

2004

Spatial Variations in Benthic Invertebrate Assemblages in and Around the Georges Banks Closed Areas

andrew Clayton Walker

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Spatial Variations in
Benthic Invertebrate Assemblages
in and around the
Georges Bank Closed Areas

THESIS

Presented to:

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Science

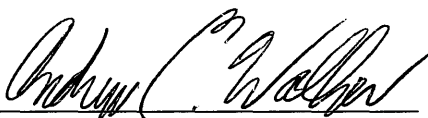
by

Andrew Clayton Walker

2004

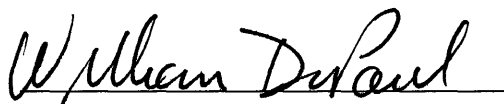
APPROVAL SHEET

This thesis is submitted in partial fulfillment of
the requirements for the degree of
Master of Science




Andrew C. Walker

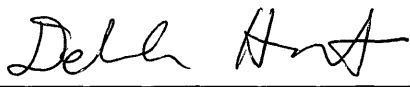
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ACKNOWLEDGEMENTS

Major Advisor – William DuPaul. For allowing me the opportunity to attend VIMS, firmly placing me into the world of scallops, and for keeping me out of debt.

Committee Members – Robert “Bob” Diaz, Deborah “Dvora” Hart (NEFSC), and Roger Mann. Bob, thank you for all your statistical help and support. Dvora, thank you for all the expertise on scallops and scallop fishery statistics that you bring to the table. Roger, thank you for all your help in making certain that my thesis was written in the best English form and not structurally American.

The Scallop Observing Program – Patricia Yoos and everyone at A.I.S., thank you all for a wonderful work experience after my undergraduate career and for propelling me into graduate school.

Technical and Moral Support – David Rudders, Todd Gedamke, Wolf Lange, John Walter, David Evans, and Chris Bonzek. Thank you all for your moral support, aid in statistics and computer software (SPSS, S-Plus, ArcView, etc.), and for making sure I did not trip over obstacles you may have went through in acquiring your own graduate degrees.

R/V *Albatross IV* Captains, Crew, and Volunteers – Too many named and unnamed individuals to recall. Thank you all for your aid and understanding in my collection of a freezer full of invertebrate samples that you all saw as “trash.”

R/V *Albatross IV* Chief Scientists – Victor Nordahl and Nancy McHugh. For helping to make sure all my sampling was completed while I was awake or asleep.

Laboratory Assistance – Tiffany Harvey. For your help lasting eight hours per day for weeks on end. Counting and weighing invertebrate samples is one thing, but being able to stick around through the smell that made all Maury Hall residents flee made you an even greater asset than I could ever have hoped for in a summer aide. Thanks again.

Species Identification – Lea Anne-Henry (Dalhousie University, Nova Scotia) for her help with hydroids and bryozoans; John Dearborn (U. Maine), Cynthia Ahearn (Smithsonian), and Sabine Stöhr (Swedish MNH) for their aid with brittlestars; and Vincent Guida (NMFS) as the best all around go-to-guy for Northeast Atlantic species identification. Additionally, I would also like to thank Barbara Hecker for both introducing me to Vincent Guida as well as teaching me the ropes in her Invertebrate Zoology course at the Marine Biological Laboratory in Woods Hole, MA as part of the Boston University Marine Program.

All of Advisory Services Staff – Special thanks go to Cheryl Teagle and Dianne Roberts for helping me through the stacks of paperwork, mailing correspondence, and knowing I was around when Bill was away.

The VIMS Community – Thanks goes out to fellow students, faculty, and all other employees for being available when help is needed. It was wonderful being able to know that the answer to any question, the need for any equipment, and any other aid in general was only a few steps, a phone call, or an e-mail away. Make sure to keep the Toilet Bowl alive, it keeps us sane.

Exam Moderators – John Graves. For controlling a room full of crazy scientists, twice.

My Family – Mom, Dad, my sister Carrie and her husband Matt. Thank you for everything from moral and financial support to guidance and wisdom. Also, a special thanks to my sister Carrie for not killing me for disembarking from the R/V *Albatross IV* roughly a week prior to her wedding. I told you I'd make it!

My Fiancé – Ann Marie Alves. How we made it through my Masters program, your Fordham Law program, and planning a wedding for August 2004, I will never know!

