IMPACTS OF BOTTOM FISHING ON COLONIAL EPIFAUNA IN THE BAY OF FUNDY AND ON THE SCOTIAN SHELF

by

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

at

Dalhousie University
Halifax, Nova Scotia
September 2003

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DATE: September 2, 2003

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TITLE: Impacts of bottom fishing on colonial epifauna in the Bay of Fundy and on the Scotian Shelf

DEPARTMENT OR SCHOOL: Biology

DEGREE: Ph.D. CONVOCATION October YEAR: 2003

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DEDICATION

Any success I have ever had has been because of my parents Gary and Lilla Henry in Ottawa, Ontario. Their love, support and humour made every difficult moment in my life diminish, and I dedicate this thesis to them.

I would also like to dedicate this thesis to Dale Calder at the Royal Ontario Museum in Toronto, Ontario for introducing me to the taxonomy and ecology of marine hydroids. His kindness, expertise and special enthusiasm for his work continue to inspire me to look at ethereal critters, to learn their life histories and to consider the nomenclature we use to categorize them:

"For I am not going to tell you *my* name, ...
For one thing it would take a long while:
my name is growing all the time,
and I've lived a very long time;
so *my* name is like a story.
Real names tell you the story of the things they belong to in my language,...
It is a lovely language but it takes a very long time to say anything in it,
because we do not say anything in it,
unless it is worth taking a long time to say and to listen to."

JRR Tolkien,
Lord of the Ring: The Two Towers (1955)

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ABSTRACT

Sessile colony-forming animals on the seafloor are susceptible to bottom fishing disturbances in marine ecosystems. Life histories of "colonial epifauna" affect the capacity for these animals to persist, however effects of bottom fishing on the richness, biomass, species composition and life histories of colonial epifauna are not well studied. A literature review demonstrated the high potential for regeneration from injuries inflicted by bottom fishing to impair sexual reproduction, growth and encounters with other individuals. A three year study with the Canadian Department of Fisheries and Oceans (DFO) on the impacts of experimentally pulsed otter trawling on the Scotian Shelf demonstrated significant changes in colonial epifauna species composition after trawling, and biologically relevant suppression of natural temporal dynamics in richness and biomass as well as impacts on biomass of sponges, bryozoans and soft corals. Inshore DFO scallop surveys in the Bay of Fundy demonstrated significant divergence between hydroid communities on heavily fished cobbles and those on relatively unfished live scallop substrata: divergence was mostly explained by the lack of large, long-lived arborescent taxa on cobbles. Dredging in the Bay of Fundy injured hydroids and significantly reduced sexual fecundity and induced colony fragmentation in the hydroid *Sertularia cupressina*. *In vitro* disturbance induced colonies of the soft coral *Gersemia rubiformis* to contract and prematurely release sexually-derived larvae to reduce injury and avoid expending resources associated with sexual reproduction. The importance of evaluating the potential for injuries to impair sexual reproduction in colonial epifauna is particularly emphasized throughout this thesis, as this may limit recruitment and recovery from bottom fishing and reduce genetic diversity in marine ecosystems.

ACKNOWLEDGEMENTS

Field and lab

I would like to thank the captains and crews of the Canadian Coast Guard Ships *Hudson*, *Needler*, *Parizeau, Teleost* and *J.L. Hart* for their assistance and expertise that was instrumental to all of the field suverys and experiments conducted in this thesis. I am particularly indebted to the chief scientists on board these cruises: Don Gordon, Mark Lundy and Dale Roddick at the Bedford Institute of Oceanography (BIO), Department of Fisheries and Oceans (DFO). The taxonomic expertise of Kevin MacIsaac and Cynthia Bourbonnais (BIO) was essential to the trawl impact study on Western Bank, and they kindly furnished me with numerous hydroids from corals, fish stomachs, cobbles and sand collected across Atlantic Canada. Kevin's unintentional humour also provided me with much respite during the progress of my thesis, whether on a research cruise or before a dive in shark-patrolled waters. I would also like to thank The Geological Survey of Canada (Atlantic), Natural Resources Canada, Dave McKeown and Gordon Fader for providing the necessary ORE Trackpoint II systems and oceanographic and geological interpretations. I wish to thank Maria Buzeta, Mike Strong and the Green's Point Lighthouse Association for assistance in the field. I thank Peter Vass (BIO) for developing and directing the operation of the videograb on Western Bank. I thank Lorraine Hamilton (BIO) for contributing the coral RAPD - PCR work, and Pål Mortensen and Lene Buhl-Mortensen (BIO) for helping with methods for quantifying coral "states". Dan Jackson (Huntsman Marine Science Centre) kindly contributed his expertise to train me with digital imaging software and photography of specimens, and for carefully divulging some *Corrie* plots. I am grateful for all the work that Rhonda Coll (BIO) has done for me, her kindness and professionalism in retrieving cryptic papers from over the globe are much appreciated. Criticisms of all manuscripts derived from this thesis research were very kindly provided by Don Gordon (BIO), Kevin MacIsaac (BIO), Kent Gilkinson (Northwest Atlantic Fisheries Centre, DFO) and Maria Buzeta (St. Andrews Biological Station, DFO).

Thesis development

My thesis committee (Michael Hart, Robert Scheibling and Martin Willison) at Dalhousie University was especially essential in helping me shape this research and for providing much needed criticisms along the way. Each committee member demonstrated his own unique expertise, professionalism and genuine curiosity in his research field that I hope to reflect in my future experiences. All contributed substantially to keeping my research on track and provided much graduate student comfort and humour whether they knew it or not. I would also like to thank Ransom Myers for his role in the early development of my thesis, and Hal Whitehead for helping me with graduate student formalities in the Department of Biology.

My supervisor Ellen Kenchington deserves substantial gratitude for actively directing my thesis and research career. Her research diversity, scientific creativity and professional success have allowed me to set very ambitious goals for my own research career, although I cannot think of ways to properly thank her for all she has contributed to me professionally and personally.

Motivation

I would like to thank friends that have played a part in my life as a graduate student and motivated me to complete this thesis, especially to those that lured me into the ocean and gave me reasons to stay there.

Funding

Funding was provided by DFO, a post-graduate NSERC scholarship, a DFO-NSERC supplemental award, a grant from Dale Calder and Cliff Cunningham through the Partnerships for Enhancing Expertise in Taxonomy program (NSF DEB - # 9978131) and the Centre for Marine Biodiversity. Travel to conferences was provided by DFO, the PEET program, Dalhousie University and a grant from the Ecological Society of America.

CHAPTER ONE: INTRODUCTION

Effects of bottom fishing in marine ecosystems: linking life history traits with observed patterns

Global concerns about the impacts of bottom fishing on marine ecosystems have prompted numerous studies into the effects of these human activities, many of which are reviewed in Hutchings (1990), Jones (1992), Jennings and Kaiser (1998), Lindeboom and de Groot (1998), Collie et al. (2000), Dayton et al. (2002), Johnson (2002), Kaiser et al. (2002) and Thrush and Dayton (2002). As this gear frequently or continuously contacts the bottom, it is not surprising that impacts on the biological communities inhabiting the seafloor have received much research attention. The severity of impacts on benthic communities depend on the gear type, fishing speed/intensity, bottom/habitat type and the life histories of the organisms inhabiting the area (e.g., Thrush et al. 1995; Collie et al. 1997, Collie et al. 2000).

Life history traits of species in chronically fished marine ecosystems

Impacts of bottom fishing can be greatest in areas that are fished for the first time, infrequently or in areas with relatively stable consolidated sediments (Jennings and Kaiser 1998; Kaiser et al. 1998; Duplisea et al. 2002) as proportionately more resident organisms are likely to exhibit life histories not well suited to habitats with intense or frequent disturbance (Dinmore et al. 2003) e.g., many species in deep-water ecosystems (Jones 1992; Probert et al. 1997; Probert 1999; Koslow et al. 2001; Thrush and Dayton 2002). A suite of life history traits are predicted to be positively correlated with habitat stability including large body size, slow growth rate, late or "delayed" sexual maturity,

and long lifespans (Grassle and Sanders 1973; Sanders 1979). Recognizing the link between life history traits and effects of bottom fishing could help to predict shifts in biological assembly by identifying vulnerable "indicator" species and understanding population dynamics of the individual species (Jennings and Cotter 1999; Jennings et al. 1999).

Fishing-related shifts in species composition are reported in fish communities and reflect changes in life history traits such as body size, age and size at maturity and reproductive potential (Jennings and Kaiser 1998; Jennings et al. 1999; Dayton et al. 2002; Jennings et al. 2002). Life history traits of benthic invertebrates also change in response to chronic bottom fishing, including body size, extent of mobility, growth rate and form, fragility and lifespan (Gili et al. 1987; Thrush et al. 1995; Auster et al. 1996; MacDonald et al. 1996; Collie et al. 1997; Frid et al. 1999; Pugh 1999; Kaiser et al. 2000a; McConnaughey et al. 2000; Smith et al. 2000; Veale et al. 2000; Bradshaw et al. 2002; Chícharo et al. 2002; Thrush and Dayton 2002), although shifts in these traits are not consistently observed e.g., Frid et al. (2000).

Adaptive potential of colonial epifauna in fished ecosystems

This thesis considers colonial animals living on the seafloor (colonial "epifauna") to be those taxa comprised of physiologically integrated repeated units ("modules") that can, if separated from the colony, potentially function in isolation e.g., an osculum-bearing sponge, a cnidarian polyp, a bryozoan or tunicate zooid *cf* Harper (1977). It is recognized that this classification may not hold for sponges (e.g., see Rosen 1979), but it

was felt that the present classification conveniently permits sponges to be included in the analyses.

The sessile emergent nature of colonial epifauna makes them highly susceptible to being killed, removed or damaged by bottom fishing activities (Hutchings 1990; Collie et al., 1997; 2000). But in contrast to unitary (or "solitary") taxa, the ability for portions of colonies to survive the death of individual modules ("partial mortality") and regenerate these damaged areas makes colonial epifauna potentially good at recovering from injuries (Jackson 1977; Buss 1979).

The considerable life history plasticity observed in many colonial epifauna species may also help adapt colonies to persisting in disturbed habitats. For example, colony "astogeny" (the way in which modules are arranged in the colony *sensu* Lasker and Sánchez 2002) can be modulated by disturbance; colonies tend to approximate linear runner- or vine-shapes in habitats where the incidence for mortality is high, and mound- or tree-shapes in more stable habitats (Jackson 1979). Modulated astogeny in disturbed habitats also endows a "refugial" growth strategy to the colony that confers relatively high "mobility" over the substrate but low competitive ranking (Buss 1979; Jackson and Coates 1986; Marfenin 1997).

Many colonial epifauna also exhibit variability in reproductive mode that can help adapt colonies to disturbed habitats. Reproduction can occur via sexually-derived larvae, or asexually ("clonally") via budding, fission, fragmentation or more rarely, parthenogenesis (Hughes and Cancino 1985; Hughes 1989; Carvalho 1994). Cloning often results in the production of large genetically identical propagules that generally have

low mortality rates, and confers the ability to rapidly colonize local and distant habitats that spreads the risk of further mortality and (in contrast to aclonal taxa) to delay senescence by extending the lifespan of the genotype beyond that of the colony (Jackson 1986; Orive 1995; Karlson 2002). The potential for recruitment limitation in colonial epifauna that rarely exploit clonal reproduction increases the contribution and thus the importance of sex in colonization processes of these taxa (Karlson 2002), but disturbances that fragment colonies would effectively induce clonality in these taxa.

Impacts of bottom fishing on colonial epifauna communities

Life history plasticity can increase the probability of long-term species persistence if it increases survivorship and fecundity (Hadfield and Strathmann 1996), but the impacts of fishing-induced changes to life history traits in colonial epifauna communities have rarely been investigated. Although the ability to regenerate is well established in these animals and thus the potential for colonial epifauna community recovery is high, long-term changes in colonial epifauna communities are becoming increasingly evident in response to chronic bottom fishing. These communities tend to have reduced species richness (Callaway et al. 2002) and biomass (Kaiser et al. 2000b; McConnaughey et al. 2000; Veale et al. 2000). Major shifts in species composition are also reported and reflect the disappearance of highly "vulnerable" taxa i.e., low resilience to fishing paired with low recovery potential *sensu* Pitcher et al. (2000). Lightly fished or unfished colonial epifauna communities can be dominated by a larger proportion of large erect rigid taxa while those exposed to heavier fishing pressure tend to be comprised of small, flexible,

runner-like or encrusting growth forms (Gili et al. 1987; Hutchings 1990; Collie et al. 2000; Pitcher et al. 2000; Bradshaw et al. 2001, 2002).

Incorporating dynamics of injured organisms into ecosystem models

In addition to the significant mortality inflicted by bottom fishing on benthic organisms (e.g., Jennings and Kaiser 1998; Bergman and van Santbrink 2000), these activities also wound a large proportion of animals. There is substantial evidence that bottom fishing inflicts injuries on both target and non-target benthic invertebrates (Caddy 1973; de Groot 1984; Rumohr and Krost 1991; Eleftheriou and Robertson 1992; Kaiser and Spencer 1995; Kaiser 1996; Currie and Parry 1993; Lindeboom and de Groot (1998); Kaiser et al. 2000a, b; Jenkins et al. 2001; Robinson et al. 2001; Gaspar et al. 2002; Moschino et al. 2003). Numerous studies report high incidences of fishing-related wounds, fragmentation or detachment from the seafloor in colonial epifauna (Tilmant 1982; de Groot 1984; Van Dolah et al. 1987; Sainsbury et al. 1993; Bavestrello et al. 1997; Freese et al. 1999; Koenig et al. 2000; Roberts et al. 2000; Fosså et al. 2002; Wassenberg et al. 2002; Kefalas 2003; Mortensen et al. 2003), including those inflicted by fixed bottom gear such as pots, crab traps and ghost-traps (e.g., Sutherland et al. 1983; Van der Knapp 1993; references in Johnson 2002).

Benthos that are not killed by bottom fishing will potentially recover from their injuries (Tilmant 1982; Van Dolah et al. 1987; Freese et al. 1999; Bradshaw et al. 2002) and possibly grow, reproduce, interact with other organisms and contribute genes to subsequent generations. But actual post-fishing states, rates and recovery potential of colonial epifauna communities may differ dramatically from that which is generally

predicted e.g., slower growth rates in detached colonies (Tilmant 1982) or impaired sexual reproduction (suggested by Jenkins et al. 2001). Altered life history processes occur because energetic and cellular resources used for colony repair and regeneration are frequently diverted away from sexual reproduction, growth and processes that govern encounters with other individuals (Rinkevich 1996; Meesters et al. 1997a). Furthermore, the potential for fishing-related loss of genetic diversity due to impaired sexual reproduction combined with colony fragmentation (considered in this thesis) and selective mortality (Jennings et al. 1999; Law 2000; Kenchington 2002) have not been considered before in colonial epifauna. Severely recruitment-limited populations combined with extensive cloning could lead to inbreeding (Jackson 1986), fixation of deleterious mutations (Gabriel and Bürger 2000) and increase the potential for extinction when environmental conditions change (Lasker and Coffroth 1999).

Attempts to predict post-fishing states, rates and potential for recovery are currently made based on how pre-fished organisms were living e.g., inferring re-growth of an organism based on its size (Wassenberg et al. 2002) or recruitment based on reproduction and colonization rates of unfished organisms (Jones 1992). But post-fishing states and rates reflect a mixture of life histories exhibited by injured as well as escaped organisms (Fig. 1). Since recovery potential affects the status of a species in post-fished ecosystems (Pitcher et al. 2000), attempts to predict post-fishing states and rates may overestimate recovery capacity and inaccurately predict the status of species in post-fished ecosystems.

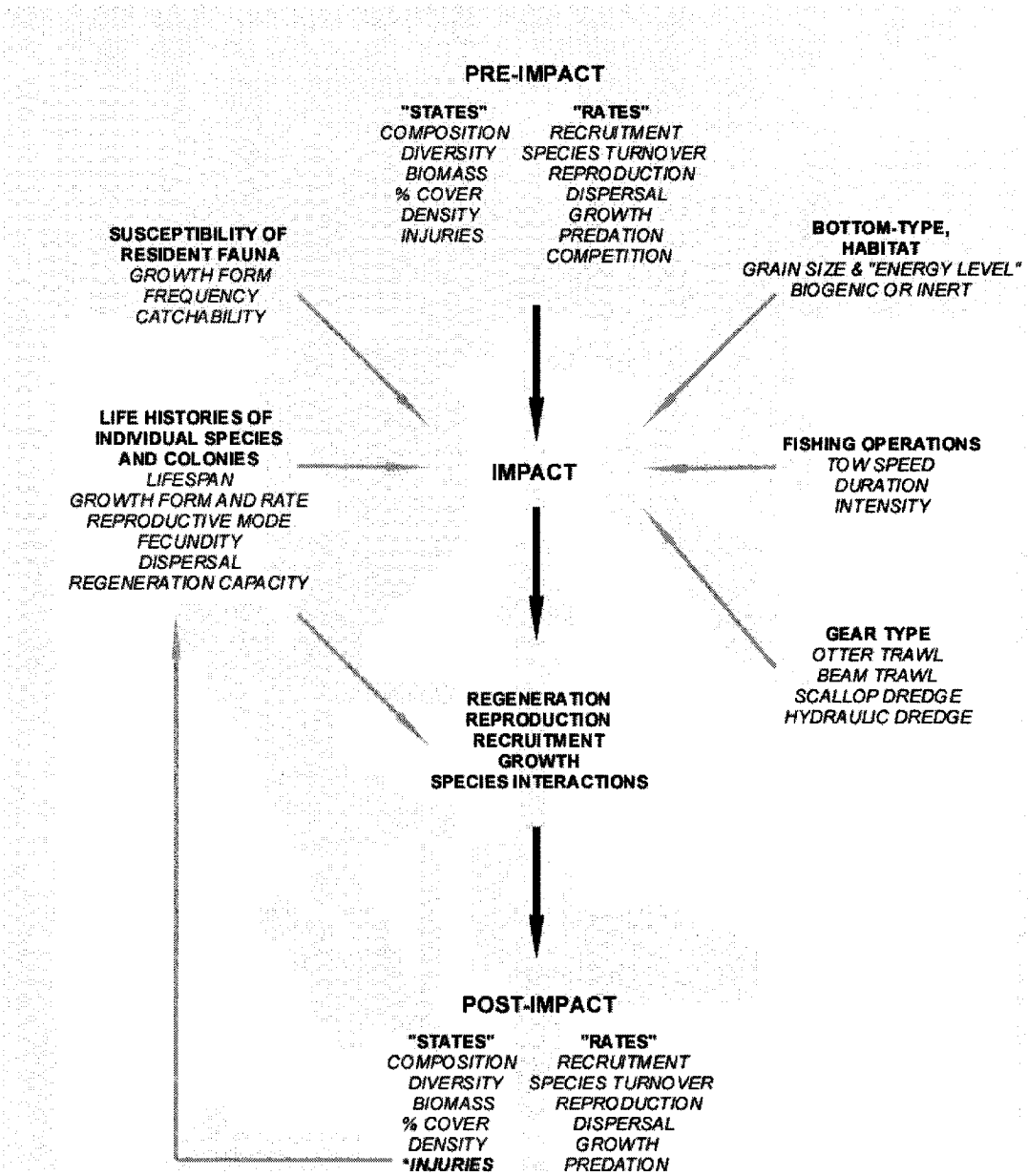

Fig. 1: Variables that affect the magnitude and direction of impacts of bottom fishing on colonial epifauna. The role of injuries in post-impact community "states" and "rates" are emphasized throughout this thesis, as fishing-related damage to colonial epifauna affects life history processes and ecological functioning e.g., regeneration, reproduction, growth and interactions with other species.

Thesis objectives

Considerable collaborations with the Canadian Department of Fisheries and Oceans (DFO) provided the basis for the current thesis research. DFO mobile bottom gear impact programs began over a decade ago in 1990, inspired by the work of the European research community particularly in the North Sea and the Irish Sea. Several areas in Atlantic Canada were selected as suitable sites to study fishing impacts including a gravel-bottom ecosystem in the 4TVW haddock nursery area on Western Bank on the eastern Scotian Shelf (Prena et al. 1996). Regular surveys of the inshore Bay of Fundy scallop (*Placopecten magellanicus*) stocks also facilitated macrofaunal sampling on commercial scallop grounds. The following overall objectives were met with a combination of experimental and survey methods in the field and in the laboratory:

(1) to identify impacts of bottom fishing on communities and life histories of colonial epifauna, and

(2) to link observed impacts to life history responses to bottom fishing activities.

Thesis overview

Chapter Two reviews regeneration from partial mortality in colonial epifauna. The first part of this review describes the cellular and physiological aspects of wound sealing, healing and repair to demonstrate the potential for colony resources to be shared between these and other life history processes such as sexual reproduction, growth and encounters with other organisms. The second part reviews how colony state, wound characteristics and species-specific factors affect regeneration in colonial epifauna. The third part reviews the ecological consequences of regeneration for other life history processes. This

part integrates the cellular and physiological aspects of regeneration with evidence for ecological trade-offs between regeneration and (often to the detriment of) sexual reproduction, re-growth and interactions with other organisms. The potential for human activities that injure colonial epifauna to alter life histories is discussed, with attention paid to how the response of an individual colony can be conferred to higher levels of biological assembly. This chapter was written primarily by the author of this thesis, but thesis committee member Dr. Michael Hart has contributed to its current form by helping to prepare the revised version for submission to a peer-reviewed journal.

In Chapter Three a three year field experiment is described on the impacts of otter trawling on communities of colonial epifauna in an area of the eastern Scotian Shelf closed to most bottom fishing since 1987. This study comprised a smaller part of a broad investigation conducted by DFO (project directed by Dr. Don Gordon and Dr. Ellen Kenchington) to examine the physical and biological impacts of pulsed bottom fishing on the closed area. This study also provided the opportunity to examine impacts on a sector of organisms that are typically lumped into taxonomically coarse groups and have spatial and temporal dynamics that are virtually unknown in most areas exposed to commercial-scale bottom fishing. Sorting and identifications of all colonial epifauna except the hydroids (performed by the thesis author) were done by Kevin MacIsaac and Cynthia Bourbonnais. The effects of trawling are interpreted in relation to large natural spatial and temporal shifts in colonial epifauna communities in the study area and in relation to mechanisms by which otter trawling modifies these communities e.g., trawl-induced fragmentation, regeneration from partial mortality followed by rapid colony re-growth.

This chapter is currently being revised mainly by the thesis author and thesis supervisor Dr. Ellen Kenchington, but also by Dr. Don Gordon, Kevin MacIsaac and Cynthia Bourbonnais for submission to a peer-reviewed journal.

In Chapter Four a field study conducted in the Bay of Fundy is described that tested the hypothesis that areas exposed to commercial-scale scallop dredging are comprised of a different set of species than those from areas with lighter to no fishing. Life history attributes of these species should differ in predictable ways, based on the potential for high mortality. Species on frequently disturbed areas should be smaller, with creeping growth strategies, little branching and the potential for high dispersal. Species on more stable areas can grow to be larger, be highly branched with a tendency towards brooding philopatric larvae with potentially lower dispersal capacity. The value of using "pseudo-controls" in the absence of any reference areas is discussed. This chapter is currently being revised by the thesis author and thesis supervisor Dr. Ellen Kenchington for submission to a peer-reviewed journal.

In Chapter Five another field study conducted in the Bay of Fundy is described that tested the hypothesis that hydroids damaged by scallop dredging have impaired sexual reproduction and are split into genetically identical colonies ("clones"). Ecological and genetic methods were used to examine the effects of injury on aspects of reproduction in colonies of the hydroid *Sertularia cupressina*. The consequences of fishing-related injuries on reproduction are discussed in relation to long-term declines in populations of hydroids and other colonial epifauna due to low recruitment of sexually-derived larvae and loss of evolutionary adaptability due to reduced genotypic ("clonal") diversity. This

chapter is currently being revised by the thesis author and thesis supervisor Dr. Ellen Kenchington for submission to a peer-reviewed journal.

In Chapter Six describes a laboratory investigation is described on the effects of experimental disturbance (cobble substrata repeatedly turned over) on aspects of responses, reproduction and regeneration from injuries in the nephtheid soft coral *Gersemia rubiformis*. This chapter began as a student project for Angela Silvaggio who was supervised by the thesis author. The thesis author presented the student with the research question, designed the experiments, helped to collect the animals, set up the aquaria and analysed the data. *In vitro* photography and measurements were combined with genetic methods to test the hypothesis that disturbed corals would behave differently and fragment from partial mortality from cobbles being frequently turned over. The capacity for regeneration in *G. rubiformis* was also explored, and results are discussed in relation to additional mechanisms for fishing-related injuries to impair sexual reproduction e.g., premature release of unviable sexually-derived larvae. This chapter is currently being revised by the thesis author, thesis supervisor Dr. Ellen Kenchington with contributions by the project student for submission to a peer-reviewed journal.

Chapter Seven summarizes the results obtained in this thesis and places these observations across different taxa, habitats and effects of different fishing gear into a more contectual outlook. Life history traits and biological responses of individual taxa are invoked in this section of the thesis to explain patterns observed during this and other studies.

CHAPTER TWO: REGENERATION FROM PARTIAL MORTALITY IN COLONIAL MARINE EPIFAUNA

INTRODUCTION

Colonial animals are characterized by body plans consisting of repeating morphological units (modules) with potentially high levels of physical connectedness, integration and genetic relatedness between modules (Rosen 1979). Colonial body plans are well represented in marine animals, and appear multiple times in sponges, cnidarians, bryozoans and tunicates.

The biological significance of coloniality to marine animals is evident in the competitive superiority of these organisms to their unitary counterparts, the adaptiveness of resource translocation between modules and their abilities to survive despite injuries and death of individual colony units (Jackson 1977; Buss 1979).

The adaptive significance of coloniality is universal across marine plants, algae and animals. But the sessile nature of colonial animals to physical or biotic disturbances and the absence of cell walls in animal taxa may favour the evolution of diverse or novel strategies to translocate intracolonial resources in these groups (Buss 1987). Therefore, these strategies are expected to be different from those exhibited by other sessile organisms such as plants or more mobile animals (Huey et al. 2002).

Colonial marine epifauna are highly vulnerable to natural (e.g., grazing, predation, waves, cyclones, ice scour) and anthropogenic (e.g., scuba diving, anchors, log battering, blast-fishing, fishing gear) disturbances that can result in partial or whole colony mortality. Regeneration from partial mortality is widely noted as a vital initial step in community recovery by compensating for damaged or dead colony parts and helping

colonies to survive, regain their initial sizes and re-establish populations to pre-disturbance levels through growth, reproduction and species interaction processes (Fishelson 1973; Loya 1976a; Pearson 1981; Fadlallah 1982; Karlson 1983; Hughes and Jackson 1985; Done 1987, 1988; Cameron et al. 1991; Bythell et al. 1993; Jokiel et al. 1993; Connell et al. 1997; Lasker and Coffroth 1999).

A major motivating factor for focusing on colonial epifauna in this review is the role that these organisms play as biogenic habitat for commercially valuable and non-target species in marine ecosystems that are exposed to chronic mechanical disturbance from bottom fishing activities such as trawling and dredging (Bradstock and Gordon 1983; Sainsbury 1987; Sainsbury et al. 1993; Auster et al. 1996; Kaiser et al. 1998; Rogers 1999). These disturbances inflict considerable partial mortality on colonial epifauna (e.g., Tilmant 1982; de Groot 1984; Van Dolah et al. 1987; Sainsbury et al. 1993; Van der Knapp 1993; Bavestrello et al. 1997; Freese et al. 1999; Koenig et al. 2000; Roberts et al. 2000; Fosså et al. 2002; Johnson et al. 2002; Wassenberg et al. 2002; Mortensen et al. 2003), where regeneration is likely to play a key role in the survival and subequent life histories of colonial epifauna exposed to bottom fishing.

The goal of this review was to highlight the ecological relevance of regeneration from partial mortality caused by physical disturbances (i.e., excluding stress events such as disease, bleaching, sedimentation) to life history aspects of colonial epifauna. Colony responses to injuries are linked with factors that limit regenerative powers. These linkages help to explain patterns in colony growth, reproduction and species interactions following partial mortality. In the first part of the review, general colony responses to partial

mortality are reviewed. Reconstitution of damaged/isolated module parts was not reviewed here as such injuries do not constitute partial colony mortality. No attempt was made to review organogenesis and the molecular control of developmental patterning of individual module regeneration. The second part of the review examines how wound characteristics, colony state and species-specific differences are related to variability in regeneration capacity among colonial epifauna taxa. Increased resource demands during regeneration may alter resource allocation to growth, reproduction and species interaction processes. Thus, the third part of the review examines how regeneration alters colony growth, sexual reproduction and outcomes of species encounters. No studies have examined the relationship between regeneration from partial mortality and community-level processes (e.g., larval recruitment, energy transfer, succession). But the observation that colony resources are frequently shared between regeneration, sexual reproduction, growth, and species encounters leads to a series of hypotheses about the role of regeneration in ecological and evolutionary processes that are physiologically and developmentally linked to injury repair.

COLONY RESPONSES TO INJURIES

Damaged colonies progress through three categories of responses: sealing, defense and module restoration from a regeneration bud (Needham 1952).

Sealing refers to events that result in wound closure to ensure that additional contents are not lost and foreign particles are prevented from entering the lesion. Closure is effected as one of two mechanisms: (1) morphallaxis (usually in the case of small wounds), entailing contraction of underlying cellular zones followed by the stretching or

re-organizing of existing cells (Hay 1966; Harrison 1972; Storr 1976) or (2) epimorphis, involving a cascade of cell migration, differentiation, and proliferation events to seal the wound (Needham 1952).

Defense refers to cell- and antibody-mediated immune responses that lead to the phagocytic destruction of foreign matter and dead cells. Remarkable antibody production and phagocytic abilities are demonstrated by wandering totipotent amoeboid cells (amoebocytes) and by lymphocyte-like cells (which may themselves be derived from amoebocytes).

Regeneration refers to the formation of an undifferentiated cell mass (blastema) followed by the budding of new modules that are likely regulated by rules of module assembly and pattern formation to ensure new modules are oriented correctly in the colony (Holyoak 1992). Progenitor blastema cells either originate from dedifferentiated somatic cells or the aggregation of totipotent stem cell reserves (Thouveny and Tassava 1998). Dedifferentiation is a return to the cell cycle through the destabilization of the differentiated state of various somatic cell types, prompted by signals from tissue surrounding the wound (Brockes 1998). Many cell types of colonial marine invertebrates are permanently committed to their differentiated states, but several cell lines can dedifferentiate to follow new fates (Galliot and Schmid 2002). For example, the choanocytes and pinacocytes of sponges, and the hemocytes and cells of the atrial epithelium, epicardial epithelium and septal mesenchyme of tunicates are all potentially able to dedifferentiate and contribute to blastema formation.

In other taxa, totipotent stem cells contribute more to the blastema bud rather than somatic cells, typically in the form of amoebocytic reserve cells. Examples include archaeocytes (in sponges), wandering amoebocytes and interstitial i-cells (in cnidarians) and wandering amoebocytes (in bryozoans and tunicates). New modules are then constituted from the subsequent redifferentiation of somatic cells or differentiation of stem cells.

The totipotency of hemocytes and their roles as possible stem cell precursors are best exemplified in botryllid tunicates, many of which regenerate whole colonies from very few hemocytes, a process known as vascular budding from totipotent stem cells (Rinkevich et al. 1993, 1995). The emerging understanding of the great totipotency potential of tunicate hemocytes and their roles as possible stem cell precursors could have important medical and biotechnology implications for human stem cell research given the close evolutionary relationship between tunicates and vertebrates.

Resources used in responses to partial mortality are summarized across colonial epifauna taxa in Table 1.

Table 1: Summary of resources required for sealing, repair and module regeneration in colonial epifauna.

Group	Molecules	Cell types	Energy sources
Sponges[1]	spongin (in the Demospongiae)	archaeocytes; choanocytes*; collencytes; gray cells; pinacocytes; sclerocytes; spherulous cells	gray cells; cyanobacteria; symbionts
Corals[2]	mineralized crystals (in species with calcified skeletons); peptide growth factors*	amoebocytes; coenochymal cells; cells from the epithelium, gastroderm, mesoglea, mesenterial filaments; globular granular cells; i-cells; sperm cells lymphocyte-like cells; "transitional" cells;	lipids, proteins, glucose from zooxanthellae; prey; dissolved free amino acids
Hydroids[3]	various molecular factors in hydranths; stolon inducing factors	amoebocytes; cnidocytes; endodermal cells; epidermal cells; i-cells	gastrovascular flow mediated by ATP-fueled contractile vacuoles
Bryozoans[4]	unknown	amoebocytes	brown body resorption*; carbon compounds circulated by funiculae
Tunicates[5]	cytokine-like molecules secreted by morula cells; substances that inhibit blastogenic budding*	amoebocytes; cells from the atrial epithelium, epicardial epithelium, mesenchyme; morula cells, lymphocyte-like cells; spherical cells	stolonal spherical cells*

* proposed

Table 1 (continued): Summary of resources required for sealing, repair and module regeneration in colonial epifauna.

[1] (Wilson 1910; Stolte 1935; Korotkova 1970; Harrison 1972; Boury-Esnault 1976; Thompson et al. 1983; Simpson 1984; Hoppe 1988; Leys and Mackie 1994; Hill and Hill 2002)

[2] (Stolte 1935; Muscatine and Cernichiaria 1969; Pearse and Muscatine 1971; Fishelson 1973; Lang da Silveira and Van't Hof 1977; Rinkevich and Loya 1983; Isa 1987; Stimson 1987; Hayes and Bush 1990; Ferrier 1991; Olano 1993; Meesters et al. 1997a; Oren et al. 1997b; Meszaros and Bigger 1999; Ben-David-Zaslow and Benayahu 2000)

[3] (Stolte 1935; Vorontsova and Liosner 1960; Tardent 1963; Hale 1964; Hay 1966; Braverman 1971, 1973; Tardent 1985; Müller et al. 1987; Buss and Blackstone 1991; Schierwater et al. 1992; Frank et al. 2001)

[4] (Stolte 1935; Vorontsova and Liosner 1960; Menon 1972; Gordon 1977; Zimmer and Woollacott 1977; Nieuwkoop and Sutasurya 1981; Best and Thorpe 1985; Hughes 1989; Harvell and Helling 1993)

[5] (Stolte 1935; Berrill 1951; Vorontsova and Liosner 1960; Sabaddin 1979; Mukai et al. 1983; Sugino and Nakauchi 1987; Rinkevich et al. 1995; Kawamura and Sugino 1999; Ballarin et al. 2001; Kawamura 2001)

FACTORS AFFECTING REGENERATIVE CAPACITY

Permanent lesions, scars and the generally exponential decline in regeneration over time e.g., as reported for scleractinians (Bak and Steward-Van Es 1980; Bak 1983; Meesters et al. 1996a, 1997a; van Woesik 1998; Lirman 2000a), are evidence of the limited regenerative potential exhibited by colonial epifauna. Wound characteristics interact with state functions of the colony and species-specific differences to limit regenerative capacities in these animals.

A taxonomically broad summary of regeneration rates from the literature is provided in Table 2. The 99 cases of regeneration rates (27 from sponges, 6 from gorgonians, 55 from scleractinians, 3 from hydroids, 6 from bryozoans and 2 from tunicates) were incorporated into this summary. Species in Table 2 are cited as they originally appeared in the referenced study. For example, noting the large differences in regeneration rates among taxa now known to be "sibling species" e.g., *Montastraea annularis* morphs (*sensu* Knowlton et al. 1992; Van Veghel and Bak 1993, 1994; Weil and Knowlton 1994; Lopez et al. 1999) helps to emphasize regeneration variability among colonies with different colony growth patterns. Studies differed in measures of wound size and regeneration, therefore data have been standardized where possible to facilitate comparisons. Effects of wound characteristics, colony state and taxon-specific differences in regenerative capacity explain much of the variability between cases in Table 2. These factors are reviewed and discussed with respect to how they restrict regeneration.

Table 2: Daily regeneration rates of colonial epifauna from published data.

Species	Wound size	Daily regeneration rate	Reference
Sponges			
Agelas clathrodes	100-300mm^2	3.6-12.1mm^2	Hoppe 1988
Anchinoe sp. (yellow morph)	layer cleared	0.4mm^2/ mm border	Ayling 1981
Anchinoe sp.	1000mm^2	3.7mm^2	Ayling 1983
Aplysilla rosea	1000mm^2	6.2mm^2	Ayling 1983
Chelonaplysilla sp.	1000mm^2	4.1mm^2	Ayling 1983
Chondropsis sp.	1000mm^2	5.7mm^2	Ayling 1983
Cliona celata	250mm^2	1.1-1.8mm^2	Bell 2002
Crambe crambe	450mm^2	8.6-10.0mm^2	Turon et al. 1998
Eurypon sp.	1000mm^2	0.9mm^2	Ayling 1983
Hymedesmia sp. (orange morph)	1000mm^2	0.5mm^2	Ayling 1983
Hymedesmia sp. (red morph)	layer cleared	0.3mm^2/ mm border	Ayling 1981
Ircinia strobilina	100-300 mm^2	12.0-41.1mm^2	Hoppe 1988
Microciona sp.	layer cleared	0.2 mm^2/ mm border	Ayling 1981
Microciona sp.	10-600mm^2	0-7.5mm^2	Ayling 1983
Neofibularia nolitangere	100-300mm^2	4.5-13.6mm^2	Hoppe 1988
Stylopus sp. (pink morph)	1000mm^2	7.0mm^2	Ayling 1983
Stylopus sp.	layer cleared	0.1-0.5mm^2/ mm border	Ayling 1981
Stylopus sp.	10-4200mm^2	0-270.0mm^2	Ayling 1983
Tedania sp. (crimson morph)	12.6mm^2	no regeneration	Jackson and Palumbi 1979
Tedania sp. (orange morph)	layer cleared	0.1mm^2/ mm border	Ayling 1981
Tedania sp. (orange morph)	1000mm^2	4.2mm^2	Ayling 1983
Tedania sp. (orange morph sp. 1)	12.6mm^2	4.2-12.6mm^2	Jackson and Palumbi 1979

Table 2 (continued): Daily regeneration rates of colonial epifauna from published data.

Tedania sp. (orange morph sp. 2)	12.6mm^2	0.5mm^2	Jackson and Palumbi 1979
Tedania sp. (pink-brown morph)	12.6mm^2	1.8mm^2	Jackson and Palumbi 1979
Tedania sp. (pink-red morph)	12.6mm^2	1.3-1.6mm^2	Jackson and Palumbi 1979
Tedania sp. (red-orange morph)	12.6mm^2	6.3mm^2	Jackson and Palumbi 1979
Tedania sp. (white morph)	12.6mm^2	0.4-0.6mm^2	Jackson and Palumbi 1979
Gorgonians			
Eunicea mammosa	20mm	6.0-7.8mm	Wahle 1983a
Paramuricea clavata	500mm	0.2mm	Bavestrello et al. 1997
Plexaura homomalla	20mm	6.8-8.6mm	Wahle 1983a
Plexaurella dichotoma	20mm	6.7-10.6mm	Wahle 1983a
Plexaurella flexuosa	40mm	1.4mm	Lang da Silveira and Van't Hof 1977
Plexaurella fusifera	4.5mm	0.3-0.4mm	Meszaros and Bigger 1999
Scleractinians			
Acropora cytherea	400mm^2	5.4-5.6mm^2	Hall 1997
Acropora formosa	not given	0-0.2mm	Stephenson and Stephenson 1933
Acropora gemmifera	not given	0-0.1mm	Stephenson and Stephenson 1933
Acropora hebes	10mm	0.4mm	Isa 1987
Acropora hyacinthus	400mm^2	2.8-4.2mm^2	Hall 1997
Acropora palifera	400mm^2	no regeneration	Hall 1997
Acropora palmata	fragment	0.1-0.5mm	Rogers et al. 1982
Acropora palmata	100mm^2	1.7mm^2	Bak 1983
Acropora palmata	100mm^2	3.6-3.7mm^2	Meesters et al. 1992
Acropora palmata	79mm^2	16.0-25.0mm^2	Meesters and Bak 1995
Acropora palmata	>=3000mm^2	3.6-10.7mm^2	Lirman 2000a
Acropora polymorpha	not given	0.2-0.3mm	Stephenson and Stephenson 1933
Acropora quelchi	not given	0-0.1mm	Stephenson and Stephenson 1933
Acropora robusta	400mm^2	5.4mm^2	Hall 1997

Table 2 (continued): Daily regeneration rates of colonial epifauna from published data.

Acropora sp. 1	not given	0-0.1mm	Stephenson and Stephenson 1933
Acropora sp. 2	not given	0-0.1mm	Stephenson and Stephenson 1933
Agaricia agaricites (forma *purpurea*)	100-500mm^2	0.7-2.2mm^2	Bak and Steward-van Es 1980
Agaricia agaricites	100-500mm^2	0.3-0.5mm^2	Bak et al. 1977
Astrangia lajollaensis	layer cleared	0-0.1 corallite	Fadlallah 1982
Diploria clivosa	570mm^2	0.6-0.8mm^2	Guzmán et al. 1994
Diploria strigosa	100mm^2	1.2-1.5mm^2	Meesters et al. 1992
Diploria strigosa	570mm^2	0.5-0.8mm^2	Guzmán et al. 1994
Favia favus	110-550mm^2	1.6-7.8mm^2	Oren et al. 1997a
Favia favus	87-274mm^2	1.3-3.5mm^2	Oren et al. 2001
Goniastrea retiformis	400mm^2	0.6-1.1mm^2	Hall 1997
Meandrina meandrites	79mm^2	1.3-3.4mm^2	Meesters and Bak 1993
Montastraea annularis (bumpy morph)	160mm^2	15.4-18.7mm^2	Van Veghel and Bak 1994
Montastraea annularis (columnar morph)	160mm^2	0.7mm^2	Van Veghel and Bak 1994
Montastraea annularis (columnar morph)	83-406mm^2	3.7-11.2mm^2	Meesters et al. 1997a
Montastraea annularis (massive morph)	79mm^2	1.6mm^2	Meesters and Bak 1993
Montastraea annularis (massive morph)	160mm^2	10.5-13.9mm^2	Van Veghel and Bak 1994
Montastraea annularis	100-500mm^2	0.75-0.94mm^2	Bak et al. 1977
Montastraea annularis	100mm^2	1.9mm^2	Meesters et al. 1992
Montastraea annularis	170mm^2	4.1mm^2	Meesters et al. 1994
Montastraea annularis	227mm^2	2.9-3.6mm^2	Mascarelli and Bunkley-Williams 1999
Oculina patagonica	200mm^2	2.8-4.4mm^2	Fine et al. 2002
Pocillopora damicornis	400mm^2	3.7-4.0mm^2	Hall 1997
Porites astreoides (brown morph)	13.7-220mm^2	1.5-5.7mm^2	Nagelkerken and Bak 1998
Porites astreoides (green morph)	15.1mm^2	1.7mm^2	Nagelkerken et al. 1999
Porites astreoides (hemisphaerical morph)	79mm^2	5.4-9.0mm^2	Meesters and Bak 1993

Table 2 (continued): Daily regeneration rates of colonial epifauna from published data.

Porites astreoides	100-500mm^2	0.9-2.1mm^2	Bak and Steward-van Es 1980
Porites astreoides	100mm^2	2.7-3.1mm^2	Meesters et al. 1992
Porites astreoides	570mm^2	0.3-0.8mm^2	Guzmán et al. 1994
Porites astreoides	<=80mm	0.02-0.03mm	Ruesink 1997
Porites australiensis	400mm^2	1.7-2.5mm^2	Hall 1997
Porites lichen	400mm^2	0.6-0.9mm^2	Hall 1997
Porites lobata	15-1310mm^2	0.4-4.1mm^2	van Woesik 1998
Porites lutea	15-1310mm^2	0.4-18.3mm^2	van Woesik 1998
Porites mayeri	400mm^2	0-1.4mm^2	Hall 1997
Siderastrea siderea	100mm^2	0.6-1.2mm^2	Meesters et al. 1992
Siderastrea siderea	570mm^2	0.1-0.7mm^2	Guzmán et al. 1994
Siderastrea siderea	<=80mm	0.01 mm	Ruesink 1997
Stephanocoenia michelinii (encrusting morph)	15.1mm^2	0.7mm^2	Nagelkerken and Bak 1998
Stephanocoenia michelinii (massive morph)	16.1mm^2	0.8mm^2	Nagelkerken and Bak 1998
Stephanocoenia michelinii (massive morph)	200mm^2	6.0mm^2	Nagelkerken et al. 1999
Hydroids			
Podocoryna carnea	explants	0.1-0.5 polyps	Braverman 1971
Podocoryna carnea	explants	0.1-0.2 polyps	Ponczek and Blackstone 2001
Hydractinia symbiolongicarpus	explants	0.3-0.6 polyps	Ponczek and Blackstone 2001
Bryozoans			
Electra pilosa	explants	1.0-3.7 zooids	Menon 1972
Membranipora membranacea	explants	1.7-2.3 zooids	Menon 1972
Reptadeonella sp.	12.6mm^2	0.3mm^2	Palumbi and Jackson 1982
Steginoporella sp.	12.6mm^2	0.3-0.9mm^2	Jackson and Palumbi 1979
Steginoporella sp.	38.5mm^2	0.2mm^2	Palumbi and Jackson 1982
Steginoporella sp.	12.6mm^2	0.1-0.3mm^2	Palumbi and Jackson, 1982, 1983

Table 2 (continued): Daily regeneration rates of colonial epifauna from published data.

