marie 1997; Paul et al. 2001). This study analyses the influence of snow crab, rock crab, and toad crab on shallow (~15-30 m deep), soft-sediment communities of Bonne Bay, a sub-arctic (~49°N) Newfoundland fjord. We used laboratory experiments to test for the individual effects of these three species on composition, richness, and density of macrobenthic organisms. We then manipulated snow crab and rock crab densities to reflect their variable abundance in different areas of the bay. These results were then compared with a field exclusion experiment to determine whether results from the controlled, small-scale laboratory experiments were consistent with those observed at larger spatial and temporal scales in the field.

5.4 MATERIALS AND METHODS

5.4.1 Study area

Bonne Bay fjord is located in Western Newfoundland, NW Atlantic (Fig. 5.1). Sediments and infauna for the laboratory experiments were collected from Small Cove (~15 m deep; 49°28'84''N, 57°54'48W), a protected site located in South Arm, one of the two main arms of the fjord. South Arm is a basin of up to ~55 m deep, open to the waters of the Gulf of St. Lawrence (Gilbert & Pettigrew 1993).

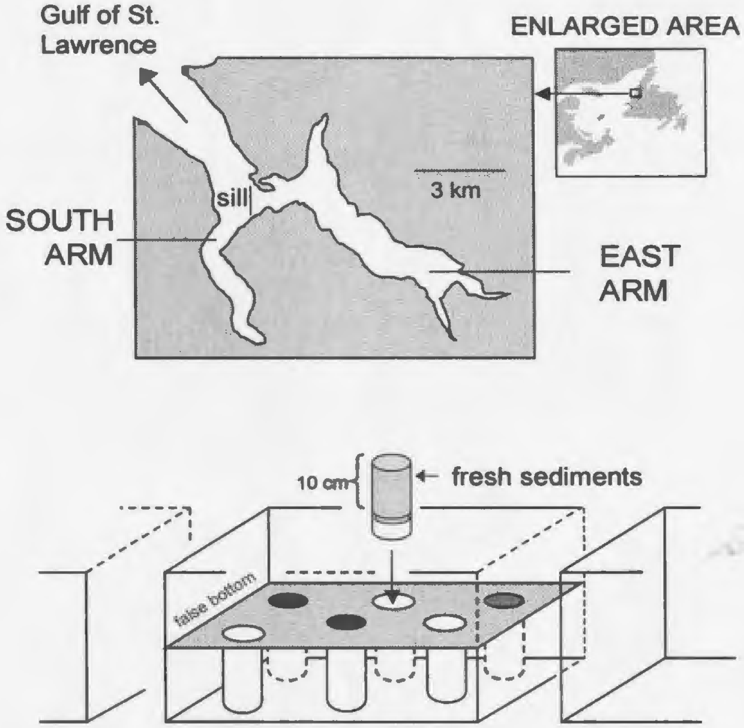

Figure 5.1 Top: Map of Bonne Bay, with the location of South Arm (the line indicates the location of Small Cove). Bottom: schematic of experimental tanks showing the arrangement of sediment cores protected from (Exclusion, with mesh at top) and exposed to (Predator, open cores) crab predation.

Small Cove sediments contain sparse gravel and pebble and are primarily fine sands (~60% in weight) with silt (~30%), and clay (~10%). C:N ratios average 15.9 (+/- 0.6, 95% CI), a value relatively high in comparison to those reported for freshly settled detritus (~13; Blackburn et al. 1996), but low compared with other sites in the bay (eg. 20.6 +/- 0.95 in South East Arm; Quijón & Snelgrove, in press). The field experiment was carried out in close proximity to that area at ~30m depth. Preliminary sampling and analyses did not indicate any differences in benthic composition and overall abundance between the two depths, and samples from both locations were considered representative of the same infaunal community.

5.4.2 Prey and predators

Infaunal species composition for this and other areas of the fjord have been described by Wieckzoreck & Hooper (1995) and Quijón & Snelgrove (in press, unpublished data). The community includes a total of ~55 species, primarily composed of polychaetes (34 spp), bivalves (10 spp), amphipods (4 spp), and cumaceans (3 spp). The most abundant species are the polychaetes *Paradoneis lyra*, *Prionospio steenstrupi*, and the bivalves *Astarte* sp., *Thyasira flexuosa*, and *Cerastoderma pinnulisum* (see 5.5.2 Field experiment and community structure, for a comparison of relative abundances). Snow crab, rock crab, and toad crab are the most abundant and frequently collected predators in the experimental area (see Chapter 2), as shown by successive deployment of 60 x 40 x 30 cm traps fitted with ~1.5 cm mesh and baited with mackerel. Mesh size was appropriate for the retention of immature and adolescent crabs (*sensu* Sainte-Marie et al. 1995) that were representative of size composition at this depth and season, particularly for snow crab populations of the area (Comeau et al. 1998). Deployments were all carried out at 30-50 m depth approximately every two weeks during the summers of 1999-2001 (see Discussion for a comparison of densities).

5.4.3 Field experiment

A field experiment including full cages or "exclusions", partial cages or "artifact treatments", and ambient undisturbed sediments or "predation treatments" was deployed at ~30-m depth in Small Cove (referred as South Arm in Fig. 5.1). Each treatment included four replicates that were haphazardly interspersed on the seafloor. Cages (1 m diameter x 15 cm high, pushed 3 cm into the sediment) were circular in shape to minimize differential erosion or deposition of sediments in different areas of the cages. Each cage was anchored to the bottom by four legs that extended into the sediment. Plastic mesh (1 cm x 1 cm) covered full cages and 50% of the area of each artifact treatment (50% of top and sides). The design of the artifact treatments was intended to allow predators to access and potentially feed on infauna while mimicking the effects of the full cages on the local hydrodynamics (see review by Ólaffson et al. 1994).

Macrobenthic organisms were sampled with tube cores (7 cm diameter; 10 cm deep; 2 cores per sample) that were collected by scuba divers. Initial sampling ("before") took place on June 25th 1999, immediately prior to deployment of full cages, artifact treatments, and ambient sediments. Cages were subsequently sampled after 4 and 8 wk periods ("after"; see data analysis below). To minimize potential disturbance effects resulting in loss of independence between 4 and 8 wk treatments, cages were removed immediately after sampling and sampling was never repeated within a given caged or ambient location. This design allowed us to evaluate the influence of predation (predator versus exclusion) at 2 time periods (4 and 8 wk) and evaluate the possibility of experimental artifacts over the 8 wk period. For this last analysis, additional sediment cores were collected from all treatments and used to evaluate grain size distribution and CHN content. Those analyses allowed us to evaluate possible sediment-mediated artifacts related to caging treatments.

5.4.4 Laboratory experiments

During the summers of 1999 and 2000, five laboratory experiments were conducted to evaluate the individual influence of snow crab (*Chionoecetes opilio* Fabricius), rock crab (*Cancer irroratus* Say), and toad crab (*Hyas* spp). Fresh sediment cores (7 cm diameter) with intact infauna were collected by divers and carefully transported to the Bonne Bay Field Station (~1.5 km away). In the laboratory, experiments were established in a series of three flow-through tanks supplied with cold-water (1-2°C) from the bay. Six sediment cores were placed in each tank (18 cores per experiment) so that the upper lip of the cores was flush with a plastic plate that served as a false bottom (see Fig. 5.1). Before placing the cores in the tanks, the sediment inside was carefully extruded so that it was flush with the upper lip of the cores and thus the sediment surface would be flush with the false bottom once positioned in the tanks. Sediments (and associated infauna) were acclimated to laboratory conditions for 24 h prior to the initiation of the experiments.

Crabs (adolescent males, 60-80 mm carapace width) were collected in regular sampling of Bonne Bay as described above. Crabs were acclimated for at least 24 hours before one individual was added to each tank. Different crabs were used for each experiment. Crabs had access to three of the cores (predator treatments) whereas the other three cores were protected from crabs with a ~0.6 x 0.6 cm plastic mesh (exclusion treatments). Predator and exclusion cores were randomly distributed within each tank (see data analysis for details on sources of variation and degrees of freedom). Experiments lasted for 96 hours, after which the crab from each tank was removed, tanks were carefully drained, and sediment cores were collected and processed as described below. Identical procedures were used to test the effects of snow crab, rock crab, and toad crab (one crab per tank; three independent experiments). For two additional experiments densities of snow crab and rock crab were doubled to two individuals per tank; these experiments were included to reflect the higher density of these species in comparison with toad crab in Small Cove as well as other areas of the bay (Quijón & Snelgrove, in press). For each experiment, fresh sediments were collected from the same site.

5.4.5 Sample processing and analysis

Cores of sediments from field and laboratory experiments were sieved through a 500-micron mesh, fixed in a 10% sea water-formalin solution, and then stored in 70% ethanol with Rose Bengal. Benthic organisms were counted and identified to species level. Samples collected for sediment characterization (study area and field experiment) were frozen and later divided into two sub-samples for grain size analyses and estimation of C:N ratios. The first analysis sorted the sediment in >350, >250, >177, >125, >88, >62.5, >53, >44, >37, >31, >15, >7.8, >3.9, >2.0, >0.98, >0.49 μm fractions (see details in Ramey & Snelgrove 2003). Each fraction was expressed as percentage of total dry weight, and pooled into mean sand (>250 microns), fine and very fine sand (>62.5 microns), silt (>3.9 microns), and clay <3.9 microns) based on the Wentworth scale (Folk 1980). A second fraction of the sediment samples was processed with a CHN analyzer (Perkin Elmer Model 2400) to estimate C and N as a function of sediment dry weight and C:N ratios (an estimator of food quality for deposit feeders, Blackburn et al. 1996).

5.4.6 Data analysis

For the field experiment and each laboratory experiment, benthic community structure was analyzed using Chord Normalized Expected Species Shared (CNESS). This similarity index estimates the number of species shared between two samples based on a random draw of m individuals (Trueblood et al. 1994). A random draw of m=10 was used for all data sets except the experiment using one rock crab (m=5; overall density of most samples exposed to rock crabs was <10 ind. per core, necessitating a smaller size for m). The CNESS dissimilarity sample x species matrix was also used to cluster samples based on unweighted pair-group mean average sorting. The program COMPAH 90 (E.D. Gallagher, U. Massachusetts, Boston) was used for this analysis. The CNESS sample x species matrix was then transformed to a normalized hypergeometric probability matrix (H), and used in a Principal Components Analysis (hereafter called PCA-H) to produce a two-dimensional metric scaling of CNESS distances among samples. This approach resembles multidimensional scaling results (authors unpublished data), but CNESS plots have the added advantage that they can be overlaid with Gabriel Euclidean Distance Biplots (Gabriel 1971) that identify species particularly important in determining CNESS variability among samples, and thus, driving community composition.