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ABSTRACT

As Congress moves towards the upcoming proposed reauthorization of the Sustainable Fisheries Act in 2005, science will be further called upon to aid in the identification of essential fish habitat and establishment of marine protected areas. Recent concerns over including the commercial species *Placopecten magellanicus* in studies that compare the effects of mobile fishing gear on benthic invertebrates across closed area boundaries have prompted this research to address the issue.

Sampling was conducted using a mesh-lined, eight-foot New Bedford-style scallop dredge 138 stations (sea scallops present at 120 stations) across the Georges Bank region during the 2002 NOAA sea scallop survey cruise. Five ecological variables were determined: density, biomass, species richness, Pielou's Evenness, and the Shannon-Wiener Diversity Index.

Analysis of the data determined that variations in overall ecological variables were attributable to environmental factors such as depth, sediment type, and geographic location, as well as defined fisheries regions, all to varying degrees. In addition, invertebrate scavenger and opportunistic predator data showed no significant change in association to open or closed area, though increased fishing pressure within open fishing regions led to decreases in observed biomass. Furthermore, distance from a closed area boundary as well as the level of fishing effort were not observed to be significant indicators of ecological variables, though transect-based research projects may illicit better results.

In analyzing for a bias due to the commercial species *Placopecten magellanicus*, removal of the sea scallop and its attached epifauna from the analysis determined that species richness was the only ecological variable found to be significantly greater within closed area regions. Species that were present in association with live sea scallop shell within open areas were additionally observed attached to benthic substrate within closed fishing regions. Epifaunal taxa within open areas were less likely to find a stable attachment site aside from small (<100mm) *Placopecten magellanicus* shells due to active fishing pressure which removed larger scallops and disturbed the benthic environment. When *Placopecten magellanicus* epifauna were included in the analysis, only biomass was found to be significantly greater within closed area regions. This increase in biomass was associated with the increased surface area of live *Placopecten magellanicus* present within the closed areas. Though the fishery shucks the scallops at sea and returns the shells to the benthic environment, attached epifauna are not found to proliferate on this substrate.

The results of this study suggest that including commercially retained species within the estimates for ecological variables can bias the data collected. In addition, these results suggest that estimates for the recovery time of benthic environments on Georges Bank should be reevaluated, with future investigations taking this bias into account.

**Spatial Variations in Benthic Invertebrate Assemblages
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INTRODUCTION

Background

Description of Georges Bank

Georges Bank is defined as a section of the Northwest Atlantic continental shelf extending east of Cape Cod, Massachusetts (Figure 1). It is one of the southernmost banks in a range that extends north to the Grand Banks of Newfoundland. Georges Bank is separated from Canada's Scotian shelf by the Northeast Channel as well as from the Nantucket Shoals by the Great South Channel. The Nantucket Shoals shelf region is occasionally studied along with Georges Bank due to its similarity in physical morphology and biologic diversity. The bathymetry of Georges Bank extends roughly 150 km in latitude and 300 km in longitude, giving an area of nearly 34,000 km² extending to the 100 m isobath (Backus, 1987; Uchupi and Austin, Jr., 1987). Surficial sediments on the bank are primarily sand with large portions being dominated by sandy shoals. Some areas of Georges Bank such as the northern portion south of Georges Basin, Great South Channel, and the northeast Nantucket Shoals, however, are composed of gravel pavements with patchy distributions of glacial erratics present to varying degrees (Twichell et al., 1987; Uchupi and Austin, Jr., 1987; Theroux and Wigley, 1998; Murawski et al., 2000). Organic carbon within the bottom sediments of Georges Bank is generally low, making up less than 0.5% by weight of the sediment (Theroux and Wigley, 1998).

The geologic morphology of the Northwest Atlantic also provides Georges Bank with a net clockwise gyre circulation. This circulation is initiated by inflow from the Scotian shelf as well as the Gulf of Maine's counterclockwise gyre and exits either off-

shelf or southeast along the continental shelf of the United States (Butman and Beardsley, 1987; Theroux and Wigley, 1998). This circulation, along with other physical processes such as stratification and nutrient recycling, promotes high year-round levels of primary production (O'Reilly et al., 1987). Circulation, however, is not truly “enclosed” as it is in locations such as the North Sea where the presence of land reduces loss from the system. Due to the outflow present on Georges Bank, seasonal strength of the gyre circulation has been strongly associated with the levels of zooplankton, larval fish, and larval invertebrate abundance present in the water column (Bourne, 1987b; Mountain and Schlitz, 1987; Sherman et al., 1987). Some species such as cod and haddock use this circulation to their advantage and reproduce during the seasons when circulation and system retention are the strongest (Fogarty et al., 1987; Mountain and Schlitz, 1987; Sherman et al., 1987).