Tunicates			
Botrylloides sp.	5-71 zooids	0.1 zooid	Rinkevich et al. 1995
Symplegma reptans	all but 1 zooid	0.1-0.2 zooids	Sugino and Nakauchi 1987

Wound characteristics

Some factors that limit regenerative capacity may be more important than others depending on the lesion characteristics (Bak et al. 1977). The effects of lesion size, perimeter and location on the colony are particularly important in determining lesion regeneration capacity, and the results of such data can be interpreted. The role that wound source (i.e., naturally versus artificially inflicted lesions) plays in colony regeneration is not well understood, but is introduced here to highlight its consideration in future studies. For example, many colonial epifauna have specialized grazing predators (including many nudibranch molluscs) to which colonies may have evolved specialized wound healing and regeneration responses. Such specializations might not be expected in response to partial mortality from recently invasive predators or from anthropogenic sources.

Wound size

Incomplete regeneration from large wounds and rapid recovery from small lesions are widely noted phenomena in sponges (*Ircinia strobilina* and *Neofibularia nolitangere*) (Hoppe 1988), scleractinians (*Acropora palmata*, *Agaricia agaricites*, *Favia favus*, *Montastraea annularis* and *Porites astreoides*) (Bak et al. 1977; Bak and Engel 1979; Bak and Steward-Van Es 1980; Meesters et al. 1997a; Lirman 2000a; Oren et al. 2001) and bryozoans (*Steginoporella* and *Reptadeonella*) (Jackson and Palumbi 1982). By extrapolating data from the studies that estimated regeneration rates in mm^2 from Table 2, it appears that there is an approximately linear decrease in daily regeneration rates with increasing wound size ($R^2 = 0.35$) (Fig. 2).

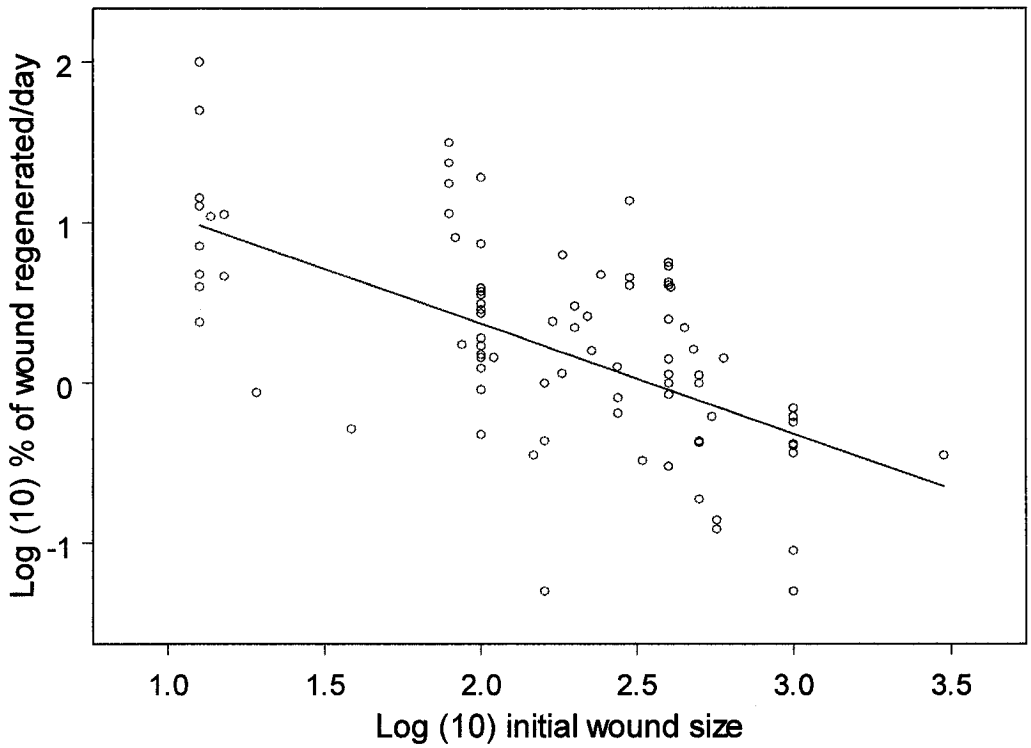

Fig. 2: Linear relationship between amount of tissue regenerated per day and initial wound size based on 91 standardized published regeneration rates of colonial epifauna ($R^2 = 0.35$).

Regenerative capacity depends on lesion size as it is costly for a colony to regenerate a large amount of tissue. Small wounds heal quicker and more completely because small injured surface areas require fewer resources than larger wounds. For example, significantly more carbon products had to be transported from healthy to damaged areas in the scleractinians *Favia favus*, *Platygyra lamellina* and *Porites* spp. when colonies exhibited large versus small wounds (Oren et al. 1997b; Oren et al. 1998). Regeneration capacity of *Montastraea annularis* was highly dependent on wound size, and the amount of tissue that could be regenerated was a function of initial lesion area (Meesters et al. 1996a, b, 1997a). Similar functions would be of enormous value: if the mean wound size of a disturbance can be measured for each species in a disturbed area, it is possible to predict the rates of colonial epifauna community recovery based on the percentage of tissue that can be regenerated.

Wound perimeter

Wound perimeter is a function of both lesion size and shape: a highly convoluted wound has a smaller surface area/perimeter ratio than a circular wound of the same surface area. Short-term regeneration rates are largely determined by wound perimeter, after which time lesion surface area and the surface area/perimeter ratio may become more important to healing (Oren et al. 1997a). The positive relationship between wound perimeter and lesion regeneration capacity was also corroborated by regenerative studies in scleractinians (Meesters et al. 1996a; Van Woesik 1998; Lirman 2000a) and ascidians (Stocker 1991).

As the perimeter of a linear versus circular lesion of the same surface area is associated with more healthy tissue bordering the wound (Oren et al. 1997a), lesion perimeter restricts regeneration by limiting the amount of resources available to wounds with small perimeters. Ultimately, perimeter-based limitations in regenerative capacity have probably evolved to reduce fitness costs associated with high resource allocation to healing large wounds (Meesters et al. 1997a).

Wound location

There is much evidence to suggest that regenerative capacity depends on where a wound is inflicted on a colony. For example, when tops of the vase-shaped sponge *Neofibularia nolitangere* were experimentally damaged, they healed more quickly than wounds inflicted on lateral surfaces (Hoppe 1988). Lesions located near the growing edges (distal wounds) of encrusting colonies of the bryozoan *Steginoporella* sp. regenerated four times faster and were fouled much less often than those inflicted closer to the centres of colonies (proximal wounds) (Palumbi and Jackson 1982, 1983).

The co-ordination of various stages of the regeneration process may also be disrupted by wounds at different locations. Distal lesions in the scleractinian *Acropora palmata* were rapidly sealed by a thin transparent layer of undifferentiated cells with no apparent calcification and no zooxanthellae. In contrast, wounds near the colony base were sealed and calcified almost simultaneously (Bak 1983; Meesters and Bak 1995). Tissue regeneration and calcification in proximal wounds on *A. palmata* were characterized by the random emergence of new polyps and calices with a slow-growing pigmented lip migrating inwards from the wound perimeter (Meesters and Bak 1993;

Lirman 2000a), a structure also observed in *Montastraea annularis* (massive morph), *Meandrina meandrites*, *Porites astreoides*, *P. lobata* and *P. lutea* (Meesters and Bak 1993; Van Woesik 1998).

In contrast to species in which distal wounds are more rapidly healed, wounds on branch tips of the gorgonian *Plexaura homomalla* regenerated much slower than injuries on primary branches (Wahle 1983a), and naturally occurring wounds on more centrally-located colony portions of the corals *Porites astreoides* and *Siderastrea siderea* healed more quickly than peripheral regions (Ruesink 1997). Deep wounds (those that injure superficial tissue and deeper skeletal elements) appeared to be regenerated faster than superficial wounds in *Porites astreoides*, but not in *Agaricia agaricites* (Bak and Steward-Van Es 1980). In some cases, wound location has no effect on regeneration rate (e.g., Meesters et al. 1992). These apprarent discrepancies can be explained by the degree to which resources can be made available to certain areas on a colony.

There is growing evidence that many species preferentially transport resources from proximal to distal modules. Kim and Lasker (1998) considered that depletion of colony resources by exterior modules, or "self-shading", is an emergent property of colonial organisms that can determine growth capacities. Best and Thorpe (1985) first demonstrated the intracolonial transport of ^{14}C from proximal "source" to distal "sink" regions in the bryozoan *Membranipora membranacea.* The adaptive significance of a predominantly proximo-distal direction of resource translocation could be the enhancement of growth and competitive abilities of peripheral modules by keeping the outermost zooids as robust as possible (Palumbi and Jackson 1983). Resource

translocation and activity of enzymes involved in skeletogenesis are also predominantly proximo-distal in scleractinians (Gladfelter 1983; Isa and Yamazato 1984) but this direction may not be important in species that perhaps lack comparable spatial gradients in functional polymorphisms between proximal and distal modules (Wahle 1983a). Enhanced regenerative capacity in *Plexaura homomalla*, *Porites astreoides* and *Siderastrea siderea* in more central portions in these cases may therefore reflect the larger amount of healthy tissue surrounding proximal wounds and not a translocation polarity gradient (*sensu* Wahle 1983a). Similar regeneration rates at the tops versus sides of hermatypic coral colonies can also be explained by sufficient resources reaching the wounded areas, as naturally shaded sides of colonies are photoadapted by accumulating more chlorophyll in side polyps (Meesters et al. 1992). If such translocation gradients are common among different colonial species, then wound location could limit regenerative capacity if it imposes gradient-based or colony-based restrictions on resource availability at some parts of a wound. The existence and direction of such gradients should be corroborated across a wider range of colonial marine invertebrates. The functional correlation between translocation gradients and spatial variation in wound healing should also be verified experimentally in more cases.

Naturally versus experimentally inflicted wounds

The spatial extent of most disturbances experienced by colonial marine invertebrates at the community-level varies from millimeters and centimeters (e.g., predation, bioerosion) to thousands of kilometers (e.g., storms) (Jackson 1991; Nyström et al. 2000). Unfortunately, regeneration from wounds found under natural conditions is

rarely examined (e.g., 3 out of 98 cases in Table 2), and *in situ* lesion properties are rarely characterized concomitantly during the same regeneration study. In contrast to the relatively rapid healing of small wounds, the regeneration of lost modules from increasingly larger lesions has not been very thoroughly investigated, despite the broad size range of wounds found under natural conditions (Table 3).

Table 3: Lesion properties found on colonial epifauna under natural conditions.

Lesions property			
Size	**Source**	**Habitat, geographic region**	**Reference**
10-240mm^2	predation	coral reef, Barbados	Ott and Lewis 1972
2410-7510mm^2	various	coral reef, Brazil (São Paulo)	Acosta et al. 2001
100-10700mm^2	fish, divers, bottom-associated processes	coral reef, Curaçao	Meesters et al. 1996b
50-300mm^2 (type I lesion), 200-6000 mm^2 (type II lesion)	fish, divers, bottom-associated processes	coral reef, Curaçao	Meesters et al. 1997b
0-50% damage	various	coral reef, Curaçao	Bak and Meesters 1998
0->2000mm^2	storms, boats	coral reef, Florida USA	Lirman 2000b
8-10% with >66% damage, 12-20% with 33-66% damage, 13-50% with <33% damage	predation	coral reef, GBR	Done 1987
40% with >66% damage, 15% with 33-66% damage, 20% with <33% damage	predation	coral reef, GBR	Done 1988

Table 3 (continued): Lesion properties found on colonial epifauna under natural conditions.

Lesions property			
Size	**Source**	**Habitat, geographic region**	**Reference**
0-45% with <33% damage, 0-47% with 33-66% damage, 0-43% with >66% damage	predation	coral reef, GBR	Cameron et al. 1991
53% fragments <50mm long	divers	coral reef, GBR	Rouphael and Inglis 1995
3-27% corals with >20% damage, 31% sponges with >33% damage	hurricane	coral reef, Jamaica	Woodley et al. 1981
11-75% with 0-25% damage, 7-85% with 25-50% damage, 0-18% with 50-75% damage, 0-22% with 75-100% damage	various	coral reef, Jamaica	Hughes and Jackson 1985
$100mm^2$	predation	coral reef, Jamaica	Kaufman 1981
$0-344mm^3$	predation	coral reef, Panama (Atlantic)	Lasker et al. 1988
$0-5590mm^3$	predation	coral reef, Panama (Atlantic)	Vreeland and Lasker 1989

Table 3 (continued): Lesion properties found on colonial epifauna under natural conditions.

Lesions property			
Size	**Source**	**Habitat, geographic region**	**Reference**
2-3% with <50% damage, 2-3% with >50% damage	various	coral reef, Red Sea	Riegl and Velimirov 1991
at least 1% of coral surface	predation	coral reef, Red Sea	Schuhmacher 1992
11-24% with lesions <100mm^2, 23-30% with lesions 100-200mm^2, 17-21% with lesions 200-300mm^2, 31-42% with lesions >300 mm^2	various	coral reef, Panama (Atlantic)	Ruesink 1997
<25mm^2	predation	coral reef, Red Sea	Oren et al. 1998
<100-10000mm^2	predation, storms	coral reef, Red Sea	Oren et al. 2001
500-4500mm^2	solar damage	coral reef, Thailand	Brown 1994
1200-4000mm^2	storms	coral reef, USVI	Rogers et al. 1982
600-910mm^2	predation	coral reef, USVI	Witman 1988
16-31% dead area	various	coral reef, USVI	Bythell et al. 1993
0-4mm^2	ice, storms, predation	subtidal fouling community, Antarctica	Stanwell-Smith and Barnes 1997

Table 3 (continued): Lesion properties found on colonial epifauna under natural conditions.

Shape	**Source**	**Habitat, geographic region**	**Reference**
lesions on side branches rectangular of uniform depth	predation	coral reef, Puerto Rico	Vreeland and Lasker 1989
small lesions circular, larger lesions circular to narrow	predation, storms	coral reef, Red Sea	Oren et al. 2001
hemisphaerical colonies have circular to elliptical wounds, annular colonies have elongate wounds	solar damage	coral reef, Thaliand	Brown 1994
Orientation	**Source**	**Habitat, geographic region**	**Reference**
14% sponges turned over, 55% gorgonians broken at bases or pulled out of seafloor	bottom-trawling	continental shelf, Gulf of Alaska	Freese et al. 1999
87% broken at base	boring sponges	coral reef, Jamaica	Tunnicliffe 1979
0-98% broken at base, 0-1% broken at branches, 0-2% broken at tips	waves	coral reef, Jamaica	Tunnicliffe 1981
0-2% detached, 60-95% at distal tips	abrasion, predation	coral reef, Jamaica	Wahle 1985
40-71% detached, 22-46% broken at base	detachment, abrasion, overgrowth	coral reef, Puerto Rico	Yoshioka and Yoshioka 1991

Table 3 (continued): Lesion properties found on colonial epifauna under natural conditions.

86% at colony margins	predation	coral reef, Red Sea	Oren et al. 1998

GBR = Great Barrier Reef; USVI = United States Virgin Island

The lack of such studies is problematic for our understanding of regeneration rates and limits. First, lesion characteristics are frequently dynamic across species, sites and seasons (e.g., Woodley et al. 1981; Wahle 1985; Witman 1988; Yoshioka and Yoshioka 1991; Meesters et al. 1996b, 1997b; Acosta et al. 2001 and see Table 3 in the present study). Descriptions and rates of regeneration phenomena may be irrelevant to marine conservation priorities if experimentally inflicted wounds do not reflect those that occur naturally on colonies. Experimental wounds are usually designed to approximate natural wounds, but experimental wound shape and location are not always considered relative to natural shapes and locations. Second, experimental wounds tend to become larger after wounding than do natural wounds (e.g., Van Veghel and Bak 1994). Uninjured modules adjacent to experimentally inflicted wounds become more susceptible to natural disturbances such as predation and fouling (e.g., Van Veghel and Bak 1994). These generalizations suggest that some experimental studies of regeneration require careful interpretation. Future experimental studies must consider the relevancy of using experimentally inflicted wounds to examine regeneration aspects of colonial epifauna under natural conditions.

Colony state

Colony state refers to colony characteristics such as size, shape, age and genetic identity (genotype), and to interactions with the biotic and physical environment and the involvement of the colony in other activities requiring the same limiting resources needed for regeneration. Colony size and age appear to be particularly important determinants of

regeneration capabilities, but there is growing evidence that colony disturbance history strongly interacts with other variables to determine regenerative capacity.

Colony size

Although larger colonies are more vulnerable to disturbance and damage (Jackson 1979), regenerative capacity is also greater in larger colonies (Bak et al. 1977; Woodley et al. 1981; Hughes 1984; Hughes and Jackson 1985; Davis 1988; Stocker 1991; Bythell et al. 1993; Bak and Meesters 1998; Acosta et al. 2001). Size-dependent survivorship of wave-generated or experimentally-derived fragments in scleractinians (Highsmith et al. 1980; Tunnicliffe 1981; Liddle and Kay 1987; Richmond 1987; Smith and Hughes 1999), gorgonians (Lasker 1990) and zoanthids (Karlson 1988a) also suggests increased regenerative capacity with greater size.

Size-dependent regeneration capacity may reflect the relative amount of tissue injured by the disturbance event: injuries occur more frequently on larger colonies, but damage relatively smaller areas in contrast to smaller colonies that would experience relatively greater tissue loss by the same disturbance (Hughes and Jackson 1985; Bak and Meesters 1998). Wounds on small colonies have higher circumference/surface area ratios that expose more of a colony to damage (Meesters et al. 1996a). Thus, regenerative capacity is reduced and whole colony mortality is greater in smaller colonies.

Lower regenerative capacities of small colonies may also reflect reduced resource availability (Korotkova 1970; Connell 1973; Loya 1976b). Although injury responses are often limited to modules adjacent to the wound (Meesters et al. 1994; Meszaros and Bigger 1999; Lirman 2000a), recent evidence suggests a more colony-wide response to

wounding in the scleractinians *Favia favus* (Oren et al. 1997a, b) and *Platygyra lamellina* (Oren et al. 1997b). The measurement of intracolonial transport of ^{14}C-labelled compounds in these species demonstrated widespread reallocation of colony resources through physiologically integrated modules, particularly in colonies with spatially extensive wounds. In these corals, larger colonies with greater resources may recover more quickly if those resources can be transported around the colony to the wound site. Similarly, rapid healing in sponges may also depend on the availability of resources from healthy tissue and could explain size-dependent regenerative capacity noted in sponges (Wulff 1991).

If enough uninjured area is available to regenerate damaged tissue, then colony size may not be relevant to the injury response. Sufficient resource availability may explain the apparent lack of relationship between colony size and regenerative capacity in *Acropora palmata* (Lirman and Fong 1997; Lirman 2000a), *Agaricia agaricites* forma *purpurea* (Bak and Steward van Es 1980), *Porites astreoides* (Bak and Steward-van Es 1980), *Montastraea annularis* (Meesters et al. 1994) and *Plexaura homomalla* (Wahle 1983a). Thus, the adaptive significance of colonial integration and therefore colony size during regeneration may only be apparent when injury response is not localized or when wounds are relatively large (Bak and Steward-van Es 1980; Wahle 1983a; Oren et al. 1997a,b, 1998, 2001).

Colony age

Regeneration from partial mortality is also an age-dependent process. Lower regenerative capacity in juvenile colonies of the ascidian *Podoclavella moluccensis*

exposed to experimental damage and high predation levels may be caused by the small sizes and lack of structural defenses in young colonies (Davis 1988). Juvenile sponges may not regenerate at all, possibly because archaeocytes are heavily invested in growth processes instead of colony maintenance during this life stage (Simpson 1984).

Menon (1972) noted greater regenerative capacity in younger versus older colony regions in the bryozoans *Electra pilosa* and *Membranipora membranacea*. Younger zooids of another bryozoan, *Steginoporella* sp., showed fewer lesions in nature, regenerated four times faster and were fouled less often by epibionts than older regions (Jackson and Palumbi 1979; Palumbi and Jackson 1982, 1983; Jackson and Hughes 1985). In the case where a juvenile colony is comprised of its first "primary" polyp, regeneration may not even proceed if its central portions are destroyed (Bak and Engel 1979) and might also reflect effects of wound location if the oral aperature of a coral polyp represents an important organizing centre for the direction of regeneration phenomena.

These patterns can potentially be explained by the age of damaged tissues. Brown body accumulation, which probably reflects the physiological age of a bryozoan, was negatively correlated to regeneration rate in experimentally damaged colonies (Palumbi and Jackson 1982). In addition to ensuring zooid survival at the colony periphery, translocation polarity gradients may direct resources from feeding "source" modules into young growing "sink" modules. Thus, age-based restrictions in regenerative capacity reflect the evolution of resource translocation strategies towards juvenile modules typically associated with the colony periphery where the risk of injury is often quite high.

In these cases, reduced regeneration rates in older (proximal) parts of the colony may be one unavoidable cost of a colonial translocation strategy designed to emphasize peripheral growth as the expense of proximal repair.

Colony morphology and genotype

The morphological architectures of colonial organisms have predictable ecological consequences related to resource allocation to different life history processes. Colonies that are increasingly more committed to persisting in their habitats should have higher degrees of integrated colony responses that result in greater investments towards somatic maintenance and repair (Jackson 1979; Kojis and Quinn 1985). Regenerative capacities may depend on the morphology and consequent resource investment strategy of the injured colony. The wide ranges in interspecific regeneration rates among shape variants (e.g., Jackson and Palumbi 1979; Van Veghel and Bak 1994; Hall 1997; Nagelkerken and Bak 1998) corroborate this prediction. In general, massive mounding corals tend to regenerate faster than plating forms (Fishelson 1973; Bak and Engel 1979; Riegl and Velimirov 1991; Nagelkerken and Bak 1998).

The individual polyp size in a colony is also correlated with regenerative capacity. For example, bush-shaped corals with small polyps, such as *Acropora variabilis* and *Pocillopora danae*, regenerate more rapidly than brain-shaped species with large polyps, such as *Favia favus* and *Platygyra lamellina* (Fishelson 1973; Riegl and Velimirov 1991). Corals with small polyps form a bilayer of encroaching soft tissue over the wound and an underlying layer of calcium carbonate that envelopes organisms and sediments that may have fouled the lesion. Macropolypal corals regenerate from remnant corallites that

eventually re-establish contact with one another to form a continuous layer (Fishelson 1973).

In contrast to these coral examples, polyp size is not inversely correlated with regenerative capacity in tropical bryzoans. For example, the bryozoans *Steginoporella* spp. typically regenerated faster than *Reptadeonella* spp., the former having larger zooids. The enhanced regenerative capacity of *Steginoporella* spp. was instead thought to reflect the ability of its large zooids to prevent the settlement of fouling organisms on wounds (Palumbi and Jackson 1982), thereby facilitating healing and regeneration.

As partial mortality events change the morphology of colonies by reducing the number of modules and their continuity within a colony, the origin of remnant tissues from which regeneration occurs could affect regenerative capacity. Several modes of tissue regeneration seem to occur across a wide range of taxa. For example, isolated tissue patches from perforated skeletal regions in *Porites compressa* can initiate tissue re-growth following partial mortality (Jokiel et al. 1993). Re-growth from remnant tissues located deep in the skeletal frameworks of apparently dead stands of *Acropora* cf *vaughani* corals could permit colony recovery following bleaching events (Riegl and Piller 2001). In alcyonaceans, blastema buds that emerged following partial mortality formed several smaller colonies that contacted each other but remained isolated within the larger framework (Fishelson 1973). In two rare studies of regeneration in fossil corals, Lee and Elias (1991, 2000) described regeneration mechanisms in the Ordovician tabulate corals *Catenipora rubra* and *Saffordophyllum newcombae*. Damage to a single polyp in *C. rubra* elicited either repair of that module, or rejuvenation by polyp fission into two

equal sized modules (Lee and Elias 1991). Damage to rows of modules elicited the lateral budding of adjacent polyps to restore colony size and shape (Lee and Elias 1991). Regeneration from partial mortality in *S. newcombae* was achieved by the formation of open spaces ("lacunae") in rejuvenated coralla first along the colony periphery and then towards the centre. In some cases lacunae transformed into normal corallites, but coenochymal "spill over" followed by new corallite growth or rapid corallite fission sometimes accompanied or even preceded corallite rejuvenation (Lee and Elias 2000). As different sources of remnant tissues likely vary in the amount of resources and the mechanisms available for their delivery to regenerating modules, it is reasonable to expect that the new morphology and distribution of remnant tissue could affect regenerative capacity.

Intraspecific variation in regeneration may also reflect genetic differences between morphs that may regulate other life history processes such as growth (Tomascik 1990). Regenerative capacities between growth forms of *Montastraea annularis* are different (Van Veghel and Bak 1994; Weil and Knowlton 1994) and could have a genetic basis (Knowlton et al. 1992; Van Veghel and Bak 1993; Lopez et al. 1999). Few studies have examined differences between genets but preliminary evidence demonstrated that regeneration rates vary among genetically distinct colonies (e.g., Meesters et al. 1996b), suggesting that genotype modulates colony responses to partial mortality.

Colony-environment interactions

Water temperature

Increased water temperatures can stimulate regeneration from sub-lethal partial mortality in bryozoans (Menon 1972). Complete acclimation to ambient conditions allowed injuries to regenerate more quickly in the scleractinian *Montastraea annularis* in areas with above average water temperatures, possibly because corals normally experience occasional influxes of much colder oceanic water that may temporarily stress the colonies (Lester and Bak 1985). Thus, regeneration may be impaired only at extreme temperatures (Menon 1972), possibly by impairing metabolism or by degrading proteins in the colony.

Short-term regeneration in hermatypic corals that are chronically exposed to abnormally high water temperatures may not be impaired due to coral acclimation to ambient conditions (Lester and Bak 1985). However, delayed mortality due to bleaching in acclimated hermatypic corals (even after water temperatures have dropped) may be attributed to exhausted resource reserves during regeneration (Meesters and Bak 1993). Depletion of zooxanthellae due to bleaching may be critical to understanding reduced regenerative potential of bleached corals as these symbionts provide energy for coral functions such as mucus production, ciliary action and amoebocytic activity that facilitate regeneration and protect corals against disease (Mascarelli and Bunkley-Williams 1999; Meszaros and Bigger 1999).

Bleached hermatypic corals tend to show reduced regenerative capacities. Regeneration is significantly reduced and sometimes completely absent following

experimentally-induced lesions in naturally bleached colonies of *Montastraea annularis*, *Porites astreoides*, *Meandrina meandrites* and *Oculina patagonica* when compared to controls (Meesters and Bak 1993; Meesters et al. 1997a; Fine et al. 2002). Artificially bleached clones of *M. annularis* also exhibited reduced regenerative rates, with some treatments showing no signs of regeneration (Mascarelli and Bunkley-Williams 1999).

Water temperature-based limitations on regenerative capacity in hermatypic colonial animals may be imposed through resource limitations that follow threshold depletion levels of symbiotic algae. A blockage of resources between bleached and unbleached areas is also likely to restrict intracolonial transport of energy and cells from healthy areas to lesions (Fine et al. 2002).

Food availability

Depth-related variation in regenerative capacities of hermatypic corals is frequently cited as evidence of food limitation on regeneration rates. Food availability varies with zooxanthellae species and density, degree of cell photoacclimation (i.e., concentrations of chlorophyll c_2), energy reserves and sources (Nagelkerken et al. 1999). Any change in these factors can result in altered regenerative capacities. For example, slower initial regeneration in deep versus shallow water colonies of the scleractinians *Porites astreoides* and *Stephanocoenia michelinii* was due to reduced energy reserves as light levels decreased with depth, and was not associated with changes in zooxanthellae density or photoacclimitization (Nagelkerken et al. 1999). Since polyp regeneration proceeded more rapidly at deeper depths that in shallow water once wounds were sealed, energy must have been acquired independently of zooxanthellae or chlorophyll

concentrations. This could be achieved heterotrophically or by reallocating energy from other life history processes (Nagelkerken et al. 1999) including the resorption of reproductive structures (Szmant and Gassman 1990; Sier and Olive 1994). The positive phototropic response demonstrated by some regenerating zooxanthellate scleractininans (Kawaguti 1937; Franzisket 1970) could also reflect an evolutionary adaptation that satisfies increased intracolonial energetic demands during regeneration. Thus, food limitation may restrict regenerative capacity for colonies in food-poor areas such as for hermatypic corals at deep depths, and may select for the evolution of life history traits such as increased dependence on heterotrophic food sources. The role of food availability in ahermatypic colonial groups should be examined, but is expected to impose similar restrictions during colony regeneration.

Sedimentation

Sedimentation stress exerts considerable energetic strains on colonies that must clear away and prevent the accumulation of sediments (Rogers 1990; Guzmán et al. 1994), but few studies have demonstrated the effects of sedimentation on regenerative capacity. High levels of sedimentation could increase intracolonial energetic demands due to the activities of "costly" sediment rejection mechanisms and reductions in zooxanthellic carbon production in colonies that host endosymbiotic algae due to reduced light availability (Meesters et al. 1992). Colonies generally exhibit slower regeneration rates in habitats with high sediment levels, particularly in species with inefficient sedimentation mechanisms e.g., *Acropora palmata* (Meesters et al. 1992).

Interestingly, Guzmán et al. (1994) found faster regeneration of lesions in several scleractinan coral species at sites polluted by the 1986 oil spill at Bahía Las Minas, Panama, than at unaffected areas. Coastal oil pollution and the subsequent sediment leaching from nearby mangroves and seagrass beds did not serve to enhance regenerative capacity directly, but instead triggered the clearing of oily sediments and polyp regeneration by reallocating resources from other life history processes including growth and sexual reproduction (Guzmán et al. 1991; 1994). Thus, sedimentation stress may not directly impair regenerative capacity, at least in species with efficient sediment rejection mechanisms (Tomascik and Sander 1987; Meesters et al. 1992). Instead, stress-based impairment of other life history processes such as calcification in hermatypic corals (Bak 1978) may trigger acute survival responses that re-direct resources into colony maintenance and sediment clearing mechanisms.

Disturbance history

Disturbances that damage colonies and stimulate regeneration include geographically broad, intense events (e.g., hurricanes, commercial-scale bottom fishing) and local, less intense events (e.g., bioerosion, predation) (Knowlton et al. 1990; Gleason 1993). Past injuries leave colonies more susceptible to mortality by limiting colonial resources and potential for regeneration from more recent injuries (Lang da Silveira and Van't Hof 1977; Jackson and Palumbi 1979; Palumbi and Jackson 1982; Cumming 2002). For example, the fate of coral colonies (i.e., whether a colony escapes or is injured/killed by a disturbance event) in response to local disturbances strongly depends on the occurrence of recent hurricane damage. Injured corals are significantly more likely

to be injured again than previously uninjured corals (Hughes 1984; Hughes and Jackson 1985; Babcock 1991). Interestingly, uninjured corals may be more likely to escape again than be injured or killed, suggesting that other factors (perhaps resistant genotypes) may affect whether a colony is injured or not (Hughes and Jackson 1985). In a second example, susceptibility to grazing by parrotfish or other local sources of partial mortality was higher in post-hurricane coral communities (Bythell et al. 1993, 2000). Wahle (1983a, 1985) documented patterns in wounds on gorgonians, and concluded that cumulative large injuries could be as important as mortality in structuring coral reef communities because of repeated resource demands on the regenerating colonies.

Allocation to other life history processes

Energy and cells are finite resources distributed within a colony and allocated to costly life history processes such as sexual reproduction, growth and interactions with other species and conspecifics. Colonies that are irreversibly committed to such processes often cannot sufficiently regenerate from partial morality, or simply do not regenerate at all. For example, experimentally excised stolons of the thecate hydroid *Clytia* sp. were prevented from regenerating when they contacted stolons of the athecate *Bougainvillia* sp. (Katô et al. 1967). The regeneration of very large wounds may halt in favour of growth and reproduction if the fitness of the colony is threatened by resource limitation, as would be the case in spatially extensive lesions (Meesters et al. 1997a). Thus, there is evidence of a general trade-off between regeneration and reproduction in both directions: reduced sexual reproduction following injury and regeneration, and impaired regeneration during episodes of sexual reproduction.

Species-specific differences

Regeneration data in Table 2 were organized as subsets of several marine invertebrate groups: sponges, gorgonians, corals, hydroids, bryozoans and tunicates. Maximum daily regeneration rates given in mm^2 from standardized wound sizes were extracted from Table 2 and transformed to the percentage of wound regenerated per day. Regeneration data were standardized by considering smaller wounds (i.e., 1 – 200 mm^2) separately from spatially more extensive wounds (i.e., greater than 200 mm^2) as initial wound size tends to affect regenerative capacity. Species were then ranked from the fastest to the slowest regenerators in Table 4 (small wounds) and Table 5 (large wounds).

Table 4: Ranked daily regeneration rates of colonial epifauna with wounds 1 - 200mm^2.

Species	**Maximum % of wound regenerated daily**	**Group**
Tedania sp. 1 (orange morph)	100.0	warm-water sponge
Tedania sp. 3 (red-orange morph)	50.0	warm-water sponge
Acropora palmata	31.7	warm-water scleractinian
Meandrina meandrites	23.7	warm-water scleractinian
Ircinia strobilina	19.2	warm-water sponge
Montastraea annularis (massive morph)	17.6	warm-water scleractinian
Tedania sp. 4 (pink-brown morph)	14.3	warm-water sponge
Tedania sp. 5 (pink-red morph)	12.7	warm-water sponge
Porites astreoides (hemisphaerical morph)	11.4	warm-water scleractinian
Porites astreoides (green morph)	11.3	warm-water scleractinian
Porites astreoides (brown morph)	11.0	warm-water scleractinian
Montastraea annularis (columnar morph)	8.1	warm-water scleractinian
Neofibularia nolitangere	7.4	warm-water sponge
Steginoporella sp.	7.1	warm-water bryozoan
Tedania sp. 6 (white morph)	4.8	warm-water sponge
Stephanocoenia michelinii (encrusting morph)	4.6	warm-water scleractinian
Tedania sp. 2 (orange morph 2)	4.0	warm-water sponge
Agelas clathrodes	3.9	warm-water sponge
Microciona sp.	3.5	cold-water sponge
Porites astreoides	3.1	warm-water scleractinian
Stephanocoenia michelinii (massive morph)	3.0	warm-water scleractinian
Stylopus sp.	2.9	cold-water sponge
Montastraea annularis	2.4	warm-water scleractinian
Reptadeonella sp.	2.4	warm-water bryozoan
Oculina patagonica	2.2	warm-water scleractinian
Favia favus	1.7	warm-water scleractinian
Diploria strigosa	1.5	warm-water scleractinian
Siderastrea siderea	1.2	warm-water scleractinian
Montastraea annularis (bumpy morph)	1.0	warm-water scleractinian
Agaricia agaricites (forma *purpurea*)	0.9	warm-water scleractinian
Porites lobata	0.9	warm-water scleractinian

Table 4: Ranked daily regeneration rates of colonial epifauna with wounds 1 - 200mm^2.

Porites lutea	0.9	warm-water scleractinian
Agaricia agaricites	0.5	warm-water scleractinian
Tedania sp. 7 (crimson morph)	0.0	warm-water sponge

Table 5: Ranked daily regeneration rates of colonial epifauna with wounds 201 - 4200mm^2.

Species	**Maximum % of wound regenerated daily**	**Group**
Ircinia strobilina	13.70	warm-water sponge
Stylopus sp.	6.07	cold-water sponge
Montastraea annularis (columnar morph)	4.74	warm-water scleractinian
Neofibularia nolitangere	4.53	warm-water sponge
Agelas clathrodes	4.03	warm-water sponge
Porites astreoides (brown morph)	2.59	warm-water scleractinian
Crambe crambe	2.20	warm-water sponge
Favia favus	1.62	warm-water scleractinian
Montastraea annularis	1.59	warm-water scleractinian
Microciona sp.	1.43	warm-water sponge
Acropora robusta	1.34	warm-water scleractinian
Acropora hyacinthus	1.06	warm-water scleractinian
Pocillopora damicornis	1.02	warm-water scleractinian
Stylopus sp. (pink morph)	0.70	cold-water sponge
Cliona celata	0.65	cold-water sponge
Aplysilla rosea	0.62	cold-water sponge
Chondropsis sp.	0.57	cold-water sponge
Agaricia agaricites (forma *purpurea*)	0.44	warm-water scleractinian
Porites astreoides	0.43	warm-water sponge
Tedania sp. (orange morph)	0.42	cold-water sponge
Chelonaplysilla sp.	0.41	cold-water sponge
Anchinoe sp.	0.37	cold-water sponge
Acropora palmata	0.36	warm-water scleractinian
Porites mayeri	0.35	warm-water scleractinian
Porites lobata	0.31	warm-water scleractinian
Porites lutea	0.31	warm-water scleractinian
Goniastrea retiformis	0.28	warm-water scleractinian
Porites lichen	0.21	warm-water scleractinian
Diploria clivosa	0.14	warm-water scleractinian
Diploria strigosa	0.14	warm-water scleractinian
Siderastrea siderea	0.12	warm-water scleractinian
Eurypon sp.	0.09	cold-water sponge
Hymedesmia sp. (orange morph)	0.05	cold-water sponge
Agaricia agaricites	0.01	warm-water scleractinian
Acropora palifera	0.00	warm-water scleractinian

The objective of this analysis was to identify taxa that are the best (or worst) regenerators. However, with the possible exception of perhaps a high frequency of rapid regeneration among sponges versus other taxa, both high and low regeneration rates were broadly distributed among taxa in Tables 4 and 5. Furthermore, in cases where sufficiently broad ranges of wounds have been inflicted, i.e., on sponges and scleractinians, the large variability of regeneration rates within a particular group (0 - 100% for sponges, and 0 - 37% for scleractinians) suggests that regeneration capacity probably does not have a strong phylogenetic basis (at least at the level of animal phyla).

Unfortunately, these taxonomic comparisons are of limited use. First, there are few regeneration studies for groups other than sponges and scleractinian corals. Although replacement of individual module body parts has been particularly well studied in tunicates and hydroids, regeneration of lost modules following partial mortality has not been investigated as thoroughly in these animals as it has been in sponges and scleractinians. Regeneration in other colonial organisms (e.g., planktonic siphonophores) has rarely been studied. There are some obvious practical barriers to the study of regeneration in, for example, large toxic pelagic colonies. Similarly, there are no studies of modular regeneration in pterobranch hemichordates, though these are probably the living descendants of one of the most well-known colony forms in the fossil record (the graptolites).

Second, module regeneration data in Table 2 could not be completely standardized because qualitatively different measures were used to characterize regeneration in different studies (e.g., area of regenerated tissue versus linear dimensions

of regenerated tissue versus appearance of new polyps or zooids over time). This variation reflected differences in the morphological architectures of the animal colonies considered in regeneration studies. Sponges, scleractinians, and to some extent the bryozoans are comprised of modular units arranged into plates, mounds and trees *sensu* Jackson (1979). The regeneration of densely arranged modules in such architectures is probably more easily described by surface area estimates, whereas the regeneration of modules in runner, vine and even sheet-shaped colonies (e.g., hydroids) *sensu* Jackson (1979) is usually described as a function of polyp densities. All of these taxa can vary in the natural density of modules, especially in contrasts between colonies that consist of only modules (e.g., bryozoans, massive corals) versus colonies that can consist of modules connected by stolons or other nonmodular tissues (e.g., hydroids, social tunicates). In the former case, measures of regenerated area should be highly correlated with counts of regenerated polyps. In the latter case, this correlation depends on whether there is natural variation in polyp density within nonmodular tissues. Alternatively, it may be more appropriate to study regeneration in terms of increases in biomass rather than surface area *sensu* Edmunds and Gates (2002).

A third factor that limits generalization about regeneration capacity is the taxonomic distribution of module polymorphism. Reproductive, nutritive and defensive roles are served by specialized modules in polymorphic colonies (e.g., many hydroids and bryozoans) instead of by one "all-purpose" module (e.g., many scleractinians and tunicates). (It is not clear how to categorize sponges in this respect as modular sponge design reflects the abundance of different feeding, defensive, or reproductive cell types

within choanocyte chambers, and these abundances are phenotypically plastic within individuals in space and time). Module regeneration is often accompanied by a loss or modification of the module type that appeared at the injury site (reviewed in Section 3). This bias suggests that comparisons of regeneration capacities across higher taxa should be limited to groups that exhibit similar levels of module specialization. In general, there appear to be few broad generalizations about regeneration differences among higher animal taxa.

Habitat-related variability

Differences in regenerative capacity may be explained by the selection for rapid re-growth in habitats where the probability for damage and partial mortality is high (Kott 1981; Meesters et al. 1996b; Bell 2002). For example, colonies in these habitats may have evolved fast regeneration capacities to recover from partial mortality caused by ice scour, tidal surges, or species interactions.

Although there were relatively fewer regeneration estimates from cold-water species, there appeared to be some tendency toward higher regeneration rates among warm-water species (Table 4 and 5). Only studies of sponges include multiple measures of regeneration rates for both cold- and warm-water species. Among 12 studies of small wounds (Table 4), regeneration rates for nine of 10 warm-water species were higher than rates for two cold-water species. Among 16 studies of large wounds (Table 5), five of the six highest regeneration rates were observed in warm-water species and nine of the 10 lowest rates were observed among cold-water species. It is not known whether the potential for partial mortality is actually higher in warmer waters than in colder regions:

thus, it is not clear to what extent selection for rapid regeneration in warm-water species occurs. Alternatively, rapid regeneration in warm-water species may reflect higher metabolic rates in tropical and sub-tropical species.

An exception to this trend is the high rate of regeneration from large wounds in the cold-water sponge *Stylopus* sp. (Table 5). This species regenerated from large wounds more quickly than many warm-water sponges, scleractinians and bryozoans (Table 5). Resources for regeneration may not be restricted in *Stylopus* sp. and some other cold-water sponges. Intense predation by spongivores may also have selected for fast regeneration in these species while tough, fibrous outer sponge ectosome skeletons could have eliminated the need for fast regeneration in others (Ayling 1981).

Selection for asexual reproduction

Interspecific differences may also be explained by the prolific use of asexual reproduction in some but not other species. In particular, the evolution of fragmentation as a tactic for dispersal and colonization of new habitats should include the evolution of quick regeneration of lost modules (Karlson 1988b). In these species, both the regeneration of the fragment ("daughter") and the original remnant ("parent") colony is relevant. Asexual reproduction followed by rapid regeneration enhances fragment survival under various environmental conditions: (1) in habitats unsuitable for the settlement of sexually-derived larvae, (2) in areas with high levels of partial morality and whole colony mortality in smaller fragments, and (3) in habitats where resource competition is particularly intense (Highsmith 1982; Heyward and Collins 1985; Karlson 1986; Lasker 1990; Lewis 1996). Parent colonies of *Acropora palmata* were also one of

the fastest regenerators in Table 3 (in the case of smaller wounds) and this species generally demonstrates rapid regeneration capacities (Bak 1983): the evolution of frequent asexual reproduction in corals thereby enhances the rapid regenerative capacity of remnant parent colonies as well as daughter fragments.

ECOLOGICAL CONSEQUENCES OF REGENERATION

Regeneration, growth, reproduction and species encounters require significant energetic resource investments from a colony. Energy allocation to life history processes is often redirected into module regeneration following partial mortality. Regeneration potentially redirects energy and other resources away from other vital life history processes such as growth, reproduction and species interactions (Meesters et al. 1997a) by isolating colony modules from each other and consequently disrupting aspects of colonial integration (Wahle 1983a).

But occasionally trade-offs are avoided, and other life history processes are sometimes enhanced following regeneration (e.g., growth). Thus, alternate explanations other than resource limitation are required to understand how regeneration may affect other vital life history processes in colonial marine epifauna.

One intensively studied interaction is the effect of regeneration from partial mortality on sexual reproduction. Rinkevich (1996) proposed three hypotheses, not necessarily mutually exclusive of one another, to explain dynamics of sexual reproduction following regeneration in corals: (1) energy may be allocated hierarchically to various life history processes, (2) energy may not be limited in a colony and (3) regeneration may not be restricted by energy, but instead by potentially limited sources of totipotent stem cells.

Support for the first two hypotheses is derived from evidence that energy availability and allocation to life history processes varies in space and time (Ben-David-Zaslow and Benayahu 1999). The third hypothesis is supported by evidence for the roles that cellular resources play in the life histories of unitary animals (reviewed by Zera and Harshman 2001) and in colonial epifauna (Table 6 in this review).

Table 6: Summary of potentially limiting cell types shared between regeneration and other life history processes in colonial epifauna.

Process	Sponges	Corals	Hydroids
Sexual reproduction	archaeocytes; choanocytes*; pinacocytes	amoebocytes	i-cells
Growth	archaeocytes; choanocytes; pinacocytes	amoebocytes	i-cells; cells from epidermis, endoderm; amoebocytes; cnidoblasts
Predators	sclerocytes; archaeocytes	amoebocyte; cnidoblasts	i-cells; cnidoblasts
Competitors	sclerocytes; archaeocytes	amoebocytes; cnidoblasts	i-cells; cnidoblasts
Conspecifics	sclerocytes; archaeocytes; collencytes	amoebocytes; cnidoblasts	i-cells ; cnidoblasts

* proposed

Table 6 (continued): Summary of potentially limiting cell types shared between regeneration and other life history processes in colonial epifauna.