Total density (N) and number of species (S) per sample (77 cm^2 in the field experiment; 38.5 cm^2 in the laboratory) were also calculated. For the field experiment, statistical comparisons were carried out with a two-factor "before-after, control-impact" (BACI) design. In this factorial design, the evidence for an impact (predator exclusion in this case) appears as a significant time x treatment interaction term (Green 1979). Because a significant interaction term does not necessarily imply predator-related causal effects (cf. Underwood 1996), results of these analyses were examined with caution and contrasted with results from the corresponding PCA-H analyses. The model of the ANOVA was $y = \mu + \text{time} + \text{treatment} + \text{time x treatment} + \varepsilon$, where y refers to each response variable, μ is a mean constant, time refers to before- after (0-4wk or 0-8 wk), treatment refers to impact (predator versus exclusion), and ε refers to the error term. Although the BACI design is powerful, more recent versions include nested terms (observation [time]) that require at least two observations "before" and "after" (cf. Stewart-Oaten & Bence 2001), which we did not have. Nonetheless, this approach is more powerful than separate predator/exclusion contrasts for 4 and 8 weeks. An additional ANOVA model excluding time and interactions factors was use to compare artifact and predator treatments at the 8th week. All the factors in the field experiment were considered fixed (Sokal & Rohlf 1994).

Statistical comparisons between predator and exclusion treatments in the laboratory experiments were carried out with a randomized block design. The model for these comparisons was $y = \mu + \text{tank} + \text{treatment} + \varepsilon$, where tank refers to replicate tanks (1-3), treatment refers to predator versus exclusion treatments inside each tank, and ε refers to the error term. In order to evaluate whether the results of these analyses were driven by strong (treatment) differences detected for instance at a single tank, preliminary ANOVAs incorporated a "tank x treatment" interaction term. None of such interaction terms was significant, and therefore, the analyses were run as described above. Tank and treatment were considered random and fixed factors, respectively. Assumptions of normality and homogeneity of residuals were checked in each analysis (the latter with the Levene test), and in the few cases where data did not fit these assumptions data were $\log_e$ (x) transformed (Sokal & Rohlf 1994).

5.5 RESULTS

5.5.1 Field experiment and community structure

The first two principal components of the PCA-H explained 35% of the variation in species density and composition (Fig. 5.2). Exclusion cages were clearly separated from predator (ambient) and artifact treatments, indicating a change in species composition and density in response to predator exclusion. The biplots identified *Pholoe tecta* and *Macoma calcarea* as the species that characterized exclusion sediments, and three polychaetes (*Tharyx acutus, Mediomastus ambiseta,* and *Aricidea nolani*) characterized predator (ambient) and artifact treatments.

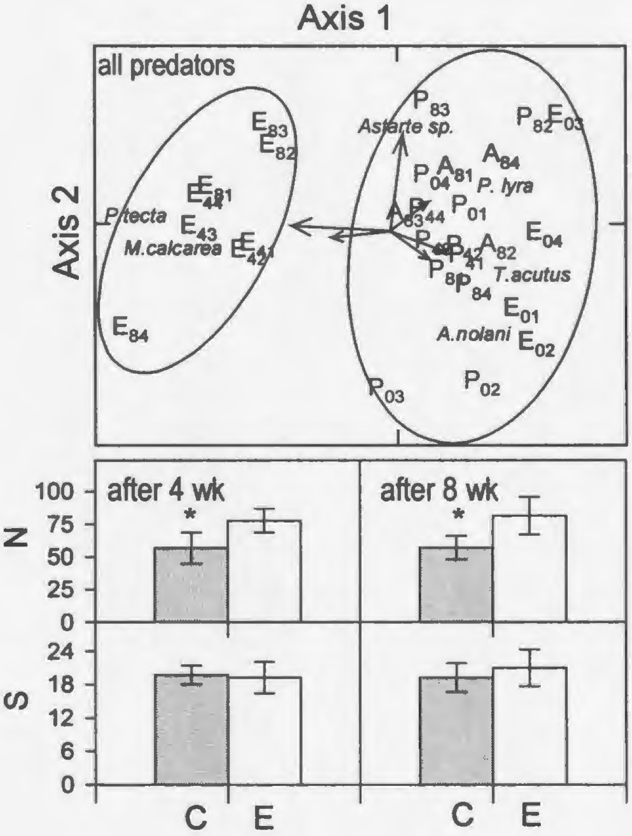

Figure 5.2 Field experiment: Upper panel: Major clusters and metric scaling plots of samples based on PCA-H of CNESS similarity for Exclusion (E), Predator (P), and Artifact (A) treatments. Subscripts denote duration (0, 4 or 8 wks) and replicate (1-4). Arrows are Gabriel biplots, which identify species that contribute the most to between-sample differences. Bottom panels: Average and 95% confidence intervals of density (N) and species richness (S) per 77 cm^2. For simplicity, only Predator and exclusions after 4 and 8 weeks are plotted (see text). Asterisks indicate significant differences between treatments (*: $P<0.05$).

Densities of the most abundant species in the area (Fig. 5.3, upper panel) were not significantly different between treatments (P>0.05). In contrast, densities of the three species identified by the Gabriel biplots (*P. tecta, M. calcarea, and T. acutus,* lower panel in Fig. 5.3) were significantly higher in the corresponding treatments (P<0.05).

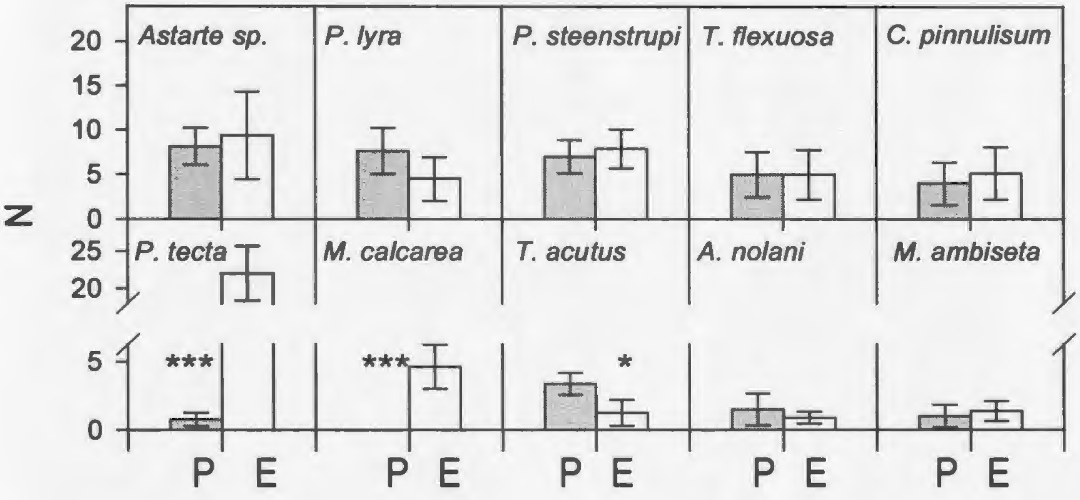

Figure 5.3 Average and 95% confidence intervals of density (N) per 77 cm^2 of the most abundant species of the area (top panel), and those identified by Gabriel biplots (lower panel; see Fig. 5.2). Given that no differences were detected between 4 and 8 weeks, the values presented correspond to averages of both sampling periods. Shaded bars stand for areas open to predators (P), and open bars for those from which predators have been excluded (E). *:P<0.05;***: P<0.001.

Predator-exclusion effects on total density were detected after 4 and 8 weeks as shown by significant time x treatment interaction terms in both ANOVAs (Table 5.1). A comparison of predator versus exclusion treatment at both times (4 and 8 wk) indicates that total densities increased with the exclusion of predators (Figure 5.2, lower panel) but no significant effects on species numbers were detected (P>0.05; Table 5.1; Fig. 5.2).

Those results were interpreted to be unrelated to caging artifacts given the absence of a significant difference between predator and artifact treatments when faunal and sedimentary variables were compared (P = 0.211-0.949; Table 5.2).

Table 5.1 Field experiment: Sum of Square (SS) values from Factorial ANOVA comparisons of total density (N) and species richness (S) per sample. Factors include time (before-after, i.e. 0-4 and 0-8 wk), treatment (impact, i.e. predator-exclusion) and their interaction. Asterisks indicate significance associated with each SS. **= P<0.01.

Source of variation		N		S	
	DF	0-4 wk	0-8 wk	0-4 wk	0-8 wk
Time	1	885.06 **	1139.06 **	2.25	7.56
Treatment	1	95.06	175.56	0.25	7.56
Time x Treatment	1	1040.06 **	1278.06 **	2.25	0.56
Error	12	946.25	1147.75	65.00	86.25

Table 5.2 Field experiment: Sum of Square (SS) values from ANOVAs comparing Artifact and predation (ambient) treatments. Response variables include density (N), species richness (S), percentages of medium sand, fine+very fine sand (f-sand), silt, clay, and C:N ratio.

Source of variation	DF	N	S	m-sand	f-sand	silt	clay	C:N
Treatment	1	0.50	0.13	63.80	3.59	20.58	28.57	0.04
Error	6	687.00	40.75	672.80	124.98	392.69	87.40	12.49

5.5.2 Laboratory experiments

The influence of the two densities of snow crab is summarized in Figure 5.4. Together, the two first principal components of each analysis explained 50% (one snow crab per tank) and 47% (two snow crab), of the overall variation in community structure. At both snow crab densities, sediments protected from predation (exclusions) were clustered and segregated from sediments exposed to predators along the first axis. Gabriel biplots identified the polychaete *Pholoe tecta* as the main species characterizing exclusion treatments. Two other polychaetes (*Euchone papillosa* and *Mediomastus ambiseta*) and a small amphipod (*Phoxocephalus holbolli*) were most important in open (predator) sediments in experiments using one and two snow crab, respectively (Fig. 5.4, top plots).