History of Georges Bank Benthic Fisheries

The hunt for Atlantic cod, *Gadus morhua* (Gadidae), was the one of the major reasons for migration to North America. The Vikings were the first to do so around 1000 AD, likely within the Newfoundland region of Canada. By the early 1500s, French, English, and Portuguese fishermen were crossing the North Atlantic to exploit the Newfoundland cod stock (Innis, 1940; German, 1987; Jennings et al., 2001). Cod were also the initiator of fishing on Georges Bank, with a true exploitation of the stock beginning during the middle of the 18th century by New England fishermen. Early development of the fishery was not overly detrimental to the stock as handlining persisted for some time. Technological changes to vessels and their gear, however, hastened the

exploitation of cod to a greater and greater extent. These advancements included: 1) the use of ice rather than salt for preservation purposes starting around the 1870s, 2) steam-powered side otter trawlers entering service around 1880, and 3) diesel-powered vessels becoming common by 1930, which allowed for the introduction of 4) stern otter trawlers around 1940 (Bourne, 1987a; German, 1987; Jennings et al., 2001).

Haddock, *Melanogrammus aeglefinus*, is another Gadidae species that has played an important role in benthic fisheries on Georges Bank. Landings on the bank steadily increased after the introduction of line trawling around 1860 (German, 1987). The haddock fishery, much like that for cod, saw the same trends in technological advancement mark a decline in the available stock biomass. In addition, due to the small cod-end mesh sizes on trawl nets, large levels of young haddock were caught as bycatch and caused further decreases in the stock (Hennemuth and Rockwell, 1987). Though haddock had been the major Georges Bank fishery during the early 20th century, the stock collapsed around 1930 and has fluctuated ever since (German, 1987; Hennemuth and Rockwell, 1987).

Several species of flatfish have also been influential to Georges Bank fisheries. Halibut, *Hippoglossus hippoglossus*, as with many other species, were originally fished inshore until stocks declined. In 1830, fishermen began to head offshore for halibut, and by 1836, a major fishery had developed on Georges Bank (German, 1987). Though the fishery primarily used handlining, the halibut stock collapsed around 1850 and has never truly recovered since bycatch of halibut in other fisheries continued to deplete the stock (Bourne, 1987a; German, 1987; Hennemuth and Rockwell, 1987). During this period, winter flounder, *Pseudopleuronectes americanus*, and yellowtail flounder, *Limanda*

ferruginea, were rarely caught as bycatch in other Georges Bank fisheries due to their relative small size (German, 1987). Inshore fisheries for flatfish increased around 1900 with the use of beam trawlers, but did not see exploitation on Georges Bank until around 1915 when otter trawlers began targeting winter flounder (Hennemuth and Rockwell, 1987). Market share also increased with the introduction of filleting in the 1920s (German, 1987). By the 1930s, winter flounder stocks began to decline, leading to increased interest in yellowtail flounder. Once these stocks began to decrease in the 1950s, fishermen began to move to the scallop fishery (Hennemuth and Rockwell, 1987).

Finally, some benthic invertebrates have made important contributions to Georges Bank fisheries as well. Sea scallops, *Placopecten magellanicus*, first fished for in the Gulf of Maine during the 1880s, were not exploited on Georges Bank until 1928 (German, 1987; Hennemuth and Rockwell, 1987). This exploitation was due to the introduction of the offshore New Bedford sea scallop dredge, capable of fishing on Georges Bank, which requires a heavier steel frame than comparable inshore dredges (Smith, 1987). In addition, if sea scallop abundance decreased, vessels were able to use the gear to target flounders in other locations (Hennemuth and Rockwell, 1987). Lobsters, *Homarus americanus*, were first fished for on Georges Bank using otter trawlers, but landings were usually damaged; by 1962, however, fishermen had decided to use strings of large lobster pots to increase the quality of their catch (Hennemuth and Rockwell, 1987; Smith, 1987). Initial landings were large with many lobsters weighing upwards of 20 pounds, but once these were fished out, levels dropped off and stabilized by 1975 (Hennemuth and Rockwell, 1987).