Process	Bryozoans	Tunicates
Sexual reproduction	amoebocytes	amoebocytes
Growth	amoebocytes	cells from atrial epithelium, epicardial epithelium, mesenchyme; amoebocytes; hemocytes
Predators	amoebocytes	unknown
Competitors	amoebocytes	amoebocytes; hemocytes; lymphocyte-like cells
Conspecifics	amoebocytes	amoebocytes; hemocytes; lymphocyte-like cells

Limited sexual reproduction following regeneration can generally be understood in terms of resource limitations including the restricted production of germ cells from stem cell precursors (Rinkevich 1996). Rinkevich's hypotheses can be extended to explain apparent trade-offs between major life history processes and regeneration in colonial marine epifauna. Resources that fuel major life history processes (i.e., energy) or that are required for structures involved in these processes (i.e., somatic cells and stem cells) are all potentially limited by the competing demands on these resources for regeneration from partial mortality. Many of these potential trade-offs are not well studied, but examples from corals suggests suggest numerous directions for further research in a broader range of colonial invertebrates.

Sexual reproduction

Regeneration frequently proceeds at the expense of sexual reproduction in colonial animals (Reiswig 1973; Tunnicliffe 1981; Wahle 1983b; Kojis and Quinn 1985; Richmond 1987; Rinkevich and Loya 1987; Hoppe 1988; Rinkevich and Loya 1989; Guzmán and Holst 1993; Van Veghel and Bak 1994; Smith and Hughes 1999; Lirman 2000b; Oren et al. 2001; Ponczek and Blackstone 2001). Hall and Hughes (1996) considered that unusually large but sexually immature corals may be circumstantial evidence of altered investments in sexual reproduction due to the energetic demands imposed by previous colony injuries. However, other physiological processes associated with disturbance could also be significant and could covary with partial mortality. For example, Ward (1995) noted reduced fecundity in overturned colonies of the scleractinian *Pocillopora damicornis*. Ward ascribed this reduction to energy limitations imposed by

reduced light availability and increased exposure to sedimentation stress of overturned corals rather than to resource demands following regeneration.

In cases where energy does not seem to be limiting, sexual reproduction may be surpressed following regeneration due to the exhaustion of stem cell resources used in gamete production. Gametogenesis proceeds epigenetically from stem cell precursors in most colonial animals (Nieuwkoop and Sutasurya 1981), and these are the same cell resources that are also heavily invested in regenerated modules.

In some cases, no trade-off between regeneration and sexual reproduction is apparent. For example, Wahle (1983a) suggested that a preset hierarchy of energetic demands, in which sexual reproduction is a high priority, may require the correlated evolution of an independent reserve energy supply for reproduction in gorgonians that cannot be tapped for module regeneration. Alternatively, energy for regeneration may not be limiting to gorgonians unless the wound is sufficiently large or colonies are chronically damaged (Wahle 1983a). Furthermore, once a colony has irreversibly committed to a reproductive phase, sexual reproduction can occur at the expense of all other processes, including regeneration (Campbell 1974), although studies in vertebrate immune responses suggest that the trade-offs between the immune response and reproduction may only be evident when the individual must simultaneously supply resources to both processes (Bonneaud et al. 2003) i.e., during the sexual reproduction season.

Enhanced sexual reproduction may occur following partial mortality and can be explained by the localized enhancement of resources at specific colony regions. For example, Soong and Lang (1992) demonstrated that significantly more polyps were fertile

closest to experimentally damaged colony margins in the corals *Porites astreoides*, *Siderastrea radians* and *S. siderea*. In a second important example, Harvell and Helling (1993) observed significant changes in the timing and pattern of sexual reproduction in experimentally damaged colonies of the bryozoan *Membranipora membranacea*. Zooids proximal to wounds inflicted on one side ("1/2-damaged colonies") became reproductive earlier than zooids from the undamaged sides of colonies. Furthermore, zooids growing along the edge of the damaged sides of colonies exhibited greater frequencies of reproduction than in undamaged sides and in control colonies. Interestingly, effects of injury on colony reproductive patterning were not observed when colonies were experimentally damaged by alternating wound infliction along the colony perimeter (i.e., "4/8-damaged colonies" referring to circular colonies divided into eight parts with every second part damaged). Harvell and Helling hypothesized that spatial gradients in sexual reproduction could be explained by a "source-sink" model of carbon translocation. A growing colony edge acts as a "sink" for carbon supplied by nearby feeding zooid "sources". Injury to this edge disrupts the strength of the sink, and carbon is kept for feeding zooids to invest in reproduction instead of edge growth. Bryozoan resources were not diverted into growth on the undamaged side of a 1/2-damaged colony, as this sink was quite distant from the carbon source. Sources were much closer to wounds in 4/8-damaged colonies, so zooids diverted carbon into the growth of nearby sinks.

The suppression of sexual reproduction in regenerating colonies that follows physical damage contrasts with observations that stress events (e.g., pollution, variable water temperatures or salinity) tend to stimulate gamete production in colonial epifauna.

For example, rapid reproductive gonophore development in hydroids can be induced by high copper concentrations, periodic emersion and increasing water temperatures (Stebbing 1980; Gili and Hughes 1995). Hydroids and other colonial epifauna may have evolved to restrain colonial resources under conditions of potentially lethal resource demands by suppressing gamete production to repair colony damage, while stress responses remain under the control of hormones (hormesis).

Growth

Colony growth is achieved by the re-iterated budding of new modules and their subsequent organization into various colonial architectures. Budding and regeneration of damaged modules might appear to be fundamentally the same process (Berrill 1951; Martínez 2002). However growth rates and patterns are frequently altered following partial mortality. The source of regenerative material in the wound milieu is different from that surrounding new modules during normal colony growth (Tardent 1963; Goss 1992), and module ontogeny itself is also influenced by the state of parent modules (Watkins 1958). These differences suggest that module production for growth and module replacement for regeneration are distinct (if related) processes.

Growth rate is often reduced in regenerating colonies (Bak 1983; Kobayashi 1984; Liddle and Kay 1987; Guzmán et al. 1991; Yoshioka and Yoshioka 1991; Brazeau and Lasker 1992; Johnson 1992; Guzmán et al. 1994; Meesters et al. 1994; Lirman 2000b; Ponczek and Blackstone 2001). Reduced growth associated with regenerating lost modules may be related to the exhaustion of a limited source of reserve cells. For example, the decline in coenochyme restoration following repeated branch injuries in the

gorgonian *Plexaura flexuosa* was thought to result from depleted cellular resources (Lang da Silveira and Van T'Hof 1977). Not mutually exclusive from the depletion of reserve cells is the possibility that greater oxygen uptake and rapid senescence of injured modules is followed by the generation of reactive oxygen species that effect changes to colony growth through altered gene expression (Blacktone 2000). Significant energy investment may also be directed into the production of anti-oxidants instead of colony growth (Ponczek and Blackstone 2001) in experimentally cloned animals where *in vitro* colony propagation is achieved by the repeated excision of colony modules.

The consequences of regeneration for growth may depend on the severity of disturbance and the overall effects on the rest of the colony (e.g., dislodgement versus fragmentation *sensu* Ward 1995), and the two processes may not always be traded off (e.g., Lester and Bak 1985). Growth rates can even be enhanced by sub-lethal injuries in colonial animals that are highly adapted to chronically disturbed environments such as shallow or seasonal marine ecosystems (Hughes and Jackson 1985; Richmond 1987) or in highly competitive habitats such as cryptic reef environments (Jackson and Palumbi 1979; Turon 1998). Regeneration of new modules is often many times faster in injured than in uninjured colonies in sponges (Ayling 1981; Ayling 1983; Hoppe 1988; Turon et al. 1998; Duckworth 2003), corals (Maragos 1972; Loya 1976b), hydroids (Braverman 1971), bryozoans (Harvell and Helling 1993) and tunicates (Hay 1966). One theory is that rapid re-growth evolved to re-establish lost colony symmetry (Wood-Jones 1907; Maragos 1972). Alternatively, a wound at the growing colony edge upsets normal

resource flow so that zooids near the wound have excess resources to divert into their own compensatory growth in undamaged modules (Harvell and Helling 1993).

When regeneration rate greatly exceeds normal growth rates, the abnormal growth of even a single module can produce massive tumours. Tumours and abnormal skeletal growth that may be related to physical disturbances and subsequent partial mortality have been reported in scleractinians (Randall and Eldredge 1976; Kaufman 1981; Bak 1983; Loya et al. 1984; Peters et al. 1986; Wielgus et al. 2002) and octocorals (Goldberg and Makemson 1981; Benayahu 1998). These malformations are often initiated by mechanical damage to colonies caused by cyclones, corallivores and boring organisms, and are followed by algal invasion and subsequent encapsulation of the damaged tissue and organisms by skeletogenic calcium deposition (Wood-Jones 1907; Kaufman 1981; Peters 1984) and amoebocyte proliferation (Goldberg and Makemson 1981). Tumours potentially affect colony survival by reducing reproductive potential and by increasing susceptibility to further damage and disease through the death of polyps and increasing colony fragility (Peters et al. 1986).

Colony pattern formation (astogeny) can also be altered during regeneration. The morphological plasticity of most sessile colonial animals is of considerable adaptive significance as it allows these organisms to alter module arrangement into various architectures e.g., runners, vines, sheets, mounds, plates and trees in different environments (Jackson 1979). In general, injured colonies and those in physically disturbed habitats tend to approximate linear arrays of modules or encrusting mounds instead of tree-shaped forms (Wood-Jones 1907; Jackson 1979, Ponczek and Blackstone

2001). For example, partial colony mortality resulted in the production of new but smaller polyps and increased peripheral stolonal growth in the hydroid *Hydractinia echinata* (Buss and Blackstone 1991). This growth pattern resulted in loose "net"-like colonies with spaces between stolons instead of tightly packed "mat" colonies in which stolons formed a continuous sheet. This change in colony astogeny may be due to altered gastrovascular flow that helps regulate colony pattern formation in hydroids (Dudgeon and Buss 1996; Lasker and Sànchez 2002). Abott (1974) considered growth patterns in regenerating bryozoan colonies of *Hippoporina* spp. to be sufficiently divergent from healthy colonies that two morphs could be distinguished: type "A" (continuous, uninterrupted growth) versus type "R", (interrupted growth from damaged or dormant zooids). Occasionally, novel morphs are observed during regeneration such as formation of double calices in the bryozoan *Barentsia discreta* (Mukai and Makioka 1978) and asymmetrical growth in normally symmetrical reef corals (Brown 1994). Because genes that regulate colonial development are likely expressed in interstitial cells in some cnidarians (Miller, 2000), altered morphology could be produced by altered levels of protein expression through interstitial or other reserve cell depletion during regeneration.

Species interactions

Colonial epifauna often inhabit space-limited ecosystems such as shallow-water coral reefs and fouling assemblages. These organisms have evolved elaborate mechanisms to cope with species encounters, e.g., anti-predator defenses, competitive strategies, co-operative fusion with conspecifics and antagonistic tissue responses that could require significant colony resource investment (Rinkevich and Loya 1985; Romano

1990; Frank and Rinkevich 1994; Tanner 1995, 1997). Therefore, to the extent that these interactions require resources also used for regeneration, it is reasonable to expect impaired species interactions during and after regeneration.

This general scenario has not been rigorously tested, but both energy and stem cells are shared between these processes. Furthermore, because colony injuries can alter ontogenetic fates of modules in species with polymorphic colonies (e.g., switching from nutritive to defensive zooids), regeneration could also alter species interactions by overriding genetic regulation of module development and thus changing species interactions whose outcome depends on the presence or absence of specific module types (Harvell 1991).

Anti-predator defenses

The acute effects of predation on production of chemical and structural defenses are not well known, and can enhance structural defenses. For example, spined avicularia replaced unmodified polypides when zooids were experimentally excised from the bryozoan *Cheilostoma* sp. (Vorontsova and Liosner 1960).

Chronic long-term effects of regeneration on defensive capabilities are less studied. However, a more commonly observed result is that of impaired defenses following partial mortality. Regenerating juvenile colonies of the ascidian *Podoclavella moluccensis* were more susceptible to predation and trampling by crabs (Davis 1988). Long sclerites are naturally produced in colony tips of the gorgonian *Briareum asbestinum*, but shorter and possibly less effective sclerites were noted in amputated tips (West 1997), suggesting reduced anti-predator capabilities in regenerating fragments.

Bythell et al. (1993) noted moderately more intense grazing by parrotfish on damaged colonies of *Montastraea annularis*, *Porites astreoides* and *Diploria strigosa*, suggesting that defensive capabilities in these scleractinians were probably reduced. It is not known whether depletion of energy stores or cells that produce anti-predator structures such as spicules or nematocyts were responsible for impaired anti-predator defense mechanisms in regenerating colonies, but it is likely that a lack of either resource impairs defense mechanisms in regenerating colonies.

Competitive abilities

Colonial animals exhibit a diverse and energetically costly (Potts 1977; Edmunds and Spencer Davies 1986; Romano 1990; Tanner 1995, 1997) set of structures and mechanisms to defend the colony growing space against encroaching species. These defenses include overgrowth, sweeper tentacles, nematocysts, allelochemicals, mucus and xenogeneic histocompatibility reactions (e.g., contact barriers in anthozoans and hydrocorals, hyperplastic stolons in hydroids, tower cells in bryozoans). These competitive encounters result in the overgrowth and subsequent phagocytosis of the inferior colony, bare zones around colonies, repeated reversals in outcomes or stand-offs associated with inhibited growth but enhanced protection at the colony periphery (e.g., Jackson and Buss 1975; Karlson 1980; Müller et al. 1983; Chornesky 1989; Harvell and Padilla 1990; Xing and Qian 1999).

Few studies have examined whether regeneration affects competitive outcomes in colonial animals. But if regeneration limits the allocation of resources to competitive processes, then one could expect to observe impaired structural defense production, as

well as cell (e.g., histocompatability, cytotoxicity) and humoral (e.g., secretion of cytokine-like molecules, antibodies) mediated immune responses.

Most evidence of impaired competitive interactions in colonial animals following partial mortality is derived from the observation that lesions are rapidly fouled by hydroids, serpulid worms and algae (e.g., Van der Knapp 1993; Bavestrello et al. 1997), suggesting strong localized inhibition of competitive abilities at the lesion site. Corals with higher degrees of existing injuries are also more susceptible to the activities of boring organisms such as sponges, polychaetes, sipunculids, echinoids and cirripeds (Hutchings 1986; Peyrot-Clausade and Brunel 1990; Scoffin et al., 1997).

Regeneration may also limit the ability of colonies to defend themselves against pathogenic endolithic fungi by restricting materials available to skeletogenic processes that would otherwise result in the encapsulation of the invading fungi (Bentis et al. 2000). Restricted resource availability may also explain the particular virulence of disease in regenerating coral fragments versus regenerating (attached) colonies (Bak and Criens 1981).

With respect to whole colony competitive abilities, damaged colonies of the scleractinian coral *Montastraea cavernosa* were more rapidly overgrown by the encrusting sponge *Rhaphidophlus venosus* (Aerts 2000). Grazing by herbivorous reef fish appeared to prevent the overgrowth of *Porites cylindrica* colonies by foliose brown algae, even permitting the regeneration of coral tissue over dead skeleton (Jompa and McCook 2002). Mechanical abrasion and smothering are both potential mechanisms that reduce

coral growth and regeneration processes by causing coral polyp retraction and therefore limiting coral access to energy and metabolites (Tanner 1995; River and Edmunds 2001).

Many competitive interactions are hierarchical: some colonies are competitively superior to others (Jackson 1979). However, some reversals in competitive outcomes that have been explained by intrinsic or environmental conditions (*sensu* Chornesky 1989) may actually reflect changes in resource availability following regeneration from wounds caused by competitive interactions. For example, regenerating colonies of the hydrocoral *Millepora dichotoma* formed callus rings of hyperplastic stolons devoid of feeding gastropores and defensive dactylopores (Müller et al. 1983). This callus growth may have impaired colony competitive abilities, but regeneration proceeds so rapidly in *M. dichotoma* that colonies can encroach and even overgrow adjacent injured hermatypic scleractinian corals (Fishelson 1973). In another case, the competitively superior octocoral *Clavularia inflata* was unable to overgrow the competitively inferior scleractinian *Acropora longicyathus*: regeneration in *C. inflata* following high predation damage by reef fish on mid-shelf reefs seemed to impair its ability to compete (Alino et al. 1992). Sexually derived colonies of the hydroid *Hydractinia symbiolongicarpus* typically overgrew another hydroid, *Podocoryna carnea*, but this competitive outcome was reversed when *Hydractinia* colonies were asexually derived clones from surgical explants of the original colonies (Van Winkle and Blackstone 2002). Damaged corals may experience long-term overgrowth and competitively exclusion by sponges (Aerts 2000) or by larger, more energy-rich conspecific colonies (Zilberberg and Edmunds 2001). Patterns of resource allocation could be measured in regenerating colonies under

competition as they have been for bleached *Oculina patagonica* corals, which exhibited significantly reduced competitive ability (Fine and Loya 2003).

Conversely, the evolution of rapid regeneration combined with continuous asexual fragmentation to escape competitive encounters can result in frequently damaged colonies actually overgrowing otherwise competitively superior species. For example, explants of the bioeroding sponge *Cliona orientalis* initially showed some signs of deterioration when grafted to various coral species, but eventually proliferated by lateral growth and fragmentation to overgrow the host coral substrate (Schönberg and Wilkinson 2001).

Self and non-self recognition capabilities

The ability of many colonial marine invertebrates to distinguish among different classes of conspecifics (allorecognition) is well documented, particularly in hydractiniid hydroids and botryllid tunicates. In laboratory mating experiments, allorecognition behaviour segregates as one or more loci that are so polymorphic that only close kin (siblings, or parents and offspring) are likely to share alleles in common by descent. Allele sharing typically regulates competitive interactions between growing colonies such that closely related colonies fuse (or at least moderate their competitive responses) while distantly related colonies avoid fusion or engage in aggressive cytotoxic rejection behaviour (Grosberg and Quinn 1988; Grosberg et al. 1996b).

Besides the potential for deficiencies in energy reserves that fuel allorecognition processes, resource limitation following regeneration may impair allorecognition capabilities by restricting the production of cell-surface markers and cell adhesion molecules (e.g. proteoglycans, polysaccharides) that regulate histocompatibility in

colonial marine invertebrates (e.g., Coombe and Parish 1988; Fernàndez-Busquets and Burger 1999; Müller et al. 1999; Schmid et al. 1999).

Reduced resources may also limit the production of structures associated with allorecognition such as fibrous contact barriers and nematocyst-laden hyperplastic stolons. For example, experimental removal of interstitial cells prevented the formation of hyperplastic stolons (but did not improve histocompatibility) in rejection interactions between colonies of the hydroid *Hydractinia echinata* (Buss et al. 1984). Allocation of interstitial cells to regeneration thus directly impairs the aggressive attack response in hydractiniid hydroids (Buss and Grosberg 1990).

Regeneration may also restrict the availability of various cell types used in cell and humoral mediated alloimmunity responses such as archaeocytes, phagocytes, amoebocytes and lymphocyte-like cells (Koyama and Watanabe 1982; Van de Vyver and Buscema 1985; Yoshino 1986; discussed in Amano 1990 and see references therein; Olano 1993; Cooper and Parrinello 2001; Parrinello et al. 2001). Thus, reduced cytotoxic and immunoglobulin antibody production functions may follow injury and regeneration.

These cell types are also precursors for somatic structures associated with fusion and subsequent cooperative abilities between two compatible colonies (e.g, formation of a shared choanoderm, gastrovascular system, skeleton). Colony responses to autogeneic tissue contact in the gorgonian *Swiftia exserta* were similar to those involved in tissue regeneration: both involved surface recognition, fusion between colonies and rearrangment of cells (Olano 1993). Thus, fusion between two otherwise histocompatible colonies may be impaired if shared resources are depleted following regeneration.

Alloimmune memory or "anamnesis" in colonial marine invertebrates may also be affected if resources are limited by regeneration. If anamnesis is limited by somatic or stem cell availability because former allogeneic interactions have exhausted these cell resources (*sensu* Frank and Rinkevich 2001), then a newly regenerated colony could exhibit reduced alloimmune memory.

These diverse and scattered studies suggest that regeneration processes may compete with allorecognition processes for resources used for structural or chemical defense and for cooperative fusion, and may interfere with the ability to remember previous allorecognition interactions and their outcomes.

Extensive studies of the genetic basis of intraspecific allorecognition behaviour (e.g., Grosberg and Quinn 1988; Grosberg et al. 1996b) have taken advantage of the utility of clonal explants created by surgical techniques. The effects of regeneration from surgery on subsequent behavioural interactions with conspecifics have not been fully explored. Partial mortality may not alter allorecognition behaviour in species with excellent regeneration capacities such as the alcyonacean *Parerythropodium fulvum fulvum* (Frank et al. 1996) in which fast regeneration is likely related to rapid, widespread intracolonial active transport of resources to injured areas (Gateño et al. 1998).

Future studies specifically designed to test the strength of associations between regeneration and allorecognition should consider both the adaptive context and the ecological conditions of interacting colonies. Species that are adapted to frequent disturbance and chronic regeneration may also have mechanisms for mitigating trade-offs between frequent regeneration demands and allorecognition interactions. Such trade-offs

could be studied in species that have or lack adaptations for dealing with chronic disturbance and frequent demands on resources for regeneration. Similarly, the outcome of allorecognition interactions may depend on environmental circumstances (Chadwick-Furman and Weissman 1995a, b). Reversals in these outcomes could affect the apparent strength of trade-offs between regeneration and allrecognition processes. A combination of laboratory and field studies might be required to measure the potential ecological and evolutionary significance of such trade-offs.

DISCUSSION

The numerous observations reviewed here, which involve altered or impaired life history functions associated with disturbance, partial mortality and regeneration in colonial epifauna, suggest that the major ecological consequences of such disturbances are mediated by the cellular and physiological processes involved in replacement of damaged modules in colonies. Major life history processes in colonial marine invertebrates share several types of resources, including energy, structural materials and some cell types (Table 6). Because these resources (and especially these cell types) are also vital to the regeneration of new modules (Table 1), regenerating colonies may be at high risk of lower sexual reproduction, altered growth, predation, competition and impaired self-nonself recognition dynamics. If wound characteristics, colony state functions and species-specific differences that define resource availability in colonial marine invertebrates are linked with the potential for shared resources between life history processes, then it becomes evident that sub-lethal injuries inflicted on colonies

will impair sexual reproduction, growth and the outcomes of species interactions if sufficient resources are not available for all of these competing functions.

This hypothesis has not been tested across a broad range of colonial epifauna, nor has it been investigated across a wide range of lesion types that occur in nature. Studies on colony injury responses, factors that limit regenerative capacity and ecological consequences of regeneration have mostly been restricted to experimentally inflicted wounds on warm-water sponges and scleractinian corals found in shallow tropical and sub-tropical habitats. Cellular and molecular aspects of regeneration of individual module parts and the signalling and genetic control of subsequent module development are well documented in experimental model organisms such as the athecate hydroids *Hydractinia*, *Podocoryna* and tubulariid hydroids. But regeneration of entire modules from partial mortality in these animals has not been studied as much and regeneration phenomena must therefore be inferred from experiments on warm-water sponges and corals. Combining data from experimental laboratory studies on these relatively small, fast-growing taxa with field observations on large, slower-growing species is difficult. However, such comparisons are necessary to test the more general hypothesis that colony regeneration from partial mortality is physiologically and evolutionarily linked to altered life history processes and community patterns.

In most cases sexual reproduction is impaired by the lack of energy and cellular resources to dedicate towards gametogenesis and the production of associated structures. It is expected that damage-induced reduction of fecundity will only increase existing limitation of sexually-derived recruits of many marine populations.

Growth rates and forms are clearly altered by resource depletion during regeneration. The formation of tumorous growths suggests that damage initiates cascades of events that result in altered gene expression. If these growth rate effects are significant with respect to the secondary productivity of colonial animals, then altered growth rates of colonies could produce a cascade of effects on biomass production at all trophic levels by changing the amount of biomass that will be consumed by these animals and by the amount of biomass available to their predators. Furthermore, altered growth patterns may indirectly influence species interactions either by attracting new or more species or by reducing associations if reduced size and structural complexity makes regenerating colonies less attractive to associated organisms that use colonial epifauna as biogenic habitat.

Energy and particularly cell depletion by regeneration will directly change the outcomes of species interactions that are highly resource-dependent. Colonies may exhibit impaired or short-lived anti-predator defenses. Competitively aggressive species that typically win their interspecific encounters may lose or tie with less aggressive taxa. Colonies may also exhibit impaired abilities to detect the genetic relatedness of conspecifics, resulting in the fusion of otherwise incompatible colonies, the rejection of otherwise compatible kin, or an inability to form barriers, destroy allogeneic tissues or mobilize other alloimmune responses.

Habitats in which colonial epifauna are frequently injured (e.g., those exposed to commercial-scale bottom fishing) are expected to be comprised of ecologically different communities from those in undisturbed or less disturbed habitats. Post-disturbance

community recovery will almost certainly be impaired under conditions of severe resource limitation driven by regeneration (the very process that helps populations re-establish themselves after partial mortality). In communities where frequent regeneration leads to resource limitation, larval recruitment may be extremely reduced, growth rates and astogeny of colonies changed, and new species hierarchies and networks established.

CHAPTER THREE: IMPACTS OF EXPERIMENTAL PULSED OTTER TRAWLING ON COLONIAL EPIFAUNA COMMUNITIES FROM A GRAVEL BOTTOM ECOSYSTEM ON WESTERN BANK (NORTHWEST ATLANTIC)

INTRODUCTION

The sessile and emergent growth forms of many colonial epifauna (numerous sponges, cnidarians, bryozoans and tunicates) make these organisms highly vulnerable to disturbances by bottom fishing on continental shelves (Bradstock and Gordon 1983; Hutchings 1990; Auster et al. 1996; Collie et al. 1997; Kaiser et al. 2000a; Pitcher et al. 2000; Wassenberg et al. 2002; Burridge et al. 2003) and in deep-water ecosystems (Jones 1992; Probert et al. 1997; Probert 1999; Roberts et al. 2000; Koenig et al. 2000; Koslow et al. 2001; Fosså et al. 2002).

Impacts of bottom fishing on colonial epifauna were until recently infrequently addressed relative to the numerous studies on mobile epibenthos and infauna (Hutchings 1990; Collie et al. 2000) due to difficulties associated with their identifications and their quantification, but a growing number of studies are emerging. High fishing effort tends to reduce colonial epifauna richness (Callaway et al. 2002) and biomass (Kaiser et al. 2000a; McConnaughey et al. 2000; Veale et al. 2000), while taxon composition shifts from assemblages dominated by large, erect, rigid colonies (highly vulnerable) to those with more flexible, runner-like or encrusting growth forms (lower vulnerability) (Gili et al. 1987; Hutchings 1990; Collie et al. 2000; Pitcher et al. 2000; Bradshaw et al. 2001, 2002).

Community-level impacts of towed bottom gear on colonial epifauna are becoming more evident, but recovery mechanisms that produce the observed post-fished communities are not well understood. Recovery will depend on the responses of resident populations to the perturbations that alter "states" and "rates" (*cf* ecosystem states and rates in Robinson and Frid 2003). Each consequence has predictable positive and negative feedback loops in these communities. First, bottom fishing inflicts considerable damage to colonial epifauna (Tilmant 1982; de Groot 1984; Van Dolah et al. 1987; Sainsbury et al. 1993; Bavestrello et al. 1997; Freese et al. 1999; Koenig et al. 2000; Roberts et al. 2000; Fosså et al. 2002; Wassenberg et al. 2002; Kefalas 2003). These injuries require costly resources for colony regeneration that could impair colony growth and sexual reproduction (Rinkevich 1996) and ultimately limit population recruitment and growth. Second, bottom fishing alters seabed characteristics e.g., sediment properties (Smith et al. 2000; Kenchington et al. 2001; Watling et al. 2001), topography (Thrush et al. 1995; Schwinghamer et al. 1998; Currie and Parry 1999; Koslow et al. 2001), sedimentation (Churchill 1989), and substrate stability (Caddy 1973; Freese et al. 1999; Robinson et al. 2001). These modifications could affect population recruitment by making habitats inhospitable to some taxa. Third, increased mortality of colonial epifauna due to lethal injuries inflicted by fishing gear creates unoccupied space that could permit new species to recruit into the community from nearby or distant sites.

Studies on the impacts of repeated, long-term bottom fishing on benthos in general are uncommon (Collie et al. 2000) but desirable as they may better reflect impacts of commercial fishing activities than an acute, one-time experimental disturbance.

Therefore, this study aimed to help fill in some of these knowledge gaps by focusing directly on the effects of pulsed experimental trawling on colonial epifauna community states and rates. The objective of this study was to characterize trawl impacts on colonial epifauna community state (taxon richness, biomass and taxon composition).

MATERIALS AND METHODS

Experimental site

Western Bank is a relatively shallow (about 70 m deep) plateau located on the outer southeastern continental shelf off the coast of Nova Scotia in the Northwest Atlantic (Fig. 3A). Surficial sediments derived from post-glacial re-working of glacial debris are mostly gravel facies of well sorted Sable Island sand and gravel (mostly granite, volcanic and metamorphic rock) (Fader et al. 1977).

Preliminary surveys conducted by the Canadian Department of Fisheries and Oceans (DFO) of the seabed on the Eastern Scotian Shelf in 1996 (Gordon et al. 1998) determined that the relatively high degree of seabed homogeneity within the 4TVW Haddock Nursery Area provided a suitable area for a bottom fishing impact experiment (Fig. 3A). This site is relatively shallow (approximately 70 m deep) with a mostly homogenous pebble to cobble bottom (4 - 256 mm) but boulders (> 256 mm) and sand (0.0625 - 2 mm) were sometimes observed (scaled *cf* Wentworth 1922). An area referred to as the "haddock box" was closed to most towed bottom fishing activities in 1987 to protect juvenile haddock and their habitats (Frank et al. 2000). Limited scallop dredging is permitted in this area, but effort data and sidescan sonar surveys conducted in 1996 (Gordon et al. 1998) suggested that the box had not been recently disturbed by bottom fishing.

Difficulties associated with offshore sampling have resulted in few studies on the benthic communities of the Scotian Shelf, but the improvement of sampling gear technology and increased survey effort has demonstrated that richness, abundance and biomass of colonial epifauna are positively related to the degree of grain size variability and sediment consolidation in this region (e.g., Lawrence et al. 1985; Kostylev et al. 2001; Hargrave and Hawkins 2002; Henry et al 2002; Kostylev 2002). The high biomass and richness of sponges, hydroids and bryozoans on Western Bank could contribute biogenic habitat for juvenile haddock (Henry et al. 2002).

Experimental design

The experimental box was a 2 km X 2 km area contained within the 4TVW Haddock Nursery Area (43° 45′N, 61° 41′W). Four 2 km long lines running north-south were randomly selected (B, E, G and I) from a possible 11 parallel lines (A through K) in 1997 (Fig. 3B). A "beyond BACI" (Before-After-Control-Impact) asymmetrical design was selected *a priori* to compare temporal changes in a single impact line (E) with those in multiple control areas (lines B, G and I) (Underwood 1992, 1994). Ten sampling stations in the impact line and ten stations in the control lines overall were randomly selected *a priori* (Fig. 3B). However logistical problems in the field prevented these sample sizes from being obtained, particularly in the control lines before trawling in 1997 and 1998 (Table 7).

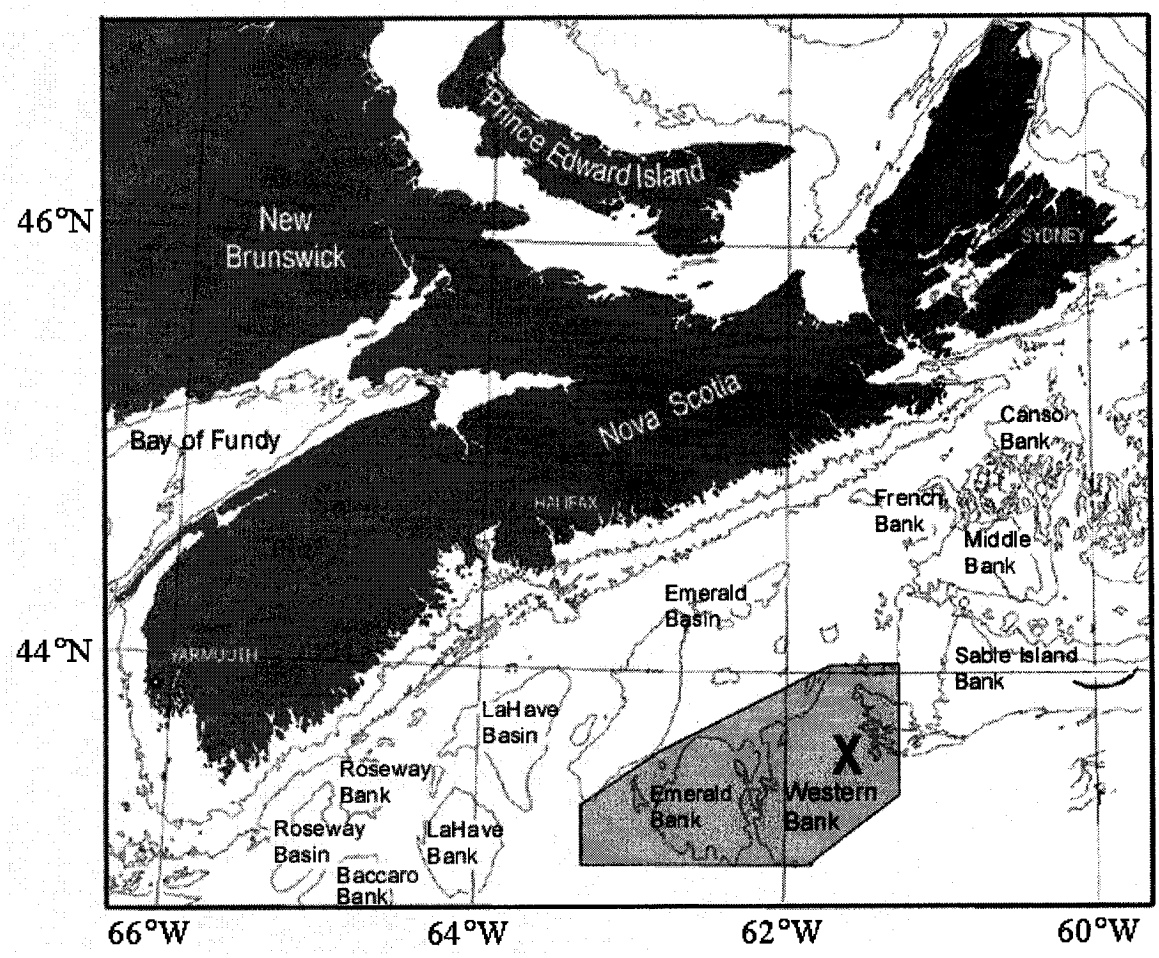

Fig. 3A: Location of experimental site on Western Bank. Study site indicated by "**X**" in the gray area that delineates the juvenile haddock box.

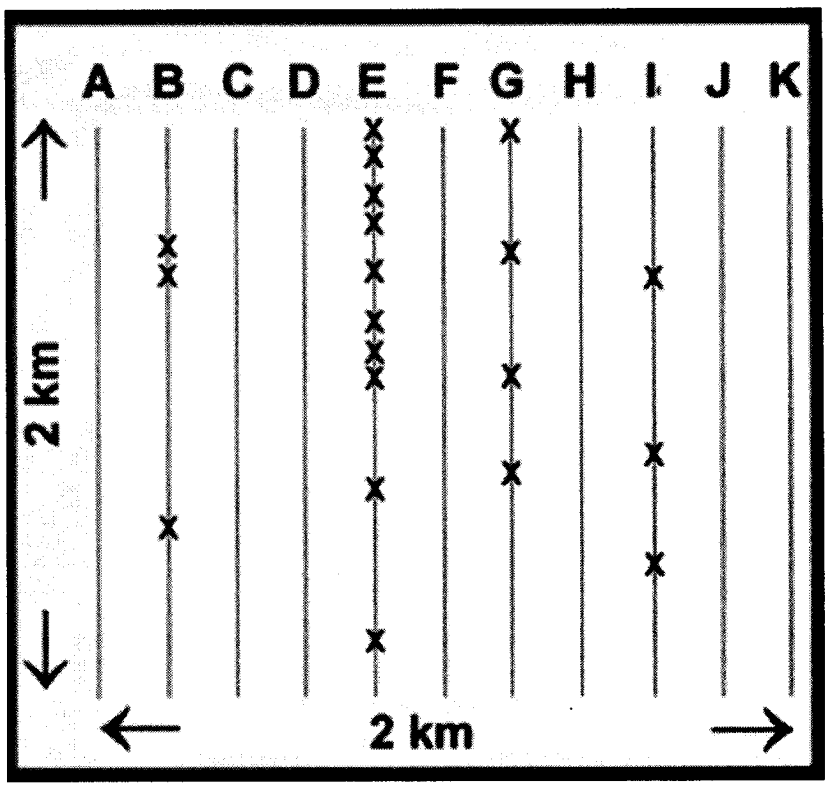

Fig. 3B: Experimental design with four randomly selected 2 km long parallel lines from a possible eleven (A through K). Lines "B", "G" and "I" were randomly selected to be the control lines, and line "E" was randomly selected to be the impact line. The symbol "x" indicates stations selected *a priori* for videograb sampling each year.

Table 7: Timing and location of videograb sampling of colonial epifauna before and after experimental otter trawling in the study site on Western Bank (N = number of samples) from 1997 to 1999.

Date	Period	Location	Treatment	N
September - October 1997	before	B	control	0
		E	impact	10
		G	control	0
		I	control	0
	after	B	control	2
		E	impact	10
		G	control	2
		I	control	2
May 1998	before	B	control	0
		E	impact	9
		G	control	2
		I	control	2
	after	B	control	3
		E	impact	10
		G	control	4
		I	control	2
May - June 1999	before	B	control	3
		E	impact	10
		G	control	4
		I	control	3
	after	B	control	3
		E	impact	10
		G	control	4
		I	control	3

Field operations

Experimentally pulsed otter-trawling

Fishing was performed using rockhopper-equipped Engel 145 otter trawl gear with a net opening (wing spread) of 20 ± 2 m and otter boards separation (door spread) of 60 ± 5 m. Net mesh size in the wings and belly was 180 mm and 130 mm respectively, with a 18.5 m long codend, the latter 9 m of which was fitted with a 30 mm square mesh liner to capture smaller organisms. Trawling was performed once each year from 1997-1999 by the C.C.G.S. *Needler* (1997, 1999) and the C.C.G.S. *Teleost* (1998). Trawl position in relation to the ship was plotted using differential global position system (dGPS) and ORE Trackpoint II ultra-short baseline acoustic tracking systems (USBS) as described in McKeown and Gordon (1997). Each year, line E was trawled 12 consecutive times in alternating directions. A trawl set began at least 500 m outside line E, and was performed at approximately 3.5 km • h^{-1} for an average of 32 minutes. Each set continued until the gear was at least 500 m outside the impact line.

Sampling of colonial epifauna

With exceptions noted earlier, benthos were sampled from each line before and two days to several weeks after trawling from the C.C.G.S. *Parizeau* (1997) and the C.C.G.S. *Hudson* (1998, 1999). This range in time between sampling periods was mostly due to poor weather conditions that prevented gear deployment. Stations were located using dGPS and USBS. A hydraulically-controlled videograb mounted on a galvanized steel platform (described in Rowell et al. 1997 and Gordon et al. 2000) was used to sample benthos from a 0.5 m^2 area to a sediment depth of 10 - 25 cm while simultaneously obtaining high resolution video of the seabed.

Benthos were dumped into a sorting tray, washed with seawater through a 1 mm mesh sieve and preserved in 10 % buffered formalin. Colonial epifauna were considered to be any organism comprised of physically integrated units (e.g., the osculum-bearing unit of a sponge, a coral or hydroid polyp, a bryozoan or tunicate zooid) that could potentially function independently. The sponges observed on Western Bank in this study were therefore considered "functionally" colonial, as were most hydroids, soft corals, bryozoans and tunicates. Colonial epifauna were sorted from other organisms in the laboratory under a dissecting microscope and preserved in 70% ethanol. Taxa were identified to the lowest possible taxonomic level and their individual wet weights were measured. Abundance was not estimated because it was not known whether colony fragments were from one or more colonies before videograb sampling. Consistent taxonomic expertise used throughout the species identification process ensured that analyses would not be affected by changes in taxonomic reliability.

Statistical analyses

Effects of trawling on colonial epifauna richness and biomass

Richness (number of taxa) and total biomass (wet weight in mg) of colonial epifauna were measured for each videograb. Levene's test for homogeneity of variances showed that biomass but not richness data were heteroscedastic: $\log_{10}$-transformations removed this heterogeneity in all cases (Levene's tests all $P > 0.05$). Since logistic constraints prevented full sampling in all lines from being performed, effects of trawling on colonial epifauna richness and biomass were measured differently each year. The absence of pre-trawl samples from control lines in 1997 left only pre- and post-trawl

samples from the impact line to be compared using a two-tailed unpaired t-test. Samples from control line B were omitted for the 1998 analyses as pre-trawl videograbs were not obtained from this line in that year. Trawl impacts were evaluated in 1998 and 1999 using two-way analyses of variances (ANOVA) to examine effects of period (before, after), location (line B, E, G, I) and the interaction period*location on richness and biomass estimates in JMP® Version 5 (SAS Institute Inc. 2002). Post-hoc contract Student t-tests of least square estimate means between periods in line E were done to test whether an interaction effect was due to a period effect in the impact line. Power analyses were performed for each ANOVA to determine the chances of detecting a significant interaction effect at $\alpha = 0.05$.

Whole-community approaches to detecting impacts of bottom fishing sometimes miss responses in individual community components that respond differentially to these disturbances (Kaiser 2003). Biomass was taxonomically decomposed across taxa (sponges, soft corals, hydroids, bryozoans and tunicates) to examine responses of individual community components more closely. Heterogeneity of variances were removed by $\log_{10}$ (biomass + 1) transformation (Levene's tests all $P > 0.05$) except in one case for tunicates ($P = 0.018$). Statistical significance of trawl impacts on biomass of these groups were analysed as above i.e., differently for each year and using post-hoc contrasts t-tests at $\alpha = 0.05$.

Effects of trawling on taxon composition

Statistical significance of trawl impacts on colonial epifauna taxon composition was examined each year using non-metric multidimensional scaling (MDS) plots and

analysis of similarity (ANOSIM) analyses in PRIMER V5.2.2 (Clarke and Gorley 2001) at $\alpha = 0.05$. Three comparisons were performed: (1) between periods every year to determine if taxon composition changed before and after trawling in line E (repeated for controls). When community divergence was evident, the similarity of percentages (SIMPER) procedure in PRIMER V5.2.2 was used to identify taxa that contributed most to dissimilarity between periods; (2) between treatments every year to determine whether spatial variability of taxon composition in line E differed from controls between periods; (3) between years before trawling to examine whether temporal variability of taxon composition varied between treatments. SIMPER analyses of communities were performed to identify whether taxa that changed from year to year in line E were the same taxa that changed in the controls.

RESULTS

Sponges, hydroids and bryozoans were the most frequently encountered colonial epifauna (Table 8). Most sponges encountered were a sycettida-type species and an unidentified species living epizoically on the brachiopod *Terebratulina* sp. Soft corals were all the stoloniferous *Clavularia* sp. and hydroids were mostly *Sertularella polyzonias*, *Symplectoscyphus bathyalis*, *S. tricuspidatus*, *Halecium muricatum*, *Calycella syringa* and *Lafoea dumosa*. Bryozoans were mostly *Dendrobeania* spp. and unidentified ascophorans, and tunicate species were all encrusting forms. On average, colonial epifauna represented only 0.25 % of the total benthic biomass, with individual estimates ranging from zero to 5.61 % of the total biomass. Colonial epifauna from the study site were relatively rich: 50 taxa were identified, 39 of which were hydroids.

Table 8: Frequency of colonial epifauna taxa collected from 99 grabs over the duration of the experimental study on Western Bank from 1997 to 1999. Frequency ≥ 25 % in bold.

Taxon	Taxonomic group	Frequency
***Dendrobeania* spp.**	**bryozoan**	**0.78**
sycettida-type sponge	**sponge**	**0.78**
ascophoran spp.	**bryozoan**	**0.40**
Sertularella polyzonias	**hydroid**	**0.38**
Symplectoscyphus bathyalis	**hydroid**	**0.38**
porifera sp. 1	**sponge**	**0.32**
Calycella syringa	**hydroid**	**0.30**
Halecium muricatum	**hydroid**	**0.30**
Lafoea dumosa	**hydroid**	**0.30**
Symplectoscyphus tricuspidatus	**hydroid**	**0.25**
Rhizocaulus verticillatus	hydroid	0.19
Clavularia sp.	soft coral	0.17
Laomedea neglecta	hydroid	0.13
Eudendrium sp.	hydroid	0.12
porifera sp. 2	sponge	0.12
ascidian sp.	tunicate	0.11
Grammaria abietina	hydroid	0.11
Scrupocellaria scabra	bryozoan	0.11
Sertularia mirabilis	hydroid	0.11
Sertularia schmidti	hydroid	0.11
Lafoea fruticosa	hydroid	0.10
Sertularia tenera	hydroid	0.08
Lafoea gracillima	hydroid	0.08
Tricellaria gracilis	bryozoan	0.07
Gonothyraea loveni	hydroid	0.06
Thuiaria articulata	hydroid	0.06
Hydrallmania falcata	hydroid	0.05
Thuiaria immersa	hydroid	0.05
athecate hydroid sp.	hydroid	0.04
Bugula harmsworthi	bryozoan	0.04
campanulariid hydroid	hydroid	0.03
Eudendrium ramosum	hydroid	0.03
Halecium sessile	hydroid	0.03
Thuiaria alternitheca	hydroid	0.03
Thuiaria laxa	hydroid	0.03
Ectopleura sp.	hydroid	0.02
Polymastia sp.	sponge	0.02
Cuspidella procumbens	hydroid	0.01

Table 8 (continued): Frequency of colonial epifauna taxa collected from 99 grabs over the duration of the experimental study on Western Bank from 1997 to 1999. Frequency ≥ 25 % in bold.