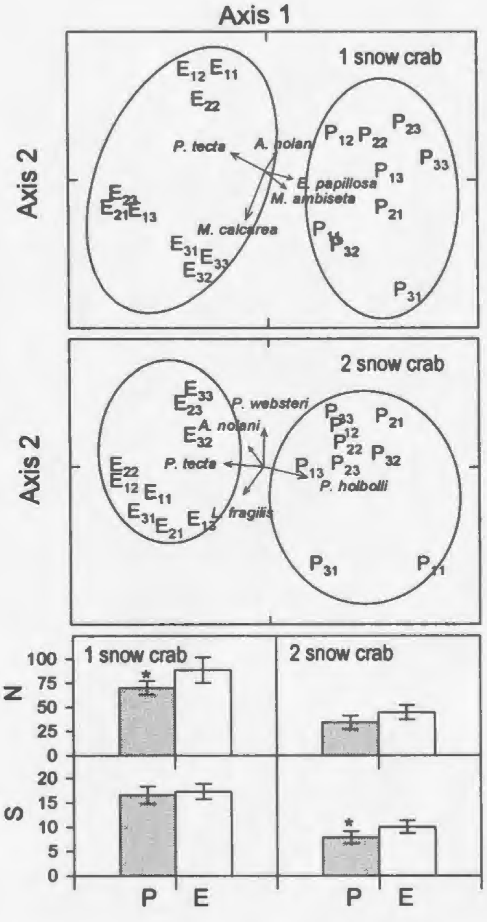

Figure 5.4 Predation experiments using one and two snow crabs. Top two panels: Major clusters and metric scaling plot of samples based on PCA-H of CNESS similarity. Letters indicate treatments: P= Predator, with snow crab; E= Exclusion. Subscripts denote tank and replicate respectively. Bottom two panels: Average and 95% confidence intervals of density (N) and species richness (S) per 38.5 cm^2 from Predator (P=with crab) and Exclusion (E) treatments.

Table 5.3 Laboratory experiments: Sum of Square (SS) values from nested ANOVA comparisons of density (N) and species richness (S) per sample. Factors include Tank and Treatment (Tank), where Treatment refers to predator versus exclusion. Asterisks indicate significance associated with each SS. *= P<0.05; ***=P<0.001.

Response variable	Source of variation	DF	snow crab		rock crab		toad crab
			1 indiv./tank	2 indiv./tank	1 indiv./tank	2 indiv./tank	1 indiv./tank
Density	Tank	2	784.33	146.78	625.33	134.30	600.44
	Treatment	1	1512.5 *	470.20	11450.9 ***	7360.90 ***	2112.50
	Error	14	3563.7	1786.10	3373.80	2228.80	11314.00
Species	Tank	2	0.44	7.44	29.78	23.11	0.11
	Treatment	3	2.72	20.06 *	338.00 ***	117.60 *	5.55
	Error	12	10.78	53.44	104.00	84.40	53.44

Between-treatment differences in the density of the main species characterizing exclusion and predator sediments (*P. tecta and E. papillosa*) were significant (P<0.001; see below). Overall, the exclusion of snow crab resulted in total density and species richness up to 30 and 27% higher, respectively. However, these changes were significant in only two of the four comparisons (Table 5.3; Fig. 5.4, lower panel).

Rock crab also influenced community composition (PCA 1 and 2 explained 36 and 38% of variation for one and two rock crab, respectively); exclusion treatments (E) were clustered and separated from predator (P) treatments along the first principal component of both PCA-H plots (Figure 5.5, top plots). The most important species in exclusion treatments of both experiments were the polychaete *Pholoe tecta* and the bivalve *Macoma calcarea*. The polychaetes *Aricidea nolani* and *Phyllodoce mucosa* were particularly important in sediments exposed to predation by one rock crab (see species density comparisons below). The amphipod, *Phoxocephalus holbolli*, the polychaete, *Laonice cirrata,* and an unidentified juvenile clam were the most important in exposed sediments in experiments with the higher density of rock crabs.

The protection from rock crab predation resulted in total infaunal densities that were two times higher than in sediments exposed to this crustacean predator. Moreover, species richness in the exclusion treatments increased more than 50%. Treatment differences were significant (P<0.05) in all comparisons (Table 5.3, Fig. 5.5, lower panel).

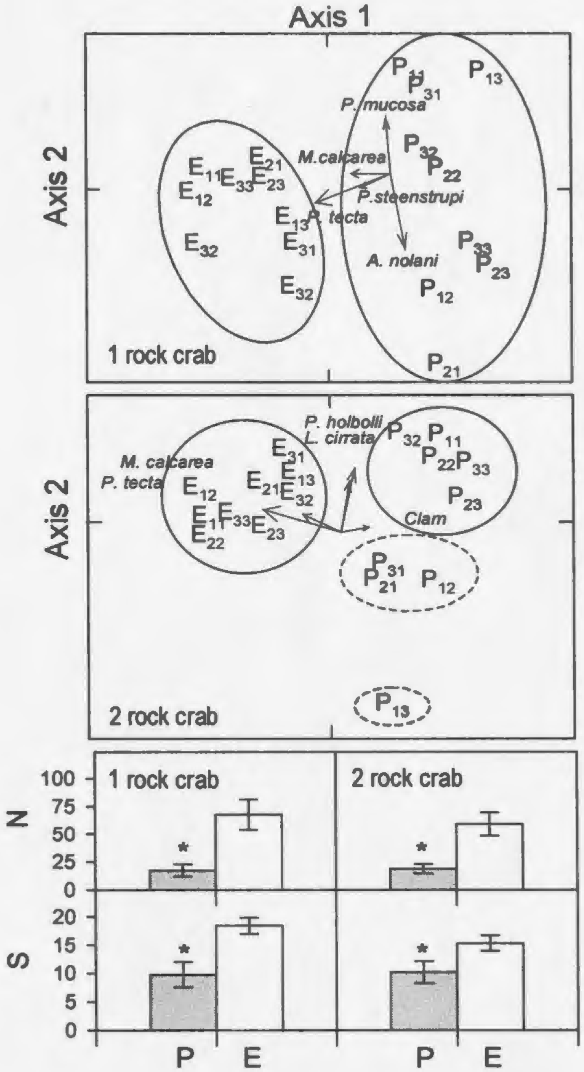

Figure 5.5 Predation experiments using one and two rock crabs. Top two panels: Major clusters and metric scaling plots of samples based on PCA-H of CNESS similarity. Bottom panels: Density (N) and species richness (S) per 38.5 cm^2. Legends as in Fig. 5.4.

The exclusion of toad crab did not result in changes in composition, total density, or species richness (P>0.05; Table 5.3, Fig. 5.6). The first two components of the PCA-H explained 40% of the observed variation, but samples from predator and exclusion treatments were all interspersed and mixed in the PCA-H plot (Fig. 5.6). Gabriel biplots identified *Macoma calcarea* and four species of polychaetes as the most important taxa in describing variability among cores: *Tharyx acutus, Eteone heteropoda, Syllides japonicus,* and *Pygospio* sp. Nonetheless, variation in infaunal composition was apparently unrelated to the exclusion of toad crab.

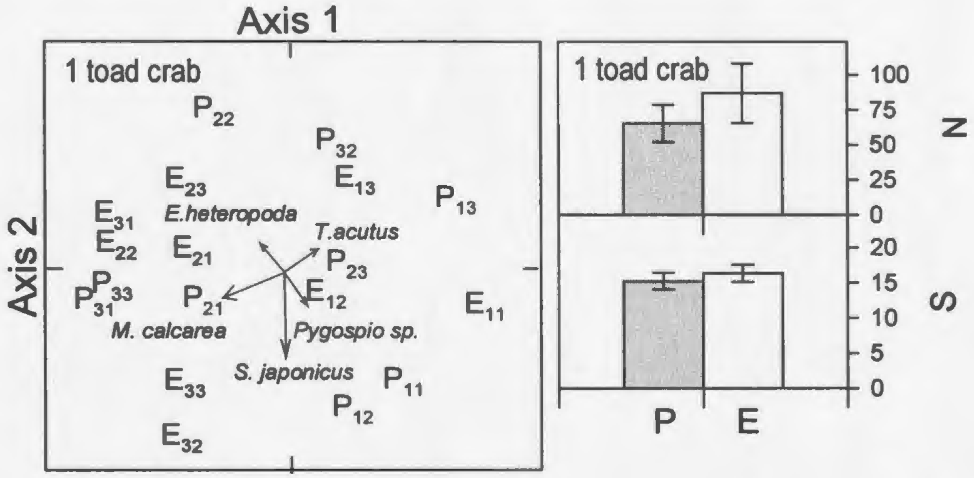

Figure 5.6 Predation experiments using one toad crab. Left panel: Major clusters and metric scaling plots of samples based on PCA-H of CNESS similarity. Right panel: Density (N) and species richness (S) per 38.5 cm^2. Legends as in Figure 5.4.

A comparison of the density of the main species characterizing exclusion and predator treatments in the three experiments using one crab is summarized in Figure 5.7. Density of *Pholoe tecta*, the species most strongly associated with snow crab and rock crab exclusion treatments, was significantly more abundant in exclusion sediments ($P<0.01$). The most abundant species in ambient sediments varied in density but did not exhibit consistent between- treatment differences.

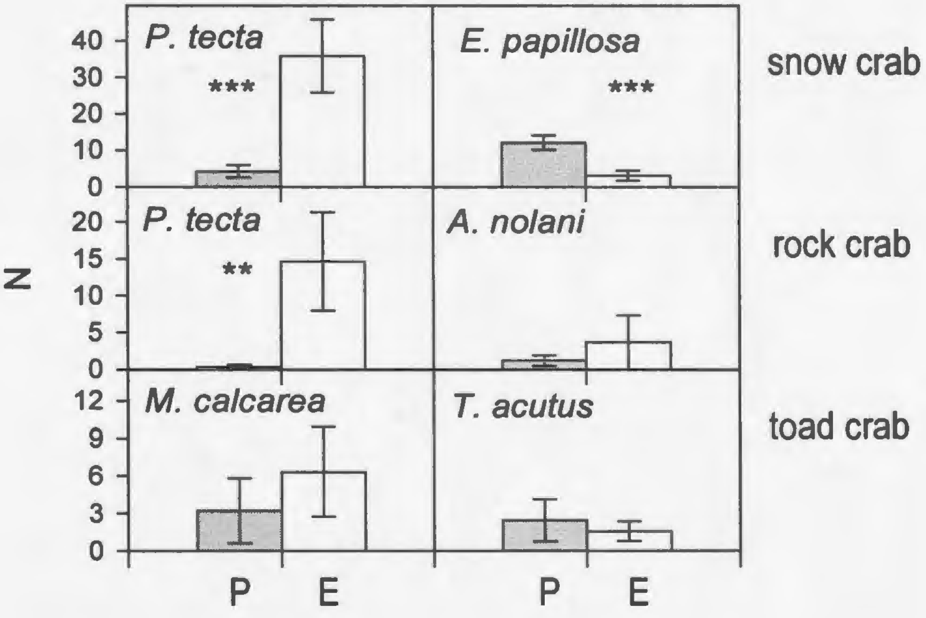

Figure 5.7 Average and 95% confidence intervals of density (N) per 38.5 cm^2 of the most important species contributing to the differences between exclusion (E, shaded bars) and predator treatments (P, open bars) in the laboratory experiments. For simplicity, only data from experiments using one crab per tank are plotted. Asterisks indicate significant difference between treatments; **: P<0.01; ***: P<0.001.