Management Strategies

In the early years of fisheries exploitation on Georges Bank, management followed the idea of the “commons” (Hardin, 1968). By the mid-19th century, however, the United States realized that their lack of basic fisheries statistics was placing themselves and certain fisheries stocks at risk. Around 1880, the U.S. Fish Commission required that fishermen reported their landings so that proper fisheries research could be conducted (Hennemuth and Rockwell, 1987). To further research, the United States, Canada, Newfoundland, and France formed the North Atlantic Council on Fishery Investigations (NACFI), and by 1930, most single-species fisheries were well known. With the formation of the International Commission for Northwest Atlantic Fisheries (ICNAF) in 1949, fisheries research grew rapidly and began to collect data on vessels, gear, and effort in addition to basic landings data.

By the 1930s, another management issue became a concern, that of bycatch. The current definition of bycatch is “fish which are harvested in a fishery, but which are not sold or kept for personal use, and includes economic discards and regulatory discards” (SFA section 3(2)). Bycatch has become an issue of importance in recent times, where as in the past, any bycatch of valuable fish could be landed along with the target species without additional permits. This issue began with the United States taking notice of the collapsing haddock stock and funding further research into the cause of it. From this research came the realization that bycatch of young haddock was due to smaller than necessary mesh in the cod-end of otter trawls and had undermined stock biomass. In 1952, the first regulation made by the ICNAF was to further study this problem by looking at increasing mesh size in the cod-end from 2.5 to 4.5 inches (Hennemuth and

Rockwell, 1987). These studies found that bycatch of undersized haddock discards sharply decreased, but no appreciable increase in yield resulted, though this was likely due to other factors such as the introduction of artificial fiber nets. This research quickly spread the use of larger mesh nets to all the Georges Bank trawl fisheries.

By 1961, however, a new larger menace beset Georges Bank as well as other regions, that being the threat of the long-distance fleet. The initial interest in Georges Bank came with the Russian fleet finding large concentrations of herring and hake present there (Hennemuth and Rockwell, 1987). With little interest in either Canada or the United States, these species were ripe for the taking. Other countries such as Poland, Spain, and Germany soon joined in. In 1963, Canada made the decision to increase its cod and haddock fisheries on Georges Bank in view of the increased pressure from the foreign fleets on other fisheries. With a significant year class recruiting to the fisheries, the Soviet Union decided to shift some of their effort to the cod and haddock fisheries as well. This increased effort quickly depleted the haddock stock and led the ICNAF to declare a total allowable catch (TAC) of 12,000 metric tonnes in 1970 (Hennemuth and Rockwell, 1987). In addition, two areas of Georges Bank were closed to trawling during the spring to protect spawning grounds (Murawski et al., 2000). This management effort largely tied the hands of local fishermen and not the foreign fleets, and with continued observed declines, ICNAF declared a TAC of zero metric tonnes in 1972 as even bycatch of haddock was deemed unsustainable. Similar problems were occurring with other stocks to such an extent that the United States and Canada convinced the ICNAF to set TACs for 18 major fisheries, with limitations for each nation involved (Hennemuth and Rockwell, 1987).

In addition to the actions taken by the ICNAF, the United States instigated its own large sweeping decisions. In 1976, Congress passed the Magnuson Fishery Conservation and Management Act (MFCMA) which removed the foreign fleets from Georges Bank and other regions by creating a two-hundred mile economic exclusion zone (EEZ) for fisheries management. In addition, eight regional management councils were created. Though the MFCMA removed the fishing pressure caused by foreign fleets, fishermen were not quick to accept additional regulations. Some management efforts, such as protecting spawning grounds and mesh size limits were accepted, while TACs were met with resentment. Throughout this, however, the National Marine Fisheries Service (NMFS) and the regional councils persevered, and by 1982, landings on Georges Bank had returned to pre-foreign fleet levels (Hennemuth and Rockwell, 1987). The final issue that the MFCMA created was the EEZ boundary issue between the United States and Canada. After much discussion, in 1984, the International Court of Justice set the final boundary giving most of Georges Bank to the United States, with Canada receiving the Northeast Peak portion of the bank (Christie, 1987; Figure 2).

A more recent method of fishery management to see increased use is that of closed areas. In 1970, seasonal closures were implemented to protect haddock spawning grounds. By the early 1990s, these closures lasted from January to June in both the United States and Canada. In 1986, a similar seasonal closure was initiated for yellowtail flounder by the Northeast Multispecies Fishery Management Plan (NEMFMP). Both of these closure systems shared a common problem in that the spawning stock aggregations were frequently present in the area either prior to or after the closure, thus leading to high fishing mortality during these periods (Murawski et al., 2000). By 1994, scientists, along

with the New England Fishery Management Council (NEFMC), had recognized that more drastic measures needed to be taken. This realization led to Amendment #5 of the NEMFMP which quickly set the stage for change in the future. Foremost among the changes was the creation of three large areas on Georges Bank and Nantucket Shoals that were closed to all bottom gear capable of retaining groundfish (i.e. dredges, otter trawls, gill nets, and hook and line gear), with the exception of lobster pots (Figure 2). In addition, other management steps in Amendment #5 and later revisions included reducing days at sea (DAS) for fishing vessels by 50% over a period of years, increased trawl mesh size, set trip length limits, and established a moratorium on new vessel entrants into any of the fisheries (Murawski et al., 2000).