Taxon	**Taxonomic group**	**Frequency**
Eudendrium sp. 2	hydroid	0.01
Halecium articulosum	hydroid	0.01
Halecium labrosum	hydroid	0.01
Halecium minutum	hydroid	0.01
Halecium tenella	hydroid	0.01
Halecium sp.	hydroid	0.01
Keratosum maximum	hydroid	0.01
Obelia geniculata	hydroid	0.01
Obelia sp.	hydroid	0.01
Sertularia similis	hydroid	0.01
thecate hydroid	hydroid	0.01
Thuiaria lonchitis	hydroid	0.01
Eudendrium sp. 2	hydroid	0.01
Halecium articulosum	hydroid	0.01

Effects on colonial epifauna species richness

Trends in colonial epifauna richness were plotted to help conceptualize spatio-temporal patterns between the controls and impact line (Fig. 4) that were analysed statistically (Table 9). Mean richness did not differ at all between periods in line E in 1997 ($P = 1$). The overall ANOVA model was not statistically significant in 1998 or 1999 ($P = 0.214$ and 0.218, respectively), and neither was the interaction effect ($P = 0.058$ and 0.981, respectively), which was also not significantly affected by the period effect in line E ($P = 0.237$ and 0.335, respectively). Power was relatively high for the ANOVA in 1998 (0.557) but very low in 1999 (0.060).

In addition to large standard deviations, mean richness tended to increase in the controls as the experiment progressed, however this increase was not as smooth in the impact line, where mean richness tended to fluctuate (Fig. 4).

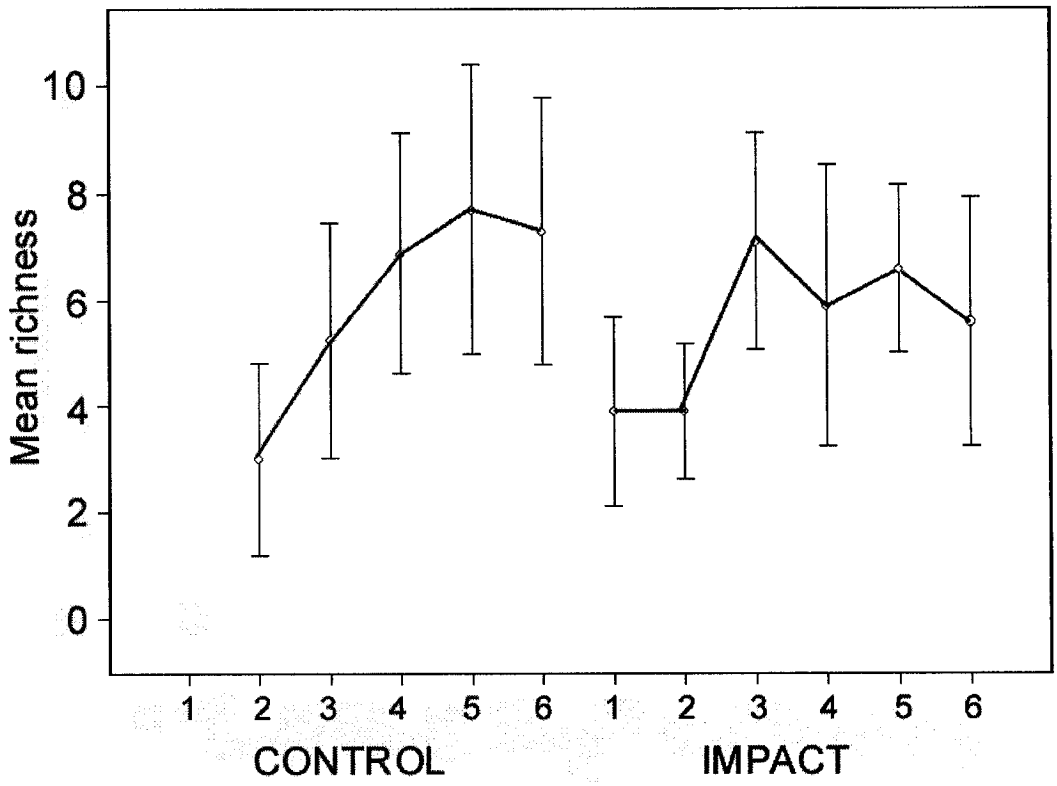

Fig. 4: Spatial and temporal changes in mean number of colonial epifauna taxa richness across treatments on Western Bank from 1997 to 1999. Numbers along x-axis represent time of sampling: 1 = pre-trawl (1997), 2 = post-trawl (1997), 3 = pre-trawl (1998), 4 = post-trawl (1998), 5 = pre-trawl (1999), 6 = post-trawl (1999). Error bars represent the standard deviations. No pre-trawl samples were obtained from the controls in 1997.

Table 9: Statistical analyses of trawling impacts estimated as effects of period (before, after), location (control: lines B, G, I and impact: line E) and the interaction between period and location (period*location) on colonial epifauna richness. Incomplete sampling in 1997 and 1998 required analyses to be performed separately each year using a two-tailed unpaired t-test between periods in the impact line (1997) and two-way ANOVAs (1998 and 1999). The symbol * indicates statistical significance at $\alpha = 0.05$.

Source of Variation	**df**	**Welch's t-value**	**P**
1997			
period	16.331	0	1

	df	***MS***	***F*-ratio**	**P**
1998				
period	1	0.847	0.180	0.675
location	2	1.245	0.265	0.770
period*location	2	15.188	3.226	0.058
contrast test:				
df = 1				
t-value = 1.215				
P = 0.237				
model	5	7.294	1.549	
error	23	4.621		
total	28			0.214
power = 0.557				

	df	***MS***	***F*-ratio**	**P**
1999				
period	1	2.309	0.442	0.511
location	3	15.811	3.027	0.044*
period*location	3	0.311	0.060	0.981
contrast test:				
df = 1				
t-value = 0.978				
P = 0.335				
model	7	7.610	1.457	
error	32	5.223		
total	39			0.218
power = 0.060				

Effects on colonial epifauna biomass

Trends in colonial epifauna biomass were also plotted to help summarize main trends in relation to natural variation across the experimental lines and across years (Fig. 5). These trends were also analysed statistically (Table 10). Mean biomass did not differ between periods in line E in 1997 (P = 0.693). The overall ANOVA model was not statistically significant in 1998 (P = 0.547) but was in 1999 (P = 0.042). The interaction effect was not significant in either year (P = 0.527 and 0.322, respectively); the contrast test in the impact line was not significant in 1998 (P = 0.978) but was in 1999 (P = 0.010). Power was relatively low for both 1998 and 1999 analyses (0.147 and 0.293, respectively).

Mean biomass estimates in the controls were associated with large standard deviations as were the estimates in the impact line. However standard deviations of means from post-trawl periods in the impact line were noticeably smaller than those in the corresponding pre-trawl periods, particularly after successive trawling i.e., in 1999 (Fig. 5).

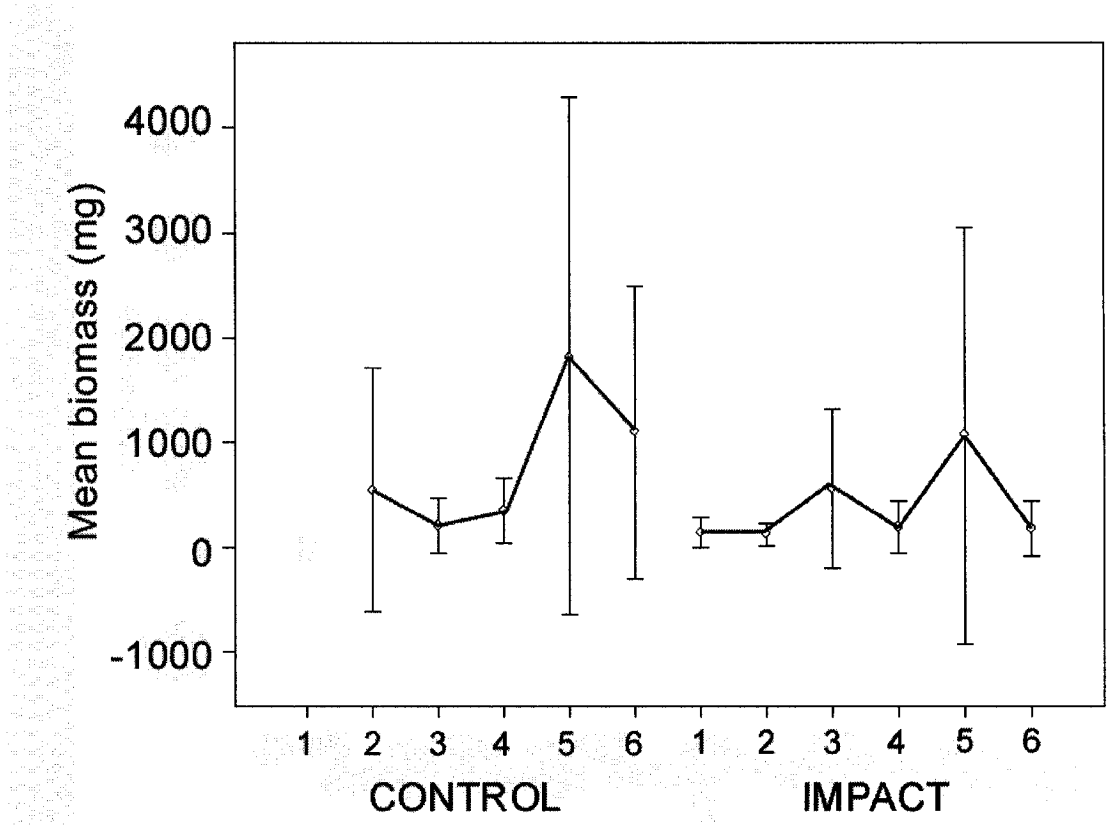

Fig. 5: Spatial and temporal changes in mean colonial epifauna biomass across treatments on Western Bank from 1997 to 1999. Numbers along x-axis represent time of sampling: 1 = pre-trawl (1997), 2 = post-trawl (1997), 3 = pre-trawl (1998), 4 = post-trawl (1998), 5 = pre-trawl (1999), 6 = post-trawl (1999). Error bars represent the standard deviations. No pre-trawl samples were obtained from the controls in 1997.

Table 10: Statistical analyses of trawling impacts estimated as effects of period (before, after), location (control: lines B, G, I and impact: line E) and the interaction between period and location (period*location) on $\log_{10}$-transformed colonial epifauna biomass. Incomplete sampling in 1997 and 1998 required analyses to be performed separately each year using a two-tailed unpaired t-test between periods in the impact line (1997) and two-way ANOVAs (1998 and 1999). The symbol * indicates statistical significance at α = 0.05.

Source of Variation		**df**	**Welch's t-value**	**P**
1997				
period		14.125	0.403	0.693
	df	***MS***	***F*-ratio**	**P**
1998				
period	1	0.103	0.295	0.592
location	2	0.141	0.404	0.673
period*location	2	0.230	0.659	0.527
contrast test:				
df = 1				
t-value = 1.674				
P = 0.107				
model	5	0.287	0.822	
error	23	0.349		
total	28			0.547
power = 0.147				
	df	***MS***	***F*-ratio**	**P**
1999				
period	1	0.378	1.066	0.310
location	3	1.041	2.935	0.048*
period*location	3	0.429	1.210	0.322
contrast test:				
df = 1				
t-value = 2.748				
P = 0.010				
model	7	0.858	2.419	
error	32	0.354		
total	39			0.042*
power = 0.293				

Effects on colonial epifauna biomass by taxonomic group

Trends in the biomass colonial epifauna combined into taxonomic groups were plotted to help explore spatio-temporal patterns between controls and the impact line (Fig. 6). Trends were also analysed statistically (Table 11). No group of colonial epifauna showed statistically significant differences in biomass between periods in line E in 1997 ($P > 0.05$ in all cases). Biomass of sponges, soft corals and bryozoans were also not significantly affected by the interaction term ($P > 0.05$ in all cases) or significantly different between periods in the impact line (contrast test $P > 0.05$ in all cases). Power was relatively low in these cases and ranged from 0.120 to 0.547. Only tunicate biomass was significantly affected by the interaction term in 1998 ($P = 0.041$), and was associated with the highest test power (0.618), but the contrast test showed that this was not due to large changes between periods in the impact line ($P = 0.504$). The contrast test between periods in 1999 was significant for biomass of hydroids ($P = 0.012$) but the interaction effect for this year was not statistically significant ($P = 0.260$) and the ANOVA had relatively low power (0.336).

Although statistically significant interaction effects on biomass of colonial groups were generally not detected, most groups demonstrated consistent period effects on the variances associated with the means in the impact line compared to the controls (Fig. 6). Standard deviations of both mean sponge and bryozoan biomass in the impact line were highest before trawling in 1997, and then consistently declined after trawling each year before increasing during the recovery phase. In the case of sponges, this produced progressively smaller deviations in the impact line as the experiment progressed i.e., from

1997 to 1999. This trend contrasted with the consistent increase in standard deviations of mean bryozoan biomass after trawling in the controls. In contrast to sponges and bryozoans, standard deviations of mean soft coral and hydroid biomass consistently increased after trawling, which progressively increased from 1997 to 1999, although similar trends were seen in controls for hydroid biomass. Trends in tunicate biomass variance were not consistent in the impact line and standard deviations were noticeably lower than those in the controls, although this could be because samples from all three control locations were combined and thus seem highly variable.

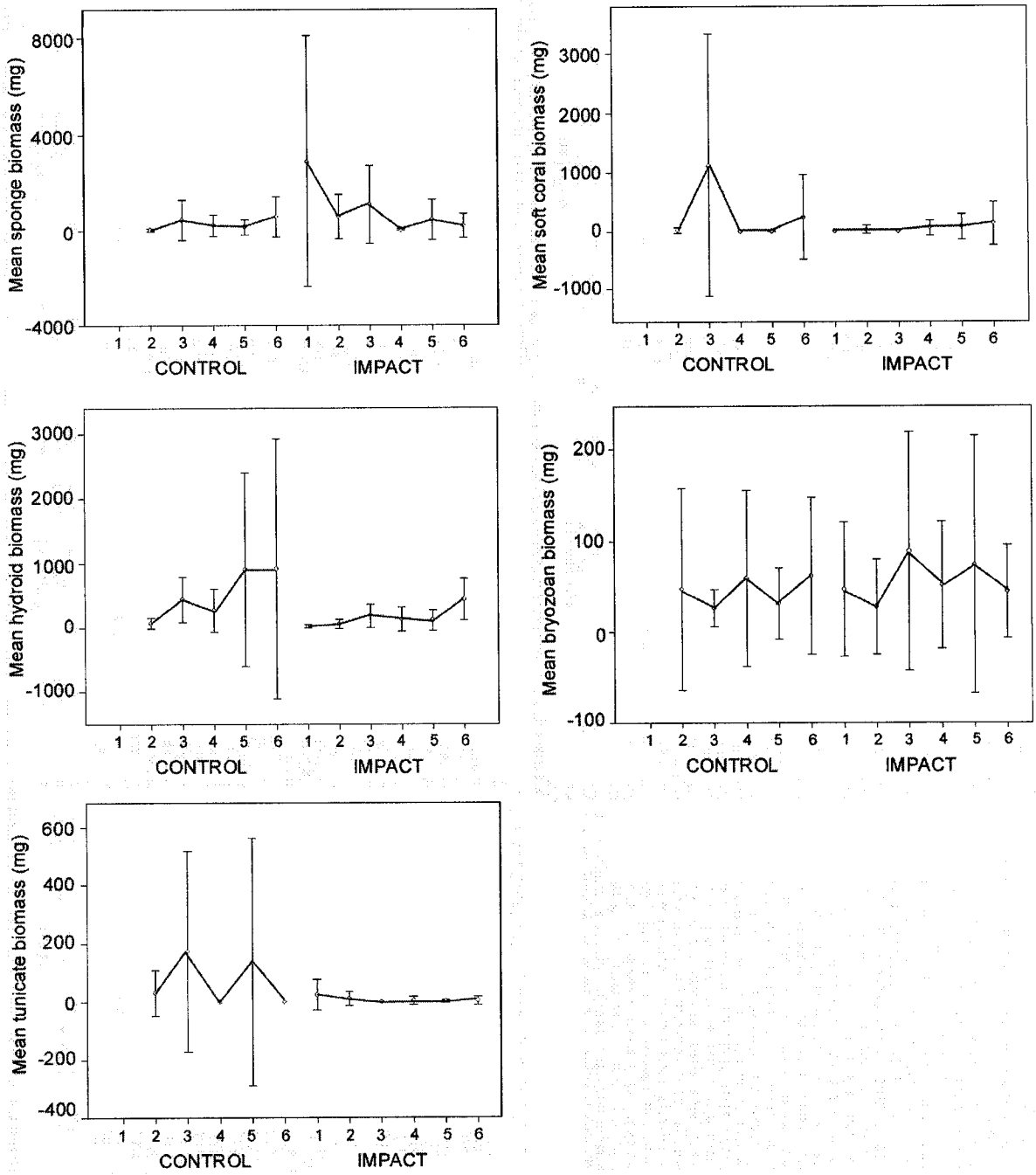

Fig. 6: Spatial and temporal changes in mean biomass of colonial epifauna groups across treatments on Western Bank from 1997 to 1999. Numbers along x-axis represent time of sampling: 1 = pre-trawl (1997), 2 = post-trawl (1997), 3 = pre-trawl (1998), 4 = post-trawl (1998), 5 = pre-trawl (1999), 6 = post-trawl (1999). Error bars represent the standard deviations. No pre-trawl samples were obtained from the controls in 1997.

Table 11: Summary of statistical analyses of trawling impacts estimated as the interaction between period and location (period*location) on $\log_{10}$ (biomass + 1)-transformed biomass data of individual colonial groups. Incomplete sampling in 1997 and 1998 required analyses to be performed separately each year using a Welch's two-tailed unpaired t-test between periods in the impact line (1997) and two-way ANOVAs (1998 and 1999). The symbol * indicates statistical significance at $\alpha = 0.05$.

Test	**Sponges**	**Soft corals**	**Hydroids**	**Bryozoans**	**Tunicates**
1997	df = 17.100 t = 0.909 P = 0.376	df = 9.000 t = - 1.656 P =0.132	df = 15.589 t = 0.023 P = 0.982	df = 17.980 t = 0.631 P =0.536	df = 17.370 t = 0.206 P =0.839
1998					
period*	df = 2	df = 2	df = 2	df = 2	df = 2
location	F = 1.098	F = 3.162	F = 0.564	F = 0.488	F = 3.688
	P = 0.351	P = 0.061	P = 0.577	P = 0.620	P = 0.041*
contrast test:	df = 1 t = 0.668 P = 0.511	df = 1 t = - 1.256 P = 0.222	df = 1 t = 1.292 P = 0.209	df = 1 t = 1.432 P = 0.166	df = 1 t = - 0.680 P = 0.504
power	0.219	0.548	0.132	0.120	0.618
1999					
period*	df = 3	df = 3	df = 3	df = 3	df = 3
location	F = 0.940	F = 1.616	F = 1.403	F = 1.041	F = 1.325
	P = 0.433	P = 0.205	P = 0.260	P = 0.388	P = 0.283
contrast test:	df = 1 t = 0.873 P = 0.389	df = 1 t = - 0.821 P = 0.418	df = 1 t = - 2.658 P = 0.012*	df = 1 t = 0.139 P = 0.890	df = 1 t = - 0.166 P = 0.869
power	0.233	0.383	0.336	0.255	0.319

Effects on colonial epifauna taxon composition

Taxon composition in control lines did not significantly differ between periods or locations in any year ($P > 0.05$); thus, each year data from controls were combined across periods and locations to increase power in subsequent ANOSIM analyses.

Between periods, within years:

ANOSIM analyses on data combined across years demonstrated no significant difference in taxon composition between periods ($R = 0.031$, $P = 0.075$). However there were annual shifts in taxon composition discussed in section (3), making it difficult to discriminate effects of period from effects of time. This necessitated separate analyses for each year. Taxon composition within line E did not change between periods in 1997 ($R = -0.080$, $P = 0.925$), but diverged after pulsed trawling in 1998 ($R = 0.209$, $P = 0.009$) and somewhat in 1999 although this effect was not statistically significant ($R = 0.102$, $P = 0.054$), which could be due to the effect of the outlier in the lower portion of the the 1999 MDS plot (Fig. 7). Over 50 % of the most common taxa (i.e., those found in at least 25% of the 99 samples, Table 8) and many rare taxa were reduced in frequency after trawling in 1998 and 1999 (Tables 12 and 13, respectively). Of the dominant taxa, only the sycettida-type sponge and the hydroid *Symplectoscyphus bathyalis* consistently increased in frequency after trawling. Taxon composition did not change significantly in any control lines between periods of any year ($P > 0.05$).

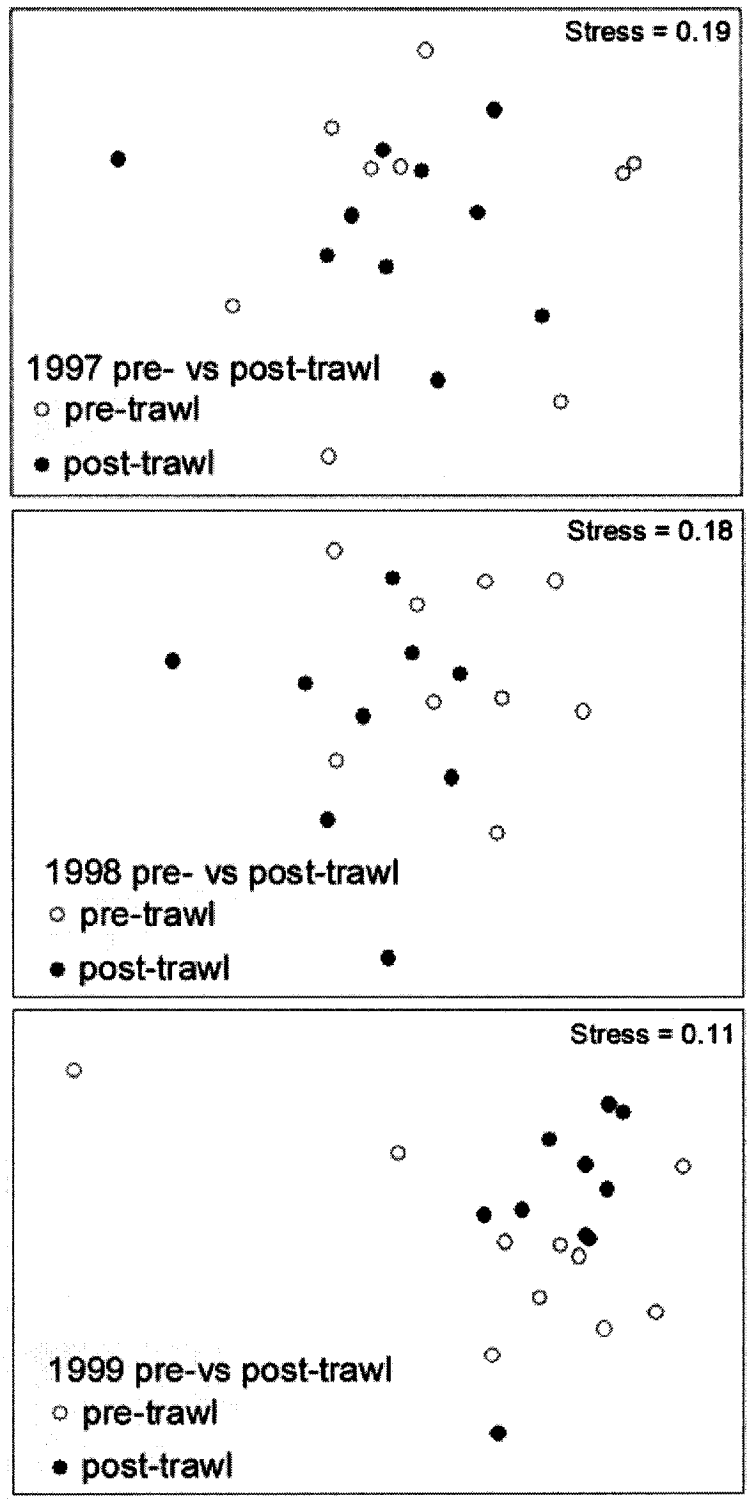

Fig. 7: Non-metric multidimensional scaling plots of colonial epifauna taxon composition between periods in the impact line on Western Bank.

Table 12: SIMPER analyses to detect effect of period on colonial epifauna taxon composition in the impact line in 1998. Taxa that contributed up to 90 % of the dissimilarity (δ) between periods are listed, with the most frequent taxa identified in bold. Average dissimilarity between periods = 71.96.

Taxon	**Frequency before trawling**	**Frequency after trawling**	**Contribution to δ (%)**	**Cumulative contribution to δ (%)**
ascophoran spp.	**0.67**	**0.30**	**7.85**	**7.85**
***Dendrobeania* spp.**	**1.00**	**0.50**	**7.71**	**15.55**
sycettida-type sponge	**0.44**	**0.90**	**7.20**	**22.75**
Sertularella polyzonias	**0.44**	**0.60**	**6.58**	**29.33**
Symplectoscyphus tricuspidatus	**0.44**	**0.20**	**5.50**	**34.83**
Sertularia tenera	0.33	0.20	5.35	40.18
Symplectoscyphus bathyalis	**0.11**	**0.40**	**4.93**	**45.11**
Lafoea dumosa	**0.11**	**0.40**	**4.39**	**49.51**
athecate hydroid	0.22	0.10	3.72	53.23
Thuiaria immersa	0.22	0.20	3.61	56.84
Gonothyraea loveni	0.33	0.00	3.61	60.45
Clavularia sp.	0.33	0.00	3.46	63.91
Sertularia mirabilis	0.22	0.10	3.29	67.21
Tricellaria gracilis	0.22	0.00	3.02	70.23
Halecium muricatum	**0.22**	**0.00**	**2.87**	**73.10**
Rhizocaulus verticillatus	0.22	0.10	2.77	75.87
Lafoea fruticosa	0.22	0.00	2.60	78.48
Eudendrium sp.	0.11	0.10	2.32	80.80
Bugula harmsworthi	0.11	0.10	2.25	83.05
porifera sp. 2	0.22	0.00	2.24	85.29
Scrupocellaria scabra	0.22	0.00	2.17	87.46
campanulariid hydroid	0.00	0.20	1.99	89.45
Eudendrium ramosum	0.11	0.10	1.93	91.38

Table 13: SIMPER analyses to detect effect of period on colonial epifauna taxon composition in the impact line in 1999. Taxa that contributed up to 90 % of the dissimilarity (δ) between periods are listed, with the most frequent taxa identified in bold. Average dissimilarity between periods = 67.02.

Taxon	**Frequency before trawling**	**Frequency after trawling**	**Contribution to δ (%)**	**Cumulative contribution to δ (%)**
Symplectoscyphus bathyalis	**0.40**	**0.90**	**7.99**	**7.99**
sycettida-type sponge	**0.50**	**0.80**	**6.43**	**14.42**
porifera sp. 1	**0.50**	**0.40**	**6.17**	**20.59**
Lafoea dumosa	**0.50**	**0.50**	**6.10**	**26.69**
Halecium muricatum	**0.60**	**0.30**	**6.01**	**32.70**
Sertularella polyzonias	**0.50**	**0.20**	**5.26**	**37.96**
***Dendrobeania* spp.**	**0.80**	**0.70**	**5.24**	**43.20**
ascophoran spp.	**0.30**	**0.30**	**4.96**	**48.16**
Lafoea gracillima	0.40	0.10	4.96	53.12
Rhizocaulus verticillatus	0.30	0.30	4.52	57.63
Symplectoscyphus tricuspidatus	**0.30**	**0.10**	**4.23**	**61.86**
Laomedea neglecta	0.10	0.30	3.69	65.55
Eudendrium sp.	0.30	0.10	3.44	68.99
Clavularia sp.	0.00	0.30	3.36	72.35
Scrupocellaria scabra	0.20	0.00	3.19	75.54
Calycella syringa	**0.30**	**0.00**	**2.83**	**78.37**
Grammaria abietina	0.10	0.20	2.50	80.87
Halecium sessile	0.10	0.10	2.25	83.11
Sertularia schmidti	0.20	0.00	2.18	85.30
Thuiaria articulata	0.10	0.10	2.08	87.37
Polymastia sp.	0.10	0.00	1.76	89.13
Hydrallmania falcata	0.10	0.10	1.67	90.80

Between treatments, within years

Post-trawl taxon composition in line E did not significantly differ from that in the controls in 1997 (R = 0.090, P = 0.094). Composition between treatments remained similar up to the pre-trawl period in 1998 (R = 0.065, P = 0.177), but subsequent trawling produced significant differences (R = 0.157, P = 0.023). Composition across treatments converged before trawling in 1999 (R = 0.107, P = 0.124), and remained similar in the post-trawl period (R = 0.014, P = 0.384). This lack of divergence between treatments was accompanied for the first time in the study by higher taxon similarity estimated by the ANOSIM within the trawled line, increasing from 30.70 % to 40.83 % in pre- versus post-trawl samples and therefore reduced taxon dissimilarity (δ) across treatments between periods in 1999 (δ = 65.13 before and δ = 58.86 after trawling, respectively), the latter which was approximately equal to the mean divergence between controls (δ = 58.11).

Between years before trawling

There were statistically significant temporal changes in taxon composition of pre-trawl communities in line E from 1997 to 1998 (R = 0.193, P = 0.021) and 1998 to 1999 (R = 0.178, P = 0.027) (Fig. 8). Over 88% of the most frequent taxa that changed in occurrence after trawling in 1998 (Table 12) also changed in the same direction between 1998 and 1999 (Table 14). Annual shifts in taxon composition in controls were also evident between years (R = 0.278, P = 0.007 and (R = 0.179, P = 0.006, respectively), although no consistent trends in the frequencies of most taxa were observed as in the

impact line e.g., increased frequencies of the sycettida-type sponge and *Symplectoscyphus bathyalis*.

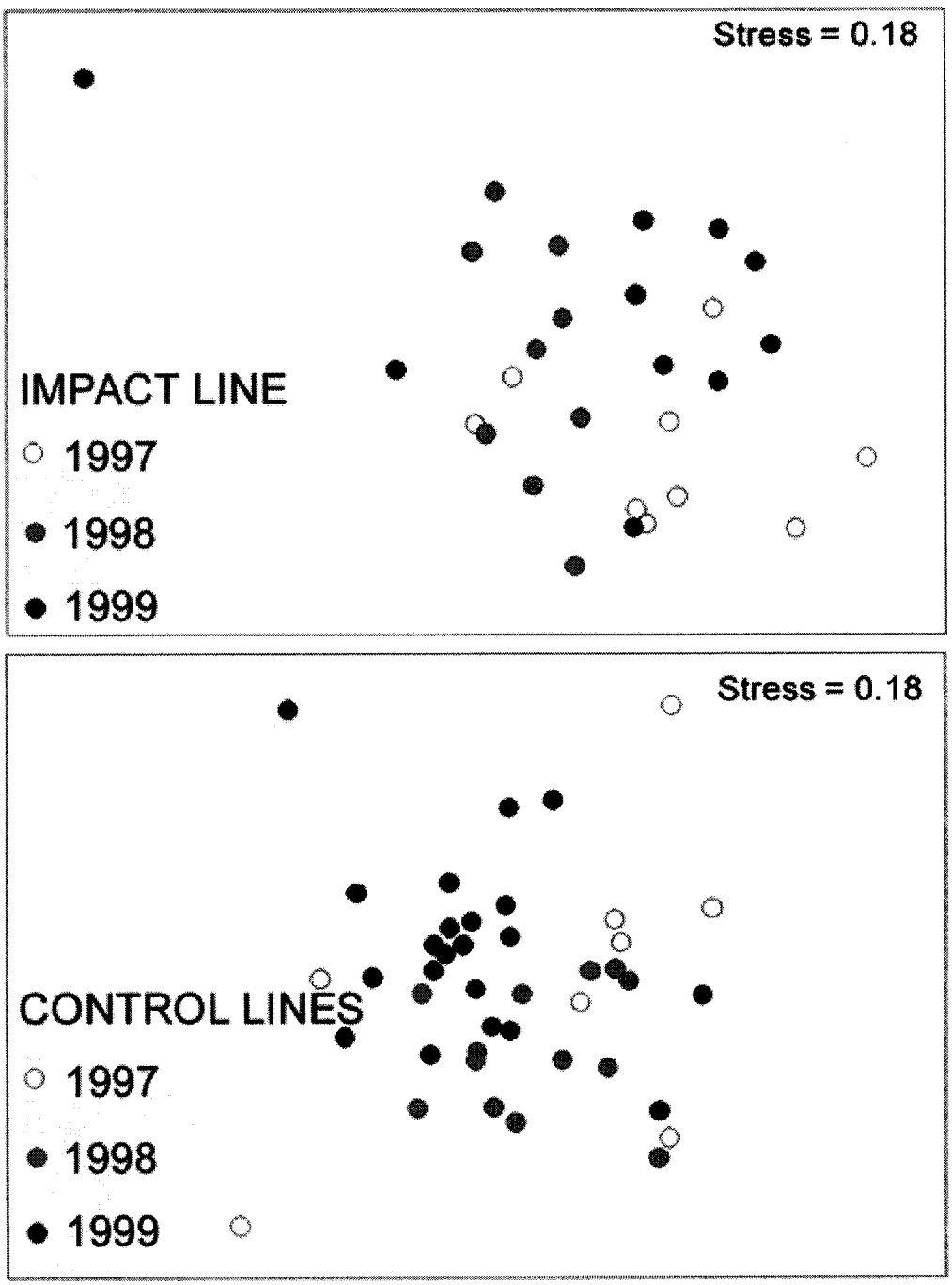

Fig. 8: Non-metric multidimensional scaling plots of annual shifts in pre-trawl taxon composition of colonial epifauna communities in the controls (B, G and I) and the impact line (E) on Western Bank from 1997 to 1999. As there were no pre-trawl samples from the controls in 1997, taxa from post-trawl samples were used in this plot for the controls.

Table 14: SIMPER analyses to detect shifts in pre-trawl taxon composition in line E from 1998 to 1999. Taxa that contributed up to 90 % of the dissimilarity (δ) between years are listed, with the most frequent taxa identified in bold. Average dissimilarity between years = 71.91.

Taxon	**Frequency in 1998**	**Frequency in 1999**	**Contribution to δ (%)**	**Cumulative contribution to δ (%)**
ascophoran spp.	**0.67**	**0.30**	**6.24**	**6.24**
sycettida-type sponge	**0.44**	**0.50**	**5.27**	**11.51**
Sertularella polyzonias	**0.44**	**0.50**	**5.26**	**16.77**
Halecium muricatum	**0.22**	**0.60**	**5.25**	**22.02**
porifera sp. 1	**0.11**	**0.50**	**5.17**	**27.20**
Symplectoscyphus tricuspidatus	**0.44**	**0.30**	**4.82**	**32.02**
Lafoea dumosa	**0.11**	**0.50**	**4.72**	**36.74**
Symplectoscyphus bathyalis	**0.11**	**0.40**	**4.02**	**40.76**
Lafoea gracillima	0.00	0.40	3.92	44.68
Sertularia tenera	0.33	0.00	3.87	48.54
Scrupocellaria scabra	0.22	0.20	3.64	52.19
Rhizocaulus verticillatus	0.22	0.30	3.51	55.69
Eudendrium sp.	0.11	0.30	3.14	58.84
Gonothyraea loveni	0.33	0.00	3.04	61.88
Clavularia sp.	0.33	0.00	2.95	64.83
Dendrobeania spp.	1.00	0.80	2.59	67.42
Lafoea fruticosa	0.22	0.10	2.58	70.00
Sertularia mirabilis	0.22	0.10	2.52	72.51
athecate hydroid	0.22	0.00	2.51	75.02
Calycella syringa	0.00	0.30	2.48	77.50
Tricellaria gracilis	0.22	0.00	2.44	79.93
Polymastia sp.	0.11	0.10	2.36	82.30
porifera sp. 2	0.22	0.00	1.92	84.21
Sertularia schmidti	0.00	0.20	1.90	86.11
Thuiaria immersa	0.22	0.00	1.80	87.91
Bugula harmsworthi	0.11	0.00	1.24	89.15
Halecium articulosum	0.11	0.00	1.24	90.40

DISCUSSION

Natural dynamics of colonial epifauna on Western Bank

The present study provided the opportunity to examine trends in colonial epifauna communities from an offshore shelf ecosystem closed to most types of bottom fishing. Several new observations support the concept that these communities are not only rich but naturally dynamic in time and space.

Colonial epifauna richness appeared to gradually increase from 1997 to 1999 (Fig. 4). Annual increases in colonial epifauna richness were reported across all benthos for the duration of the study (E. Kenchington, unpublished data). Temporal variability in processes that affect benthic species richness must have operated at the scale of several kilometres e.g., natural mortality schedules of local species and recruitment of new taxa. Annual shifts in taxon composition across all lines (Fig. 8) also support the idea of temporally dynamic processes controlling richness.

Colonial epifauna biomass also fluctuated over time but was highly variable between locations (Fig. 5). Natural birth and death schedules of resident colonial epifauna directly affect space availability, inter- and intraspecific encounters and subsequent growth of colonial epifauna. Reduced space availability increases the frequency of competitive interactions between sessile colonial epifauna that result in overgrowth, "stand-offs" and repeated reversals that can inhibit colonial growth (Jackson and Buss 1975; Karlson 1980; Chornesky 1989). But biomass tended to increase over time and could reflect steady growth of sessile epifauna that have not saturated resources and that do not frequently encounter other colonies. Still photographs and video of many

unoccupied hard substrata on the seabed in the experimental site suggest that most local habitats and resources are probably not yet saturated (E. Kenchington, personal observation), which might indicate on-going long-term recovery since the most fishery closures in the haddock box in 1987, although it could also reflect effects of other factors that reset hard-bottom communities to earlier stages of succession e.g., disturbances by predation, storms.

Impacts of trawling on colonial epifauna richness and biomass

Trawling was expected *a priori* to reduce colonial epifauna richness, but the interaction effects in the ANOVA models were not statistically significant and the power of these tests was generally low (Table 9). Trawling seemed to have the effect of perturbing natural dynamics in the impact line. Progressive smooth increases in richness over the duration of the experiment in the controls were not paralleled in the impact line (Fig. 4). Here, richness increased over time but appeared to do so more erratically. The effect of pulsed otter trawling on colonial epifauna richness in this area could be to suppress natural annual changes by killing or removing species present in the pre-trawl period and to instead make space available for recruitment during the recovery phase. Recruitment by species from adjacent unimpacted areas could exclude new taxa from recruiting by reducing substrate availability (Osman and Whitlach 1998).

Trawling was also expected *a priori* to reduce colonial epifauna biomass, but the ANOVA model did not detect a significant interaction between location and period (Table 10). The post-hoc contrast test in 1999 demonstrated that biomass was significantly reduced in the impact line, but the ANOVA had low power (Table 10).

Alternatively, trawling may not have reduced biomass in line E because otter trawl gear damages benthos but tends to be relatively inefficient at actually removing sessile epifauna (Prena et al. 1999).

Progressively more suppressed variances of biomass estimates in the post-trawl period in the impact line (Fig. 5) could be biologically significant. These may reflect the effect of pulsed otter trawling on the distribution of colonial epifaunal biomass. Although the distribution of colonial epifauna is often highly patchy or "contagious" on continental shelves of Atlantic Canada (Schneider et al. 1987; Kostylev et al. 2001), intense and pulsed otter trawling may have progressively homogenized biomass by killing or removing much of the colonial epifauna after 12 trawl sets each year for three years (= 36 sets). The partitioning of biomass analyses across colonial epifauna groups in the present study helped to demonstrate the potential for homogenization of various taxa and is discussed next.

Differential effects of otter trawling across taxonomic groups

The ANOVA models did not detect statistically significant impacts of trawling on the biomass of various taxonomic groups except in the case of tunicates, although this was due to variability between controls and not treatments (Table 11). Statistically significant increases in hydroid biomass in the impact line in 1999 were probably mostly due to increased frequency of the species *Symplectoscyphus bathyalis* (Tables 11 to 13), which may reflect an ability to fragment and rapidly regenerate. Power was generally low for all these tests (Table 11), but biologically significant trends in biomass variances cross taxa e.g., homogenization of biomass, were observed (Fig. 5) and can be explained by

examining the biology and life histories of the various colonial groups encountered in this study.

The standard deviations of both sponge and bryozoan biomass consistently decreased after trawling (Fig. 6). Effects on the biomass of the two most frequent sponges (the sycettida-type sponge and the epizoic species) could have greatly contributed to this reduction, but in different ways. Trawling could have damaged, fragmented and spread the delicate calcareous sycettida-type sponge into numerous sponges evenly over the impact line and nearby areas (this species increased in frequency after trawling, Tables 12 and 13). Trawling could have also indirectly removed the other epizoic sponge species by efficiently killing or removing its host, the brachipod *Terebratulina* sp., which became less frequent after trawling (E. Kenchington, unpublished data). Sponge re-growth and re-establishment of large standard deviations over the next year could be explained by the excellent regenerative capacities of the Porifera: sponge re-growth can even exceed normal growth rates (Ayling 1981; Ayling 1983; Hoppe 1988; Turon et al. 1998; Duckworth 2003). Rapid regeneration in sponges may have evolved to prevent the settlement of fouling organisms that smother the animal (Duckworth 2003). The regenerative capacities of the bryozoans encountered in this study (mostly *Dendrobeania* spp. and ascophorans) are not well known, but trawl-induced damage to erect taxa could be followed by regeneration and abnormally high growth rates that reflect an interruption in normal resource flow so that parts of the bryozoan near the wound take advantage of localized excess resources to divert into their own compensatory growth (Harvell and Helling 1993). The mostly erect bryozoan taxa in the present study became less frequent

after trawling (Tables 12 and 13), so were probably not fragmented like the sycettida-type sponge, but instead were probably evenly removed or killed after intense trawling, which would effectively homogenize their distributions each year.

In contrast to sponges and bryozoans, biomass variance of soft corals (all *Clavularia* sp.) consistently increased after trawling and progressively increased over the duration of the experiment (Fig. 6). Species of clavulariid soft corals usually consist of retractable polyps connected to reticulated root-like stolons and organized into small colonies with often clumped distributions (Fabricius and Alderslade 2001). Instead of being removed by otter trawling e.g., *Gersemia* sp. on low-relief sandy bottoms, some *Clavularia* colonies may have retracted into protective refugia between cobbles and escaped removal or death on Western Bank, thereby increasing the clumped distribution and therefore biomass variance after trawling. *Gersemia rubiformis* also defensively retracts into a compact form when its substrate is rolled over (Chapter Six); this response and the observation that many soft corals bend or pass under trawl gear (e.g., Wassenberg et al. 2002) may help *Clavularia* to escape or survive injuries inflicted by otter trawling. Patchiness of trawl effort may also explain reduced homogeneity in these animals in highly fished areas (e.g., McConnaughey et al. 2000), or an uneven re-distribution or epifauna that re-settle after passage of the otter trawl (Eleftheriou and Robertson 1992; Prena et al. 1999). Differential responses to bottom fishing across colonial epifauna groups should be investigated over a broad range of habitat types to test the hypothesis that bottom type influences the magnitude and direction of the impact.

Dynamics of post-trawl taxon composition

Statistically insignificant shifts in taxon composition after trawling in 1997 (Fig. 7) could reflect relatively minor impacts of the first trawl event followed by rapid recruitment from adjacent unimpacted areas since post-trawl species compositions was not statistically different from that in the controls. This supports the idea that trawled benthic populations can persist by recruitment of locally abundant taxa and not necessarily just by opportunistic taxa (Osman and Whitlach 1998; Pranovi et al. 1998; Frid et al. 2000). It also supports the concept proposed earlier that annual increases in richness could be suppressed if adjacent taxa rapidly settled into disturbed areas and prevented recruitment of new taxa. Recruitment mechanisms used to recolonize the trawled line could have included re-seeding by sexually produced larvae, asexually derived propagules (Bradshaw et al. 2001, 2002), or by reattachment of resuspended colonies (Schratzberger et al. 2002).

The impacts of the second trawl event in 1998 were larger in magnitude than the first disturbance (Fig. 7, Table 12). Taxon composition significantly differed between periods in the impact line, and post-trawl composition differed from that in the controls. This is interpreted as recruitment by impacted taxa, as the frequency of both the sycettida-type sponge and the hydroid *Symplectoscyphus bathyalis* increased after trawling (Table 12) and could have re-settled, regenerated in the impact line. Increased frequencies of sponges after dredging have been recorded (Kefalas et al. 2003) and could be related to damage that causes sponges to split and regenerate (Fenner 1991). Reduced frequencies of the other species after trawling in 1998 (Table 12) could be explained by damaged-

induced reductions in fecundity associated with the healing and/or regeneration of colonies from partial mortality that diverted resources away from sexual reproduction that could limit recruitment (Rinkevich 1996). Differential recruitment mechanisms support the idea that immigration is restricted in large repeatedly trawled areas (Schratzberger et al. 2002).