5.6 DISCUSSION

The results reported here indicate that the influence of the exclusion of predators is not simply a function of the number of epibenthic predators in a given area (Quijón & Snelgrove in press) but also depends on their composition. Irrespective of the densities used here, snow crab and rock crab, two species that are relatively common in Bonne Bay (Quijón & Snelgrove in press), displayed a strong influence over one or more community response variables, so that exclusion treatments were quite distinct from sediments exposed to predators.

5.6.1 Influence on species composition

Gabriel biplots generally identified similar species response to the exclusion of snow crab and rock crab: *Pholoe tecta* and *Macoma calcarea* were key species in describing infauna in exclusion treatments. *P. tecta* is a mobile predatory polychaete (Fauchald & Jumars 1979), and its high abundance in the exclusion sediments in comparison with predator treatments suggests that: i) this species actively escapes predation by moving into "refuge" habitats, and ii) that more than two trophic levels may be involved in the effects detected in community structure (Ambrose 1984; Commito & Ambrose 1985). Ambrose (1984) argued against the classical idea of two trophic levels represented by epibenthic predators (e.g. crabs, shrimps, fishes) and infaunal prey, and instead proposed an additional "predatory infauna" level that mediates the interactions between top epibenthic and non-predatory infauna. Wilson (1986) questioned this view, arguing that in order to verify the existence of such trophic complexity in soft-sediments top (epibenthic) predators should display strong preference for predatory infaunal species (as demonstrated later by Kneib 1988). The design used here was not intended to resolve this debate, but using Wilson's arguments, our results clearly support the view of Ambrose (1984): *P. tecta* was several times more abundant in exclusion than in predator treatments, both in field and in laboratory experiments. Further studies are required in order to clarify the interactions between *P. tecta* and non-predatory infaunal species such as *Tharyx acutus*, a cirratulid polychaete that occurred in higher numbers in sediments exposed to predators relative to sediments that excluded top (epibenthic) predators (cf. Kneib 1991; Posey & Hines 1991).

The higher density of *M. calcarea* in exclusion treatments may be the result of increased mortality in exposed sediments, and active immigration into predator exclusion treatments. Both possibilities are consistent with studies indicating that species of *Macoma* are an important dietary component of snow crab (Wieczoreck & Hooper 1995), and have the capacity for secondary (adult) dispersal following disturbance or predation (Armonies 1992). Intriguingly, *P. tecta* has not been reported from stomach contents of any of those predators. However, similar polychaetes classified as "Sigalionidae", "Polynoidae", and "scale worms" have been listed among the most frequent prey of snow crab (Lefevre & Brêthes 1991). This overlap may not be a coincidence given the taxonomic affinity between these three groups and Pholoidae (originally part of Sigalionidae, Rouse & Pleijel 2001), and their potentially problematic identification in partially digested specimens. The importance of *M. calcarea* and potentially *P. tecta* in the diet of snow crab and other crustaceans in the area suggests that the results of the laboratory exclusions are causally related to the foraging/consuming and not just to the presence of predators. However, further studies are required to evaluate potential responses of infaunal species to predator chemo (odor)-tactical signals, as demonstrated for example for clam and crab species (e.g. Finelli et al. 2000; Salierno et al. 2003).

As expected, a different set of species was associated with sediments exposed to snow crab or rock crab. In the experiments using toad crab, however, samples did not segregate as a function of treatment, suggesting little influence of this species on benthic composition. Toad crabs were observed feeding on exposed sediment cores and generating some degree of sediment disturbance. Therefore, the absence of stronger effects may result from some degree of re-colonization of exposed cores by fauna coming from cores protected from predation (cf. Zajac et al. 1998). Re-colonization was presumed to occur in all the other laboratory experiments (using snow crab and rock crab), but only for toad crab feeding did re-colonization by mobile infauna obliterate any predation effect. The mesh used to exclude predators and the distance among cores inside each tank were intended to allow migration and interchange of infauna. Two arguments justified such a decision. First, adult or juvenile dispersal and re-colonization have been demonstrated in the literature (eg. Commito et al. 1995), particularly at small spatial scales (Norkko et al. 2001). Second, this is an escape opportunity available only to those species without strict sedentary habitats at the adult stage (cf. Günther 1992). The lack of laboratory evidence for predator-mediated changes in composition suggests that toad crab play a minor role on the regulation of these benthic communities.

5.6.2 Influence on density and species richness

Beyond their similar influence on species composition, snow crab and rock crab did play different roles with respect to overall density and species richness. As expected from active predators (Moody & Steneck 1993; Yamada & Bouldry 1997), the exclusion of both species enhanced density and species richness. However, snow crab effects were not always significant. In contrast, the exclusion of rock crab produced a stronger and more consistent increase in density and richness. Differences among predator effects are likely a result of their different feeding rates and the degree to which they disturb the sediment while feeding or searching for prey (Kneib 1985; Thrush 1986; Palomo et al. 2003). Rock crab feeding rates are far higher than those measured in snow crab (cf. Elner & Jamieson 1979; Thompson & Hawryluk 1989; Barbeau & Scheibling 1994a,b). We did not quantify predator-related sediment disturbance but in observations carried out during the experiments, rock crab consistently disturbed the upper cm of sediment while feeding. In contrast, disturbance by snow crab was restricted to a more careful digging and scraping of sediment while feeding, a behavior already reported from field observations in the area (Wieckzoreck & Hooper 1995).

Given the influence of snow crab and rock crab as individual predators, we expected similar (density-independent predation) or more intense (additive) effects when adding a second crab to each tank (cf. Real 1979; Weissberger 1999). Overall, different predator numbers resulted in similar effects on benthic abundance and species richness. Whether these results reflect density- independent predation, a threshold prey density below which predators are no longer effective, or simply the existence of some degree of agonistic response that restricts predation, is uncertain. These relationships are usually measured in terms of predation (feeding) rates on individual species rather than as generalized predation effects on species assemblages (cf. Stephen & Krebs 1986; Seitz et al. 2001). However, observations carried out during the experiments suggest that agonistic behaviors may be the main factor, at least for rock crab. This behavior explains the apparent contradiction between the voracious feeding activity of individual crabs and the absence of an additive effect when more than one crab was added, particularly at such a small scale.

5.6.3 From the laboratory to the field

Results of the field experiment were remarkably similar to those detected in the feeding experiments using snow crab and rock crab. This similarity suggest that even when there is a variety of other invertebrate and vertebrate predators in the area, decapod crustaceans, and these two species in particular, are likely the major players in benthic community structure. The same species (*Pholoe tecta* and *Macoma calcarea*) were associated with exclusion treatments and similar clustering and segregation of these treatments from predator and artifact treatments was detected. The clustering of ambient (with predators) and artifact treatments is also consistent with the lack of apparent artifact effects as indicated by the non-significant differences in the corresponding ANOVAS. Both results suggest that the observed changes are causally related to the exclusion of predators and not to hydrodynamic interference created by the deployment of cages (cf. Hulberg and Oliver 1980; Hall et al. 1990; Steele 1996).

A more variable set of species dominated sediments exposed to predation. As discussed above, *Tharyx acutus* was significantly more abundant in exposed than in exclusion sediments. We did not identify a specific mechanism to explain this pattern with certainty, but potential negative interactions between this species and those most favored by the exclusion of epibenthic predators (e.g. *Pholoe tecta*) are a possibility. The length and timing (June-August) of the field experiment suggest that some degree of settlement or recruitment could have taken place during experiment. However, the lack of artifact effects resulting from the deployment of cages, and the similarity between species composition after 4 and 8 weeks (as shown by the PCA-H plots) suggest that cumulative recruitment effects were not a significant factor contributing to our results.

Similarities between field and laboratory experiments suggest that predator consumption, and not just predator presence, is an important, if not the main, mechanism contributing to community structure at the local (m to 100's m) scale (Seitz & Lipcius 2001). Extrapolation beyond this scale, however, requires caution. Processes acting at larger spatial scales may change in intensity (Fauchald & Erikstad 2002) or may simply be different (Schneider et al. 1997; Pace 2001). Overall these results suggest that experimental manipulations involving habitats with contrasting numbers of snow crab and rock crab will likely result in different outcomes. This hypothesis is consistent with the view that design of predator-exclusion experiments should always incorporate an explicit spatial component (Fernandes et al. 1999). Otherwise, natural variability in predator numbers (and not just prey numbers) cannot be properly incorporated in models of benthic regulation.

An examination of the abundance of predators in the experimental site (Small Cove, Table 5.4) suggests that local changes in infaunal composition are most easily attributed to differences in snow crab abundance. This conclusion is supported by the affinity between snow crab diet and the species composition in exclusion treatments (see above), the higher density of snow crab at Small Cove (South Arm in Fig. 5.1) relative to other crab species (0.92 crab • $trap^{-1}day^{-1}$), and the unexpected absence of a significant reduction in species richness.

Table 5.4 Relative abundances of snow crab, rock crab, and toad crab during the summers of 1999-2001. Sites compared are Small Cove (experimental site) and Mike's Cove, both in South Arm, and South East Arm in East Arm (see Fig. 1). Values correspond to means (+/- 95% confidence intervals) of crabs $trap^{-1}$ day^{-1} estimated from deployment of traps multiple times (N).

Sites (Main Arm)	N	Snow crab	Rock crab	Toad crab
Small Cove – South Arm	16	0.96 (0.59)	0.08 (0.06)	0.15 (0.09)
Mike's Cove - South Arm	14	0.24 (0.18)	0.44 (0.28)	0.03 (0.04)
South-East Arm - East Arm	15	0.21 (0.16)	0.30 (0.20)	0.10 (0.07)

Changes in species numbers are more likely related to feeding by rock crab. This was the only predator that consistently modified this variable, but rock crab was the least abundant crab species at the study site (0.08 crab • $trap^{-1}day^{-1}$). As is true of predators elsewhere (cf. Hines et al. 1990; Fauchald & Erikstad 2002), rock crab will likely be more influential in areas of the bay where it aggregates in higher densities (cf. Table 5.4). At the scale of the bay, that prediction has been confirmed by experiments carried out in East Arm (Quijón & Snelgrove in press), where rock crab is more abundant and the outcome of predator exclusion experiments shows significant changes in species richness. Moreover, species richness in South Arm ambient sediments, where experimental cores were collected, is significantly higher than in East Arm where rock crab are more abundant, suggesting that rock crab may play a key regulatory role.