Much of this change came as scientists and managers alike realized that protecting habitat, both physical and biologic, was as important as managing the exploited stocks. Congress also recognized this and stated that “one of the greatest long-term threats to the viability of commercial and recreational fisheries is the continuing loss of marine, estuarine, and other aquatic habitats. Habitat considerations should receive increased attention for the conservation and management of fishery resources of the United States” (SFA section 2(a)(9)). With this knowledge, Congress passed the amended Magnuson-Stevens Fishery Conservation and Management Act (also known as the Sustainable Fisheries Act [SFA]) in 1996 (initially reauthorized in 1994). Included within the SFA was a measure requiring “essential fish habitat [EFH]” to be described and was defined as “those waters and substrate necessary to fish for spawning, breeding, feeding or growth to maturity” (SFA section 3(10)). To accomplish this, Congress required that

“the Secretary [of Commerce] shall, within 6 months of the date of enactment of the Sustainable Fisheries Act, establish by regulation guidelines to assist the [Regional Fishery Management] Councils in the description and identification of essential fish habitat in fishery management plans (including adverse impacts on such habitat) and in the consideration of actions to ensure the conservation and enhancement of such habitat. The Secretary shall set forth a schedule for the amendment of fishery management plans to include the identification of essential fish habitat and for the review and updating of such identifications based on new scientific evidence or other relevant information.” (SFA section 305(b)(1)(A))

Additionally, recognition of “habitat areas of particular concern” (HAPC) and regulation of such areas was to be made possible through fishery management plans (Murawski et al., 2000). Since that time, the NEFMC has adopted the recommendation and set aside a portion of Closed Area II (Figure 2) south of the area’s northern 50 fathom depth limit as it was known to be a nursery ground for cod and haddock (Lough et. al, 1989; Collie et al., 1997; Murawski et al., 2000, Fig. 2)

Finally, the Atlantic Sea Scallop Fishery Management Plan (ASSFMP) also took measures to better manage future stock biomass with the passing of Amendment #4 in 1994. In addition to using several of the same steps as the groundfish plan, scallop dredges have been regulated by increasing their ring size and twine top mesh size, both as methods to reduce bycatch of groundfish as well as small unmarketable scallops. Furthermore, the ASSFMP included a measure to reduce crew size to nine men (later decreased to seven) as a method to control the overall available fishing effort per fishing vessel. In 1998, as an additional deterrent to fishing violations within the closed areas, scallop vessels were required to possess vessel monitoring systems (VMS) to track each vessel via the Global Positioning System (GPS). By 1998, both total biomass and

abundance of sea scallops had increased by roughly an order of magnitude within the groundfish closed areas, as well as marginally outside the boundaries (Murawski et al., 2000). In 1999, a section of Closed Area II (Figure 2), south of 41°30'N, was briefly opened to the scallop fleet through a special limited access program. This program set two TACs, one for the directed scallop fishery as well as another for yellowtail flounder bycatch. This helped to control bycatch issues previously uncontrollable during the years of foreign fleet overexploitation (Hennemuth and Rockwell, 1987). As an additional management effort, NMFS also placed fishery observers on over 25% of the vessels entering the closed area (NEFMC, 2000). The system showed such a great level of success that in 2000 all three closed areas were briefly opened in succession which has allowed for record scallop landings in recent years.

Literature Review

Since 1990, many studies have examined factors that affect benthic habitats. The first obvious division is that of natural and anthropogenic effects. Natural effects, such as storms, tides, and currents, all play significant roles in shaping benthic habitats. Organisms, in general, are adapted to the continuous factor that tides and currents play, though these can help to reshape the sediment on or within which benthic organisms inhabit. Storms, however, are not generally predictable, and likely cause some degree of unexpected change to the environment. Additionally, storms are likely a factor in removing visible anthropogenic effects such as gear tracks. With a large portion of Georges Bank being of average continental shelf depth (50-100m), storm impacts are somewhat limited in comparison to nearshore and estuarine waters.