Pre-trawl taxon composition in the impact line remained skewed by high frequencies of the sycettida-type sponge and *Symplectoscyphus bathyalis* in 1999. Trawling reproduced compositional divergence between periods in the impact line (Fig. 7, Table 13), the magnitude of which could be argued was statistically significant given the arbitrarily set $\alpha = 0.05$ and the estimated significance level for the ANOSIM was $P = 0.054$. Contrary to the prediction that successive trawling would produce increasingly divergent taxon composition, post-trawl composition did not differ between treatments in 1999. Re-seeding of trawled areas may have involved recruitment from unimpacted areas as in 1997. Alternatively, this third pulsed trawl event may have homogenized species composition observed elsewhere in post-fished benthic communities (Bradshaw et al. 2001; Thrush and Dayton 2002) by substantially reducing the proportion of vulnerable taxa leaving more resilient species (Pitcher et al. 2000). The effect of this homogenization would be to indirectly magnify natural variability between control lines, which could hinder the ANOSIM from detecting differences between treatments. This hypothesis was supported by increased taxon similarity within the impact line between periods in 1999.

Overall, the short-term impacts of otter trawling on colonial epifauna in the study area appear to be relatively minor compared to changes that naturally occur over space

and time as observed for other benthic communities (Drabsch et al. 2001; Kenchington et al. 2001). The effect of pulsing otter trawling seems to produce effects observed over the longer-term e.g., suppressed natural increases in richness, homogenization of colonial epifauna assemblages, increased frequencies of trawl-resilient taxa. This study was careful not to overshadow the relevance of these longer-term biologically significant effects (i.e., suppression of changes in richness, altered dynamics associated with biomass and across colonial epifauna groups) that underlie biological processes producing the observed patterns (Smith et al. 1993). This study also highlights the value of longer-term observations needed to detect impacts on community states and rates that affect higher-order marine ecosystem states and rates.

CHAPTER FOUR: DIFFERENCES BETWEEN EPILITHIC AND EPIZOIC HYDROID ASSEMBLAGES FROM COMMERCIAL SCALLOP GROUNDS IN THE BAY OF FUNDY, NORTHWEST ATLANTIC

INTRODUCTION

Many interdependent factors affect recruitment of sessile marine epifaunal organisms (pre-settlement processes) and/or the ability of a recruit to acquire resources once it has settled (post-settlement processes) (Osman 1977; Todd 1998). Global interest in disturbances caused by towed bottom fishing gear (trawls, dredges) has prompted many investigations into the consequences of such activities on sessile epifaunal organisms that sustain much of the impacts (e.g., de Groot 1984; Auster et al. 1996; Collie et al. 1997; Jennings and Kaiser 1998; Bremec and Lasta 1999; Freese et al. 1999; Prena et al. 1999; Kaiser et al. 2000a; McConnaughey et al. 2000; Bradshaw et al. 2001, 2002; Wassenberg et al. 2002). The vulnerability of sponges and colonial epifauna e.g., many cnidarians, bryozoans and tunicates, is particularly important to address in such studies (Hutchings 1990; Kaiser et al. 1999; Collie et al. 2000) as these animals provide biogenic habitat for juvenile and demersal fish and shellfish (Bradstock and Gordon 1983; Auster et al. 1996; Kaiser et al. 1998; Stevens 2003; Stoner and Titgen 2003).

Bottom fishing removes fragile emergent epifauna and shifts these communities from high diversity/low abundance to low diversity/high abundance configurations (Veale et al. 2000). Taxon composition shifts from assemblages dominated by large rigid colonies to those with more flexible runner-like ("guerilla" *sensu* Lovett Doust 1981) or

encrusting growth forms (Gili et al. 1987; Hutchings 1990; Collie et al. 2000; Pitcher et al. 2000; Bradshaw et al. 2001, 2002).

The objective of this study was to examine colonial epifauna assemblage structure in a region exposed to chronic bottom fishing. The study was conducted in the lower Bay of Fundy (Northwest Atlantic) on heavily fished scallop grounds near Digby, Nova Scotia where sea scallop *Placopecten magellanicus* (Gmelin, 1791) has been commercially fished for about a century. Commercial dredge gear consists of seven drags linked by a 7 m long metal bar. Each drag is made of 74 mm diameter steel rings knit together with rubber washers, a 76 cm wide iron frame opening and a steel bar at the tail (Fuller et al. 1998).

Benthic hydrozoans ("hydroids") are frequently encountered in this region (Fuller et al. 1998, Magee et al. 1999, 2000), and historically clogged dredge nets (Caddy 1970). Hydroids colonize a variety of substrata in this region e.g., upper shells of sea scallops and mussels, cobbles and wharves (Caddy 1970; Logan 1988; Fuller et al. 1998; Magee et al. 1999; 2000; Fig. 9). They exhibit great life history diversity, ranging from large slow-growing, arborescent forms to those with fast growth and small stolonal colonies. Approximately half of the species produce free medusae, while the rest liberate less motile planulae (Cornelius 1981).

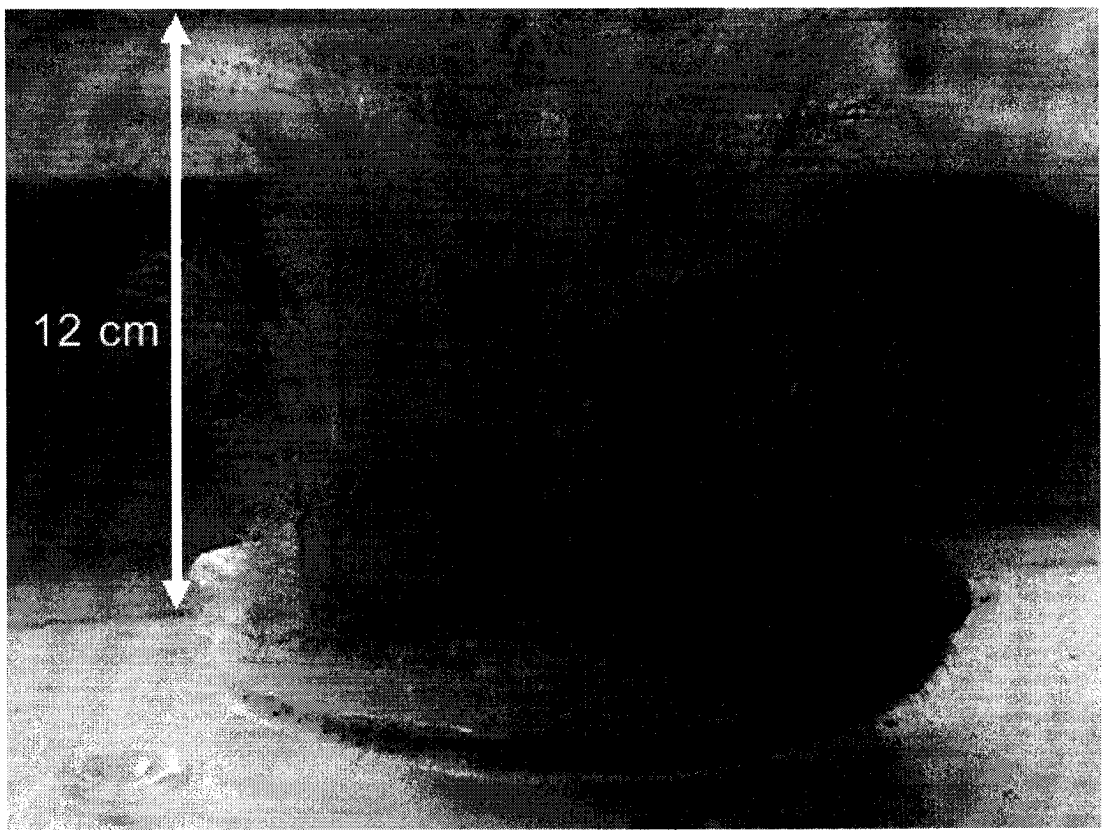

Fig 9: Dense hydroid growth observed on a live sea scallop (*Placopecten magellanicus*) from commercial scallop grounds in the Bay of Fundy.

Potentially confounding natural variability in community analyses due to species replacements can be reduced by using coarser taxonomic information (Warwick 1988; Smith and Simpson 1993) that can discriminate between heavily fished and unimpacted biological communities (e.g., Coggan et al. 2001). However, aggregation of species data to coarser levels can result in a loss of information, particularly when strong data transformations are used in community analyses (Olsgard et al. 1997; Chapman 1998). Thus, the present study also set out to evaluate the practical utility of using coarser taxonomic information versus species-level information.

Due to the absence of permanently closed areas in the Bay of Fundy, we chose to explore the use of living biogenic substrata as psuedo-controls as these represent naturally replicated "island habitats" (Schoener 1974) that can be examined over different spatial and temporal scales (Ward and Thorpe 1991; Berkman 1994). Old-growth live bivalves may provide relatively unharmed epifaunal refuges from dredging and are naturally interspersed with other substrata, which facilitates attributing assemblage divergence to fishing impacts instead of spatial habitat differences.

Assemblage structure of epifauna on cobbles ("epilithic" fauna) i.e., rocks 4 - 256 mm diameter, is expected to differ from that on live scallops ("epizoic" fauna) as these two substrata are impacted differently by dredging. Of those scallop that are not fished out and retained, *Placopecten magellanicus* < 100 mm avoid being caught by swimming away, while larger individuals are either killed, injured, temporarily captured by gear or temporarily bury themselves in bottom sediments to escape the dredges (Caddy 1968; 1973). In contrast, cobbles have experienced cycles of being displaced, turned over,

buried, or even processed on board before being discarded (Caddy 1973; Robinson et al. 2001). As microhabitat differences e.g., the presence of bacterial films or mineralogy, influence hydroid settlement and assemblage succession (Nishihira 1973; Orlov 1996a, b; Bavestrello et al. 2000a), colonization experiments were undertaken to test effects of microhabitat on taxon composition in a shallow subtidal area of the Bay of Fundy not known to be heavily impacted by dredging.

MATERIALS AND METHODS

Field methods for surveying hydroid assemblages

Sampling was performed on board the C.C.G.C. *J.L. Hart* in June 2000 during an annual inshore Bay of Fundy scallop survey with the Canadian Department of Fisheries and Oceans. Inshore seasonal closures concentrated near Digby permitted fishing from October 1 to January 31 during the 1999 - 2000 season, while the rest of the bay was fished year-round. Tows were made using four-gang dredge gear identical in construction to the seven-gang commercial gear, except that two bags had 38 mm polypropylene stretch mesh netting to sample smaller scallops.

Stations were located using a global positioning system. In total, 39 tows were made, each approximately 800 m long X 4 m wide (each about 8 minutes in duration) and each in approximately the same bottom-type (M. Lundy, personal communication). In total, 240 substrata (104 legal-size live scallops i.e., $\geq$ 95 shell height in the year 2000, 136 cobbles) were collected between 38 and 108 m water depth (Fig. 10).

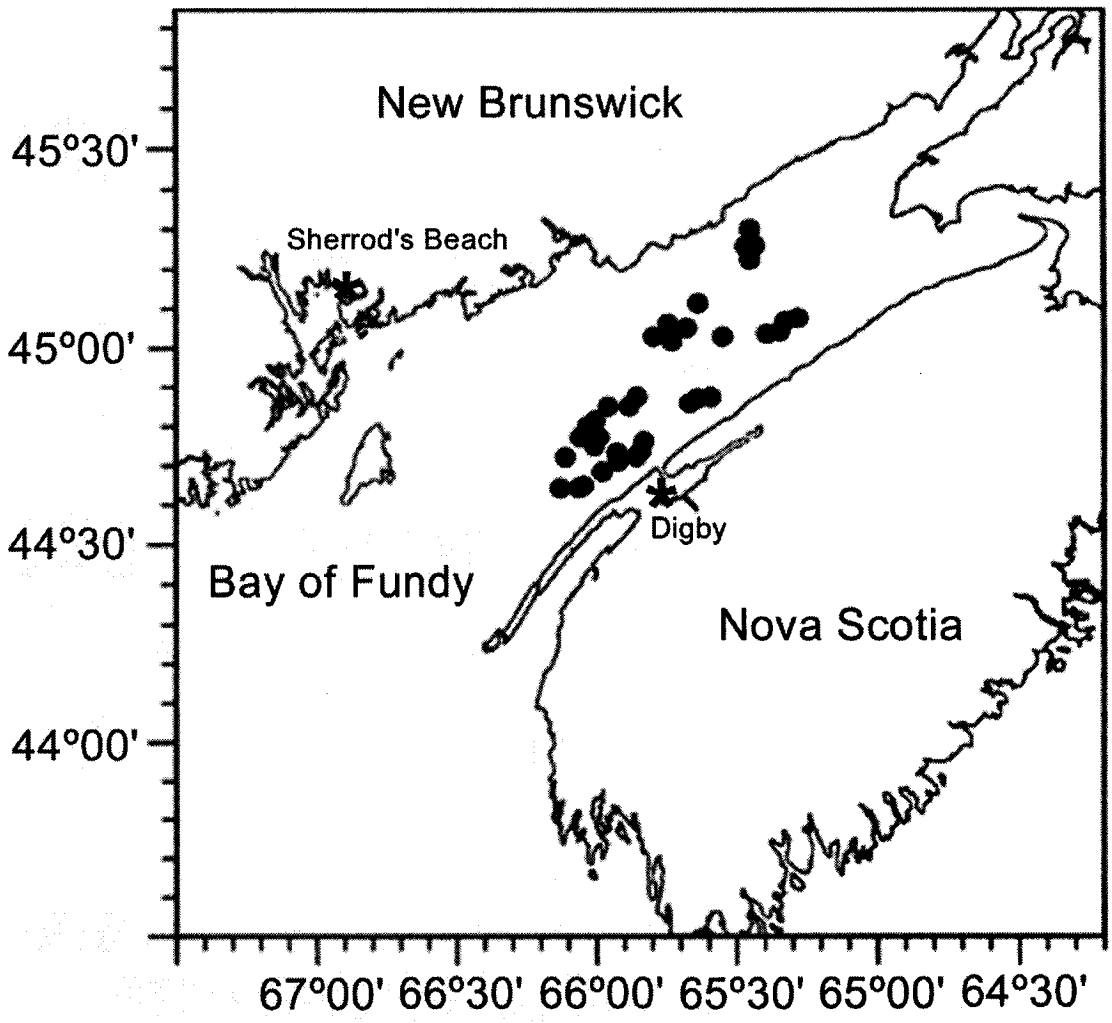

Fig. 10: Dredge survey sites of hydroids from the Bay of Fundy in June 2000. Each dot represents one tow sample (39 in total).

The naturally interspersed distribution of live scallops and cobbles permitted both substrata to be collected from each tow in most cases. Between two and five of each substratum were randomly sampled from dredge bags. Only cobbles with approximately the same surface area as that of the minimum legal size of scallops ($\geq$ 71 cm^2 = 95 mm shell height) were collected, and careful attention was made as often as possible to collect only scallops in pristine condition e.g., those with unchipped shells or growth deformations that could reflect past damage by dredging gear. Each substrate collected had to be colonized by at least one hydroid colony.

Cobbles and scallops were placed in Ziploc™ bags and kept in an open tank with a steady supply of seawater while on board, then frozen at - 72 °C upon return to the laboratory. The presence or absence of all hydroids was determined to the lowest possible taxonomic level using a Nikon SMZ 1500 dissecting microscope. Only hydroids with intact hydranths and/or stems were included in the analyses.

Statistical analyses of hydroid assemblages

Assuming that many hydroid taxa in the collections would be very small, uncommon and difficult to physically separate from their substrata, taxon biomass estimates were considered to be too inaccurate for assemblage analyses. Thus, all analyses were performed simply on raw presence/absence data.

Taxon richness was estimated as the number of distinct taxa per substratum. Mean taxon richness (μ_s) was compared between substrata with an unpaired two-tailed t-test assuming unequal variances (Levene's test $P < 0.05$).

Differences in taxon composition were analysed using PRIMER v5 (Clarke and Gorley 2001). A similarity matrix of pairwise Sörensen indices was constructed from presence/absence data using the SIMILARITY procedure. Multidimensional scaling (MDS) and analysis of similarity percentages (ANOSIM) procedures were performed on the similarity matrix to determine whether the assemblages could be discriminated based on the two substrate types. Characteristic taxa of each assemblage and those that best discriminated between substrate types (i.e, those that explained up to 90 % of the dissimilarity between assemblages) were identified using the similarity percentages (SIMPER) procedure.

Taxa were assigned *a priori* into categories of several "biological attributes" (*cf* Bremner et al. 2003): growth, maximum colony height, typical degree of branching and sexual reproduction mode (Table 15) based on published reports and observations of specimens from the present study. The null hypothesis that hydroids on cobbles would possess the same frequencies of life history traits in each category as those on scallops was tested using G-tests for goodness of fit for each life history category (Sokal and Rohlf 1995). Only taxa that discriminated up to 90% of the SIMPER dissimilarity between substrata were included in these analyses.

Table 15: Life history traits of colonial hydroids in relation to committment to long-term colony survival (modified from Jackson 1979 to reflect biology of hydroids).

Growth strategy	**Maximum colony height**	**Degree of branching**	**Dispersive reproductive stage**
guerilla	< 2 mm	no branching	medusa
mixed	2 – 50 mm	branches once	sessile medusoid
phalanx	> 50 mm	branches twice	planula
		branches three or more times	

MDS and ANOSIM analyses were repeated for data resolved to genera and families. The abilities of these data to discriminate between epizoic and epilithic assemblages were assessed by correlating similarity matrices in a pairwise manner (i.e., species-level with genus-level matrices, and species-level with family-level matrices) to estimate Spearman's rank coefficients using the RELATE procedure in PRIMER.

Fisheries data from the Marine Science Virtual Data Centre (2003) were compiled to relate differences in hydroid assemblages to recent scallop fishing effort in the study area. Logged effort data for the previous three and a half years were aggregated into latitude and longitude (to the nearest 1 / 1000 of a minute) in the MS VDC. These data were used to categorize each of the 39 study sites into three groups as evenly as possible: 0 - 75 hours (14 sites), 75 – 150 hours (13 sites), > 150 hours (12 sites). Separate ANOSIM analyses were done (1) between substrata and (2) within substrata to examine whether taxon composition changed with increasing fishing effort.

Field manipulations of hydroid assemblages

Short-term hydroid colonization experiments were undertaken from July to October 2002. Ten live scallop and ten small cobbles devoid of epifauna were collected between 50 and 80 m depth near Digby in June 2002, scraped clean with a bristle brush and kept in running seawater upon return to the laboratory. Colonies on these substrata were kept in one aquarium with a steady supply of seawater for two weeks to prepare them for transplantation.

Square plastic tabs with circular holes punched through were epoxied onto the ear of each live scallop. Each scallop was individually tethered by 30 cm long string run

through the tag, and tied to a building brick. Each brick and transplanted cobble substrate was marked with red acrylic paint to identify the upper surface.

The substrata were transported to the experimental site at Sherrod's Beach (Fig. 10), a sheltered cove located in Passamaquoddy Bay, southwestern New Brunswick in July 2002. Substrata were deployed at two metres depth below mean low water by snorkelling parallel to a straight stretch of beach at low tide. Substrata were haphazardly interspersed by drawing them from mesh dive bags and placing them at approximately one metre intervals. Substrata were checked approximately every three weeks for substrate turnover until October 2002, at which point they were retrieved and placed in individual Ziploc™ bags and transported to the laboratory for taxonomic sorting. The effects of substrate type in the absence of dredge disturbances on taxon composition were analysed using the SIMILARITY, MDS and ANOSIM procedures.

RESULTS

Hydroid assemblage analyses

In total, 51 taxa from 24 genera were observed. Several specimens were degraded or not sexually mature thus preventing their assignments to species level. Campanulariids, bougainvilliids, the campanuliniid *Calycella syringa* and the sertulariid *Sertularia cupressina* were the most frequently encountered hydroids from the scallop fishing grounds in the study region (Table 16).

Table 16: List of 51 hydroid taxa ordered by their frequencies in 240 collections of cobbles live and scallops combined from the Bay of Fundy in June 2000.

Species	Family	Overall frequency	Rank
Campanularia volubilis (Linnaeus, 1758)	Campanulariidae	0.9872	1
Clytia hemisphaerica (Linnaeus, 1767)	Campanulariidae	0.6992	2
Clytia sp.	Campanulariidae	0.6968	3
Obelia dichotoma (Linnaeus, 1758)	Campanulariidae	0.6648	4
Calycella syringa (Linnaeus, 1767)	Campanuliniidae	0.6168	5
Obelia geniculata (Linnaeus, 1758)	Campanulariidae	0.6040	6
Sertularia cupressina Linnaeus, 1758	Sertulariidae	0.5856	7
Rhizocaulus verticillatus (Linnaeus, 1758)	Campanulariidae	0.4824	8
bougainvilliid (erect)	Bougainvillidae	0.4352	9
Bougainvillia sp. (stolonal)	Bougainvillidae	0.4000	10
Obelia longissima (Pallas, 1766)	Campanulariidae	0.3648	11
Halecium undulatum Billard, 1922	Haleciidae	0.3116	12
Gonothyraea loveni (Allman, 1859)	Campanulariidae	0.2216	13
Halecium sessile Norman, 1867	Haleciidae	0.2176	14
Symplectoscyphus tricuspidatus (Alder, 1856)	Sertulariidae	0.2168	15
Abietinaria abietina (Linnaeus, 1758)	Sertulariidae	0.1904	16
Sertularella polyzonias (Linnaeus, 1758)	Sertulariidae	0.1760	17
Sertularia tenera G.O. Sars, 1874	Sertulariidae	0.1592	18
Hydrallmania falcata (Linnaeus, 1758)	Sertulariidae	0.1488	19
Diphasia fallax (Johnston, 1847)	Sertulariidae	0.1208	20
Lafoea dumosa (Fleming, 1820)	Lafoeidae	0.1160	21
Sertularia sp.	Sertulariidae	0.1040	22
Diphasia margareta (Hassall, 1841)	Sertulariidae	0.0968	23
Eudendrium ramosum (Linnaeus, 1758)	Eudendriidae	0.0952	24
Filellum serpens (Hassall, 1848)	Lafoeidae	0.0856	25
Bougainivillia superciliaris (L. Agassiz, 1849)	Bougainvillidae	0.0784	26
Ectopleura crocea (L. Agassiz, 1862)	Tubulariidae	0.0760	27
Eudendrium capillare Alder, 1856	Eudendriidae	0.0728	28
Obelia sp.	Campanulariidae	0.0720	29
Sertularia latiuscula Stimpson, 1853	Sertulariidae	0.0552	30
Abietinaria filicula (Ellis and Solander, 1786)	Sertulariidae	0.0544	31
Sertularia fabricii Levinsen, 1893	Sertulariidae	0.0448	32
Diphasia sp.	Sertulariidae	0.0416	33
Grammaria borealis (Levinsen, 1893)	Lafoeidae	0.0344	34
Halecium sp.	Haleciidae	0.0344	
Sertularia similis Clark, 1877	Sertulariidae	0.0312	35

Table 16 (continued): List of 51 hydroid taxa ordered by their frequencies in 240 collections of cobbles and live scallops combined from the Bay of Fundy in June 2000.

Species	**Family**	**Overall frequency**	**Rank**
Halecium muricatum (Ellis and Solander, 1786)	Haleciidae	0.0272	36
Lafoea fruticosa M. Sars, 1851	Lafoeidae	0.0272	
Grammaria abietina (M. Sars, 1850)	Lafoeidae	0.0240	37
campanulariid	Campanulariidae	0.0208	38
Halecium corrugatum Nutting, 1899	Haleciidae	0.0208	
Thuiaria sp.	Sertulariidae	0.0208	
Bougainvillia sp. (erect)	Bougainvilliidae	0.0136	39
Keratosum maximum (Levinsen, 1893)	Incertae Sedis	0.0136	
Nemertesia americana (Nutting, 1900)	Plumulariidae	0.0136	
Sarsia tubulosa (M. Sars, 1835)	Corynidae	0.0136	
Cuspidella sp.	Campanuliniidae	0.0104	40
Diphasia rosacea (Linnaeus, 1758)	Sertulariidae	0.0104	
Eudendrium sp.	Eudendriidae	0.0104	
Halecium labrosum Alder, 1859	Haleciidae	0.0104	
Thuiaria articulata (Pallas, 1766)	Sertulariidae	0.0104	

Taxon richness

The number of hydroid taxa ranged from one to ten on live scallops and one to nine on small cobbles. Taxon richness was significantly lower on cobble substrata (μ_s = 3.750) than on live scallops (μ_s = 4.356) according to the two-sample t-test assuming unequal variances (t = 2.670, df = 192, two-sided P = 0.006). However the high degrees of freedom associated with this test likely increased the type I error rate; it is unlikely that a mean of 3.750 taxa on cobbles was significantly different from a mean of 4.356 taxa on scallops.

Taxon composition

The MDS ordination produced two divergent hydroid assemblages from epizoic versus epilithic substrata (Fig. 11). Despite moderate convergence of shared taxa between the two assemblages (stress = 0.2), divergence was statistically significant at all taxonomic levels (ANOSIM global $R \geq 0.280$, $P < 0.05$). However the correlation between species and coarser data similarity matrices declined from species- to family-levels, and a decline in discriminating ability with higher-level assemblage information was evident (Fig. 11, Table 17).

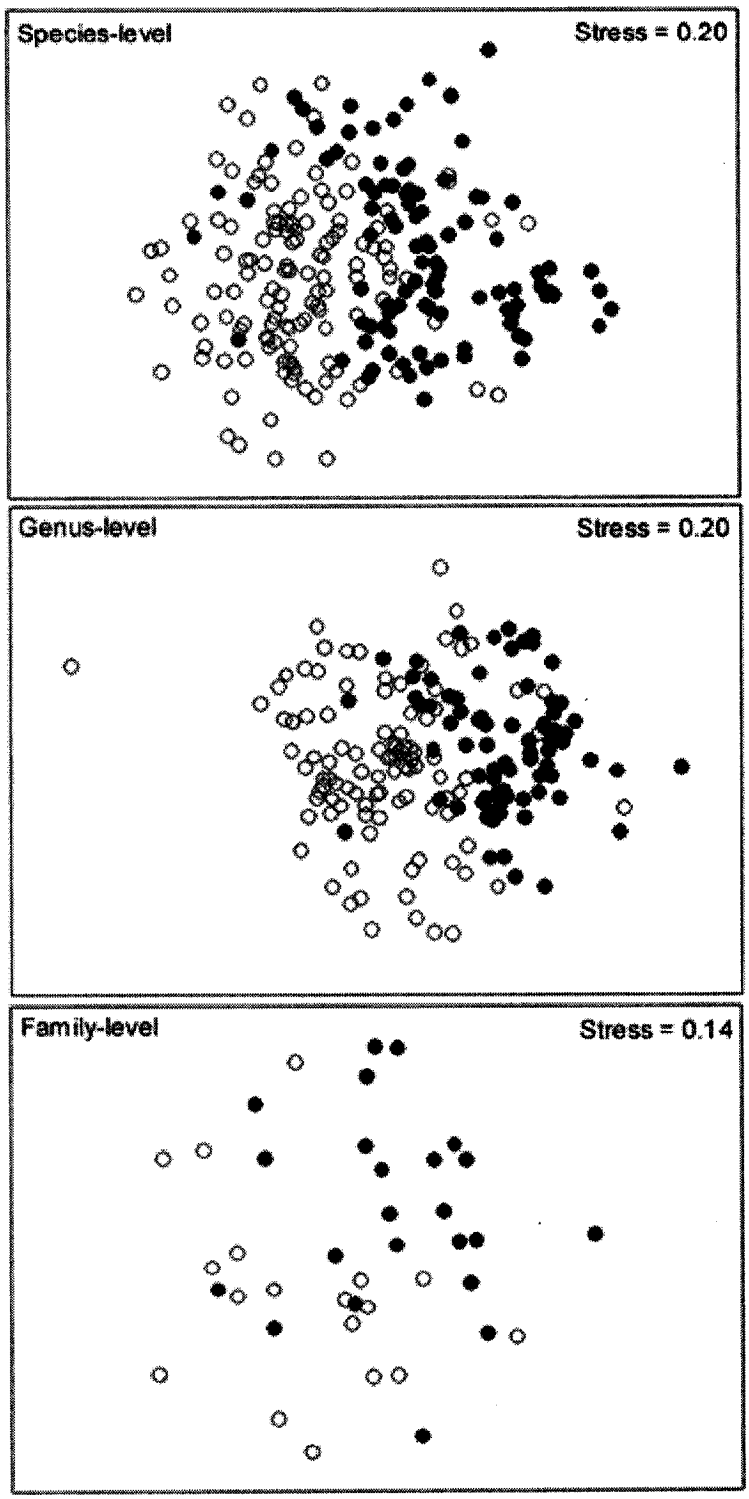

Fig. 11: Non-metric multidimensional (MDS) ordination of hydroid communities from scallop (closed circle) and cobble (open circle) substrata at different levels of taxonomic resolution. Te apparent reduction in the number of samples in genus- and family-level analyses reflects overlapping of shared genera or families in MDS plots.

Table 17: Ability for species-level and more coarse taxonomic resolution (i.e., taxonomic information at the genus- and family-levels) to detect differences in hydroid communities in the Bay of Fundy using analysis of similarities (ANOSIM) and similarity of percentages (SIMPER) analyses.

Taxonomic level	**ANOSIM Global R**	**Average SIMPER δ**	**Spearman's ρ (correlation with species matrix)**	**Spearman's ρ (correlation with genus matrix)**
Species	0.339*	87.33	-	-
Genus	0.352*	73.92	0.637*	-
Family	0.280*	47.19	0.317*	0.431*

* denotes statistical significance at $\alpha = 0.05$

Similarity within epizoic assemblages was explained primarily by nine taxa including *Calycella syringa*, *Obelia dichotoma* and *Sertularia cupressina* (Table 18). Similarity within epilithic communities was largely due to eight taxa, especially the campanulariids *Campanularia volubilis*, *Clytia hemisphaerica* and *Clytia* sp. (the latter taxon possibly being the same species as *C. hemisphaerica*, but several specimens of *Clytia* sp. could not be firmly diagnosed to species-level) (Table 18).

Average dissimilarity between epizoic and epilithic assemblages ($\delta = 87.33$) was mostly explained by 25 of the 51 species (Table 19). *Calycella syringa* was the principal discriminating species between the two communities, most commonly found on *Obelia dichotoma* and *Sertularia cupressina* (*a posteriori* Sörensen indices for association with *C. syringa* = 46.512 and 43.333, respectively).

Differences in life history traits

The life history traits of these 25 hydroid taxa (Table 20) were also significantly different between epizoic and epilithic assemblages. Hydroid assemblages on cobbles exhibited significant differences from those on scallops across all life history categories (Table 21). Taxa on cobbles tended to be low-lying runner-like guerilla and mixed growth forms and tended to be smaller with less branching and possess medusa life stages (Table 21). Hydroid taxa on scallops were more typically erect tree-shaped phalanx growth froms, with larger and more branched colonies and planula larvae life stages (Table 21).

Table 18: Characteristic hydroid taxa of assemblages on cobbles and live scallops in the Bay of Fundy. Mean similarity within assemblages on live scallops = 24.21, mean similarity within communities on cobbles = 25.33.

	Frequency on substrate	**Contribution to mean similarity (%)**	**Cumulative c contribution to mean similarity (%)**
Characteristic taxa on live scallops (n = 104)			
Calycella syringa	0.59	28.16	28.16
Obelia dichotoma	0.42	20.40	48.57
Sertularia cupressina	0.36	11.72	60.28
Rhizocaulus verticillatus	0.33	9.14	69.42
Obelia geniculata	0.30	7.79	77.21
Obelia longissima	0.21	4.27	81.48
Campanularia volubilis	0.23	3.81	85.29
Halecium sessile	0.19	2.82	88.11
Clytia sp.	0.16	2.20	90.31
Characteristic taxa on cobbles (n = 136)			
Campanularia volubilis	0.55	30.23	30.23
Clytia hemisphaerica	0.43	18.87	49.11
Clytia sp.	0.39	16.32	65.43
bougainvilliid (erect)	0.32	9.91	75.34
Obelia geniculata	0.23	4.92	80.25
Bougainvillia sp. (stolonal)	0.21	4.01	84.26
Halecium undulatum	0.20	3.88	88.14
Obelia dichotoma	0.16	2.89	91.03

Table 19: Hydroid taxa that can best discriminated between assemblages on cobbles versus live scallops in the Bay of Fundy. Mean dissimilarity (δ) between assemblages on scallops and cobbles = 87.33.

	Frequency on scallops (n = 104)	**Frequency on cobbles (n = 136)**	**Contribution to % δ**	**Cumulative contribution to % δ**
Discriminating taxa				
Calycella syringa	0.59	0.01	7.92	7.92
Campanularia volubilis	0.23	0.55	7.86	15.78
Obelia dichotoma	0.42	0.16	7.18	22.97
Clytia hemisphaerica	0.12	0.43	6.60	29.57
Clytia sp.	0.16	0.39	6.44	36.00
Sertularia cupressina	0.36	0.14	5.88	41.88
Obelia geniculata	0.30	0.23	5.71	47.59
Rhizocaulus verticillatus	0.33	0.11	5.18	52.76
bougainvilliid (erect)	0.00	0.32	4.60	57.36
Obelia longissima	0.21	0.10	3.94	61.31
Bougainvillia sp. (stolonal)	0.10	0.21	3.76	65.07
Halecium undulatum	0.01	0.20	2.98	68.05
Halecium sessile	0.19	0.03	2.79	70.84
Gonothyraea loveni	0.03	0.14	2.27	73.11
Symplectoscyhpus tricuspidatus	0.15	0.06	2.27	75.37
Sertularella polyzonias	0.13	0.03	2.00	77.37
Abietinaria abietina	0.00	0.14	1.95	79.32
Sertularia tenera	0.14	0.01	1.79	81.11
Hydrallmania falcata	0.12	0.01	1.77	82.88
Sertularia sp.	0.10	0.00	1.65	84.53
Diphasia fallax	0.09	0.02	1.32	85.85
Ectopleura crocea	0.06	0.01	1.11	86.95
Lafoea dumosa	0.03	0.07	1.10	88.05
Eudendrium ramosum	0.00	0.07	1.08	89.14
Eudendrium capillare	0.08	0.00	0.96	90.10

Table 20: Life history categories of hydroids predicted *a priori* to differ between assemblages on cobbles versus live scallops in heavily disturbed areas. Life history traits of hydroid taxa were gleaned from the literature and from observations made in the present study.

Discriminating taxa	**Growth form**	**Maximum colony height (mm)**	**Typical degree of branching**	**Dispersive reproductive stage**
Calycella syringa	guerilla	< 2	0	planula
Campanularia volubilis	guerilla	< 2	0	planula
Obelia dichotoma	guerilla	> 50	= 3°	medusa
Clytia hemisphaerica	guerilla	< 2	0*	medusa
Clytia sp.	guerilla	< 2*	0*	medusa
Sertularia cupressina	phalanx	> 50	= 3°	planula
Obelia geniculata	guerilla	2 - 50	0	medusa
Rhizocaulus verticillatus	phalanx	> 50	1°	planula
bougainvilliid (erect)	phalanx	2 - 50*	= 3	?
Obelia longissima	guerilla	> 50	= 3	medusa
Bougainvillia sp. (stolonal)	guerilla	< 2*	0*	medusa
Halecium undulatum	phalanx	2 - 50	= 3°	planula
Halecium sessile	phalanx	> 50	= 3°	planula
Gonothyraea loveni	phalanx	2 - 50	= 3°	sessile medusoid
Symplectoscyphus tricuspidatus	phalanx	> 50	2°	planula
Sertularella polyzonias	phalanx	> 50	= 3°	planula
Abietinaria abietina	phalanx	> 50	2°	planula
Sertularia tenera	phalanx	2 - 50	0	planula
Hydrallmania falcata	phalanx	> 50	= 3°	planula
Sertularia sp.	phalanx	2 - 50*	0*	planula
Diphasia fallax	phalanx	> 50	2°	planula
Ectopleura crocea	phalanx	> 50	0*	medusa
Lafoea dumosa	mixed	> 50	= 3°	planula
Eudendrium ramosum	phalanx	> 50	= 3°	planula
Eudendrium capillare	phalanx	2 - 50	= 3°	planula

*observation based on specimens from the present study

Table 21: Mean frequencies and statistical differences in life history categories in epizoic versus epilithic hydroid assemblages. Sum of frequencies in a category do not equal one because only traits from the 25 discriminating hydroid taxa were used. Expected frequencies were calculated by multiplying cobble sample size by the mean frequency of a trait on scallop.

Life history category	**Frequency on scallops**	**Frequency on cobbles**	**G**
Growth strategy			*12.350 > $X^2_{0.5, 2}$ = 5.991
guerilla	0.522	0.579	
mixed	0.002	0.015	
phalanx	0.386	0.345	
Colony size			*69.079 > $X^2_{0.5, 2}$ = 5.991
< 2 mm	0.253	0.447	
2 - 50 mm	0.117	0.244	
> 50 mm	0.512	0.249	
Colony branching			*37.296 > $X^2_{0.5, 3}$ = 7.815
no branches	0.319	0.399	
1° branching	0.072	0.027	
2° branching	0.076	0.172	
≥ 3° branching	0.415	0.342	
Dispersive stage			*23.191 > $X^2_{0.5, 2}$ = 5.991
medusa	0.295	0.404	
sessile medusoid	0.023	0.041	
planula	0.565	0.495	

*statistically significant at $\alpha = 0.05$

Effects of fishing effort category

There was evidence of increasing divergence between the taxon composition of epilithic and epizoic hydroid assemblages when sites were categorized into levels of recent fishing effort: sites with the highest fisheries effort showed the greatest hydroid assemblages divergence between cobbles and scallops (Table 22), but sites with lower fishing effort also showed significant divergence between substrate types.

Effects of substrata in undisturbed conditions

Nine hydroid taxa were found on the transplanted substrata after three months. Nineteen of the original 20 substrata were retrieved: one scallop had broken free of the tag and could not be relocated. Hydroids that colonized these substrata were dominated by tubulariids, bougainvilliids and campanulariids with rapid stolonal growth and short lifespans. Differences in taxon composition between epizoic and epilithic assemblages were not statistically significant (Global R = - 0.099, P = 0.948) and two assemblages could not be distinguished (Fig 4). All substrata were colonized by *Obelia longissima*, and both *Gonothyraea loveni* and *Opercularella lacerata* were approximately as frequent on live scallops as they were on cobbles (Table 23).

Table 22: ANOSIM comparisons of hydroid assemblages on cobbles and scallops at three levels of fishing effort. Divergence in hydroid taxon composition was also analysed separately for cobbles and scallops, and assemblages from each of the two most extreme fishing effort categories (0 – 75 and > 150 hours) were compared.

Fishing effort (hours)	**ANOSIM R-value**
Comparisons between assemblages on scallops versus cobbles	
0 – 75 hours	0.307*
75 – 150 hours	0.386*
> 150 hours	0.356*
Comparisons between fishing effort categories	
Assemblages on cobbles	0.124*, pairwise comparison between the two most extreme ranges of effort 0 –75 and > 150 hours) = 0.199*
Assemblages on scallops	0.030*, pairwise comparison between the two most extreme ranges of effort (0 –75 and > 150 hours) = 0.046*

*statistically significant at $\alpha = 0.05$

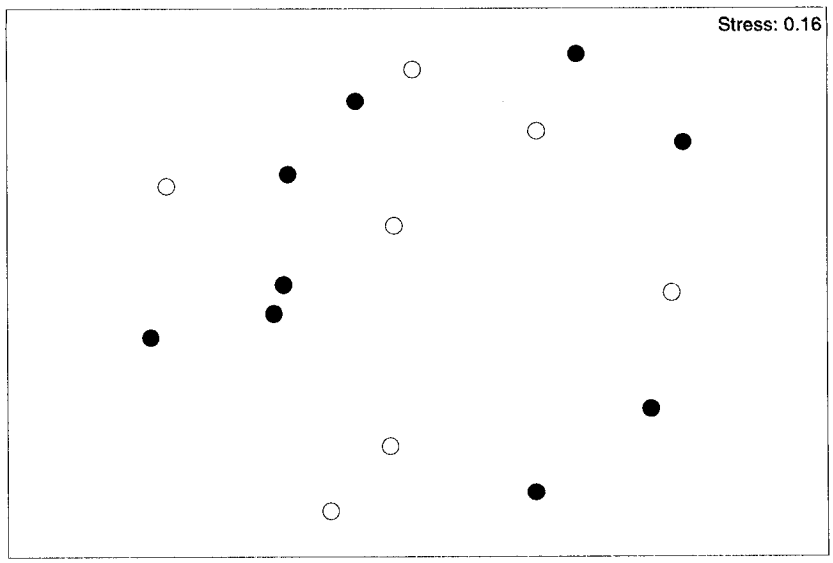

Fig 12: Non-metric multidimensional (MDS) ordination of hydroid communities that colonized transplanted scallop (closed circles) and cobbles (open circles) substrata at Sherrod's Beach in Passamaquoddy Bay. Assemblages were not divergent after three months transplantation in the shallow (2 m below mean low water) subtidal area (ANOSIM R = - 0.099, P = 0.948).

Table 23: Frequencies of hydroid taxa that colonized transplanted substrata (2 m depth) over three months at Sherrod's Beach in Passamaquoddy Bay.

Taxon	**Frequency on scallops (n = 9)**	**Frequency on cobbles (n = 10)**
Bougainvillia sp. (erect)	0.33	0.50
Ectopleura crocea (L. Agassiz, 1862)	0.33	0.30
Ectopleura larynx (Ellis and Solander, 1786)	0.00	0.10
Obelia sp.	0.11	0.10
Obelia longissima (Pallas, 1766)	1.00	1.00
Gonothyraea loveni (Allman, 1859)	0.56	0.60
Opercularella lacerata (Johnston, 1847)	0.33	0.40
Clytia hemisphaerica (Linnaeus, 1767)	0.11	0.00
Halecium sp. (stolonal)	0.22	0.10

DISCUSSION

Mechanisms for hydroid assemblage divergence

Commensalisms between hydroids and bivalves are highly reciprocal relationships. Juvenile bivalves use hydroids for spat attachment and protection from predators (Pulfrich 1996) that later offer the host camouflage, defense from predators, parasites and injuries (Vance 1978; Piraino et al. 1994; Cerrano et al. 2000). Bivalve hosts provide hydroids with space for settlement and adult colonies receive water currents, nutrition, protection from predators and space to grow (Boero 1981; Kubota 1983; Piraino et al. 1994; Cerrano et al. 2000). Divergence in taxon composition (Table 17 and Fig. 11) and life history traits (Table 21) between epizoic and epilithic hydroid assemblages observed in dredged areas in the present study could be due to several effects of microhabitat: (1) larval preferences for biofilms or other surface properties; (2) competitive interactions among epizoic taxa and (3) more intense disturbance by predation on immobile cobbles versus live scallops.

However despite well documented obligate associations, the majority of hydroids are substrate generalists (Boero 1984; Calder 1991; Gili and Hughes 1995) including most of the taxa that discriminated between substrata in the present study e.g., *Sertularia cupressina* (Schmidt and Warner 1991) and *Obelia dichotoma* (Cornelius 1995). Competition among hydroids and other epifauna is not well understood in this region, but the ability for some species e.g., *Obelia dichotoma* (Standing 1976) to pre-empt others may influence epizoic assemblage structure. However epizoic assemblages in the present study supported taxa with a range of life histories and competitive abilities. Although the

effects of predation on cobble epifauna cannot be eliminated, Caddy (1970) noted that epizoic hydroids in the Bay of Fundy at the time of his study also occurred as associated fauna on rocky substrata, and that these hydroids still exhibited no apparent faunal relationships over a decade later with other taxa including *Placopecten magellanicus* (Caddy and Carter 1984). Furthermore, 40 % of the taxa reported in the present study were frequently found on cobbles in an area on the nearby Scotian Shelf closed to most bottom fishing since 1987 even in the presence of *Placopecten magellanicus*, which rarely supported any epizoites (Chapter Three, K. MacIsaac personal communication). Many of the same species in the Gulf of Maine south of the Bay of Fundy occurred in high frequency on boulders, and responded in similar ways to bottom fishing e.g., reduced *Calycella syringa* and *Symplectoscyphus tricuspidatus*, and increased *Clytia* spp. (Pugh 1999).

Assemblage divergence could also reflect effects of host distribution. Hydroid larvae and stolons often colonize nearby hosts (Kubota 1983; Piraino et al. 1994; Bavestrello et al. 2000b; Cerrano et al. 2000), the distribution of which affects hydroid populations (Rayyan et al. 2002). Epifaunal occurrence is directly proportional to distribution of live scallop in the Bay of Fundy (Caddy 1970) and may promote the colonization of shells by the same taxa repeatedly. If microhabitat effects and host distribution control hydroid assemblage structure, then an alternative way for bottom fishing to impact faunal associations (*cf* Langton and Robinson 1990) is by removing *Placopecten magellanicus* substrata crucial to the long-term persistence of associated epifauna, which may necessitate protection from bivalve fisheries (Saier 2002).