These results suggest that two species currently targeted by large- and small-scale commercial fisheries (snow crab and rock crab, respectively) play significant roles in benthic community structure. In principle, this agrees with the view that indirect interactions such as fishery-related trophic cascades are taking place on the North Atlantic (Agardi 2000; Quijón & Snelgrove, in press). The individual sizes of snow crabs manipulated in the laboratory and in the depth range at which the field experiments were deployed are representative of the spring-summer populations in Bonne Bay and other coastal areas in the region (Hooper 1986; Ennis et al. 1990; Comeau et al. 1998). However, they are not necessarily representative of populations living in deeper waters and characterized by larger proportions of exploitable crabs (>95 mm CW males, Sainte-Marie 1997). Given that adolescent and adult (exploitable) snow crab display different feeding habits (e.g. Lovrich & Sainte-Marie 1997), the extrapolation of these results to complete populations, or specifically to the exploitable fraction of the snow crab populations, should be undertaken with caution until similar experiments are done with larger crabs. Given that this species constitutes the main fishery resource in Eastern Canada, the stability of its stocks (cf. Orensanz et al. 1998; Paul et al. 2001) may have important consequences for the recruitment to sizes as those manipulated here, and subsequently, for processes that regulate benthic communities. If, like cod, snow crab collapse and the species fail to recover in the short term (cf. Sainte-Marie 1997 for a review of temporal trends and resource management), parallel changes in benthic community structure are likely to occur.

Although the rock crab fishery is prosecuted somewhat differently, caution is again needed in extrapolating our results to larger (exploitable: >102 mm CW) individuals. Although fishery landings are smaller than those of snow crab, the growth of the rock crab fishery in areas such as the Gulf of St. Lawrence has been substantial over the last decade (Mallet & Landsburg 1996). If that growth continues and indirectly reduces the recruitment and subsequent abundance of the juvenile and adolescent stages manipulated here, changes in benthic communities can also be expected. These changes would not be limited to variations in density and species composition, but would also include species diversity, given the strong influence of rock crab on every aspect of the benthic community structure analyzed here.

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CHAPTER 6

THE USE OF COARSER TAXONOMIC RESOLUTION IN STUDIES OF PREDATION ON MARINE SEDIMENTARY FAUNA.

6.1 PREFACE

Chapters 4 and 5 examined predation as a form of biological regulation that, alternatively, can be seen as a source of disturbance to which benthic communities respond. This Chapter uses this idea to evaluate whether infaunal responses detected at the species level can also be verified after aggregating species into coarser taxonomic levels (e.g. family and order). Ultimately, this Chapter examines whether taxonomic "surrogates" of species can be used reliably to assess changes in benthic diversity.

6.2 ABSTRACT

Given the difficulties and time involved in species-level identifications, several authors have proposed the use of coarser taxonomic resolution (e.g. family, order) in studies of pollution. The use of surrogates instead of species relies on their sufficiency to detect community responses to the pollution gradient without appreciable loss of information. No studies, however, have applied this approach to experimental studies such as community responses to predation disturbance and evaluated the performance of

surrogates at the spatial scales typical of experiments (m -10's m). Both problems were addressed by analyzing the results of three predation experiments in Bonne Bay, Western Newfoundland. Species data were pooled into coarser taxonomic categories (family to class) and determined whether effects of predation that were evident at the species level were also evident with the use of each coarser surrogate. The results indicate that data at the family level do represent a reasonable surrogate of species when un-transformed data were used. However, the ability to discriminate between ambient and (predator) manipulated sediments is gradually lost with data transformation and with the pooling of species into coarser taxonomic categories. These results also suggest that the varying reliability of surrogates precludes the identification of a single general level of taxonomic sufficiency to be used in experimental studies. The use of surrogates is therefore suggested only after scrutiny and evaluation, and should be limited to preliminary studies where biodiversity has been well described.

6.3 INTRODUCTION

The last decade has seen renewed interest in marine biodiversity and concern for our inability to identify large numbers of marine invertebrates (Snelgrove 1999, Gray 2001). Most of this problem derives from the time, skills, and resources required for identification, particularly at the species level (Ferraro & Cole 1995). The lack of taxonomic expertise and the worldwide growth of research and exploration are the two main components of what Giangrande (2000) calls the "taxonomic impediment". Several surrogates of species have been proposed in order to circumvent this problem. Proposals include indicator groups such as some highly diversified polychaetes (Olsgard et al. 2003), indicator ratios such as 'nematodes: copepods' for meiobenthos (Amjad & Gray 1983) or 'polychaetes: amphipods' for macrobenthos (Gomez Gesteira & Dauvin 2000), and sub-sampling of pre-defined numbers of specimens (King & Richardson 2002). Each of these approaches has proven useful in some applications, but have failed to accurately predict patterns of biodiversity elsewhere. A fourth approach is the use of coarser taxonomic categories such as genera, families, orders, etc. (Somerfield et al. 1995). The feasibility of using coarser taxonomic levels has been studied in freshwater habitats (Bowman & Bailey 1997), rocky shores (Pagola-Carte & Saiz-Salinas 2001), gravel and sandy beaches (Schoch & Dethier 2001; Defeo & Lercari 2004), lagoons (Mistri & Rossi 2001), and coastal (e.g. Gray et al. 1988; Somerfield & Clarke 1995; James et al. 1995) and deep-sea sedimentary communities (Narayanaswamy et al. 2003).

The use of coarser taxonomic resolution relies on the idea of “taxonomic sufficiency” (hereafter TS) formally introduced by Ellis (1985). This approach justifies the use of coarser taxonomic categories instead of species, when loss of information has no significant effect on the comparison of communities in question (e.g. a pollution gradient, Gray et al. 1988; Warwick et al. 1988; Olsgard et al. 1997). Broader taxonomic categories appear not only to “suffice” in detecting pollution gradients but also remove some degree of redundancy attributed to the use of species that arguably may mask pollution effects (Gray et al. 1988; Warwick 1988; 1993). Moreover, coarser taxonomic resolution is less affected by the lack of taxonomic consistency frequently detected in species-level comparisons, and that otherwise would preclude the proper comparison of surveys (Olsgard et al. 2003). Despite these arguments and its increasing popularity, taxonomic sufficiency remains controversial (May 1990; Maurer 2000). More studies are therefore required to verify the applicability of TS in studies of natural as well as anthropogenic related sources of variation.

Three observations suggest that further exploration of TS in studies of natural variation is necessary and relevant. First, anthropogenic gradients (e.g. oil fields or sewage dumps) likely represent more intense forms of perturbation than natural gradients, and therefore, community responses and surrogate performance are expected to change (cf. Vanderklift et al. 1996; Olsgard et al. 1998). Second, the spatial scale of patterns typically studied with surrogates, (oil fields, surveys) is far larger than the typical scales of studies and experiments on natural variation (Kemp et al. 2001). Studies on predation, for example, may account for differences in benthic community structure (Olafsson et al. 1994) that are far more localized and less severe than the changes expected from pollution. Like other sources of natural variation in benthic communities, predation often induces species replacement and changes in numbers rather than in number of species.

A third observation is methodological. Traditional analyses comparing results obtained with different taxonomic levels rely on the visual comparison of non-metric multidimensional scaling plots (nMDS). A much-needed aspect in studies determining adequate taxonomical resolution is therefore the application of quantitative criteria (Vanderklift et al. 1996). Three of these criteria are used here to analyze the feasibility of using species surrogates in experimental predation studies on soft-sediment communities: i) correlation between similarity matrices resulting from data aggregated at different taxonomical levels, ii) MDS stress and similarity of control and exclusion treatments in cluster analyses, and iii) analysis of Similarity (ANOSIM) between controls and manipulated communities to evaluate discriminating ability at different taxonomic resolutions. To examine this question we used data from three field experiments (two predator exclusions, one predator inclusion) carried out in sedimentary habitats in Bonne Bay, Western Newfoundland. Previous analyses of the three experiments have already shown the existence of significant predation effects on a number of community response variables (Quijón & Snelgrove, in press & unpublished data). Thus, the three data sets can be used to evaluate the TS performance for experimental studies at relatively small spatial scales.

6.4 MATERIAL AND METHODS

6.4.1 Field experiments

Two exclusion experiments were implemented in each main arm (South and East Arms) of Bonne Bay, Newfoundland, and described in detail by Quijón & Snelgrove (submitted). Briefly, the experiments consisted of full (exclusion) and partial cages (potential artifact effects) deployed in sedimentary habitats at ~30 m deep. Fauna from the cage treatments was compared with ambient sediments by collecting replicated samples (7- cm diameter cores, 2 cores per sample, 0-10 cm deep) to monitor for changes after 4 and 8 weeks of predator exclusion. An additional experiment was carried out in East Arm and involved the inclusion of snow crabs (*Chionoecetes opilio*; the most abundant epifaunal predator in the bay) in full cages similar to those used in the exclusion experiments. Snow crabs were confined in cages for four days, after which time faunal samples similar to those described above were collected from cages and ambient sediments.

Original statistical analyses of both exclusion experiments as well as the inclusion experiment (Quijón & Snelgrove in press) were carried out with univariate (ANOVA) and multivariate methods (clustering and Principal Component Analysis of Chord Normalized Expected Species Shared, CNESS). All of the above analyses were carried out with un-transformed data of organisms identified at the species level. Overall, these analyses indicated i) the lack of cage-artifact effects on sedimentary or faunal variables; and ii) the existence of significant effects of predation on species composition, abundance and, in some cases, the diversity of the communities. The effects detected in the (snow crab) inclusion experiments were consistent with the results obtained in the exclusion experiments and with additional laboratory experiments carried out with two different densities of snow crab and rock crab (*Cancer irroratus*; Quijón & Snelgrove, submitted).

6.4.2 Analysis of taxonomic resolution

In order to test whether the differences between ambient and manipulated (exclusion or inclusion of predators) detected at the species level are also observed at coarser taxonomic resolution, the three sets of data were analyzed using PRIMER routines (Clarke & Warwick 1994). Because no artifacts effects were detected in the exclusion experiment data, only control and manipulated (exclusion or inclusion) treatments after 4 and 8 weeks of experimentation were used in the procedures described below. This reduced the pool of species from 78 to 50-51 per site (Table 6.1).

Table 6.1 Number of sampling units (replicates x treatments x sampling periods) and taxonomic units at each level of taxonomic resolution.

	Exclusion South Arm	Exclusion East Arm	Inclusion East Arm
# Sampling units	4 x 2 x 2 = 16	4 x 2 x 2 = 16	4 x 2 x 1=8
# Taxonomic units			
- Spp	50	51	39
- Fam	39	40	33
- Ord	20	18	13
- Cla	6	5	5

First, data at the species level were successively aggregated into family, order, and class levels (cf. Table 6.1). Data at the genus level were not considered because they were almost identical to species data; genera with more than one species were restricted to a few cases with relatively low abundances. Bray-Curtis similarity matrices using raw and transformed data were then created for each taxonomic resolution. Data transformation included square root (hereafter $\sqrt{}$), fourth root ($\sqrt{}\sqrt{}$), and presence-absence (+/-). The purpose of the transformations was to diminish the contribution of numerically dominant species (expressed in raw data) to emphasize community-wide attributes and rare species (√, √√) to the point where every species weighted equally (+/-) (Olsgard et al. 1997).

Next, the sixteen similarity matrices generated for each original data set were compared pair-wise using the RELATE routine and Spearman Rank Correlation (ρ). High ρ values (close to 1) suggest highly similar matrices and therefore no overall changes between data analyzed at the different taxonomic levels. Similarity matrices were then used to generate Multidimensional Scaling (MDS) plots to represent the relatedness of samples and treatments in a two-dimensional space. Stress values associated with each MDS plot reflect how well the distance among samples in the plot represent the actual distance among samples (Clarke & Warwick 1994) and were also used to compare between taxonomic levels. Group Average cluster analysis was subsequently applied to Bray-Curtis dissimilarities of the groups visualized in the MDS plots. In particular, we focused on the level of similarity at which the groups of samples from controls and manipulated sediments were linked together, and were therefore not distinguished.

Finally, controls and exclusions were compared with Analysis of Similarity (ANOSIM). This test compares a-priori defined groups of samples in a similar way as an ANOVA analysis, weighting variation within versus between groups (treatments). The ANOSIM routine generates an R-statistic (-1 to +1) and a significance test. High R-statistic values indicate that ANOSIM discriminates between treatments at the particular taxonomic level under analysis. Exclusion experiments data include two independent comparisons (after 4 and 8 weeks of exclusion), so they were treated separately (cf. Table 6.3).

6.5 RESULTS

6.5.1 Similarity matrices

Pair-wise comparisons of similarity matrices for each dataset are shown in Table 6.2. Spearman rank correlations (ρ) higher than 0.90 were restricted to comparisons of species -family matrices using raw or √ transformation (East Arm exclusion). Species-family correlations decreased with data transformation (to ρ=0.74) but were always significant ($P<0.05$) and higher than any other pairwise correlation between taxonomic levels.

Table 6.2 Spearman correlation coefficients (ρ) between pairs of similarity matrices from different taxonomic resolution. Analyses were carried out with raw and transformed (√,√√, + / -) data. Values in italic and underlined correspond to no-significant correlations ($P>0.05$) between the corresponding similarity matrices.

Experiment	Level	Raw			√			√√			+ / -		
		Spp	Fam	Ord	Spp	Fam	Ord	Spp	Fam	Ord	Spp	Fam	Ord
Exclusion South Arm	Spp	----			----			----			----		
	Fam	0.94	----		0.84	----		0.78	----		0.74	----	
	Ord	0.71	0.79	----	0.65	0.81	----	0.55	0.82	----	0.36	0.68	----
	Cla	0.46	0.49	0.57	0.19	0.27	0.47	*0.01*	*0.08*	0.31	*-0.05*	*0.04*	0.28
Exclusion East Arm	Spp	----			----			----			----		
	Fam	0.95	----		0.91	----		0.89	----		0.88	----	
	Ord	0.83	0.84	----	0.76	0.80	----	0.66	0.71	----	0.55	0.60	----
	Cla	0.63	0.63	0.85	0.45	0.47	0.68	*0.24*	*0.21*	0.38	*0.08*	*0.10*	0.22
Inclusion East Arm	Spp	----			----			----			----		
	Fam	0.94	----		0.84	----		0.78	----		0.74	----	
	Ord	0.71	0.79	----	0.65	0.81	----	0.55	0.82	----	0.36	0.68	----
	Cla	*0.29*	0.36	0.49	*0.19*	0.38	0.47	*0.13*	*0.33*	0.43	*0.10*	*0.25*	*0.36*

Overall, ρ values gradually decreased with the successive comparison between taxonomic levels (family-order, order-class), and with data transformation (raw to +/-) (Table 6.2). Non-significant correlations were detected for 8 species-class comparisons, 6 family-class, and 1 order-class comparisons (P>0.05); all other comparisons were significant.

6.5.2 MDS and cluster analyses

Samples from ambient (open symbols) and manipulated (filled symbols) communities plotted in two-dimensional space are shown in Figures 6.1, 6.2, and 6.3.

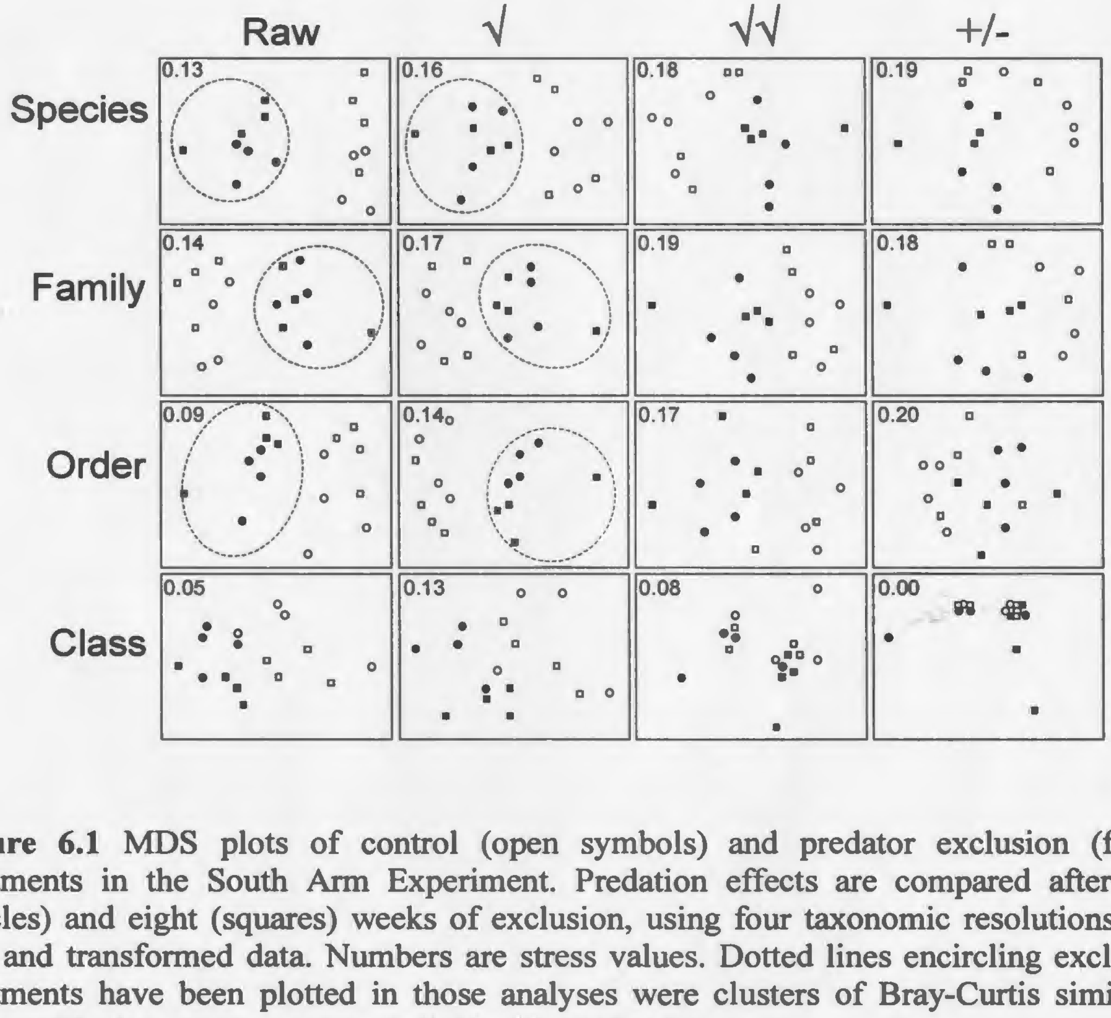

Figure 6.1 MDS plots of control (open symbols) and predator exclusion (filled) treatments in the South Arm Experiment. Predation effects are compared after four (circles) and eight (squares) weeks of exclusion, using four taxonomic resolutions, and raw and transformed data. Numbers are stress values. Dotted lines encircling exclusion treatments have been plotted in those analyses were clusters of Bray-Curtis similarity distinguished treatments as two individual branches (see text).

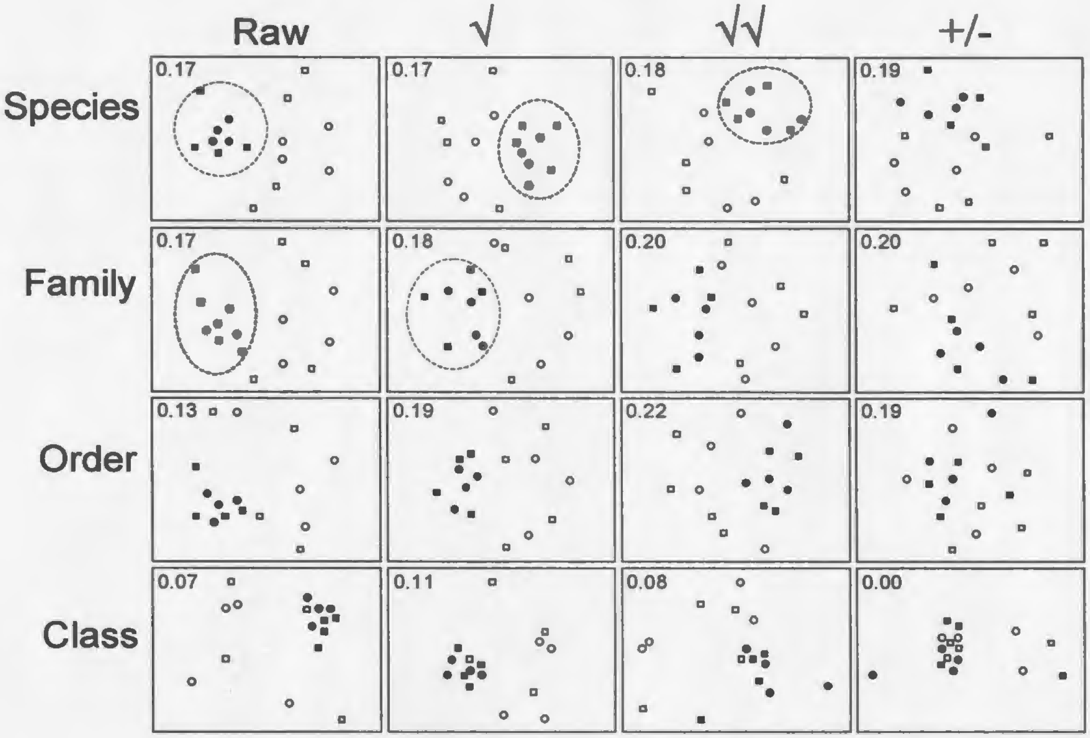

Figure 6.2 MDS plots of control (open symbols) and predator exclusion (filled) treatments in the East Arm experiment. Other details as in Fig. 6.1.