Alternatively, assemblage divergence could be related to differential impacts between cobble and scallop substrata exposed to dredging. Several lines of evidence support the concept of cobbles being more heavily disturbed than scallops. First, cobbles are repeatedly disturbed and likely re-settle in different configurations than before, thereby smothering any surviving epilithos on those surfaces. In contrast, some scallops do not escape or bury themselves but are injured e.g., evidence of "mud blisters" on the upper valves (Caddy 1968), however these can re-right themselves and clear sediments from their surfaces (Caddy 1968) where epizoites are attached. Second, a parallel comparative study of epilithic and epizoic *S. cupressina* demonstrated significantly more colony damage on cobbles than on scallops, as well as reduced sexual fecundity and genotypic diversity that might reflect colony fragmentation (Chapter Five). Third, differences in life history traits (discussed here in the next section) concur with the hypothesis that divergence could be produced by chronic and intense disturbances experienced by cobble epifauna. Fourth, assemblage divergence increased somewhat with fishing effort (Table 22), although contrasting levels of divergence in areas with no fishing with those from commercially fished areas might provide a more clear understanding of how fishing produces divergence instead of qualitatively aggregating data into imprecise categories that may be irrelevant to hydroids. Fifth, the high similarity of hydroid assemblages (Table 23, Fig. 12) between transplanted substrata suggests that these taxa may not exhibit strong preferences for cobbles or live scallop substrata. But the highly dynamic nature of shallow subtidal marine habitats to epizoic colonizers (Berkman 1994) may not enable these results to be extended to deeper water hydroid colonization

processes. Thus, although divergence could be related to microhabitat differences, host distribution, and occurrence of other epizoites, there is preliminary evidence to suggest that it could also be linked to post-settlement dredging disturbance. Substrate manipulations could be combined with experimental variations of bottom-fishing pressure to further test these ideas. Future settlement experiments should also be performed across a wider depth range to include more species with long lifespans and erect growth forms.

Differences in taxon richness

Intermediate levels of mechanical fishing disturbance and epifaunal patchiness are associated with both persistent and opportunistic taxa, and therefore high richness (Fraschetti et al. 2001), while epifaunal "desertification" (*sensu* Fanelli et al. 1994) is associated with increasing fishing disturbances (Callaway et al. 2002) as it is following substrate turnover disturbances during subtidal diamond fishing operations (Pulfrich et al. 2003). Thus, epizoic assemblages may be predicted to have higher richness because they experience less severe disturbances (Tanaka and Magalhães 2002) and because they inhabit a dynamic host that continually offers new space to recruiting taxa as the scallop grows (Berkman 1994). However despite statistical significance due to high degrees of freedom and therefore a high type I error rate, mean richness on cobbles and scallops did not appear to greatly differ, which could reflect the abundance and richness of hydroid taxa ubiquitously present in this region to colonize disturbed substrata.

Differences in taxon composition

All levels of taxonomic resolution discriminated two significantly distinct assemblages, but the greatest average dissimilarity between assemblages was produced using species-level information. It should be noted that although coarse taxonomic data can be used to indicate perturbation impacts, higher resolution data are required to fully understand species' responses to human activities (Lasiak 2003).

Epilithic hydroids were predominantly characterized by the campanulariids *Clytia hemisphaerica*, *Clytia* sp. and *Campanularia volubilis* and an erect bougainvilliid species. Colonies were usually patchily distributed over cobble surfaces, but the stolonal growth strategies of the campanulariids produced rather diffusely organized colonies within patches. Scallop shells hydroid assemblages were characterized by the presence of *Calycella syringa*, a minute stolonal annual species usually found on other hydroids (an "auto-epizoite" *sensu* Millard 1973). This species also characterized lighter fished areas in the Gulf of Maine, south of the Bay of Fundy (Pugh 1999). In the present study, *C. syringa* was almost exclusively found on the large arborescent hydroids *Sertularia cupressina* and *Obelia dichotoma* (pairwise similarity = 43.333 and 46.512 respectively), both of which also characterized scallop shell assemblages.

Calycella syringa was also the species that best discriminated between communities. The relatively lower frequency of erect arborescent hydroids on cobbles probably explains the virtual absence of *C. syringa* from these substrata except in rare instances when it occurred on dead sertulariid stems still attached to rock surfaces (L. Henry, personal observation). The close association between assemblage structure of

other marine organisms and their hydroid hosts (Bradshaw et al. 2003 in press) suggests that the relative absence of large, long lived and arborescent hydroids on cobbles could have consequences for the distribution of associated fauna.

Auto-epizoism itself may not be a phenomenon associated with relatively undisturbed benthic marine assemblages. Both *Campanularia volubilis* and *Halecium undulatum* can be auto-epizoic and yet were more frequent on cobbles than scallops in this study. At present the insufficient knowledge about the autoecology of these (and many) hydroid species prevents the formulation of a definitive explanation for these auto-epizoic associations. But the availability of older, dying or dead colonies may be critically important factors that affect the diversity and frequency of auto-epizoic hydroids as it does for epiphytes of trees in old growth undisturbed forests (Schulz and Wagner 2002).

The large arborescent species *Obelia dichotoma* also discriminated between assemblages. *Obelia dichotoma* has a relatively longer lifespan than other campanulariids that characterized epilithic assemblages. *Obelia dichotoma* exhibits wide substrate host generalism, and has been found attached to both inert and living substrata, both sessile and mobile including shark fins, turtles, sea horses and crustaceans (Cornelius 1995). Therefore it is unlikely that its predominance on scallop substrata reflected an affinity for scallop hosts over cobbles.

Differences in life histories

Further insight into assemblage divergence was gained by contrasting the life history strategies of taxa on cobbles versus live scallops. Taxa with relatively good recovery capacities mature early, have high fecundity and wide dispersal, and are

predicted to eventually dominate epifaunal assemblages in heavily fished areas (Pitcher et al. 2000). Post-fished assemblage structure therefore depends on life history traits of resident taxa and the timing of life history events that determine recovery potential (Van Dolah et al. 1987; Hutchings 1990; Jones 1992; Auster et al. 1996; Christie et al. 1998; Bergman and Van Santbrink 2000; McConnaughey et al. 2000; Bradshaw et al. 2001; Jennings et al. 2001; Kenchington et al. 2001; Bradshaw et al. 2002; Gordon et al. 2002).

Similarity between assemblages on scallop shells was largely explained by taxa with a wide range of life histories. This diversity in life history traits suggests that the shells of live scallops are sufficiently undisturbed so as to support large slow-growing erect hydroids and yet have enough resources (e.g., unoccupied space, food availability) to allow the colonization of more opportunistic taxa. Physically variable marine habitats tend to be dominated by opportunistic hydroids characterized by rapid recruitment, early resource exploitation and good recovery abilities following perturbations (Calder 1991). For example, opportunistic hydroids dominated commercially trawled fishing grounds on the Catalan shelf in northeast Spain (Gili et al. 1987). Similarly, small stolonal unbranched campanulariids with medusa stages discriminated cobble assemblages from those on scallops in the present study.

"Attribute syndromes" are positive associations between life history traits that characterize organisms found in certain habitats (Dupré and Diekman 2001). A particular trait in the syndrome may truly have evolutionarily adaptive value, but it may also be correlated to another trait that is adaptive, or it may simply be constrained by phylogeny. For example, allometric constraints imposed by colony architecture affect investment into

other life history aspects e.g., colony dimensions, shape and parental investment in young (Jackson 1979; Lasker and Sánchez 2002). The production of medusae versus sessile medusoids versus planulae may have little consequence for substrate colonization (Boero 1984; Bavestrello 1985), as the potential for wide dispersal is often not realized. Instead, the distribution of reproductive strategies on certain substrata probably reflects the correlation of this trait to other life history traits such as colony size and growth strategy (Cornelius 1990, 1991). Phylogeny may also constrain the distribution of life history traits. For example, it is thought that most sertulariids produce planula larvae (but see e.g., Migotto 1998 and Gravier-Bonnet and Lebon 2002) while *Obelia* spp. release free medusae. Substrata colonized by small fast-growing guerilla strategists may simply be populated by species that produce medusa because this reproductive strategy has evolved in those particular taxa. However attribute syndromes are still useful as they point to traits associated with habitat disturbance and could be used to assign "indicator" status to certain taxa.

Using live scallops as "pseudo-controls"

The lack of unfished reference areas necessitates finding alternative methods for examining biological impacts of bottom fishing e.g., conservative approaches using historical datasets (Frid et al. 1999, 2000; Rumohr and Kujawski 2000; Bradshaw et al. 2002) or using sites near shipwrecks that impede bottom fishing (Ball et al. 2000). Bivalves are relatively stable hard substrata to hydroids, which typically are one of the earliest taxa to colonize shells (Vance 1978). Thus, the results of this study may not extend to colonial epifauna with lifespans or biomass greater than the scallop. For example, mollusc shells are not "stable" substrata for scleractinian corals because mollusc

hosts cannot grow fast enough to support continual growth of the corals, and eventually topple under the weight of the corals (Yamamoto et al. 1998). This study demonstrated the ability for coarse taxonomic resolution to discriminate between hydroid communities between the two substrata: a rapid survey of hydroids at the family-level in areas not heavily impacted by dredging but inhabited by scallops e.g., boulder fields off Grand Manan in the Bay of Fundy, would help discern effects of microhabitat and host distribution on community structure. Following additional experimental studies that examine the effects of live scallop activities on associated epifauna, the use of live bivalves as "pseudo-controls" may be a novel way to include controls in studies that examine bottom fishing impacts in areas with no closed or relatively unfished areas.

CHAPTER FIVE: ECOLOGICAL AND GENETIC EVIDENCE FOR IMPAIRED SEXUAL REPRODUCTION AND INDUCED CLONALITY IN THE HYDROID *SERTULARIA CUPRESSINA* (CNIDARIA: HYDROZOA) ON COMMERCIAL SCALLOP GROUNDS IN ATLANTIC CANADA

INTRODUCTION

Global initiatives to study effects of bottom fishing on benthic marine ecosystems identified the critical need to examine impacts on colonial epifauna (Hutchings 1990; Collie et al. 2000), e.g., many species of sponges (considered here as "functionally" colonial), corals, zoanthids, hydroids, bryozoans and tunicates.

The sessile, often fragile and emergent nature of colonial body plans make colonial epifauna susceptible to damage by bottom fishing gear e.g., on continental shelves (Bradstock and Gordon 1983; Hutchings 1990; Auster et al. 1996; Bavestrello et al. 1997; Collie et al. 1997; Kaiser et al. 2000a; McConnaughey et al. 2000; Pitcher et al. 2000; Veale et al. 2000; Wassenberg et al. 2002; Burridge et al 2003; Kefalas et al. 2003) and in deep-water ecosystems (Jones 1992; Probert et al. 1997; Probert 1999; Koslow et al. 2001). Evidence for damage to colonial epifauna by fishing gear is becoming well documented. Colonies are often wounded, tipped over, fragmented and/or resuspended (Tilmant 1982; de Groot 1984; Van Dolah et al. 1987; Sainsbury et al. 1993; Van der Knapp 1993; Bavestrello et al. 1997; Freese et al. 1999; Koenig et al. 2000; Roberts et al. 2000; Fosså et al. 2002; Wassenberg et al. 2002; Kefalas 2003; Mortensen et al. 2003).

Such disturbances may alter the life histories of benthic species by inflicting injuries that disrupt growth and reproductive processes (Tilmant 1982; Jenkins et al.

2001). Life history responses of colonial epifauna to injuries sustained by human activities are relevant to examine since resource allocations to growth and reproduction affect recolonization abilities (Dayton et al. 2002) and long-term persistence (Forbes 2002) of these species. Injuries reduce colony fecundity as wounded colonies reallocate energetic and cellular resources from sexual reproduction to regenerate damaged areas (e.g., Kojis and Quinn 1985; Rinkevich and Loya 1987, 1989; Van Veghel and Bak 1994; Lirman 2000a). Long-term declines in colonial epifaunal populations can be related to factors that reduce recruitment (Cropper and DiResta 1999) such as reduced sexual fecundity (Hughes et al. 2000). The potential for injuries inflicted by bottom fishing gear to impair sexual reproduction in non-target benthic species has not been addressed. Strong evidence for a "trade-off" between regeneration and sexual reproduction in colonial animals suggests that colonial epifauna in heavily fished areas should exhibit reduced fecundity compared to those from areas with less fishing pressure.

Many colonial epifauna also naturally reproduce asexually ("clonally") through budding, fission or fragmentation processes that produce genetically identical but physically separate colonies (Jackson and Coates 1986). Capacity for asexual reproduction tends to be positively correlated with the adaptiveness of resource translocation between modules and regenerative powers (Needham 1952; Vorontsova and Liosner 1960; Jackson 1977; Buss 1979). Therefore the ability for colonial epifauna to exploit clonal reproduction could enhance colony survival following fragmentation induced by bottom fishing, but reduce genotypic (clonal) diversity. Very high disturbance levels further reduce clonal diversity by killing most colonies (Coffroth and Lasker 1998).

Effects of bottom fishing on the genetic diversity have not been examined for any non-target benthic organism. Reduced genetic biodiversity associated with the exploitation of clonal reproduction (Jackson 1986; Jackson and Coates 1986) and high mortality will likely impair the genetic health of marine populations (Robinson and Frid 2003).

The objective of this study was to examine whether commercial-scale scallop dredging in the Bay of Fundy region of Atlantic Canada has the potential to alter reproduction in the macrobenthic hydroid *Sertularia cupressina* (Fig. 13). This species is distinctly gonochoric and becomes sexually fertile between May and October in Atlantic Canada (personal observation). Fertilisation and initial planula larval development occurs internally in sessile gonophores. Development terminates in extracapsular acrocysts located adjacent to the gonophores. The free-living demersal planulae typically settle close to the parent (Schmidt and Warner 1991; Berghahn and Offermann 1999), and metamorphose into erect pinnate colonies up to 60 cm high that can persist for up to three years (Cornelius 1995). This species resembles the (probably) congeneric species *S. argentea*, which together with another sertulariid, *Hydrallmania falcata*, were historically fished as "white weed" in northern Europe (described in von Reitzenstein 1913) and sold as decorations in North American markets until the latter part of the nineteenth century (Hancock et al. 1956; Wagler and Berghahn 1992; Berghahn and Offermann 1999). The documented disappearance of once-extensive white weed fields (Riesen and Reise 1982; Buhs and Reise 1997) were related to increases in sedimentation and over-exploitation of oyster beds due to commercial dredging (Wagler and Berghahn 1992; Buhs and Reise 1997; Berghahn and Offermann 1999).

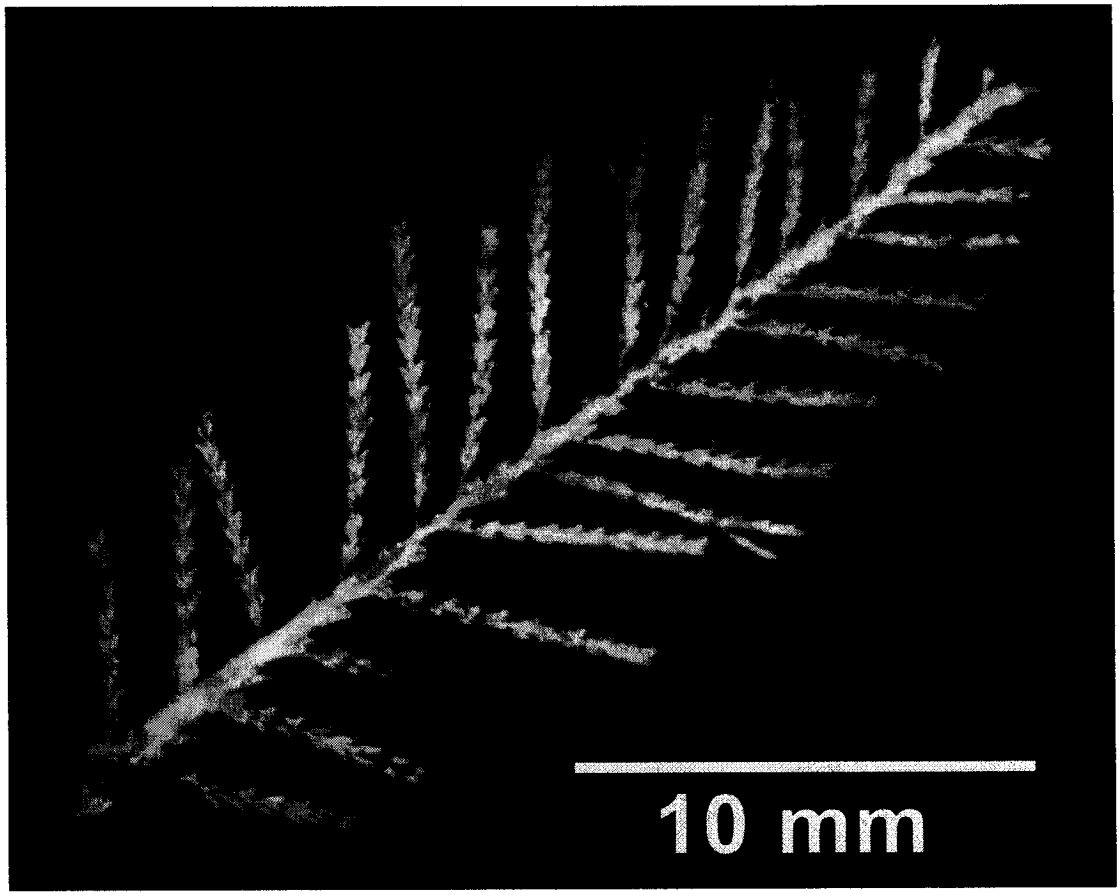

Fig. 13: A single colony "module" of the sertulariid hydroid *Sertularia cupressina* from the Bay of Fundy.

The role of asexual reproduction in the natural life history of *S. cupressina* is not known, but accidental fragmentation of hydroid colonies is possible (Boero et al. 2002). Impaired hydroid sexual reproduction and reduced clonal diversity could help explain the disappearance of historically luxuriant white weed beds.

As there are no areas permanently closed to fishing for the sea scallop *Placopecten magellanicus* in the Bay of Fundy, an alternative method to examine impacts of scallop dredging on hydroid sexual reproduction had to be considered. Living biogenic substrata may serve as "pseudo"-controls because they provide epifauna with small naturally replicated "island habitats" (Schoener 1974). Old-growth live scallops provide relatively unharmed "mini-island" refuges for epibenthos. Scallops in the Bay of Fundy are also naturally interspersed with cobbles that have been repeatedly rolled over, sorted through for scallops and dumped overboard (Caddy 1973, Robinson et al. 2001), processes that damage emergent fragile colonies. Scallops smaller than 95 mm in shell height avoid being caught by swimming away, while larger individuals are either fished out or temporarily bury and re-right themselves in bottom sediments to escape dredges (Caddy 1968). Thus, aspects of sexual and asexual reproduction in colonies of *Sertularia cupressina* on cobble substrata are expected to be altered relative to populations on the shells of live, large *P. magellanicus* scallops due to higher frequencies of injuries sustained by hydroids on cobbles during fishing. Effects of sub-lethal injuries and microhabitat differences (shells of live large scallops = "epizoic" versus the surfaces of cobbles = "epilithic") on sexual and asexual reproduction in *Sertularia cupressina* were tested using field transplantations of epizoic and epilithic colonies.

MATERIALS AND METHODS

Hydroid field collection

Sampling was performed on board the C.C.G.C. *J.L. Hart* in June 2001 during an annual inshore Bay of Fundy scallop survey with the Canadian Department of Fisheries and Oceans. Tows were made with four-gang dredge gear (described by Fuller et al. 1998) identical in construction to seven gang commercial gear in this region. Stations were located using a global positioning system. In total, 33 tows were made, each approximately 800 m long X 4 m wide (Fig. 14, Table 24). Altogether, 179 substrata (104 live scallops and 75 cobbles) with attached live *Sertularia cupressina* colonies (n = 1071 colonies overall) were randomly collected from depths of 53 - 94 m at water temperatures 5.6 - 9.7 °C. The naturally interspersed distribution of live scallops and cobbles permitted both substrata to be collected simultaneously in most cases. Samples were placed in Ziploc™ bags and kept in an open tank with a steady supply of seawater while on board, and preserved in 95 % ethanol upon return to the laboratory.

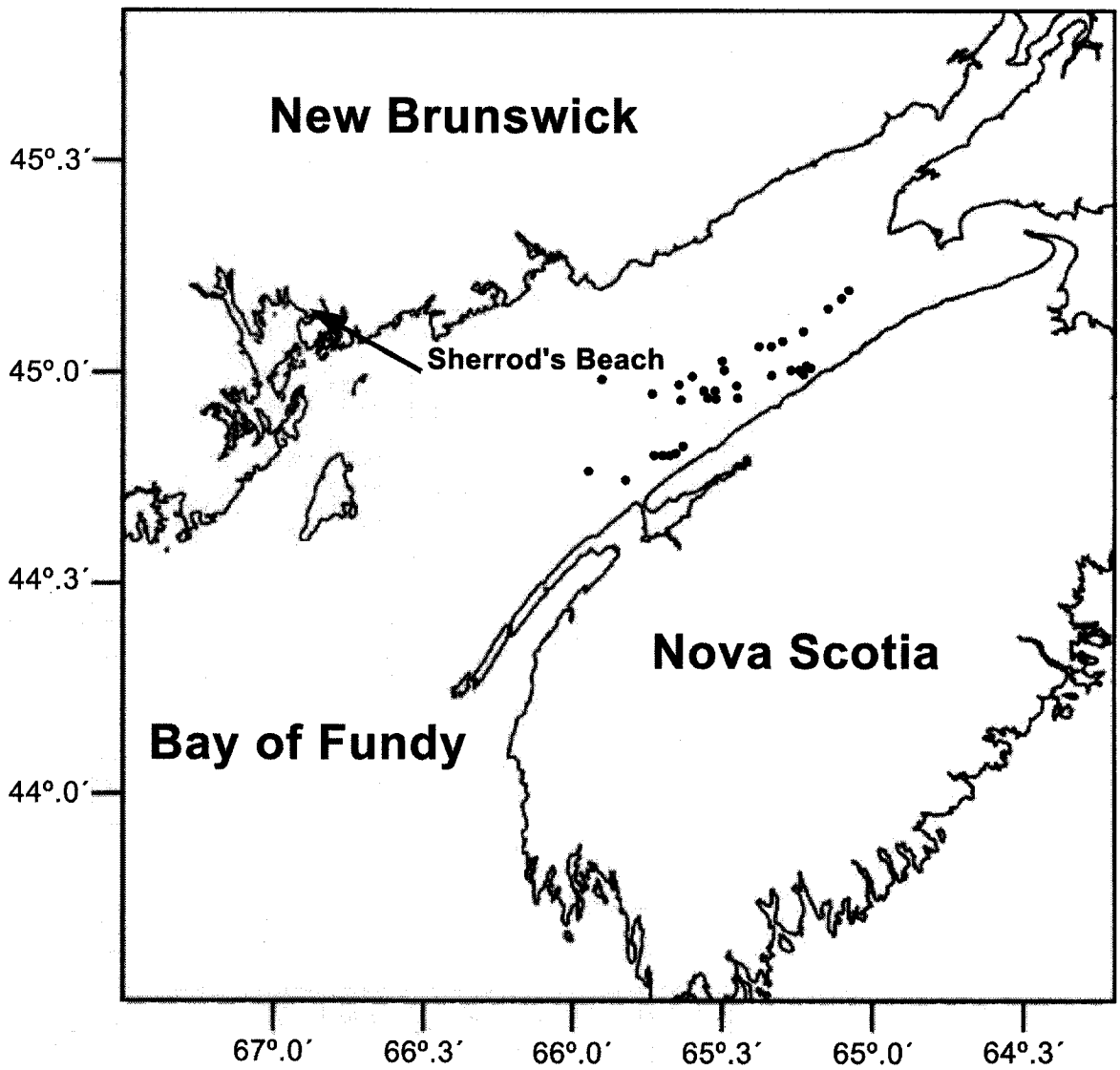

Fig. 14: Locations of 33 survey sites for epizoic and epilithic hydroids in the Bay of Fundy in June 2001. Each point represents one 800 m long scallop tow where 75 cobbles and 104 live scallops were collected. The field experiment site (Sherrod's Beach) is also indicated on map.

Table 24: Characteristics of the 33 sites in the Bay of Fundy where epilithic and epizoic colonies of *Sertularia cupressina* were sampled in June 2001 (na = no data available).

Tow #	Latitude (N)	Longitude (W)	Depth (m)	Cobbles sampled	Scallops sampled	Fishing effort (hours dredged from June 1998 to June 2001)
41	44°57′.45	65°56′.08	93	0	1	38
63	44°55′.21	65°43′.39	94	1	0	34
91	44°59′.39	65°39′.62	86	0	3	94
93	44°56′.71	65°45′.88	75	1	2	70
123	45°01′.62	65°33′.03	82	1	2	5
125	45°04′.36	65°32′.65	85	2	2	141
179	44°52′.13	65°43′.80	86	3	0	126
181	44°56′.93	65°35′.19	77	4	7	30
182	44°55′.59	65°34′.25	76	2	0	28
183	44°55′.21	65°31′.56	76	5	6	78
184	44°53′.77	65°29′.03	75	1	4	10
190	44°51′.10	65°42′.45	84	4	0	79
202	44°44′.52	65°49′.70	65	5	2	0
210	44°41′.36	65°58′.33	78	1	4	0
214	44°59′.62	65°25′.96	73	3	2	22
219	45°02′.82	65°21′.53	74	6	0	0
220	45°03′.03	65°19′.48	77	1	4	0
222	45°04′.01	65°16′.86	72	3	7	0
236	45°14′.55	65°10′.10	60	1	2	12
237	45°13′.95	65°11′.36	65	2	5	61
239	45°11′.16	65°17′.00	53	1	0	28
244	44°46′.79	65°47′.15	66	2	3	0
276	44°50′.24	65°42′.92	81	5	5	0
277	44°50′.66	65°41′.36	80	5	4	0
279	44°50′.76	65°40′.67	82	5	4	0
280	44°53′.63	65°39′.85	77	3	3	0
284	45°01′.54	65°17′.87	66	0	4	55
285	45°00′.47	65°16′.64	65	0	5	0
287	44°59′.32	65°19′.16	63	0	3	9
288	44°59′.03	65°20′.44	64	0	8	0
293	45°00′.04	65°15′.52	60	1	0	0
296	44°57′.26	65°21′.73	58	5	5	0
299	44°52′.61	65°37′.15	80	2	7	0

Laboratory analyses of hydroid fertility, fecundity and injury

Colony abundance, maximum colony height and injury frequency (evidence of broken hydrocauli with sealed, snapped off stems indicating past damage unrelated to the scientific survey e.g., Fig. 15) of all colonies on the 179 substrata were measured under a Nikon SMZ 1500 dissecting microscope. Fertility was estimated as the percentage of sexually fertile colonies on each substrate.

Another aspect of sexual reproduction, fecundity, was measured at the module-level (i.e., the level of an individual upright hydrocaulus stem that is repeated in the colony) two ways. One module was randomly selecting from each colony and two parameters were digitally measured: (1) the number of full intact gonophores per module (either gravid with gonads or larvae) and (2) the maximum length and width of one randomly selected gonophore (Fig. 16). Maximum colony height and the number of full intact gonophores were not highly correlated (Pearson correlation $\rho = 0.422$, Fig. 17), therefore differences between substrata on a standardized fecundity estimate i.e., number of gonophores (number of gonophores / millimetre of stem height, were not examined. Measurements were made using a Nikon SMZ 1500 dissecting microscope and *Optimas* v 6.1 digital imaging software from which mean values were calculated. The overall average of each module-level fecundity estimate was calculated per substrate to remove any potentially confounding effects of non-independence between colonies on the same substrate.

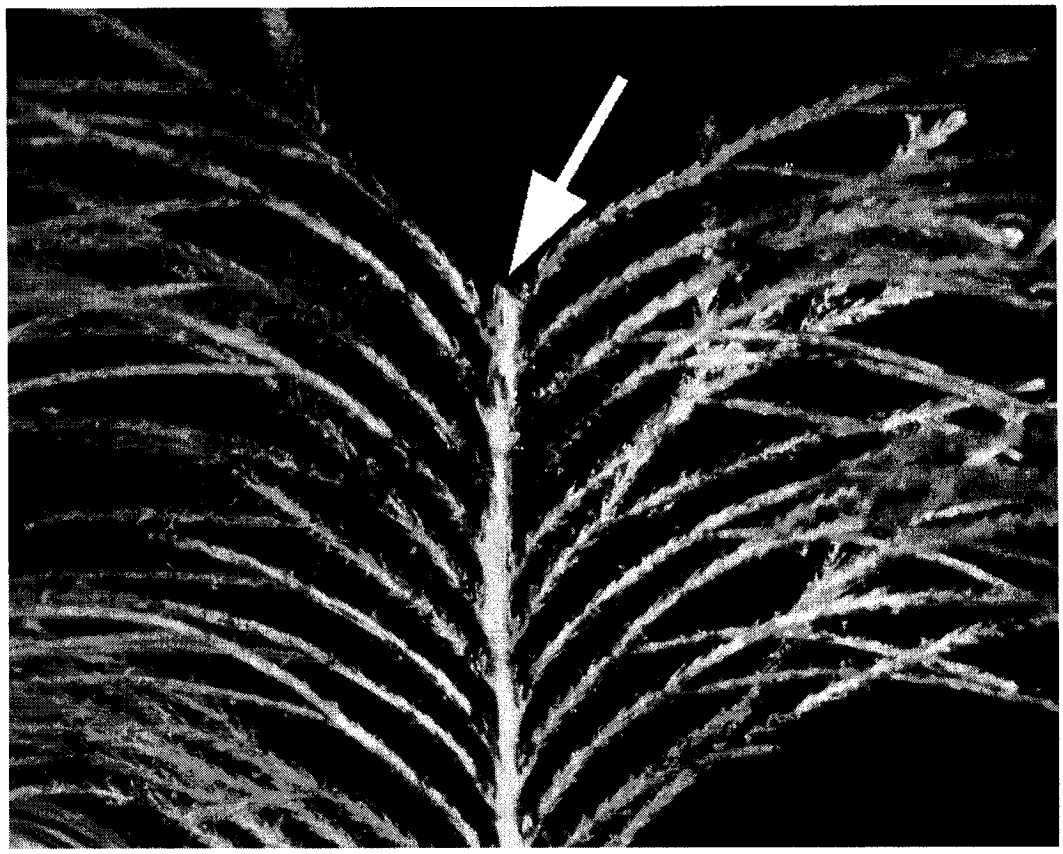

Fig. 15: Evidence for past damage to *Sertularia cupressina* caused by scallop dredging indicated by arrow. The distal portion of the stems (the "hydrocaulus", singular) of *S. cupressina* are often snapped off and sealed at the end, indicating that the injury did not happen during the field sampling programme.

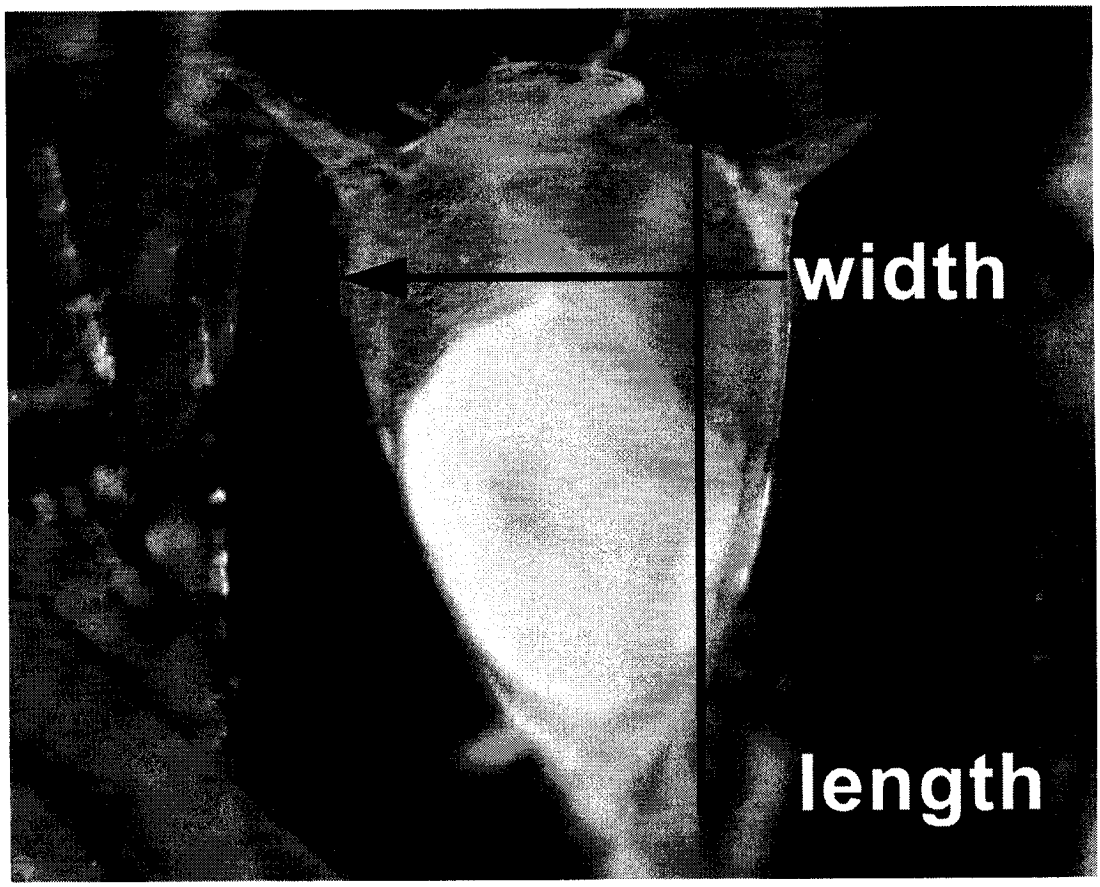

Fig. 16: Digital estimation of gonophore dimensions in *Sertularia cupressina*. Maximum length and width of a module gonophore was measured under a dissecting microscope using *Optimas* v 6.1 imaging software.

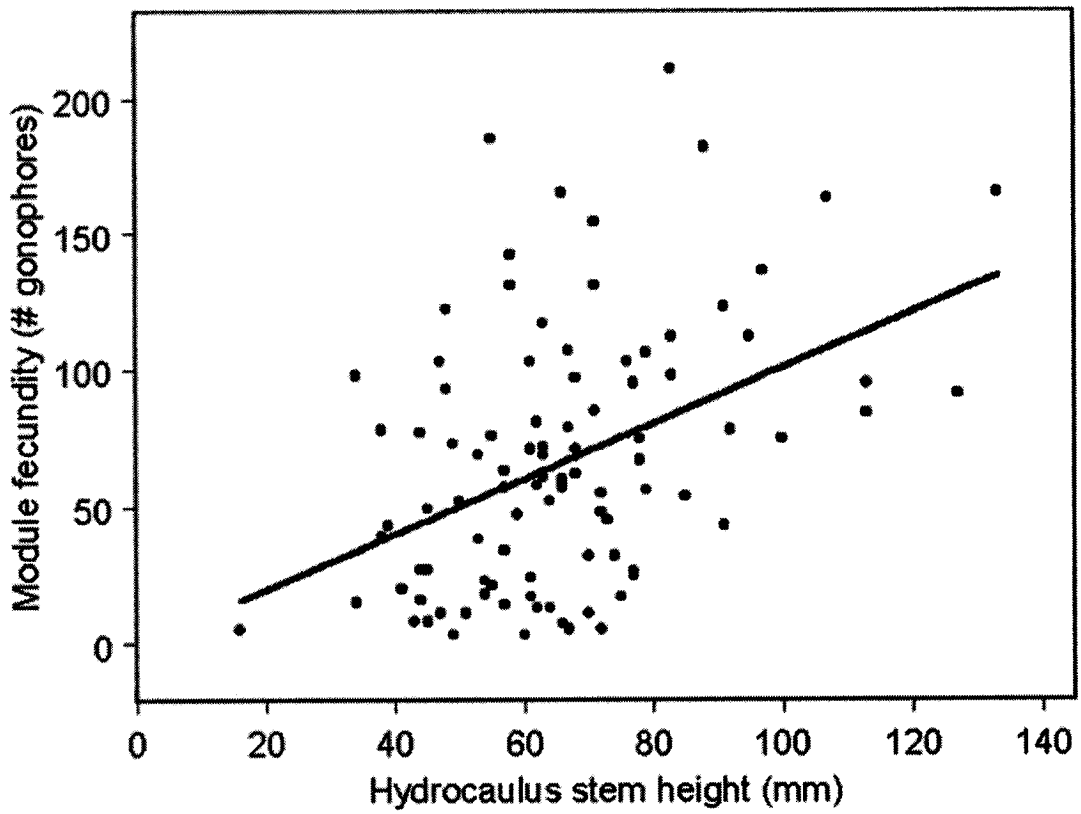

Fig. 17: Correlation between gonophore fecundity and hydrocaulus height in *Sertularia cupressina*. The Pearson correlation coefficient (ρ = 0.422) between the number of gonophores and module size did not justified estimating a "standardized fecundity" measure.

Statistical analyses

Three sets of analyses were performed to examine statistical differences in parameters: (1) between substrata, (2) across substrata covarying with fishing effort categories assigned *a priori* and (3) within epilithic substrata between categories of fishing effort.

The first set involved a series of one-tailed unpaired t-tests and G-tests (Sokal and Rohlf 1995) to test the hypotheses that mean hydroid abundance, percent fertility, number of gonophores and gonophore dimensions would be higher on scallops than on cobbles, and that injury frequency would be higher on cobbles than on scallops.

The second set involved a series of post-hoc two-way analyses of variances (ANOVAs) to test the hypotheses that mean abundance, percent fertility and injury frequency would be significantly affected by the interaction between substrate and fishing effort at a statistical significance level of $\alpha = 0.05$. Logged scallop fishing effort data aggregated across minutes in the Bay of Fundy from June 1998 to June 2001 were obtained from the Maritime Science Virtual Data Centre (2003). Effort ranged from 0 – 141 hours of dredging per square minute of area (Table 24). Data were used to create two categories of fishing effort: low effort (0 – 50 hours) and high effort (> 50 hours).

The third set involved a series of G-tests to test the hypothesis that colonies on cobbles would be more frequently damaged and less often sexually fertile in areas of high fishing effort, and later, that they would be more clonal than on scallops (see next section).

Genetic analyses of asexual reproduction

Clonal diversity of epizoic and epilithic colonies was assessed using randomly amplified polymorphic DNA (RAPD) markers amplified by polymerase chain reactions (PCR). This is a relatively inexpensive genetic method that does not require any previous knowledge of nucleotide sequences. RAPD-PCR techniques can rapidly produce hundreds of markers that tend to be inherited as dominant neutral Mendelian alleles (Grosberg et al. 1996a), and can yield much information about hydroid population structure (Hart and Grosberg 1999).

DNA salt-extraction protocol

A 20 mm portion of hydrocaulus was removed from each colony, snipped into fragments with sterilized scissors and cleaned in 2 mL of TE (10 mM Tris-ethylenediamine tetraacetic acid, 1.0 mM EDTA, pH 7.4) for 30 minutes. The sample was transferred to a 1.5 mL microtube containing 600 µL of lysis buffer (10mM Tris, 100mM EDTA, 400mM NaCl, pH 8.0), 24 µL of SDS (10 % w / v sodium dodecyl sulfate solution) and 20 µL proteinase K solution (1 µg / µL), and incubated in a water bath at 55°C for 12 hours. The sample was centrifuged in a Centronix Microcentrifuge 1236V machine (Montreal Biotech Inc.) at 14000 rpm for 60 seconds, and the aqueous portion was pipetted into 250 µL saturated NaCl solution. The sample was gently mixed using a Fisher Vortex Genie 2® vortexer (Fisher Scientific) for three minutes, centrifuged at 14000 rpm for ten minutes, and the solution was carefully pipetted and transferred into 400 µL of chloroform. This mixture was then gently mixed for three minutes, centrifuged at 14000 rpm for ten minutes, and the upper aqueous layer carefully transferred to an

equal volume of isopropanol and frozen at -72 °C for three hours. The DNA was centrifuged at 14000 rpm for 30 minutes, after which time the alcohol was pipetted off and the DNA pellet was washed three times with 70% ethanol and centrifuged again at 14000 rpm for 30 minutes. The ethanol was pipetted off and the microtube containing the DNA was air dried for approximately ten minutes. The DNA was resuspended in TE, and 2 µL of RNase A (10mg/mL) was added and left for 12 hours. The DNA was cleaned with a QIAquick PCR purification kit (Qiagen Inc.) and resuspended in the supplied ethanol buffer.

RAPD-PCR protocol

A RAPD-PCR protocol described in Edwards (1998) was slightly modified to initially test the suitability of this method to amplify DNA extracted from twelve test colonies of *Sertularia cupressina*. The PCR mixture included 14.3 µL of distilled water, 1 µL 10 X PCR buffer with $(NH_4)_2SO_4$ (MBI Fermentas), 1.5 µL $MgCl_2$ (25mM/mL), 2 µL dNTP (0.2 mM each dNTP), 0.2 µL *Taq* DNA polymerase (5 units / µL), 1 µL of primer and 1 µL of genomic DNA for a total reaction volume of 21 µL, which was overlayed by 21 µL of mineral oil. PCR steps were performed in a PTC-100™ (Programmable Thermocycler Controller) machine (MJ Research, Inc.). The initial denaturation was performed at 95 °C for two minutes and followed by 47 cycles of denaturation at 95 °C for 20 seconds, primer annealing at 37 °C for 60 seconds and extension at 72 °C for 60 seconds. The last extension was prolonged by ten minutes, and incubated at 4 °C indefinitely. PCR products were run adjacent to a GeneRuler™ 100 DNA ladder plus (MBI Fermentas) on 1.5 % agarose gels in 1 X TAE (Tris-acetate EDTA) buffer at 90 V

for three hours, stained for 20 minutes in ethidium bromide and destained in distilled water for ten minutes. Bands were photographed under ultraviolet light using a BIO-RAD Gel Doc 1000 system (Bio-Rad Laboratories, Canada, Ltd.). All visible bands were scored by hand in Molecular Analyst™ (Bio-Rad Laboratories, Canada, Ltd.). Fifty primers from the University of British Columbia (UBC) were initially screened for polymorphisms between the 12 colonies, but only the ten most polymorphic primers were selected and used in subsequent genetic analyses of clonal diversity of hydroids on 34 epizoic and 37 epilithic substrata subsampled from the above 179 substrata (n = 414 colonies overall).

Band reproducibility

The fidelity ("reproducibility") of RAPD bands varies due to polymorphisms that arise from molecular protocol artefacts (Grosberg et al. 1996a), and was examined in the present study by genotyping two different parts of each of the 12 colonies across all ten primers used in preliminary RAPD screening protocol as described above. Mean band reproducibility was estimated for each primer as the mean of $R_b = 2b_{12} / (b_1 + b_2)$ (modified from Pérez et al. 1998) where b_{12} = number of bands amplified by a primer that appear in both replicates, b_1 = number of bands in the first replicate and b_2 = number of bands in the second replicate, averaged over all 12 colonies (R_b = 1.00 for a completely reproducible banding pattern).

Estimates of clonal diversity

Clonal diversity was estimated as the ratio between the number of genotypes distinguished by RAPD-PCR (N_C) and the sample size (N). Clonal diversity equals one when colonies were established strictly by sexual reproduction, and approaches zero when most colonies are represented by only one clone (Ellstrand and Roose 1987). The potential for scallop dredging to alter asexual reproduction was evaluated by comparing the statistical significance of differences in mean clonal diversity between substrata using a one-tailed unpaired t-tests at $\alpha = 0.05$.

Field study of the role of microhabitat differences versus injuries

Post hoc short-term field experiments were performed to investigate mechanisms for suppressed sexual reproduction and reduced clonal diversity of hydroids on cobble substrates to determine: (1) if differences in sexual and asexual reproduction naturally occur between live scallop and cobble substrata in the absence of dredging disturbances, and (2) if injury results in suppression of sexual reproduction and clonal propagation in damaged colonies.

Fresh colonies were collected between 50 - 80 m depth near Digby in June 2002 during the inshore DFO scallop survey. Ten live scallops and 30 cobbles colonized by sexually immature colonies of *Sertularia cupressina* were obtained and kept in running seawater until transportation to the laboratory less than a week later. Colony abundance was standardized by removing all but three colonies of *S. cupressina* (each approximately 40 mm high) and all other visible epibenthos per substrate.

Effects of microhabitat differences on sexual and asexual reproduction were examined using the 10 scallops and randomly selecting 10 cobbles. Square plastic tabs with circular holes punched through them were epoxied onto the auricle of each live scallop to individually tether the live animal to a building brick by 30 cm long string run through the tag. Effects of injuries on sexual reproduction were examined using the remaining 20 cobbles sampled earlier.

All 40 substrata were marked with red acrylic paint to identify upper surfaces and transported to the experimental site at Sherrod's Beach (Fig. 14), a sheltered cove in Passamaquoddy Bay, southwestern New Brunswick in July 2002. Substrata were deployed at two metres depth below mean low water by snorkelling parallel to a straight stretch of beach at low tide (depth approximately 10 metres at high tide in this area). Each experiment was run in its own lane parallel to the other experiment, but separated by about 2 metres. Substrata were randomly interspersed by drawing them from a mesh dive bag and placing them at approximately one metre intervals.

Experimental injuries were inflicted *in situ* to ten cobbles randomly selected selected in the lane designated for the injury experiment by excising the distal most 5 mm of one hydrocaulus stem using scissors: the remaining ten cobbles in that lane served as controls. Substrata were checked approximately every three weeks for substrate turnover until September 2002, at which point they were retrieved and placed in individual Ziploc™ bags and transported to the laboratory.

Measures of fertility and fecundity were estimated as in the field survey, and the extent of clonal reproduction was assessed by comparing the number of distinct colonies

at the end of the field experiment. Substrate- and module-level parameters were compared between treatments using a χ^2-test and a one-tailed unpaired t-test respectively at a significance level of $\alpha = 0.05$.

RESULTS

Substrate-level analyses

Hydroid abundance

Colony abundance of *Sertularia cupressina* ranged in abundance from one to 13 colonies per substrate, and was significantly larger on scallops ($P < 0.001$, Table 25). Substrate significantly affected abundance, but this effect did not seem to significantly depend on the interaction between fishing effort category and substrate according to the two-way ANOVA ($F = 0.395$, $df = 1$, $P = 0.531$).