Samples from ambient and manipulated communities were clearly segregated when species- level data were used (Figures 6.1, 6.2, and 6.3). However, treatments become increasingly similar (and samples intermixed) with the aggregation of data to coarser taxonomic categories (family to class) and with more severe data transformation. In both exclusion experiments (Figs. 6.1 and 6.2) the stress values generally increased from species to order (0.09-0.20), but then decreased at the class level (0-0.13). In the inclusion experiment (Fig. 6.3) the stress increase from species to family (0.06-0.11), and decreased in order and class (0.00-0.04). Some cluster analyses separated control from manipulated communities as two simple branches (dotted lines in Figs 6.1-6.3), sometimes making the distinction between treatments straightforward. However, these cases were restricted to species and family level analyses for experiments conducted in East Arm, and to species through order levels for experiments conducted in South Arm.

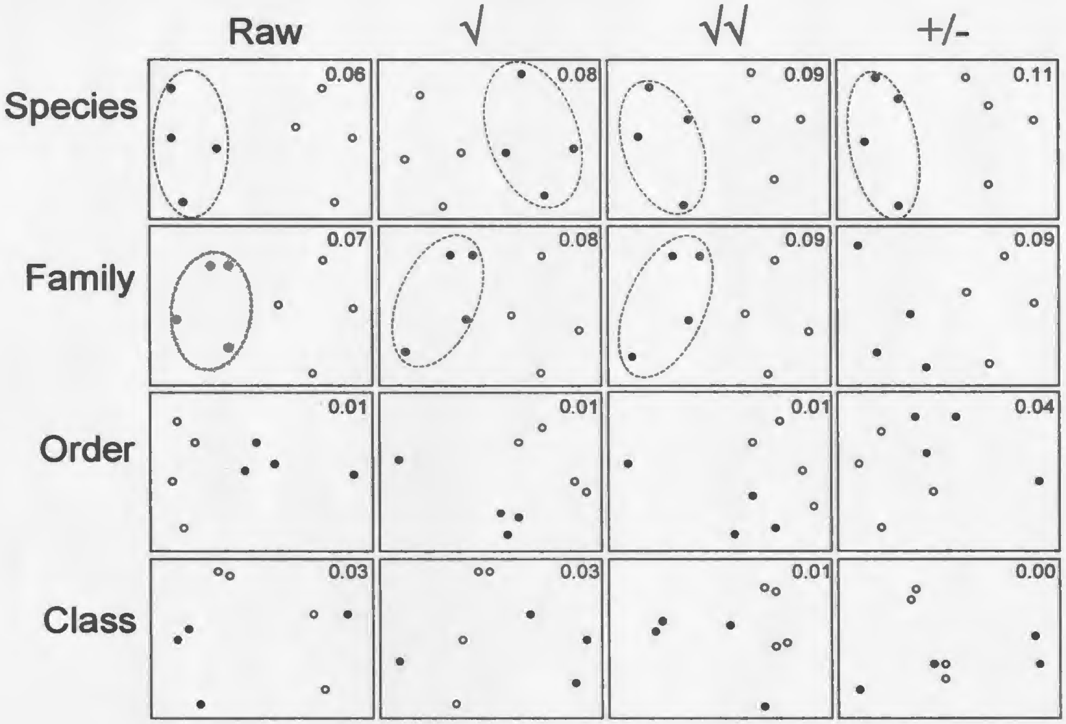

Figure 6.3 MDS plots of control (open symbols) and predator inclusion (filled) treatments in the (snow crab inclusion) experiment conducted in East Arm. Other details as in Fig.6.1.

The comparison of Bray-Curtis similarities linking control and manipulated groups of samples is presented in Table 6.3 and Fig. 6.4. For the three sets of data, Bray-Curtis similarity values consistently increased 30-40% with the aggregation of species in coarser taxonomic categories (rows of Table 6.3) but rate of change was small between species and family relative to coarser taxonomic levels (Fig. 6.4). The transformation of data also contributed to increased similarity between treatments, but this increase was ~10% (compare columns of Table 6.3).

Table 6.3 Bray-Curtis similarity values linking controls and manipulated (exclusion or exclusion of predators) treatments in Group-average cluster analyses. Data from different taxonomic resolutions and using raw and transformed (√,√√, + / -) data are compared.

Experiment	Transformation	Species	Family	Order	Class
Exclusion	Raw	42.54	46.59	57.48	71.69
South Arm	√	51.00	47.60	69.07	84.10
	√√	50.83	51.04	73.15	82.98
	+/ -	54.53	54.07	74.76	80.44
Exclusion	Raw	35.82	39.37	51.98	61.49
East Arm	√	41.38	46.55	63.47	75.23
	√√	42.18	49.62	69.00	82.99
	+/ -	42.82	52.26	74.58	84.82
Inclusion	Raw	30.52	34.05	43.57	62.84
East Arm	√	35.81	39.90	54.99	72.60
	√√	38.20	38.97	60.97	73.51
	+/ -	40.37	40.85	66.86	73.33

6.5.3 Analysis of similarity

The ability to discriminate between treatments (indicated by a significant R-statistic value) was evaluated with ANOSIM (Table 6.4). In general, with the aggregation of data at coarser taxonomic levels, the R-statistic values decreased and the number of cases with no significant differences (P>0.05) increased. The ability to discriminate between controls and predator exclusions (or inclusions) was greatest at the species level (16/20 comparisons) and was almost completely lost at the class level (significant differences in only 7 of 20 comparisons). Family and order level comparisons provided somewhat similar findings (14 out of 20 significant differences) to species-level comparisons but the

R-values were generally higher at the family level. As in the earlier analyses, increased severity of data transformation was more frequently associated with non-significant differences between treatments (i.e. reduced discriminating ability; Table 6.4).

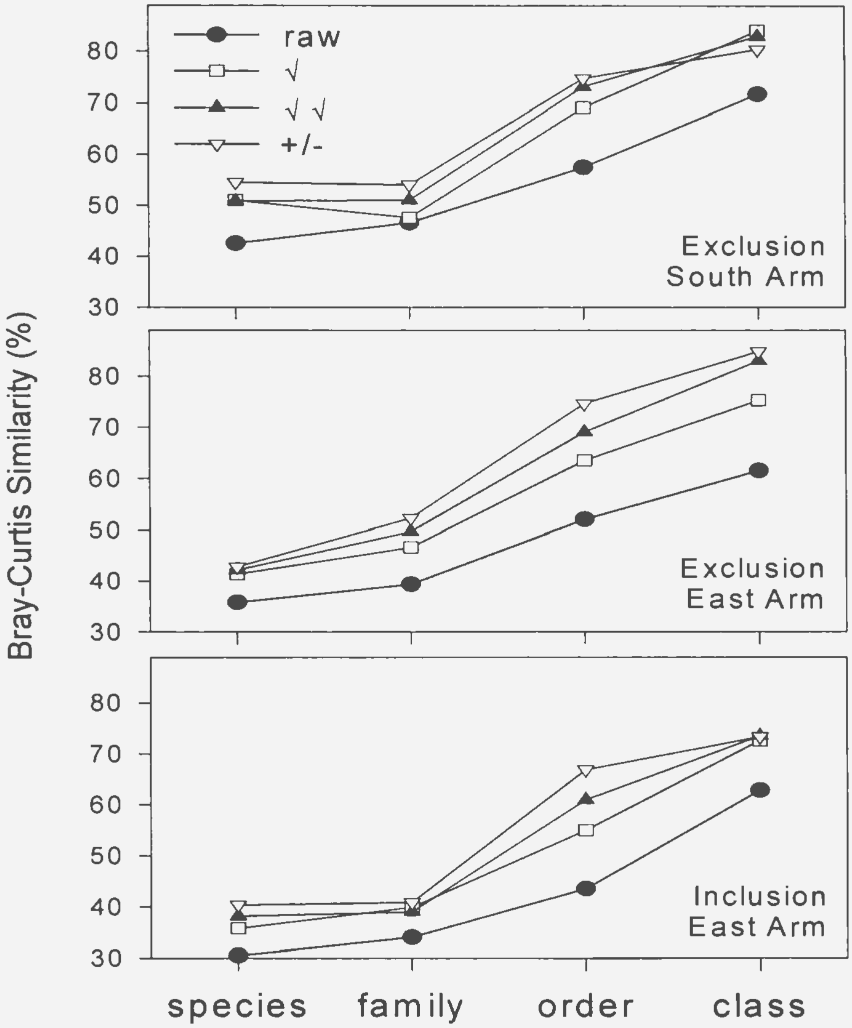

Figure 6.4 Variation in Bray-Curtis similarity linking controls and manipulated (exclusion / inclusion) treatments along different taxonomic resolution (species – class) in the three sets of experimental data. Results from raw and increasingly transformed data are plotted.

Table 6.4 Values of the R-statistic from one-way ANOSIM comparing between ambient (control) and manipulated (predator exclusion or inclusion) communities, at different taxonomic resolutions. For the exclusion experiments, comparisons were done separately for predation effects after 4 and 8 wks. Asterisks and "NS" indicate significant and non-significant differences, respectively.

Experiment	Time	Transformation	Species	Family	Order	Class
Exclusion South Arm	4 wk	Raw	0.95*	0.93*	0.65*	0.39*
		√	0.85*	0.92*	0.87*	0.32NS
		√√	0.65*	0.74*	0.88*	0.22NS
		+/ -	0.36NS	0.50NS	0.73*	0.06NS
	8 wk	Raw	0.83*	0.83*	0.67*	0.67*
		√	0.41*	0.41NS	0.60*	0.55*
		√√	0.23NS	0.20NS	0.49*	0.29*
		+/ -	0.13NS	0.04NS	0.32NS	0.12NS
Exclusion East Arm	4 wk	Raw	0.77*	0.73*	0.67*	0.64*
		√	0.69*	0.65*	0.66*	0.73*
		√√	0.63*	0.50*	0.38NS	0.51*
		+/ -	0.54*	0.44*	-0.14NS	0.12NS
	8wk	Raw	0.40*	0.52*	0.30*	0.21NS
		√	0.44*	0.45*	0.38*	0.30NS
		√√	0.40*	0.29NS	0.23NS	0.18NS
		+/ -	0.25NS	0.23NS	0.12NS	-0.13NS
Inclusion East Arm		Raw	0.92*	0.73*	0.55*	0.06NS
		√	0.88*	0.65*	0.51*	0.32NS
		√√	0.82*	0.59*	0.41*	0.35NS
		+/ -	0.74*	0.60*	0.26NS	0.30NS

6.6 DISCUSSION

Few studies have applied TS in the analysis of factors generating natural rather than of anthropogenic variation of benthic community structure (Dauvin et al. 2003). This is likely related to the lower performance that TS is expected to play in less polluted areas, as recently shown in Norwegian benthos by Olsgard & Somerfield (2000). The results include three lines of evidence to suggest that the use of surrogates may be adequate in order to detect differences in experimental studies such as those looking at predation effects (see below). However, these results also suggest that not just any taxonomic resolution will suffice.