Injury frequency

Overall incidence of damage to hydroids was generally low (Table 25), but in a few cases up to 100 % of colonies on cobbles were injured. Injury frequency of *Sertularia cupressina* on cobbles was significantly higher than that on scallops ($P < 0.05$, Table 25), and was affected by both substrate ($F = 73.381$, $df = 1$, $P < 0.001$) and the interaction between substrate and the covariate fishing effort category ($F = 4.458$, $df = 1$, $P = 0.036$) in the two-way ANOVA. Injury frequency on cobbles was also significantly higher in areas of high versus low fishing effort ($P < 0.05$, Fig. 18).

Fertility

No colonies below 27 mm were observed to be sexually fertile. The number of fertile colonies on a substrate ranged from 0 to 100 %. Significantly fewer epilithic

colonies were sexually fertile colonies than those on scallops ($P < 0.05$, Table 25). Fertility was also significantly affected by substrate ($F = 10.109$, $df = 1$, $P = 0.002$), but not by the interaction between substrate and the covariate fishing effort category ($F = 1.807$, $df = 1$, $P = 0.181$) according to the two-way ANOVA. Reductions in the frequency of sexually fertile colonies on cobbles in areas with high fishing effort were not statistically significant ($P > 0.05$, Fig. 18).

Clonal diversity

In total, 212 polymorphic bands were scored from 414 hydroid colonies (Table 26). Clonal diversity ranged from 0.2 to 1: epilithic colonies exhibited significantly lower clonal diversity than on epizoic substrata (Table 25), the latter which were more frequently comprised of sexually derived colonies ($P < 0.001$, Table 26, 27). Most primers demonstrated good reproducibility, ranging from 80 –100 % repeatability (Table 26). Thus, protocol artifacts would have had to have occurred fairly consistently on hydroids genotyped only on cobbles in order to observe higher clonality on this substrate. Colonies on cobbles also showed a significantly higher degree of clonality in areas of high versus low fishing effort ($P < 0.05$, Fig. 18).

Module-level analyses

Module fecundity varied between 0 and 211 gonophores per hydrocaulus stem. Gonophore dimensions exhibited some variability: maximum length (from aperature to attachment point on colony) ranged from 638.9 to 1429.4 μm, and width (excluding spines) ranged from 324.1 to 791.9 μm. No measure of module-level fecundity differed significantly between substrata ($P \geq 0.395$, Table 25).

Table 25: Statistical differences in mean abundance, fertility, injury frequency and sexual fecundity between epilithic and epizoic colonies of *Sertularia cupressina* surveyed in June 2001. Standard deviations (sd) also given. Statistical significance at P = 0.05 indicated by an asterisk (*), significance of G-statistic evaluated at chi-squared of $\chi^2_{0.5,1}$.

Parameter	Mean on cobbles ± sd	Mean on scallops ± sd	Statistic	df	P
Substrate-level					
Colony abundance*	4.7 ± 1.8	7.0 ± 1.9	t = - 8.101	77	< 0.05
% Injured*	22.9 ± 26.5	0.7 ± 3.1	G = 57.27	1	< 0.05
% Fertile*	4.4 ± 12.0	10.6 ± 15.5	G = 4.410	1	< 0.05
Clonal diversity *	0.8 ± 0.3	1.0 ± 0	t = - 4.849	36	< 0.05
Module-level					
Number of gonophores	47.9 ± 39.9	63.2 ± 40.3	t = - 0.754	50	0.454
Gonophore length (μm)	1154.8 ± 96.2	1113.2 ± 169.5	t = 0.745	50	0.460
Gonophore width (μm)	613.9 ± 103.4	583.1 ± 101.5	t = 0.859	50	0.395

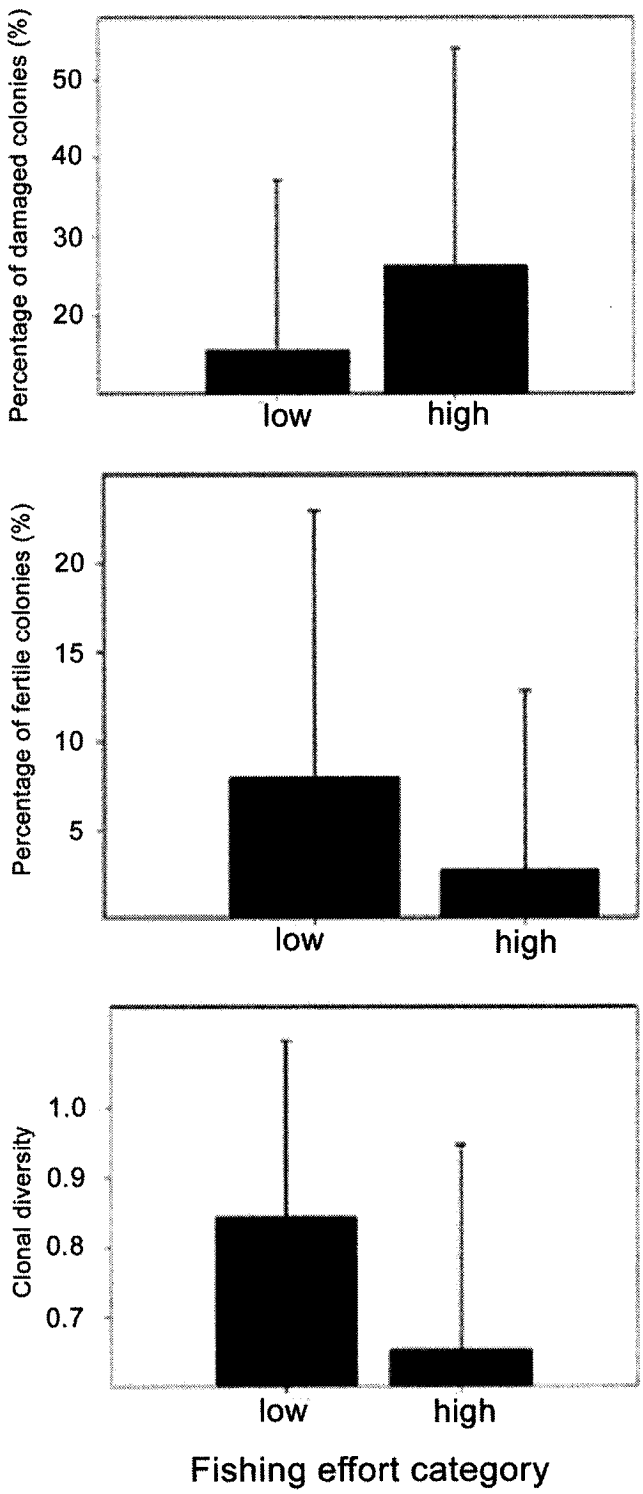

Fig. 18: Effect of scallop dredging effort (low = 0 – 50 hours, high = > 50 hours over the last three years) on injury frequency ($G = 5.049$, $df = 1$, $P < 0.05$), percentage of fertile colonies ($G = 1.505$, $df = 1$, $P > 0.05$) and clonal diversity ($G = 5.402$, $df = 1$, $P < 0.05$) of *Sertularia cupressina* colonies on cobble substrata in the Bay of Fundy. Vertical bars represent the standard deviations of the means.

Table 26: Characteristics of bands amplified by RAPD-PCR primers used to examine clonal diversity of *Sertularia cupressina*. Band size (number of base pairs) was estimated visually by alignment with GeneRuler™ 100 DNA ladder plus (MBI Fermentas). Mean reproducibility R_b of each banding pattern (formula in text) estimated from two replicates from each of 12 colonies is also given for each primer.

Primer nucleotide sequence (5′ - 3′)	Band size (bp)	Frequency of polymorphic bands	Number of polymorphic bands	Number of bands scored / colony	Mean R_b
UBC 472 AGGCGTGCAA	100 - 3000	0.010 - 0.412	24	1 - 8	1.00
UBC 474 AGGCGGGAAC	200 - 3000	0.065 - 0.565	24	1 - 12	0.82
UBC 475 CCAGCGTATT	100 - 3000	0.016 - 0.492	22	1 - 7	0.89
UBC 476 TTGAGGCCCT	100 - 2000	0.016 - 0.516	21	1 - 6	0.89
UBC 477 TGTTGTGCCC	150 - 2000	0.020 - 0.392	20	1 - 5	1.00
UBC 478 CGAGCTGGTC	100 - 3000	0.026 - 0.718	25	1 - 9	0.80
UBC 479 CTCATACGCG	150 - 1750	0.030 - 0.478	17	2 - 6	1.00
UBC 483 GCACTAAGAC	200 - 2000	0.018 - 0.309	19	1 - 5	1.00
UBC 486 CCAGCATCAG	200 - 3000	0.019 - 0.472	21	1 - 8	0.92
UBC 487 GTGGCTAGGT	200 - 3000	0.021 - 0.646	19	1 - 7	0.92

Table 27: Differences in clonal diversity between epilithic and epizoic populations of *Sertularia cupressina* assessed with RAPD-PCR.

Cobble ID	N_C / N	Scallop ID	N_C / N
125R1	4 / 6 = 0.67	91S2	4 / 4 = 1.00
125R2	3 / 3 = 1.00	91S3	7 / 7 = 1.00
179R1	1 / 3 = 0.33	125S1	4 / 4 = 1.00
179R2	1 / 5 = 0.20	125S2	2 / 2 = 1.00
179R3	4 / 4 = 1.00	181S4	3 / 3 = 1.00
181R4	4 / 5 = 0.80	183S4	3 / 3 = 1.00
182R2	3 / 5 = 0.60	183S6	7 / 7 = 1.00
183R1	3 / 3 = 1.00	190S1	2 / 2 = 1.00
183R2	3 / 4 = 0.75	190S2	3 / 3 = 1.00
183R3	1 / 4 = 0.25	190S3	2 / 2 = 1.00
190R1	3 / 4 = 0.75	210S1	3 / 3 = 1.00
190R2	2 / 4 = 0.50	210S2	4 / 4 = 1.00
190R3	1 / 2 = 0.50	210S4	6 / 6 = 1.00
190R4	7 / 8 = 0.88	220S1	4 / 4 = 1.00
219R1	4 / 5 = 0.80	220S2	4 / 4 = 1.00
219R2	7 / 7 = 1.00	220S4	3 / 3 = 1.00
219R3	5 / 5 = 1.00	222S4	3 / 3 = 1.00
219R4	1 / 5 = 0.20	222S5	5 / 5 = 1.00
219R5	6 / 6 = 1.00	222S6	5 / 5 = 1.00
219R6	2 / 2 = 1.00	222S7	5 / 5 = 1.00
220R1	1 / 3 = 0.33	236S1	5 / 5 = 1.00
222R1	2 / 2 = 1.00	236S2	2 / 2 = 1.00
222R2	3 / 3 = 1.00	244S1	3 / 3 = 1.00
222R3	1 / 3 = 0.33	244S2	5 / 5 = 1.00
236R1	2 / 4 = 0.50	244S3	4 / 4 = 1.00
244R1	4 / 5 = 0.80	280S1	5 / 5 = 1.00
244R2	4 / 4 = 1.00	280S2	7 / 7 = 1.00
276R3	3 / 3 = 1.00	285S1	3 / 3 = 1.00
276R5	7 / 7 = 1.00	285S2	4 / 4 = 1.00
277R1	8 / 8 = 1.00	285S3	6 / 6 = 1.00
277R2	4 / 4 = 1.00	285S4	6 / 6 = 1.00
277R4	3 / 3 = 1.00	288S7	3 / 3 = 1.00
277R5	2 / 2 = 1.00	288S8	5 / 5 = 1.00
279R1	5 / 5 = 1.00	299S2	8 / 8 = 1.00
279R2	5 / 7 = 0.71		
279R4	3 / 3 = 1.00		
296R5	4 / 4 = 1.00		

Effect of microhabitat differences versus injuries

Over half of the transplanted substrata possessed colonies that became sexually fertile during the field study: 5 / 10 on epilithic substrata, and 6 / 9 on epizoic substrata (one scallop broke free after three weeks and could not be relocated). Percentage of sexually fertile colonies on a substrate ranged from 0 to 66.7 %. Module fecundity ranged from 0 to 20 gonophores per hydrocaulus. Gonophore dimensions varied from 925.4 to 1339.5 μm in length, and 490.4 to 714.7 μm in width. Substrate- and module-level parameters were not statistically different between treatments (all $P > 0.05$, Table 28). Clonal diversity did not change during the field study as colony abundance did not change from three.

Injured colonies regenerated distal tips relatively rapidly: a new distal white bud was observed at the wound site after the first three weeks, and had already regenerated the excised 5 mm portion of hydrocaulus stem. New feeding polyps had emerged from the wounded tip after nine weeks. None of the injured colonies became fertile during the field experiment, in contrast to 6 / 10 epizoic substrates bearing sexual mature colonies. Substrate-level fecundity ranged from 0 to 66.7 %. Module-level fecundity varied from 0 to 24 gonophores. Gonophore dimensions ranged from 985.5 to 1329.5 μm in length, and 390.9 to 720.5 μm in width. Differences in percent fertility and module-level fecundity between treatments were statistically significant ($P < 0.05$ and $P = 0.013$ respectively, Table 29). Clonal diversity did not change during the field study as colony abundance did not change from three (Table 29).

Table 28: Effects of microhabitat differences on fecundity of transplanted colonies of *Sertularia cupressina* (na = not applicable). Standard deviations (sd) also given.

Parameter	Mean on cobbles ± sd	Mean on scallops ± sd	Statistic	df	P
Substrate-level					
% Fertile	23.1 ± 27.7	36.7 ± 30.6	G = 0.854	1	> 0.05
Clonal diversity	1.0 ± 0	1.0 ± 0	na	na	na
Module-level					
Number of gonophores	2.5 ± 3.0	3.8 ± 3.2	t = 0.905	17	0.378
Gonophore length (μm)	1138.1 ± 63.5	1119.2 ± 91.9	t = 0.388	8	0.708
Gonophore width (μm)	605.5 ± 54.9	607.8 ± 46.9	t = 0.072	8	0.945

Table 29: Differences between percentage of fertile colonies and sexual fecundity of transplanted injured versus control colonies of *Sertularia cupressina* (na = not applicable). Statistical significance at P = 0.05 indicated by an asterisk (*), significance of chi-squared (χ^2) statistic evaluated at $\chi^2_{0.5,\,1.}$

Parameter	Mean on injured colonies ± sd	Mean on control colonies ± sd	Statistic	df	P
Substrate-level					
% Fecundity *	0 ± 0	29.7 ± 28.9	$X^2 = 4.225$	1	< 0.05
Clonal diversity	1.0 ± 0	1.0 ± 0	na	na	na
Module-level					
Fecundity*	0 ± 0	3.3 ± 3.8	t = 2.768	18	0.013
Gonophore length (µm)	na	1149.9 ± 125.8	na	na	na
Gonophore width (µm)	na	567.1 ± 103.9	na	na	na

DISCUSSION

Increased siltation and reduction of substrate availability from over-exploitation of oyster beds in the Wadden Sea likely prevented dense aggregations of *Sertularia cupressina* from persisting because of reduced successful larval settlement and metamorphosis (Buhs and Reise 1997; Berghahn and Offermann 1999). The present study offers alternative (but not mutually exclusive) theories on the disappearance of white weed beds. Colonies may have been induced to clone and regenerate from injuries that subsequently reduced fecundity and genetic diversity, preventing populations from adapting to changing environments.

The high levels of sub-lethal damage to *Sertularia cupressina* observed in the present study (Table 25) likely reflect wounding by scallop dredging and are associated with reduced sexual fecundity and increased clonality of epilithic populations (Tables 25 and 29, Fig. 18). Evidence for divergence in taxon composition seen between epizoic and epilithic hydroid assemblages (Chapter Four) combined with the association between high fishing effort and life history responses in the present study suggests that some species of hydroids, notably *S. cupressina*, are highly susceptible to the effects of scallop dredging in Atlantic Canada.

The susceptibility of *Sertularia cupressina* to injuries by dredging is related to its emergent and arborescent colony form. Regeneration from wounds probably plays a critical role in epifaunal community recovery from fishing disturbances (Bradshaw et al. 2001). Damage to *S. cupressina* may be offset by the rapid regeneration of broken hydrocauli (Schmidt and Warner 1991) as seen in *S. argentea* (Hancock et al. 1956). But

since regeneration and sexual reproduction in colonial hydroids share the same resources e.g., energy, stem cells (Tardent 1963; Nieuwkoop and Sutasurya 1981; Tardent 1985), it is likely that resource consumption during repair and restorative processes suppresses sexual reproduction in these animals as it does in other colonial epifauna (Rinkevich 1996).

Attributing differences in hydroid reproduction between substrata to dredge-inflicted injuries is confounded by potential effects of microhabitat features that could differ between live scallops and cobbles. Sexual reproduction in hydroids is positively associated with food availability (Paffenhöfer 1968; Burykin 1984; Coma et al. 1998) that may be enhanced by living on a filter-feeding host. Asexual reproduction of autonomous propagules (e.g., stolons, frustules) in hydroids can be induced by water currents (Bavestrello et al., 2000b) or under environmentally stressful conditions e.g., starvation (Gravier-Bonnet 1992), smothering (Jarms and Tiemann 1996), high temperatures (Rungger 1969) or death of the epibiotic host (Hirai 1960). Cloning in hydroids is thought to favour the dispersal of the genet to new habitats (Gravier-Bonnet 1992; Cerrano et al. 1997, 1998; Bavestrello et al. 2000b) and extend the lifespan of the clone beyond that of the hydroid colony (Coma et al. 1992).

But the low frequency of sexually fertile *Sertularia cupressina* colonies on cobbles (Table 25) and the reduction in fertility following experimental wounding (Table 29) supports the idea of injury-related suppression of sexual reproduction in favour of vital life-saving regeneration processes i.e., not to microhabitat differences between cobbles and live scallops, since transplanted epilithic colonies were as fecund as those

living on live scallops (Table 28). When fertile epilithic colonies were observed in the field survey, they were as fecund at the module-level as those on epizoic substrata (Table 25). This suggests that sexual reproduction of *S. cupressina*: is an "all-or-none" process: either colonies invest resources into sexual reproduction or they do not, instead of gradually reducing fecundity by limiting gonophore production or dimensions. The absence of any sexually fertile colonies in the experimentally injured treatments was also associated with the relatively rapid regeneration of the distal tips of these colonies. The idea of an "all-or-none" process does not necessarily conflict with results gained from the field experiments: significant differences in module-level fecundity in transplanted injured versus control colonies reflected a statistical artefact produced the absence of any sexually fertile damaged colonies.

Similar levels of module-level sexual fecundity between epilithic and epizoic colonies of *Sertularia cupressina* (Table 25) contrasts with studies on another hydroid (Braverman 1963) and warm-water corals (Wahle 1983b; Rinkevich and Loya 1989) where both the percentage of fertile colonies and the number of gonophores were reduced. These differences may reflect more efficient resource translocation to injured modules in the latter taxa. Enough resources could be left behind for other modules to become sexually reproductive, producing reproductive "asynchrony" within the same colony (Rinkevich and Loya 1989). The efficiency of resource translocation in *S. cupressina* is not known, but its good capacity for regeneration suggests that an "all-or-none" response to injury would have to reflect rapid sequestering of resources but a substantial resource drain for other modules.

Maximal clonal diversity of colonies on epizoic substrata observed in the field survey (Table 27) is likely produced by pre- and post-settlement processes that favour the recruitment and survival of genotypes on the shells of live scallops. *Sertularia cupressina* does not preferentially settle on rocks, shells or other hard substrata (Berghahn and Offermann 1999). High clonal diversity can be explained by high proportion of sexually fertile colonies as the production of philopatric planulae by several colonies increases the probability of successful recruitment back onto that substrate. High fecundity combined with philopatry may also explain why higher colony abundance was observed on scallops versus cobbles.

The absence of clonality on epizoic substrata (Table 25) may be explained by the longevity of the scallop host. Whole colonies of *Sertularia argentea* and *S. cupressina* naturally senesce and detach from substrata (Schmidt and Warner 1991), but asexual propragation of the remaining hydrorhizae and subsequent colony re-growth are possible (Hancock et al. 1956; Schmidt and Warner 1991). Adult colonies on commercial fishing grounds may live for several years, but by this time the scallop host has probably attained a commercially legal size (i.e., 95 mm shell height in the Bay of Fundy) and is fished out before epizoic colonies fully senesce.

Significantly reduced clonal diversity on cobble versus scallop substrata (Table 25) and at higher levels of fishing effort (Fig. 18) could be explained by pre-settlement processes such as lack of recruitment, and / or by post-settlement processes such as high mortality of juvenile or adult colonies. The philopatric nature of *Sertularia cupressina* planulae suggests that a lack of recruitment of sexually derived colonies on a cobble

reflects the low frequency of fertile colonies (Table 25) available to establish more genotypes on that substrate. Reduced clonal diversity can also arise from high post-settlement mortality that eliminates most clones and therefore most genotypes (Coffroth and Lasker 1998). But *S. cupressina* survives and regenerates well from wounds. It also does not seem to propagate asexually under natural conditions (see above discussion) and increased water currents generated by scallops did not favour clonality in transplanted colonies as it does in the hydroid *Hydractinia pruvoti* on gastropod shells (Bavestrello et al. 2000b). Clonality in *S. cupressina* is therefore hypothesized to have resulted from injury-induced fragmentation of the hydrorhizal system that connects the upright modules of a colony to each other and to the substrate.

Fragments of live hydroids, including *Sertularia cupressina*, have been found floating as pelagos in the Northwest Atlantic over the last century (Bigelow 1915, reported as *Thuiaria cupressina*; Madin et al. 1996), and could be related to colony displacement by bottom fishing (Concelman et al. 2001). The mechanism for hydrorhizal fragmentation could be extrinsically caused by grinding substrata against other objects and effectively severing colonies. Fragmentation could also occur intrinsically if the colony "aborts" damaged modules by severing hydrorhizal connections to that part of the colony. Experimental damage of colonies did not induce clonality of *S. cupressina* in the field (Table 28), so the mechanism for clonality in *S. cupressina* is still unclear. A similar mode of clonal propagation in the related species *S. argentea* was induced by experimental damage (Hancock et al. 1956), but injuries were located much lower down the hydrocauli than in the present study. Extrinsic fragmentation is still a possible

mechanism to explain reduced clonal diversity of epilithic populations, but the experimental evidence for induced clonality in *S. argentea* is intriguing enough to warrant future analyses of injury-induced asexuality in *S. cupressina*. Colony-regulated abortion of damaged modules may represent a strategy similar to frustule production in other hydroids to undergo dormancy or potentially disperse to more favourable habitats.

It is possible that the timing of the field sampling biased the sampling of sexually fertile colonies. The physiological condition of the animal, resource availability and potential for high mortality interact to produce schedules of sexual reproduction in clonal animals (Harvell and Grosberg 1988; Hall and Hughes 1996). Low fecundity observed in colonies on cobbles may have reflected delayed sexual reproduction of colonies until conditions became more suitable. Extended field surveys could be conducted to test this hypothesis, but the reduced levels of clonal diversity, high injury frequency and reduced fertility of colonies on cobbles suggests that the low proportion sexually fertile colonies was related to damage and not to season.

The literature on the effects of fishing on submerged aquatic vegetation has addressed the need to determine impacts on sexual reproductive processes in marine seagrasses (Stephan et al. 2000). Partial fisheries closures during reproduction seasons were recommended to mitigate effects of bottom fishing, propellers and moorings that shear off reproductive structures, scar and fragment seagrasses (Francour et al. 1999; Stephan et al. 2000; Bell et al. 2002).

The potential for life history impairment in colonial epifauna damaged by destructive fishing methods has not received the same attention as it has in seagrasses.

Yet life history responses characterize the recolonization potential of colonial epifauna and the overall capacity for community recovery from fishing disturbances (Dayton et al. 2002; Burridge et al. 2003). Impaired sexual reproduction reduces recolonization potential as it limits recruitment into disturbed areas. Recruitment limitation will be particularly relevant in communities comprised of taxa that do not normally exploit alternative reproductive modes of propagation i.e., asexual reproduction (Karlson 2002). To our knowledge, this study is the first to examine the potential for towed bottom fishing operations to impair sexual reproduction in a colonial epifaunal species, and the first to examine how bottom fishing potentially impairs reproductive strategies in a non-target organism.

Long-term declines in sponge, hydroid and coral populations may be related to diminished recruitment related to colony injury and mortality (Buhs and Reise 1997; Connell et al. 1997; Berghahn and Offermann 1999; Cropper and DiResta 1999). The present study demonstrated the possibility for injury-induced suppression of fecundity and enhanced clonality to be a mechanism for recruitment limitation in animals exposed to commercial-scale scallop dredging. Direct suppression of sexual reproduction by regeneration from partial mortality and extensive cloning could also have diminished fecundity and colonial growth of new potentially sexually mature modules (Ponczek and Blackstone 2001) or by lowering the density of sexually mature animals (Cropper and DiResta 1999; Kefalas et al. 2003). Bottom-fishing could also limit recruitment by destroying patches of larval "sources" that potentially sustain "sink" populations (Frid et al. 1999, 2000; Fosså 2002), or by direct removal of hard substrata (Buhs and Reise 1997;

Berghahn and Offermann 1999). If epizoic populations act as "sources" for hydroid recruitment and genetic variability in Atlantic Canada, then limiting scallop dredging to seasons that do not bear upon sexual fertility of epifauna could help further sustain benthic assemblages that use sea scallops and inert objects for habitat.

CHAPTER SIX: EFFECTS OF MECHANICAL DISTURBANCE ON COLONY RESPONSES, REPRODUCTION AND REGENERATION IN THE COLD WATER OCTOCORAL *GERSEMIA RUBIFORMIS* (EHRENBERG, 1834)

INTRODUCTION

Global concerns over the impacts of bottom fishing (e.g., trawling, dredging) on sessile epifauna have prompted investigations into the effects of these disturbances on scleractinian, gorgonian and alcyoniid corals (Tilmant 1982; Sainsbury et al. 1993; Freese et al. 1999; Rogers 1999; Koenig et al. 2000; Roberts et al. 2000; Fosså et al. 2002; Reed 2002; Mortensen et al. 2003). The nephtheid octocoral *Gersemia* spp. comprises much of the coral biomass caught as invertebrate by-catch during bottom trawling in the North Pacific (Krieger 2001), and in the northwest Atlantic, the biomass of *Gersemia rubiformis* (Ehrenberg, 1834) was significantly reduced by experimental otter trawling on the Grand Banks off Newfoundland (Prena et al. 1999; Kenchington et al. 2001). These "soft" corals may be damaged, dislodged from their substrata, crushed, tipped or dragged during fishing operations and are consequently considered highly vulnerable to bottom gear disturbances (Krieger 2001).

However, colonial cnidarians have the ability to survive some degree of damage due to their body plan, which is comprised of physiologically connected modular units called polyps or anthocodia. Cnidarian responses to natural disturbance events such as storms, predation or sediment abrasion have been investigated in several octocoral Orders (e.g., gorgonians, alcyonaceans and pennatulaceans). They include inflation or retraction of polyps (Fadlallah 1982; Riegl 1995; Tanner 1995; River and Edmunds 2001) which

may disrupt daily feeding and waste exchange activities, production of clonally-derived propagules, (e.g., colony fission, fragmentation or budding; Highsmith 1982; Fabricius 1995), and reallocation of intra-colonial resources to damaged or regenerating modules (Wahle 1985; Oren et al. 1997b, 2001). Partial mortality may also result in the loss of entire branches (Brazeau and Lasker 1992) and the abnormal regeneration of damaged polyps (Benayahu 1998). Some octocorals (particularly xeniids and nephtheids) are adapted to disturbance and have evolved a "fugitive" life history by increasing the ability of asexual propagules to migrate into open spaces and act as "pioneers" of recently disturbed habitats (Fabricius 1995; Karlson et al. 1996).

Gersemia rubiformis is a cold water ahermatypic nephtheid with a northern circumpolar distribution. It is eurybathic, occurring from less than one metre below the extreme low spring tide level (L. Henry, personal observation) to 3600 m depth (Madsen 1944; Carlgren 1945). The goal of this study was to investigate the effects of disturbance on *G. rubiformis* with respect to 1) colony and anthocodia physiognomy, 2) reproduction, and 3) regeneration, by simulating mechanical injuries that would be experienced by this coral during bottom fishing operations.

It is hypothesized that mechanical disturbance will impair cycles of colony and anthocodium expansion and retraction by reducing the frequency of time spent in more expanded states. *Gersemia fruticosa* (Sars, 1860), a possible conspecific, is known to have endogenous, cyclical rhythms of expansion and retraction of 18 to 48 hours or more duration (Slephkova and Seravin 1983; Seravin and Gudkov 1990). These rhythms may be modified by external factors such as light regimes or disturbances, as chronic

experimental sedimentation lead to reduced tentacular motion in warm-water alcyonaceans (Riegl 1995).

Gersemia rubiformis is gonochoric and broods its larvae (Nørrevang 1973). The extent to which this species naturally undergoes asexual reproduction is not known. Injuries, high turbulence and other disturbances promote asexual reproduction in warm-water zooxanthellate species (Fabricius 1995; Brazeau and Lasker 1992), but asexual reproduction may not be common in some temperate and cold-water octocorals (Farrant 1985; McFadden 1986; Gotelli 1991; McFadden 1991, 1999). Injuries can suppress sexual reproduction in soft corals (e.g., Wahle 1983a) as resources (e.g., energy and stem cells) are invested into colony repair and regeneration rather than into gamete production or larval brooding. The association between exogenous disturbances and clonal propagation in other octocorals suggests that substrate turnover perturbations could promote asexual reproduction and impair sexual reproduction in *G. rubiformis*.

Most studies of regeneration from injuries in octocorals have been made on warm water gorgonians (Wahle 1983a, b; Lang da Silveira and Van't Hof 1977; Gateño et al. 1998; Meszaros and Bigger 1999). But the potentially long lifespan, slow growth and fragility of cold-water octocorals could make these animals highly vulnerable to long-term impacts of bottom fishing disturbances (Breeze et al. 1997; Krieger 2001; Stone and Wing 2001), unless damage can be repaired quickly. The capacity for *Gersemia rubiformis* to regenerate lost polyps following the experimental excision of colony branches was examined.

Together, these results provide insight into the vulnerability of *Gersemia rubiformis* to bottom fishing gear and other disturbances, and the effect such disturbances may have on life-history processes.

Materials and methods

Specimen collection and rearing

Eight colonies of *Gersemia rubiformis* were collected along with their cobble substrata by SCUBA at approximately 10 m depth in June 2002 from three sites in the Passamaquoddy Bay region of the lower Bay of Fundy in the northwest Atlantic (approximately 45° 0' N, 66°4' W). Corals were transported in a 25 L cooler and maintained in individual 11.4 L gallon tanks containing three other cobbles devoid of epifauna. Close inspection and photography of corals immediately after transportation to the laboratory under a dissecting microscope showed that no larvae of adult organisms inhabited the cobble surfaces. Separate aquaria and water supplies ensured that cross-fertilization and larval dispersal between corals were prevented, as it was unknown if and when this species might become sexually active in the laboratory. No soft coral larvae or polyps have ever been brought into the laboratory via the water supply (B. MacDonald, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, personal communication).

Aquaria were supplied with a steady flow of 20 μm - filtered seawater at 5.7 °C and 33.5 $^{0}/_{00}$ water salinity and light regimes of approximately 10 hours light (8 AM – 6 PM) and 14 hours dark (6PM – 8AM) consistently throughout the study. Corals were acclimatized for one week before experimentation. Although ahermatypic octocorals may regularly gain much of their nutrition from soluble organic particles and suspension

feeding on small plankton, instead of zooplankton predation (Marsical and Bigger 1977; Fabricius et al. 1995; Orejas 2001; Orejas et al. 2003), coral diets were supplemented with 1mL cultured *Artemia* spp. once every two weeks.

Corals were randomly allocated into control and disturbed treatment groups (Table 30). Beginning at time = zero, experimental treatments were disturbed in the early morning by continuously rolling the colonies and their attached cobbles over 360 degrees, ten times back and forth while keeping the coral constantly submerged in the aquarium. This protocol ensured that all polyps even in the largest corals (Table 30) were crushed. Colonies were left to recover in their original configurations i.e., the cobble substrate was replaced in the same orientation as before the disturbance with the coral on the upper surface. Disturbances were inflicted once every two weeks, over a period of two months (i.e. five times; therefore, each disturbed coral was crushed 50 times).

Table 30: Characteristics of experimental colonies of the soft coral *Gersemia rubiformis* collected from the Bay of Fundy randomly assigned *a priori* into control and disturbed (mechanically crushed) treatments.

Coral colour	**Coral size range (cm) (height when fully contracted – height when fully expanded)**	**Treatment**
light - dark pink	1.8 - 8.0	control
light orange	1.0 - 8.0	control
light orange - light pink	2.0 - 8.0	control
light orange	4.0 - 10.0	control
deep pink	2.9 - 7.5	disturbed
light pink - dark pink	3.0 - 12.0	disturbed
light - dark pink	5.0 - 12.4	disturbed
deep pink	3.0 - 14.5	disturbed

Colony responses

Coral response was examined by recording the degree of colony expansion and retraction both four days and one week post-disturbance for two months. All corals were assigned into one of three colony states: "State 1" corresponded to a strongly retracted berry shape with no open or extended polyps, "State 2" corresponded to an elongated body stalk with some polyps out, and "State 3" corresponded to a fully inflated coral with 100 % of the polyps extended (Fig. 19). Colony state was measured for each coral early in the morning prior to turning lights on and afternoon on the recording day producing 18 recording times in total. Each coral was also photographed *in vitro* using a Nikon Coolpix 990 digital camera with an 8 - 25 mm lens mounted next to each aquarium. A Nikon fiber illuminator was used to provide extra lighting for enhanced picture clarity and imaging of daughter offspring.

General trends in the periodicity of colony contraction and expansion were evaluated separately for control and disturbed corals using G-tests for goodness of fit (Sokal and Rohlf 1995). These tests compared the mean frequencies of corals found in each state between the nine morning and nine afternoon observations, the statistical significance of the chi-squared statistic was evaluated at $\alpha = 0.05$ with 2 degrees of freedom.

Fixed effects of treatment (two levels, disturbed and undisturbed) and time (18 recording times) and a random effect of subject nested within treatment on coral response were examined using a repeated measures analysis of variance (RMANOVA) with JMP® Version 5 (SAS Institute Inc. 2002). Because the dependent measured response (coral

state) was an ordinal variable, JMP® fits the cumulative response probabilities to the logistic distribution function of the linear model using maximum likelihood analysis and estimates Wald statistics for each effect (SAS Institute Inc. 2002).

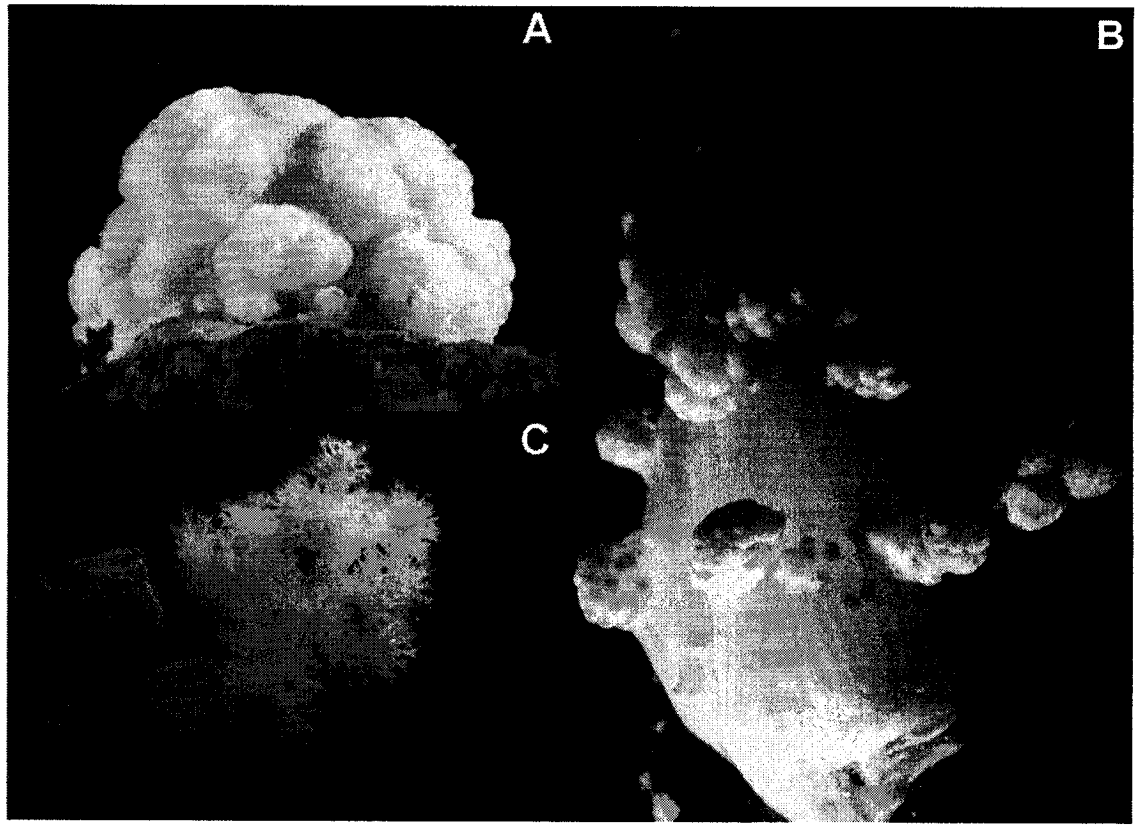

Fig. 19: Three states of colony contraction and expansion in a single colony of *Gersemia rubiformis*: A = State 1 (colony = 2 cm high), B = State 2 (colony = 6 cm high), C = State 3 (colony = 8 cm high).

Asexual and sexual reproduction

Effects of crushing on reproduction were examined through enumeration of juvenile colonies that appeared during the experiment and with genetic techniques to determine whether the daughter colonies were sexually or asexually derived.

As discussed above, any colonies observed during the experimental period had to have been propagated while *in vitro*. New colony propagation was measured by counting the appearance of new daughter colonies around the base of each adult coral in each separate aquarium, and measuring their growth over time.

Since corals were not visibly sexually fertile at the time of collection and based on the relationship between disturbance and asexual propagation in other soft corals, the *a priori* prediction was that any new colonies would be propagated asexually. However since juveniles were at first comprised of a single initial polyp that might indicate a sexual origin instead of asexual where the new colony is often comprised of multiple polyps (Dahan and Benayahu 1997), it was decided *a posteriori* that genetic methods should be used to confirm the origins of these juveniles. However since sampling for DNA analysis is destructive, a separate experiment was performed at the conclusion of the disturbance and coral response experiment (i.e., after 90 days) to elucidate the origins of daughter colonies. Coral and substrate turnover was repeated for all colonies after 90 days to see if producing offspring was repeatable by this method. All new daughter colonies and a branch from each parent were sampled after two weeks.

Colony parentage was determined genetically using randomly amplified polymorphic DNA – polymerase chain reaction (RAPD – PCR) methods optimized for

Gersemia rubiformis. Tissue was digested in proteinase K for three hours at 55° C using a Qiagen DNeasy kit with the RNase digestion step following the manufacturer's instructions (Qiagen, Mississauga, Ontario). DNA concentrations were determined using PicoGreen analysis (Molecular Probes, Eugene, Oregon). Parental and putative offspring tissues were eluted in 200 µL and 100 µL elution buffer, respectively. Ten primers developed by the University of British Columbia (UBC, Vancouver, British Columbia) were tested for inter-colonial variability using *G. rubiformis* specimens collected by the Canadian Department of Fisheries and Oceans during previous offshore groundfish surveys on the Scotian Shelf of the Canadian northwest Atlantic.

Four of these primers were highly variable between corals: UBC 601 (5′ - CCG CCC ACT G - 3′), UBC 602 (5′ - GCG AAG ACT A - 3′), UBC 603 (5′ - ACC CAC CGC G - 3′) and UBC 604 (5′ - GGC CCA TTG C - 3′). PCR was performed on a cocktail containing 10 ng of DNA, 0.75 µM primer and 1X SIGMA RED*Taq* ReadyMix PCR reaction mix (Sigma-Aldrich, Mississauga, Ontario) (2X stock solution composed of 20 mM Tris - HCl at pH 8.3, 100 mM KCl, 3 mM $MgCl_2$, 0.002% gelatin, 0.4 mM dNTP mix of dATP, dCTP, dGTP and dTTP, stabilizers and 0.06 units *Taq* DNA polymerase / µL, MBI) to a final reaction volume of 10 µL. PCR cycling began at 94 °C for two minutes, followed by 47 cycles of 94 °C for 20 seconds, 42 °C for one minute and 72 °C for another minute. PCR products were run on 2 % agarose in 1X TAE from a 20X stock solution of buffer (0.8 *M* Tris, 0.4 *M* NaAc, 0.02 *M* ethylenediamine tetraacetic acid adjusted to pH 8.0 with acetic acid) containing ethidium bromide. MBI Fermentas 100 bp ladder (MBI Fermentas, Burlington, Ontario) was run alongside the products. Images

were visualized on a SynGene Genius (Syngene Gene Genius, Frederick, Maryland) gel documentation system and all distinctly visible bands were sized and scored as present or absent in every coral. Band fidelity or "repeatability" was observed to be good, although intensity of bands varied within a colony (L. Hamilton, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, personal communication).

Genetic dissimilarity was estimating as genetic distance $d = 1 - [2n_{11} / 2n_{11} + n_{10} + n_{01}]$ (Nei and Li 1979) where n_{11} is the number of shared bands between corals *i* and *j*, n_{10} is the number of bands in coral *i* but not *j*, and n_{01} is the number of bands in coral *j* but not *i*. Daughter colonies with no genetic dissimilarity (i.e., $d = 0$) with the respective parent colony were considered to be asexual progeny, while offspring with *d* greater than zero were assumed to have been sexually derived. Mean genetic distance between parents and daughter colonies was also contrasted with mean distance between offspring from different parents to explor genetic relatedness between daughter colonies.

Assuming that RAPD markers are inherited in a Mendelian fashion in *Gersemia rubiformis*, offspring are expected to possess approximately 50 % of the bands present in the mother colony. This assumption was tested using Monte-Carlo randomization tests to determine whether the frequency of shared bands relative to the total number of bands between offspring from the same parent significantly differed from that expected i.e., 50 %. The chi-squared test statistic (χ^2) was obtained by generating samples from the null hypothesis binomial distribution and calculating the χ^2 statistic for the probability of observing this frequency across 1000 replications.

Regeneration

Following the colony response and reproduction observations, one branch containing four to five polyps was experimentally excised from each of the four control corals using a scalpel. Coral condition was monitored over the next four weeks and photographs were taken to document macroscopic colony responses, repair and regeneration.

RESULTS

General observations on coral health

The overall health of crushed corals appeared to decline over time. Disturbed corals retracted all anthocodia and their entire body stalks within a minute of being crushed the first time. After the pulsed disturbances, the body stalk remained weak throughout the morning and afternoon, and the degree of stalk inflation also continued to deteriorate over time (Fig. 20). Control coral health remained stable throughout the experiment, and continues to do so after being maintained *in vitro* 12 months after collection from the field (L. Henry, personal observation).

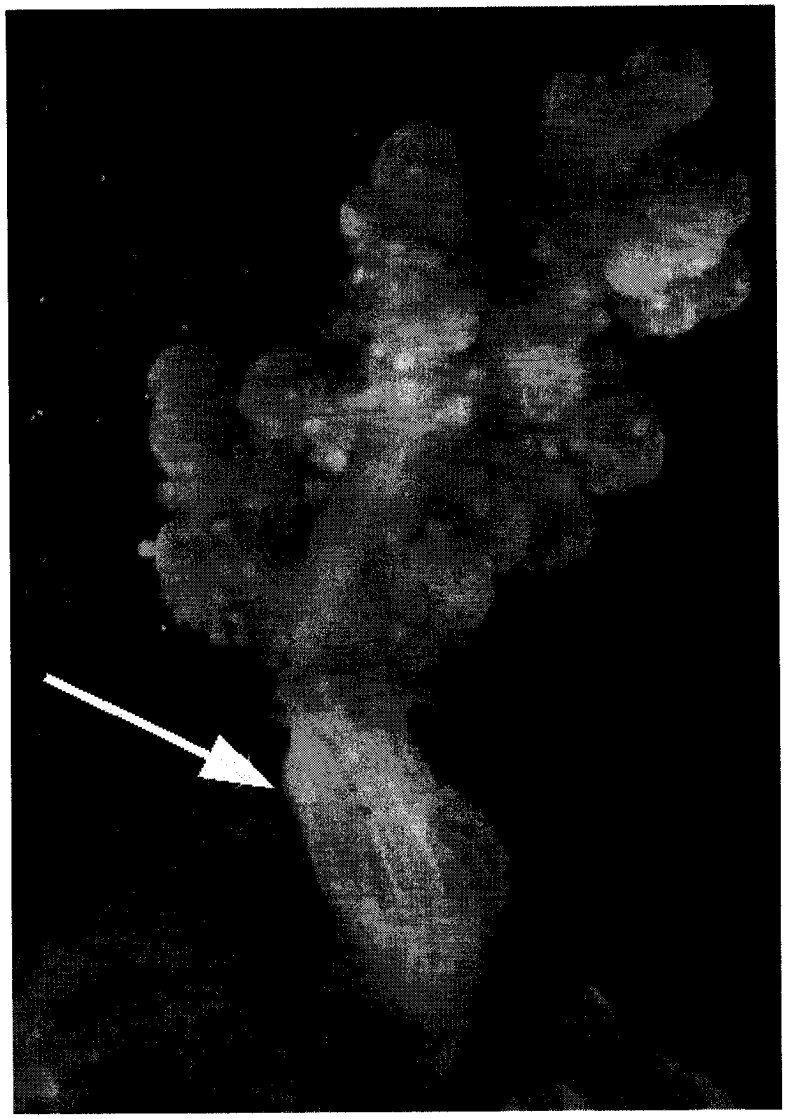

Fig. 20: General weakening of the body stalk was observed (shown by arrow) in mechanically injured *Gersemia rubiformis* colonies.