6.6.1 Correlation of similarity Matrices

Species-family correlations were the highest among all possible pair-wise comparisons in the three sets of data. This result is particularly important given that correlation of similarity matrices is the most powerful tool to evaluate TS performance (Somerfield et al. 2002). Although an "acceptable" value of Spearman ρ is rather arbitrary, values ~0.95 reflect an almost perfect correspondence between similarity matrices (Clarke & Warwick 1994). Species-family correlations of untransformed data (0.94-0.95) were the only ones to meet this criterion. Species-family correlations after data transformation did not perform as well (up to 0.91 in √), whereas correlations between species and order or class levels were clearly lower. These results suggest limitations for the use of surrogates other than genus or family, as already shown in studies on macrobenthos (James et al. 1995) and meiobenthos (Gray et al. 1988).

6.6.2 MDS and cluster analyses

MDS plots do not offer an objective criterion for separating good from poor taxonomic resolution (Vanderklift et al. 1996). However, they help to visualize gradual changes in sample similarity and the smothering effect of coarser resolution and data transformation

(Olsgard et al. 1997). This is relevant in studies of natural variation (e.g. Schoch & Dethier 2001), where community responses are generally weaker than in pollution studies (Olsgard et al. 1998; Karakassis et al. 2002). In predation studies, for instance, "strong" effects result in changes ≥ 100% of prey density (Olafsson et al. 1994). This is not the norm in sedimentary communities, and in fact does not represent the more modest predation effects detected in Bonne Bay (Quijón & Snelgrove, submitted). In this area, exclusion of predators significantly increased total densities (up to ~57% on average) but not the number of species (up to ~30%). Cluster analyses separated controls and manipulated treatments as individual branches in only a few cases, confined mostly to raw and weakly transformed data at the species or family levels. Coarser resolution (order and class) increasingly intermixed different treatments, suggesting limitations for their use as surrogates of species.

Stress values increased from species to family or order, and then decreased in the class level. A similar pattern of variation was reported in a pollution study (Vanderklift et al. 1996), although previous studies have also found a simple decrease or no major changes in stress (e.g. Somerfield & Clarke 1995). Variation of stress along increasing taxonomic resolution may be related to the reduction in the "# taxa : # samples" ratio, and with the increase in non-zero values in the data sheets (Vanderklift et al. 1996). Although the biological significance of both ratios is not straightforward, the lower stress values detected at the class level simply suggest that these MDS plots are better representations of the actual distances among samples (Clarke & Warwick 1994). However, it does not imply that class is a better surrogate of species than family or order in this study.

6.6.3 Analysis of Similarities

The ability of ANOSIM to discriminate decreased with coarser taxonomic resolution and with increasingly strong data transformation. When aggregated at coarser taxonomic levels, species response to stress may undergo compensatory changes that reduce the sensitivity of some surrogates (Frost et al. 1992). That appears to be the case at the class level, where ANOSIM frequently failed to discriminate between treatments ($P>0.05$). Previous studies have found that in some intertidal habitats class or even phyla are useful surrogates of species (Krassulya 20016; Defeo & Lercari 2004). However, those disturbances were strong and persistent enough to be likely reflected at almost any taxonomic resolution (Olsgard et al. 1998; Warwick 1988). The ANOSIM R-statistic is also a useful tool to evaluate discriminating ability (Clarke & Warwick 1994). As expected, R-statistic values decreased with species aggregation (Warwick 1988) and data transformation (Bowman & Bailey 1997; Somerfield & Gage 2000). Correlation coefficients were calculated to visualize how close surrogates resemble species in terms of R-statistic values (see Table 6.4) and they declined from 0.91 (species-family) to 0.41 (species-order) and 0.43 (species-class). Although the rigor of these comparisons may be argued, this and previous analyses showed that data at the family level approximated species data considerably better than did order or class.

6.6.4 Natural variation and the use surrogates

Several studies have suggested that family is a good surrogate of species (Somerfield & Clarke 19956; Dauvin et al. 2003), and the best compromise between accuracy and cost-effective processing (Ferraro & Cole 1995). For Bonne Bay, the use of family as an acceptable surrogate of species relies on two aspects of our data. First, it is the result of low number of species per family (cf. Table 6.1). This attribute reduced the chances of comparing families with very different number of species, a problem that constrains the use of TS in spatial comparisons (May 1990; Prance 1994). Second, the effects of predation included the aggregation and quick dominance of few species in predator exclusion treatments (e.g. the polychaete *Pholoe tecta*; Quijón & Snelgrove, in press). This change resembles the local effects of a pollution gradient, where few tolerant/opportunistic species become dominant (e.g. Pearson & Rosenberg 1978). None of these aspects are peculiar to our experiments, but they restrict the use of surrogates such as families to systems where predation induces strong changes in dominance among prey species.

The acceptable level of taxonomic resolution is a function of the (anthropogenic or natural) gradient to which communities are responding (Rakocinski et al. 1997). Indeed, some studies have found that family level data do not perform well as species surrogates (Narayanaswany et al. 2003; Bowman & Bailey 1997). Therefore, this study does not constitute a call for a generalized use of family (or other surrogate) instead of species. Identification to the species level must be achieved whenever possible (Terlizzi et al.

2003), because it constitutes the most traditional entity to define and study biodiversity (Gray 2001; Hutchings 1998). This is not a reason to ignore a cautious use of surrogates in studies on natural gradients or experimental ecology, as demonstrated here. But the fact that TS approaches are of varying reliability in different applications suggests that in exploratory studies they will be most useful in well-known systems. In experimental studies, its potential use may be justified given the large proportion of effort invested in preliminary studies that might be re-allocated by using properly identified surrogates.

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CHAPTER 7

GENERAL CONCLUSIONS

The main goal of this study was to document spatial variation in epifaunal predators and infaunal prey, and to provide a mechanistic understanding of benthic community responses by experimental manipulation of predators. The main conclusions of each chapter and further implications in the temporal and spatial contexts delineated in the introductory Chapter are detailed below.

The shallow sill that limits exchange with Eastern Arm appears to be an inflexion point in the distribution of snow crab and at least one species of shrimp (Chapter 2). Although no sill-related pattern was observed for early larval stages, adult spatial pattern was clearly related to the distribution of zoea II and later larval stages, suggesting a role for larval supply in establishing adult benthic distribution. Because late-stage larval distribution, and likely settlement and recruitment, are closely related to adult predator distribution at the scale of the fjord, the subsequent influence of predatory decapods may be more closely related to predator pre-settlement and early post-settlement processes than expected (Chapter 2). As discussed in the Overview (Chapter 1), pre-settlement processes are likely to be even more influential at spatial scales larger than those analyzed here (10’-100’s km). Data on day-night dynamics and flux of larvae through the sill with high-resolution data on the emigration-immigration cycle are needed in order to provide a more comprehensive description of the plankton-benthos linkage.

Although polychaetes are generally representative of sedimentary biodiversity, their value as predictors of overall biodiversity is limited by habitat variation, and the variable degree of correspondence between composition and a given habitat type (Chapter 3). In general, two contrasting habitats (sandy and muddy sediments) supported infaunal assemblages that were significantly different in terms of composition, density, and species richness. The exploration of that variation at the local (fjord) and regional scales (Nova Scotia to Labrador) suggests that the polychaetes of the fjord are representative of a broader region of the North Atlantic (Chapter 3). To reach more specific conclusions, however, a more systematic study of this and other invertebrates from the Gulf of St. Lawrence is needed, particularly in the subsystem to which Bonne Bay belongs. Such studies will contribute to a greater understanding of how the diversity of Bonne Bay relates to the overall diversity of the region.

As shown here (Chapter 4), predation regulates composition, density, and in some circumstances, species richness and diversity of infaunal sedimentary communities. As expected, spatial variation in the intensity of these effects was detected from simultaneous experiments set in communities with different infaunal diversity. Differences in predator composition, as well as in diversity of prey communities, help to explain these spatial differences, and emphasize the advantages of experiments that encompass more than a single/uniform community or habitat. Moreover, the overall similarity in the results gathered from three different approaches (field- exclusion and inclusion, and laboratory experiments) re-enforce the idea that the role of predation and its spatial variation as inferred from the experiments are realistic and representative of the interactions occurring in this system (Chapter 4). A further step in the study of the role of predation is to explore its relative contribution as a top-down process in relation to bottom-up processes (see Overview; Chapter 1). Although several studies have examined this question at a local scale, evidence from sedimentary habitats is far from conclusive.

Although predation in general contributes to community structure, the fact that some predators are targeted by fisheries suggests that the fishery may actually play a greater role in ecosystem dynamics than that inferred from single species analysis (Chapters 4 and 5). The individual role of the main predators of the bay demonstrate that two species targeted by fisheries (snow crab and rock crab) were precisely the ones that contributed the most to community effects detected in the field and laboratory experiments (Chapter 5). The switch in predator composition experienced in coastal Newfoundland with the depletion of cod and the increase in decapods could imply a broad-scale change in predation rates (or predation pressure) on infauna, thereby affecting their community structure. Unfortunately, long-term data on predation rates or population structure are almost non-existent for most shrimp and crab species in Atlantic Canada. More research is needed in order to generate those data and verify models to evaluate the magnitude of the changes in sedimentary communities that have been driven indirectly by over-fishing.

The use of taxonomic categories coarser than species has been rarely applied to community studies except in relation to anthropogenic pollution. The detection of predation effects on infaunal data aggregated up to the family level suggests that the use of surrogates may be possible without significant losses of information (Chapter 6). This was the first experimental study to test the applicability of surrogates, and therefore more studies are required in order to compare their utility. Although the use of surrogates is recommended only under certain conditions (e.g. only after evaluation of surrogate performance and only at areas where biodiversity is well described) further studies should focus on other types of natural disturbance, and test the applicability of surrogacy in relation to community gradients (e.g. species diversity). For instance, no current studies have systematically studied the variation in the ratio of species to genus (or any other taxonomic category) and attempted to relate that variation to surrogate performance.

In summary, exploratory and experimental studies summarized here suggest that predatory crab and shrimp play a significant role as regulators of benthic community structure. This conclusion coincides with the general notion that predation is the main post-settlement factor shaping soft-sediment communities at this and most commonly studied lower latitudes. It also suggests that external factors such as the fishery, that affect predator numbers and composition at spatial and temporal scales far larger than those manipulated here, may have indirect cascading effects on the bottom component of the North Atlantic ecosystem.