Colony responses

Neither treatment exhibited statistically significant periodicity in the mean frequencies of corals found in different colony states between the early morning (dark) to late afternoon (daylight) times ($\chi^2_{0.5,\ 2} = 5.991 > G = 0.026$, G = 3.472 for control and disturbed treatments respectively). Corals were generally most often found in State 3, less so in State 2 and much less so in State 1, regardless of the time of day (Table 31), although no strictly nocturnal observations were made.

The RMANOVA demonstrated that effects of treatment, subject and time were not statistically significant at $\alpha = 0.05$: Wald $\chi^2 = 0.999$, df = 1, P = 0.317 for treatment, Wald $\chi^2 = 0.7.428$, df = 6, P = 0.283 for subject, and Wald $\chi^2 = 0.24.450$, df = 17, P = 0.108 for effect of time. The lack of significance indicates that cumulative disturbances had no significant effect on coral states during the observation schedule, although the power of the test to detect differences was low due to the number of subjects.

Table 31: Mean frequencies of all four control colonies and all four mechanically disturbed colonies of *Gersemia rubiformis* colonies in the three colony states during the early morning and late afternoon under laboratory conditions. Mean values and standard deviations (sd) for the morning and afternoon obtained by averaging frequency across each of nine days (= 18 observations for each coral summed over morning and afternoon).

State		**Mean frequency of control corals in state ± sd**	**Mean frequency of disturbed corals in state ± sd**
Morning			
1	AM	13.875 ± 13.967	8.325 ± 10.627
2	AM	33.325 ± 20.302	24.975 ± 13.967
3	AM	52.775 ± 24.650	66.700 ± 9.063
Afternoon			
1	PM	15.625 ± 15.729	25.000 ± 17.678
2	PM	31.250 ± 7.217	46.875 ± 6.250
3	PM	53.125 ± 18.750	34.375 ± 18.750

* indicates statistical significance at $\alpha = 0.05$

Asexual and sexual reproduction

Daughter colonies appeared in the disturbed treatments within 13 days of the first disturbance event (Fig. 21). By the end of the experiment, all disturbed corals had propagated new daughter colonies at different times, and this effect was repeatable even after 100 days in two control and three disturbed corals. Early development of a daughter colony was characterized by the settlement of a single pinnately arranged "founder" polyp (Fabricius and Alderslade 2001) with characteristic pinnules on the tentacles (Fig. 22) very close to the base of the adult colony. Polyp growth was also monitored over time, ranging from 0.02 to 0.40 polyps / day with a mean colony growth rate of 0.36 polyps/day ± 0.16 sd (a mean averaged across 39 daughter colonies over the entire study period). However no colonies survived beyond the seven polyp stage, so appearance and disappearance of daughter colonies was regularly observed.

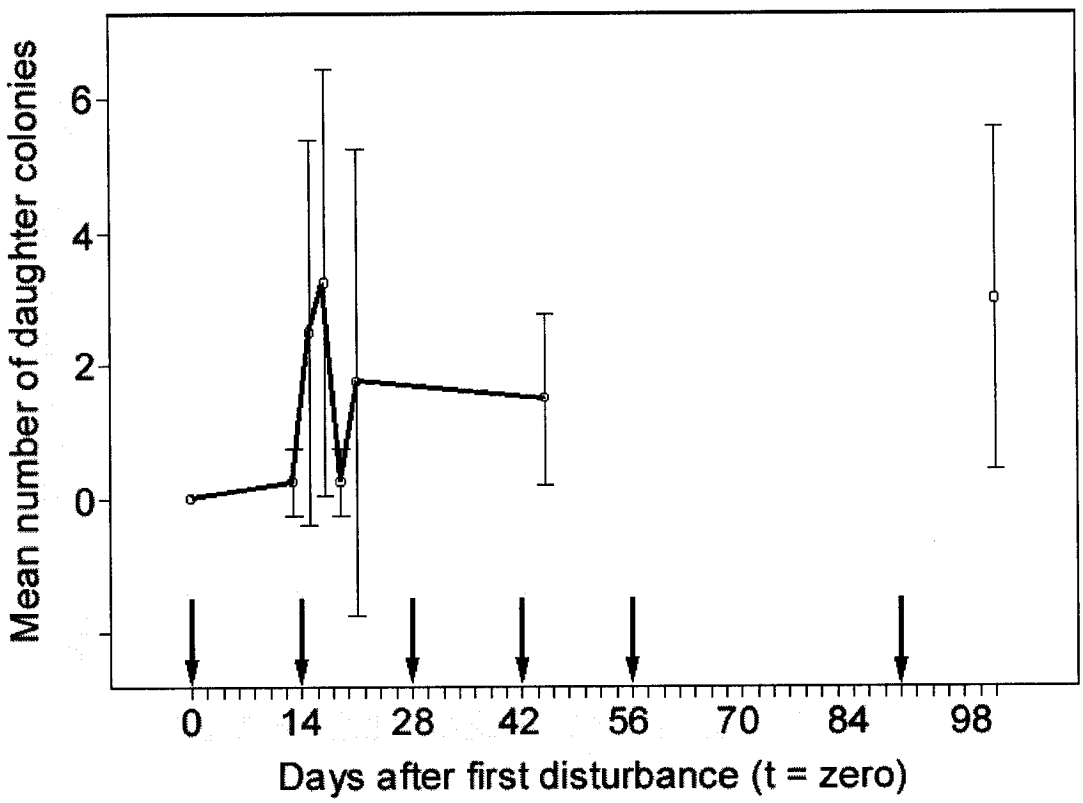

Fig. 21: Mean abundance and standard deviations of daughter colonies found near the four disturbed parent colonies (no offspring were found near the bases of control colonies). Arrows indicate day of disturbance, beginning at day zero and repeating for a total of five times until day 42. The last (sixth) arrow indicates the time at which disturbance was inflicted after the initial experiment to see if juvenile propagation was repeatable by this method.

Fig. 22: New single-polyp offspring of *Gersemia rubiformis* visible soon after colony disturbance. Extended polyp diameter approximately 2 mm.

Band sizes obtained from the RAPD-PCR analyses demonstrated that all adult and juvenile colonies were genetically dissimilar from each other (Fig. 23, Table 32), indicating sexual propagation of juveniles in contrast to our *a priori* expectations, but confirming the concept that a single founder polyp of *Gersemia rubiformis* was unlikely asexually produced. Although the mean genetic distance between siblings (mean = 0.496, standard deviation = 0.204) was slightly higher than the mean distance between offspring collected from the bases of different adults (mean = 0.447, standard deviation = 0.167), this difference was not statistically significant according to a two-sample t-est ($t = -1.009$, $df = 30.516$, $P = 0.321$). The sex ratio of corals used in this study was not known *a priori*, but the production of sexually derived offspring from six of the eight corals indicated that at least six of the eight corals were female.

Inheritance of bands in offspring from three of the five parents did not significantly differ from the expected 50 % frequency (all $P > 0.05$), indicating a high likelihood that these offspring were derived from the corals where they were found. The other offspring exhibited statistically significant departures from 50 % ($P > 0.05$), but in both cases these colonies inherited more bands than was expected, which is still consistent with the assumption that thee juveniles were derived from that parent and that they were not clonally-derived.

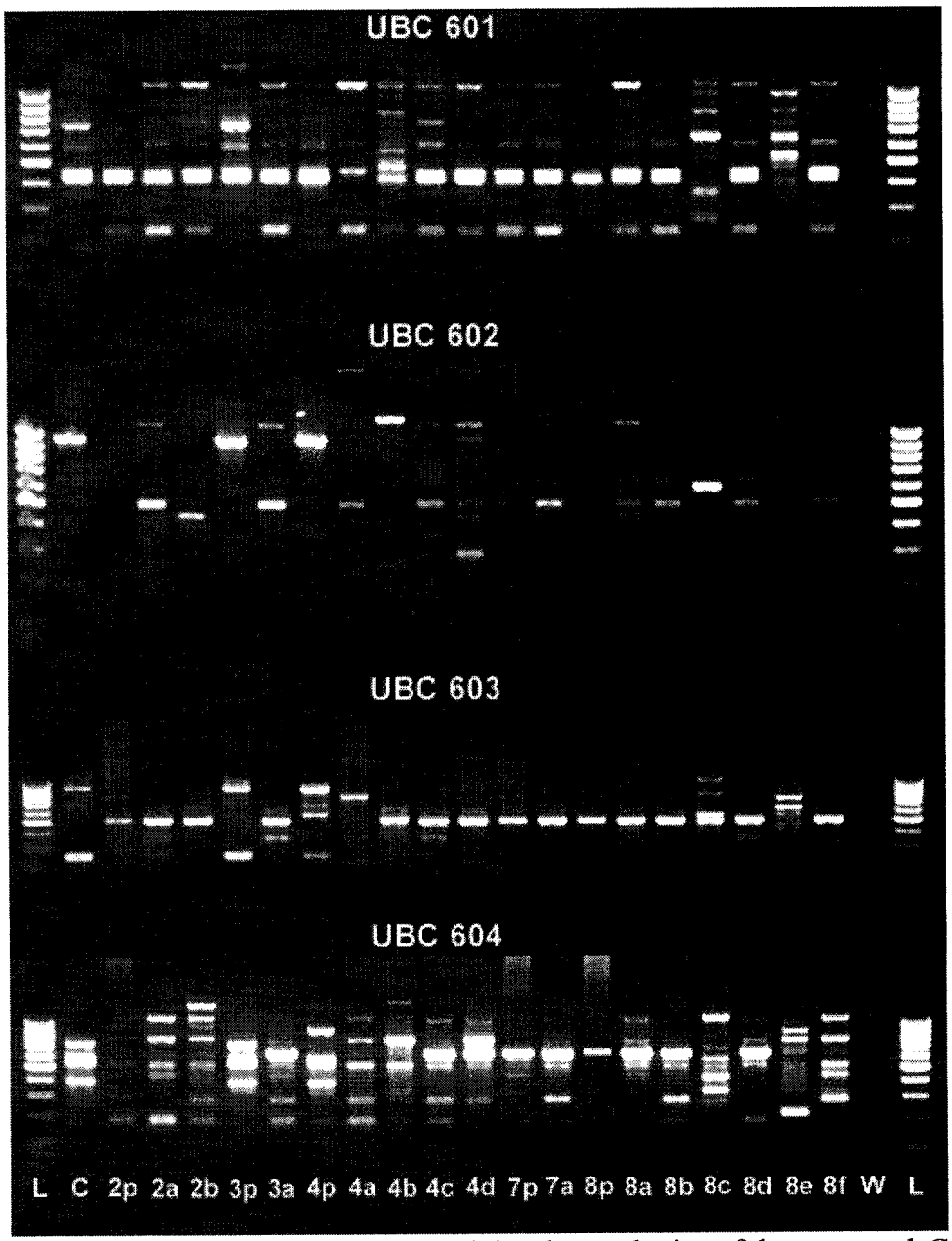

Fig. 23: RAPD – PCR results of parents and daughter colonies of the octocoral *Gersemia rubiformis*. Primer number (UBC 601, 602, 603, 604) indicated at top of each gel. L = 100 bp ladder (each band = 100 bp, ranging from 1 kb at the top to 100 bp at the bottom of each gel), C = control sample of *Gersemia* obtained from a branch on a colony from the Scotian Shelf, "p" indicates parent coral, subsequent lettering represents offspring from that parent, W = RAPD quality H_2O control.

Table 32: Genetic distance between all parent and daughter colonies of the octocoral *Gersemia rubiformis* collected in a separate experiment at the conclusion of the disturbance and coral response experiment. Number refers to the initial parent coral, the letter "p" identifies the coral as the parent and letters "a" to "f" refer to the offspring of that parent.

	2p	**2a**	**2b**	**3p**	**3a**	**4p**	**4a**	**4b**	**4c**	**4d**
2a	0.545									
2b	0.500	0.267								
3p	0.800	0.615	0.581							
3a	0.619	0.259	0.448	0.440						
4p	0.652	0.483	0.517	0.452	0.593					
4a	0.636	0.429	0.533	0.692	0.481	0.517				
4b	0.565	0.517	0.484	0.778	0.500	0.533	0.586			
4c	0.520	0.290	0.333	0.724	0.333	0.437	0.484	0.375		
4d	0.580	0.333	0.375	0.714	0.379	0.613	0.533	0.548	0.273	
7p	0.600	0.432	0.500	0.583	0.440	0.437	0.538	0.481	0.310	0.357
7a	0.600	0.385	0.429	0.583	0.440	0.481	0.538	0.556	0.310	0.214
8p	0.667	0.667	0.300	0.250	0.647	0.789	0.889	0.789	0.619	0.600
8a	0.667	0.333	0.462	0.636	0.304	0.600	0.583	0.520	0.333	0.231
8b	0.524	0.333	0.379	0.680	0.385	0.500	0.481	0.357	0.200	0.310
8c	0.769	0.687	0.765	0.867	0.742	0.697	0.812	0.576	0.600	0.647
8d	0.524	0.259	0.379	0.600	0.385	0.500	0.481	0.500	0.200	0.310
8e	0.733	0.722	0.684	0.882	0.829	0.622	0.778	0.568	0.641	0.737
8f	0.538	0.250	0.294	0.667	0.419	0.455	0.500	0.394	0.200	0.353

	7p	**7a**	**8p**	**8a**	**8b**	**8c**	**8d**	**8e**
7a	0.169							
8p	0.600	0.500						
8a	0.364	0.182	0.429					
8b	0.360	0.280	0.529	0.217				
8c	0.467	0.533	0.818	0.714	0.677			
8d	0.360	0.280	0.529	0.304	0.231	0.677		
8e	0.647	0.706	0.923	0.875	0.714	0.400	0.771	
8f	0.467	0.400	0.727	0.429	0.290	0.667	0.226	0.650

Regeneration

Immediate coral responses to experimental excision of four to five polyps were colony retraction of all remaining polyps and body stalks within five minutes. Corals did not inflate substantially over the next 24 hours but eventually resumed polyp extension and body stalk expansion after 36 to 48 hours. Macroscopic observations of wounds showed no fouling of lesions by other organisms or scarring. After ten to fourteen days, new tissue was superficially aggregated in sparse clumps over the wound surface (Fig. 24), that eventually merged over the regenerating area between 18 and 21 days. Tissue regeneration proceeded rapidly at this point and later stages were characterized by aggregates of new tissue that eventually spread and merged over the wounded surface. A single new polyp emerged from the regenerated tissue (Fig. 24) after 25 to 30 days.

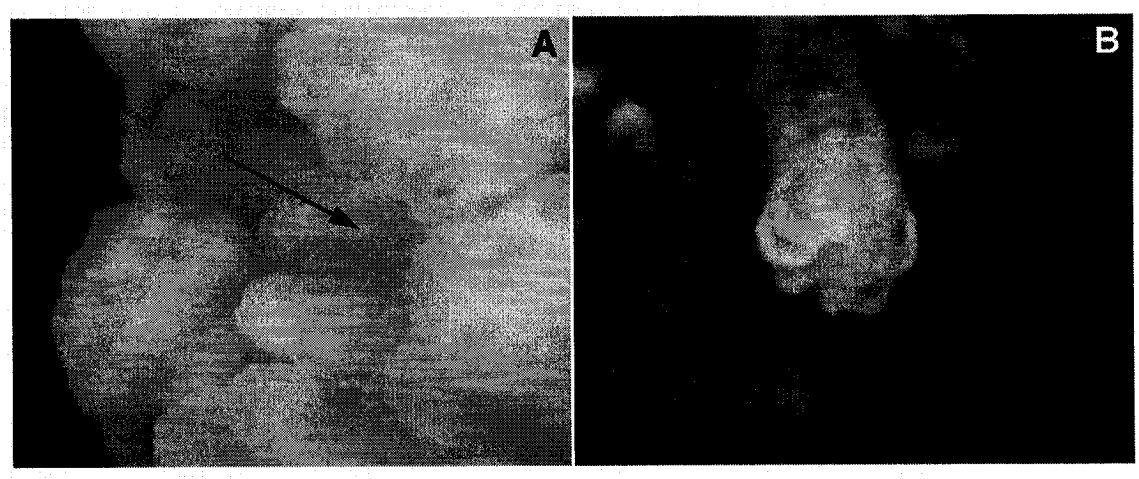

Fig. 24: One of many aggregates of new tissue (shown by arrow) (A) and the emergence of a newly regenerated polyp (B) following partial mortality in *Gersemia rubiformis*.

DISCUSSION

The responses of octocorals to injuries and partial mortality have been most often documented in warm water gorgonians e.g., (Brazeau and Lasker 1992; Fabricius 1995; Karlson et al. 1996; Benayahu 1998). But it is important to consider responses of cold water coral fauna in light of increasing threats to these organisms through commercial-scale bottom fishing in increasingly deeper waters where many of these corals are found.

In the present study, the effect of crushing disturbances that simulated what happens during bottom fishing resulted in immediate colony retraction and an apparent decline in condition of *G. rubiformis* colonies over time as demonstrated by weakened body stalks (Fig. 20). Similar declines in octocoral appearance were also seen after sedimentation damage in Antarctic soft corals (Slattery and Bockus 1997). Reduced polyp extension and weak body stalks could inhibit the ability for *G. rubiformis* to feed and transfer wastes, and could result in overall reduced growth rates. However, repeated mechanical disturbance over two months did not significantly impair the degree of colony expansion and retraction. This may be because corals immediately retracted 100% of their polyps and their body stalks into compact forms when first disturbed.

Gersemia rubiformis maintained *in vitro* were not observed to have cycles between full colony retraction and expansion, although the majority of corals were found in a fully expanded state (State 3) in periods of light and dark (Table 31). No differences were found between control and disturbed animals. Thus no disruptions to circadial rhythms induced by mechanical disturbance were detected. The *in vitro* aquaria conditions in the present study may have prevented critical external stimuli (e.g., tidal movements, light regimes) from controlling endogenous colony rhythms, if indeed they

were absent. It is likely that *G. rubiformis* exhibits circadial rhythms in nature as observed in *G. fruticosa* (Slephkova and Seravin 1983; Seravin and Gudkov 1990).

The likelihood for these types of mechanical disturbances to occur in areas such as intensively chronically fished areas is quite high. For example, *Gersemia rubiformis* often represent a ubiquitous part of the invertebrate by-catch in scallop dredges in the Bay of Fundy (Fuller et al. 1998) where it is hauled up, rolled around to separate the scallops from the "trash" and eventually discarded overboard. The ability for *G. rubiformis* to retract but rapidly recover from these disturbances may be vital to its survival in these areas, and may mean it is less vulnerable to effects of bottom fishing than other soft corals with rigid skeletons and unretractable colonies e.g., *Paragorgia arborea* (Linnaeus, 1753) and *Primnoa resedaeformis* (Gunnerus, 1763).

All corals in the disturbed treatments propagated offspring during the experiment, and some juveniles appeared after less than two weeks following the first disturbance event (Fig. 21). Juveniles aggregated at the base of the parent colony on the same cobble, as is often seen under natural conditions (L. Henry, personal observation) and may explain the patchy aggregated distribution of *Gersemia* spp. in the Atlantic region (Schneider et al. 1987; Gilkinson et al. 2003). This tendency to aggregate might reflect an evolutionary mechanism for juveniles of *G. rubiformis* to settle and metamorphose in habitats already occupied by, and therefore hospitable to, adults. Juvenile survivorship in another cold water alcyonacean, *Alcyonium siderium* (Verrill, 1922), was inversely correlated with distance to the parent colony, probably as an adaptation to avoid predation (Sebens 1983).

Although colony growth of *Gersemia rubiformis* juveniles was fast initially, the short lifespans observed could reflect competitive inferiority of juveniles to adult colonies. Food depletion and reduction of water movement in highly aggregated stands of adult *A. siderium* colonies probably resulted in the negative correlation between growth of *A. siderium* juveniles and proximity to parents (Sebens 1983). *In vitro* aquaria conditions may have inadequate food quality for newly metamorphosed *G. rubiformis* juveniles. Premature larval release may also have resulted in inadequate resource acquisition in sexually-derived planulae that reduced life expectancies in a similar way that larval energetic content and planulae longevity appear to be positively correlated in other soft corals (Ben-David-Zaslow and Benayahu 1998; Cordes et al. 2001). Combined field and laboratory growth experiments could help explain the effects of reproductive timing and critical resource requirements on colony growth and survival of juvenile soft corals.

Contrary to expectations, daughter colonies generated after disturbances were sexually-derived and were not a result of asexual budding or fragmentation (Table 23). This was surprising for several reasons: (1) corals were not visibly sexually fertile at the time of sampling, (2) specimens were not given enough time to develop eggs and become fertilized between the time of sampling and the beginning of the experiment and (3) damage induced by substrate turnover was expected to increase demand for energetic and cellular resources for repair processes and result in reduced resource availability for gamete production, larval brooding, etc.

Gersemia rubiformis planulae may have initially gone undetected in the experimental corals because its eggs, embryos and subsequent larvae (approximately 250 μm, 475 μm and 1500 μm long, respectively) are brooded deep in the mesenteries of the gastrovascular cavities in individual polyps (Verrill 1922; Nørrevang 1973). Egg development, fertilization and larval brooding was unlikely to have occurred during the pre-experimental acclimatization period of one week as complete cycles of soft coral sexual reproduction can take weeks to months (McFadden 1991; Fabricius and Alderslade 2001). Therefore the female colonies were probably already brooding larvae when they were collected and planulae may have been missed because they were underdeveloped.

No planulae were released from control colonies during the mechanical disturbance experiment. These were only observed after the second post-experimental attempt to repeat offspring propagation in all colonies approximately 100 days after being collected from the field. Either these female colonies became sexually fertile *in vitro*, or they underwent prolonged larval brooding and planulae competence periods. As all eight colonies were maintained in separate aquaria, cross-fertilization and larval dispersal were prevented, while hermaphrodites and selfing are also rare among soft corals (Dahan and Benayahu 1997; Fabricius and Alderslade 2001). But since soft coral planulae can remain competent for several months after release from parent colonies (Farrant 1985; Ben-David-Zaslow and Benayahu 1998; Cordes et al. 2001) and even the disturbed colonies continued to propagate offspring after 100 days *in vitro*, the latter hypothesis of prolonged

larval brooding and lifespan appears to be the most reasonable explanation for observing sexually derived offspring from control colonies.

There are two hypotheses consistent with disturbance-induced propagation of sexually-derived juveniles: (1) crushing induces intrinsic mechanisms that cause the coral to expel resource-costly larvae that potentially uptake material from the parent through their epidermal layer (Nørrevang 1973), and (2) crushing extrinsically mediates larval release by tearing larval brooding tissues. Whether intrinsic or extrinsic, premature larval expulsion in response to mechanical disturbance may have lead to the observed mortality of all daughter colonies if larvae did not have sufficient resources for subsequent long-term growth. Stress induces premature release of gametes and abortion of planulae in warm water corals (Loya and Rinkevich 1979, 1980; Szmant-Froelich et al. 1980; Fadlallah 1983) that can lead to unviable recruits (Loya and Rinkevich 1979). *In vitro* "bail-out" of polyps containing larvae was also observed in stressed scleractinians but larvae recruited successfully (Sammarco 1982). Disturbance may perturb cold-water corals such as *Gersemia* spp. and induce expulsion of highly unviable larvae, but survival experiments should be conducted in the field to eliminate bias in mortality estimates due to unnatural conditions. Interestingly, the excision of polyps at the conclusion of the experiment did not initiate the production of daughter colonies.

Genetic distances between siblings were not statistically different from distances between offspring collected from different females (Table 32). Fertilization of a female colony by multiple local males may explain this lack of significance (Barki et al. 2000). Co-dominant genetic markers that can detect more variation and that are more suitable to

quantifying genetic distances and paternity (e.g., microsatellites) could be used to test this hypothesis.

The regeneration of damaged polyps in octocorals is largely directed by the intra-colonial transportation of energy and cellular resources. Amoebocyte accumulation at the wound site originates from adjacent uninjured tissues (Meszaros and Bigger 1999) while polyp regeneration is due to migration of epidermal interstitial and "transitional" cells (Lang da Silveira and Van't Hof 1977). Adult *Gersemia rubiformis* colonies demonstrated good regenerative capacities following experimentally inflicted partial mortality, with new polyps emerging (Fig. 24) after less than 30 days. No fouling of the lesions by filamentous algae, hydroids or other organisms as seen in some warm water gorgonian octocorals (Wahle 1983b) was observerd. Octocorals tend to show good regenerative abilities, and future studies could determine whether histological repair processes in *G. rubiformis* proceed in a similar manner as those documented in other octocorals e.g., migration of epidermal interstitial and "transitional" cells, amoebocyte accumulation etc. (Lang da Silveira and Van't Hof 1977; Meszaros and Bigger 1999).

These preliminary results suggest that mechanical disturbances caused by crushing corals, designed to mimic disturbances caused by bottom fishing, appear to minimally impact *Gersemia rubiformis*. Although overall deteriorating colony conditions were noted in crushed corals, mechanical disturbances did not impair colony retraction and expansion for very long and experimentally-inflicted wounds that might occur during bottom fishing were rapidly regenerated. However, the premature explusion of brooded planulae may

have longer-term consequences for *G. rubiformis* populations by increasing mortality in juvenile stages and impairing coral recruitment.

CHAPTER SEVEN: CONCLUSIONS

The objectives of this thesis were to:

(1) identify impacts of bottom fishing on communities and life histories of colonial epifauna, and

(2) link observed impacts to life history responses to bottom fishing activities.

These objectives were met through a network of collaborations established within the Canadian Department of Fisheries and Oceans. Several impacts were identified *a priori* to occur as a result of commercial-scale fishing or after repeated experimental disturbance, and the results of this thesis concur with observations made by several others. This thesis also demonstrated potential mechanisms for how post-fished assemblages and taxa are produced by bottom fishing disturbances, all of which are related to the life histories of the individual taxa. Life history traits and biological responses of individual taxa are invoked in this section of the thesis to explain patterns observed during this and other studies.

Short- and long-term consequences of bottom fishing for colonial epifauna communities

The studies that comprised this thesis demonstrated that the potential for bottom fishing to alter communities of colonial epifauna is very high. These effects can be produced after very short time periods e.g., immediate damage to hydroids and expulsion of larvae by soft corals (Chapter Five, Chapter Six), or over periods of longer duration e.g., shifts in taxon composition (Chapter Three, Four) and reduced allocation to sexual reproduction processes (Chapter Five).

In the short term, bottom fishing alters taxon composition in colonial epifaunal communities (Gili et al. 1987, Hutchings 1990, Collie et al. 2000, Pitcher et al. 2000, Bradshaw et al. 2001, 2002). For example, repeatedly trawled communities in the impact line on Western Bank were significantly different from those observed before otter trawling (Chapter Three). Several important mechanisms can produce shifts in the relative proportions of taxa including fishing-induced clonality (Chapter Five), regeneration from partial mortalities and injury-related impairment of sexual reproduction (Chapter Two, Chapter Five) that lead to the increase in frequency of some but declines in the frequencies of other taxa. Colonies can become fragmented but survive and regenerate e.g., the sycettida-type sponge and the hydroid *Symplectoscyphus bathyalis* while others are killed e.g., the erect bryozoans *Dendrobeania* spp. and other sponges (Chapter Three), or have reduced fecundity e.g., the hydroid *Sertularia cupressina* (Chapter Five). Other short term effects of bottom fishing include mortality of small colonies but rapid regeneration of larger colonies (Chapter Two). For example, increased variation in biomass of the soft coral *Clavularia* sp. in the post-trawl periods on Western Bank could reflect size-dependent mortality of small corals and the resilience or rapid recovery from injuries caused by otter trawling in larger corals relegated to spatial refuges (Chapter Three).

Long-term effects of bottom fishing on colonial epifauna communities include suppressed natural changes in richness and reduced biomass variance (Chapter Three), shifts of life history traits exhibited by taxa in frequently disturbed areas (Chapter Four) and low clonal diversity (Chapter Five). Suppressed natural increases in colonial epifauna

richness observed in the impact line during the three year otter trawling experiment on Western Bank could be due to reduced recruitment of new taxa as a result of resident fauna rapidly sequestering available space after disturbance and therefore excluding other taxa from recruiting (Chapter Three). Long-term shifts in taxon composition of heavily fished colonial epifauna communities are reflected in the life history attributes of resident taxa (Gili et al. 1987, Hutchings 1990, Collie et al. 2000, Pitcher et al. 2000, Bradshaw et al. 2001, 2002). For example, moderately divergent taxon composition in the colonial hydroid assemblages between disturbed and relatively more stable substrata in the Bay of Fundy reflected major differences in the life histories of epilithic versus epizoic taxa (Chapter Four). Long-lived, slow-growing and arborescent taxa are not suited to frequent disturbance regimes imposed by commercial-scale scallop dredging in this region, and the potential for injury-related impairment of sexual reproduction seen in such species as *Sertularia cupressina* (Chapter Five) to limit recruitment combined with philopatric larval dispersal appears to limit the appearance of these taxa in heavily fished areas.

Consistent versus factor-dependent impacts

Several effects of bottom fishing on colonial epifauna communities were consistently observed across regions, habitats and gear/disturbance type e.g., shifts in taxon composition from vulnerable to less vulnerable taxa (Gili et al. 1987, Hutchings 1990, Collie et al. 2000, Pitcher et al. 2000, Bradshaw et al. 2001, 2002). The frequency of emergent colonial epifaunal taxa was often reduced after otter trawling on Western Bank e.g., the erect bryozoans *Dendrobeania* spp. and most sponges, including the species epibiotic on the brachiopod *Terebratulina* sp. (Chapter Three), the abundance of

which was also reported to decrease after trawling (E. Kenchington, unpublished data). Although life history traits of pre- and post-trawl taxa were not compared, chronic otter trawling may eventually produce levels of community divergence between fished and unfished areas similar to those observed for colonial epifauna exposed to opposite ends of a spectrum of intensity of commercial-scale scallop dredging in the Bay of Fundy (Chapter Four). Frequently disturbed substrata in this region were dominated by small, guerilla-growth strategists with little branching and mechanisms for potentially wide dispersal (Chapter Four). A second pattern that emerged across these studies was the potential for bottom fishing to fragment colonies and reduce clonal diversity (Chapter Two, Chapter Five). Increased frequencies of some sponges and hydroids after otter trawling on Western Bank were consistent with the idea of colonies being fragmented and essentially "cloned" (Chapter Three), ecological and genetic evidence for which was observed in hydroid colonies injured by scallop dredging in the Bay of Fundy (Chapter Five). A third effect that was consistently observed was the capacity for injuries and subsequent regeneration to impair normal sexual reproduction processes in colonial epifauna (Chapter Two, Chapter Five, Chapter Six). Impaired sexual reproduction was a highly ubiquitous response across colonial epifauna taxa in response to regeneration from injuries, including reduced sexual fecundity (Chapter Two, Chapter Five) or premature release of larvae (Chapter Six) that would subsequently limit recruitment of sexually-derived propagules. Low sexual fecundity of epilithic *Sertularia cupressina* colonies was probably due to damage inflicted during scallop dredging activities in the Bay of Fundy (Chapter Five), and in combination with reduced larval dispersal potential, may explain

the reduced frequency of this and other species on disturbed substrata in this region (Chapter Four). Frequently disturbed *Gersemia rubiformis* colonies shed sexually-derived larvae that did not survive for long, although this may have also been an artefact of *in vitro* aquaria conditions (Chapter Six). Species that decreased in frequency after otter trawling on Western Bank continued to decline in frequency throughout the study (Chapter Three), and this could reflect injury-related impairment of sexual reproduction and subsequent limitation in the recruitment potential of these taxa.

Other impacts of bottom fishing on colonial epifauna communities appear to depend on gear type, habitat type and the species themselves (Chapter One; Thrush et al. 1995; Collie et al. 1997, Collie et al. 2000). For example, significant decreases in colonial epifauna biomass were not observed after otter trawling on Western Bank (Chapter Three). Otter trawls are relatively less efficient than bivalve dredges and beam trawls in removing organisms inhabiting the seafloor (Prena et al. 1999), although the passing of the net, ropes and the doors that spread the trawl open likely inflict partial mortality to underlying colonial epifauna. Since the capacity to survive after injury depends on many factors including taxon-specific responses (Chapter Two), bottom fishing impacts should be taxon-specific in some cases (Thrush et al. 1995; Collie et al. 1997, Collie et al. 2000). For example, calcareous sycettida-type sponges and the hydroid *Symplectoscyphus bathyalis* were probably fragmented by otter trawling on Western Bank but regenerated and re-grew well after each disturbance (Chapter Three), whereas damaged colonies of other taxa probably did not survive as well as they declined in frequency in the impact line throughout the study (Chapter Three). Another example of taxon-dependent impacts

is demonstrated by the way in which taxa respond to mechanical disturbance. Rapid colony contraction responses to mechanical disturbances and fast regeneration from partial mortality may enable the soft coral *Gersemia rubiformis* to avoid being caught or killed by fishing gear (Chapter Six). These colony responses and rapid regeneration could also explain the survival and increased variability of *Clavularia* sp. soft corals after otter trawling on Western Bank, while spongs and bryozoans were probably fragmented and spread evenly over the disturbed and adjacent areas (Chapter Three). Taxon-specific effects are also combined with the effects of habitat type on impacts of bottom fishing. The ability for *G. rubiformis* and many other soft corals to retract their colonies may enable these corals to avoid fishing-induced mortality by permitting some corals to survive in refuges within gravel crevices e.g., persistence of *Clavularia* sp. on Western Bank (Chapter Three). This observation contrasts with the removal of large *Gersemia* sp. soft corals and overall soft coral biomass by otter trawling on a sandy bottom ecosystem on the Grand Banks of Newfoundland reported by others (Prena et al. 1999; Kenchington et al. 1999) where colonies probably received little refuge behind smaller sand sediments.

Unexpected impacts of bottom trawling on colonial epifauna communities

The *a priori* hypothesis that bottom fishing reduces taxon richness and biomass of colonial epifauna communities (Kaiser et al. 2000b; McConnaughey et al. 2000; Veale et al. 2000; Callaway et al. 2002) was not consistently observed in either study on Western Bank (Chapter Three) or in the Bay of Fundy (Chapter Four). Richness was affected by bottom fishing on Western Bank, but in an unexpected way: natural annual increases in the number of species were suppressed in the impact line (Chapter Three). Furthermore,

this effect would only be observed if the entire time series was examined over the three year period of the experiment. If suppressed annual increases in richness are observed after only three years, then commercial-scale chronic bottom fishing could produce species-poor communities of colonial epifauna.

Future research directions

Develop life history metrics

This thesis provided evidence for community divergence in colonial epifauna communities that was reflected in the life history traits exhibited by resident taxa on commercial fishing grounds (Chapter Four). This thesis was the first study to investigate how bottom fishing impacts sexual reproduction and the genetic consequences of these human activities on non-target benthic organisms (Chapter Five, Chapter Six). Mechanisms for community divergence include differential mortality and susceptibility to injuries (that depends on the degree of emergence from the seafloor and colony flexibility) (Chapter Three, Chapter Four, Chapter Six), regeneration (Chapter Three, Chapter Five, Chapter Six) and ecological consequences of injury repair including impaired sexual reproduction and reduced clonal diversity (Chapter Two, Chapter Five). Even at a smaller and shorter time scale, bottom fishing suppressed natural temporal dynamics of richness and biomass variance that also could be associated with injury-related impairment of other processes such as colony growth (Chapter Three), and demonstrated that experimentally trawled areas in a closed area could be rapidly colonized by local recruitment of sexually-derived larvae, colony fragments or re-settled colonies (Chapter Three). Differential effects of bottom fishing in the closed area could

also be related to variability in life histories including susceptibility to disturbances mediated by colony contractability (Chapter Three, Chapter Six), the potential to survive colony fragmentation and the ability to rapidly regenerate from injuries (Chapter Five, Chapter Six). Results of this thesis support conclusions by others that life history "syndromes" *sensu* Dupré and Diekman (2001) of colonial epifauna from chronically fished marine ecosystems are characterized by taxa with flexible or physically robust colonies with high mobility over the substrata, and small unbranched runner- and vine-shaped growth forms with potentially wide dispersal and short lifespans (Gili et al. 1987; Hutchings 1990; Pugh 1999; Collie et al. 2000; Pitcher et al. 2000; Bradshaw et al. 2001, 2002). This thesis also demonstrated that the relative absence of some taxa that typically live epibiotically on long-lived large colonial epifauna (e.g., the auto-epizoic hydroid *Calycella syringa* on the hydroid *Sertularia cupressina*) should be noted, as it suggests that community divergence in response to bottom fishing has consequences for associated fauna and marine biodiversity (Chapter Four). Results from this thesis also provide preliminary evidence for fishing-related impairment of sexual reproduction and reduced genetic biodiversity in non-target benthic organisms (Chapter Five, Chapter Six).

Although immediate community-level impacts of bottom fishing are detectable using more traditional metrics e.g., taxonomic composition or feeding guilds, long-term shifts in species composition might be better characterized by examining the differences in biological attributes (e.g., life history traits) between fished and unfished communities (Thrush and Dayton 2002; Bremner et al. 2003). The ecological significance of life history divergence in marine ecosystems is that species replacements and shifts in life

history traits could lead to altered functional diversity i.e., the diversity of ways in which component organisms contribute to the functioning of that ecosystem (Bremner et al. 2003). With respect to functions provided by colonial epifauna, replacement of large emergent arborescent colonies by more "mobile" refugial runner- and vine-shaped colonies could lead to impaired ecosystem functioning by limiting recruitment, plankton production and survival of other marine organisms that use these three-dimensionally complex animals as living "biogenic" habitat (Bradstock and Gordon 1983; Sainsbury 1987; Hutchings 1990; Sainsbury et al. 1993; Walters and Juanes 1993; Auster et al. 1995, Tupper and Boutilier 1995; Auster et al. 1996; Probert et al. 1997; Jennings and Kaiser 1998; Collie et al. 2000; Kaiser et al. 1998, 2000a; Thrush et al. 2001; Rogers 1999; Dayton et al. 2002; Kaiser et al. 2002).

Life history metrics that could indicate long-term biological impacts of bottom fishing on colonial epifauna must consider growing evidence, both from this thesis and that of others, of community shifts towards smaller, less emergent and more mobile, robust taxa with high dispersal and short lifespans, as well as changes or absence of associated fauna. In the short-term, evidence provided in this thesis for impaired sexual reproduction and a loss of genetic biodiversity could be used to indicate biologically significant impacts of bottom fishing.

Developing useful life history metrics as indicators to detect biological impacts of bottom fishing on colonial epifauna requires more detailed life history information including an understanding of species' population dynamics (Jennings and Cotter 1999; Jennings et al. 1999), particularly aspects of sexual reproduction and genetic structure

(Hutchings 1990). Thus, the caveat to incorporating life histories into metrics for impact analyses is that it requires categories of life histories to be accurately assigned to individual taxa where there may be little to no life history information. Future research effort could be directed into elucidating which attributes best discriminate areas exposed to variable levels of fishing intensity across gear and habitat types to find useful metrics that require less detailed life history information e.g., body form and flexibility *sensu* Bremner et al. (2003). In the likely event of resource-limited bottom fishing impact studies, genetic studies could be limited to taxa where the extent of fishing-related impairment of sexual reproduction and colony damage are predicted to be fully realized e.g., vulnerable species (Henry et al. 2002) with large emergent growth forms, slow growth rates, delayed sexual reproduction and potentially limited dispersal capacities such as many deep-water corals sponges (Jones 1992; Probert et al. 1997; Probert 1999; Rogers 1999; Koslow et al. 2001; Thrush and Dayton 2002).

Investigate consequences of regeneration in colonial epifauna exposed to bottom fishing

The importance of colony regeneration as an ecological process in recovery from disturbance in colonial epifauna communities has long been recognized (Fishelson 1973; Loya 1976a; Pearson 1981; Fadlallah 1982; Karlson 1983; Hughes and Jackson 1985; Done 1987, 1988; Cameron et al. 1991; Bythell et al. 1993; Jokiel et al., 1993; Connell et al. 1997; Lasker and Coffroth 1999). Few studies on bottom fishing impacts refer to this process (but see Tilmant 1982; Van Dolah et al. 1987; Freese et al. 1999; Jenkins et al. 2001; Bradshaw et al. 2002), although this may reflect the relative paucity of studies on

colonial epifauna relative to solitary fauna (Collie et al. 2000), the former which possess the ubiquitous ability to survive some degree of colony death (Jackson 1977; Buss 1979).

The review provided in this thesis offers substantial evidence for resource-driven alterations to other colony life history processes including sexual reproduction, growth and encounters with other organisms (Chapter Two) suggested by others (Rinkevich 1996; Meesters et al. 1997a). Concurrent with this review and evidence for impaired sexual reproduction demonstrated in this thesis (Chapter Five, Chapter Six) is the following hypothesis: fishing-related injuries sustained by colonial epifauna and their subsequent regeneration have most likely resulted in altered colony processes that have likely limited recruitment of sexually-derived propagules, reduced growth in some species but accelerated growth in others (possibly inducing tumour formation), and altered species interactions including the ability to deter predators, compete with other species and engage in histocompatibility-mediated fusion-rejection processes between conspecifics. The full extent of altered colony processes as a result of injury and regeneration is not known, but the existence of novel competitive hierarchies in fished ecosystems suggests that these ecological consequences can be realized. For example, gorgonian and scleractinian corals damaged by bottom fishing are fouled by competitively inferior organisms such as algae, hydroids, serpulid worms and boring sponges (Van der Knapp 1993) that compromise the physical integrity and survival of the colony. This hypothesis is testable and would offer further insight into how long-term changes in colonial epifauna communities exposed to chronic bottom fishing are achieved, and what shifts can be predicted in the future.

Incorporate sexual activity of colonial epifauna into fisheries closures measures

The potential for injury and regeneration to impair sexual reproduction is particularly relevant to address, as the long-term decline in populations of colonial epifauna are often related to recruitment limitation (Buhs and Reise 1997; Connell et al. 1997; Berghahn and Offermann 1999; Cropper and DiResta 1999), which in turn is related to sexual fecundity (Hughes et al. 2000). The high incidence of fishing-related injuries reported on colonial epifauna (e.g., 23% of epilithic hydroid colonies reported in this thesis, Chapter Five) and the potential for premature release of potentially unviable larvae (e.g., demonstrated by *Gersemia rubiformis* in this thesis, Chapter Six) suggest that the potential for injury and regeneration to impair sexual reproduction and recruitment can be very high in populations from chronically fished marine ecosystems.

Fishery closures during seasons of sexual activity of marine seagrasses were recommended to mitigate impacts of bottom fishing operations e.g., scarring and loss of reproductive structures, on these aquatic plants (Francour et al. 1999; Stephan et al. 2000; Bell et al. 2002). Provided that partial closures are a management option, similar measures may help mitigate impacts on colonial epifauna by restricting bottom fishing from breeding seasons of potentially vulnerable taxa e.g., those with high probability of experiencing impaired sexual reproduction after injury and regeneration, or those with naturally low fecundity or delayed sexual maturity.

Link bottom fishing with recruitment limitation and genetic diversity

Limited scientific resources necessitate restricting research studies on bottom fishing impacts that are defined by global, regional and/or political priorities. Much

attention has been given to the need for mapping fishing effort and associated habitats, studies at the scale of actual fisheries and on actual fishing grounds, and more information on deep-water ecosystems that have been relatively less fished than ecosystems on continental shelves (e.g., Thrush et al. 1995, Probert et al. 1997; Thrush et al. 1998; Probert 1999; Collie et al. 2000; Kaiser et al. 2000b, 2002).

This thesis demonstrated preliminary evidence for fishing-related impairment of sexual reproduction and induced clonality in a colonial epifaunal organism at the spatial and time scale of a commercial scallop fishery on a continental shelf of Atlantic Canada (Chapter Five). Suppressed sexual reproduction and colony fragmentation not only limit recruitment of sexually-derived propagules, but they can also reduce genetic variability in colonial epifauna, especially under conditions of high colony mortality (Coffroth and Lasker 1999). The hypothesis that bottom fishing limits recruitment and reduces genetic variability in clonal taxa at the scales of real fisheries is testable and probably most tractable using genetic techniques and combining results with fisheries effort data to infer relationships between effort and impacts.

Identify "sources" and "sinks"

This thesis demonstrated that live scallop substrata support highly fertile hydroid colonies in the Bay of Fundy, and the results suggest that epizoic colonies may help sustain epilithic colonies. Therefore in addition to injury- and regeneration-based impairment of sexual reproduction, bottom fishing could also limit recruitment of sexually-derived propagules by destroying patches of larval "sources" that potentially sustain "sink" populations (Frid et al. 1999, 2000; Fosså 2002). Genetic studies will help

reveal recruit sources and sinks that could overlay maps of commercial-scale fishing effort to identify areas critical to the maintenance of genetic diversity in colonial epifauna metapopulations. The potentially high vulnerability of colonial epifauna in deep-water ecosystems to bottom fishing disturbances should place these organisms at a high level of research priority, particularly as fishing-related injuries are expected to exacerbate colony resource limitations that are reflected in the slow growth rate of many deep-water organisms (Jones 1992; Probert et al. 1997; Probert 1999; Rogers 1999; Koslow et al. 2001; Thrush and Dayton 2002).

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