Though some stationary fishing gear is used on Georges Bank, their effects on the benthic environment are generally quite localized. Anthropogenic effects caused by mobile fishing gear, however, are by most accounts the greatest threat to benthic habitats in the region. Depending on gear type as well as the gear's individual factors such as weight, size, tow speed, and sediment penetration, various effects occur to the benthos (Jones, 1992; Johnson, 2002). These effects include damage to the physical and biogenic structure of the bottom, sediment resuspension, changes in sediment and water chemistry, and changes to the organism assemblages present locally and within the ecosystem as a whole (Brylinsky et al., 1994; Johnson, 2002).

Previous Fishing Effects Studies

Research into fishing effects on habitat, as well as the use of protected areas as a means of increasing species abundance, biomass, and habitat diversity, has occurred throughout the Northwest Atlantic and the rest of the world. Two mobile gear types: 1) otter trawls and 2) scallop dredges, are associated with most of the habitat destruction occurring in the Georges Bank region. Other gear types such as clam dredges and lobster pots are also currently used within the region. These gears may cause a great deal of injury to physical and biologic structures, but this damage is generally quite localized (Johnson, 2002; NEFSC, 2002).

Several studies have examined fishing effects of otter trawls on the benthic environment. In sandy environments, otter trawl impacts are generally moderate. Otter trawl doors leave physical tracks across the sediment to several centimeters in depth that persist for a period of days to as long as a year depending on the depth of the site

(Churchill, 1989; Kaiser and Spencer, 1994; Schwinghamer et al., 1998; NEFSC, 2002). Gilkinson et al. (1998), using a test tank, found that these tracks displaced infaunal bivalves, though relatively few were damaged by this disturbance. Also in 1998, Schwinghamer et al. found that trawls generally smoothed the benthic environment by flattening both sand ripples and biogenic mounds. In areas of recurrent fishing, studies also found decreases in abundance and biomass of epibenthic macrofauna (de Groot et al., 1984; Brylinsky et al., 1994; Kaiser and Spencer, 1994; Engel and Kvitek, 1998; Frid et al., 1999; Prena et al., 1999; McConnaughey et al., 2000; Moran and Stephenson, 2000; Drabsch et al., 2001; Kenchington et al., 2001; Schratzberger et al., 2002). Small benthic infauna and epibenthic scavengers were generally unaffected or showed a slight increase in abundance, though organisms exhumed from the sediment were likely to be preyed upon (de Groot, 1984; Engel and Kvitek, 1998; Frid et al., 1999; Jennings et al., 2002; Johnson, 2002).

Otter trawls have an even greater effect on gravel habitats than comparable sandy locations. Impacts to physical and biogenic structures last months to years, while permanent removal of physical features can occur as boulders may be moved some distance by fishing gear (NEFSC, 2002). Auster et al. (1996) found that modifications to trawling gear had opened up structurally complex areas of benthic habitat to fishing in the Gulf of Maine in the early 1990s. The study found that the gravel base had been exposed from under a previously existing fine sediment layer, boulders were displaced, and sponges and other epifauna had been removed. A study in the Gulf of Alaska found similar results with large amounts of attached epifauna damaged by only a single pass of the otter trawl gear (Freese et al., 1999).

The other major gear used on Georges Bank is the New Bedford-style sea scallop dredge. Though not used in mud habitats, its effects elsewhere on physical and biogenic structures are generally high (NEFSC, 2002). In sandy environments, dredging is known to smooth sand structures, though large seasonal storms will periodically reform them (Butcher et al., 1981; Thrush et al., 1995; Auster et al., 1996; Currie and Parry, 1996, 1999; Black and Parry, 1999). Black and Parry (1999), among others, noted that dredges can leave tracks up to 6 cm deep within soft sediments, as well as ridges due to the ring bag (Caddy, 1968; Thrush et al., 1995; Currie and Parry, 1996, 1999). Epifaunal communities and structures were generally disrupted by dredging, with reductions in abundance and diversity lasting from months to years, while that of infauna showed little change (Poiner and Kennedy, 1984; Eleftheriou and Robertson, 1992; Currie and Parry, 1996, 1999; Watling et al., 2001; NEFSC, 2002). In some areas, indirect effects on the benthos, such as a change in substrate due to dredging, may also be a factor affecting biodiversity (Jones and Candy, 1981).

In gravel habitats, dredges cause even greater damage to biogenic and physical structures than in sand environments, with effects lasting from months to years (NEFSC, 2002). As with sandy substrates, dredges also cause a smoothing of substrate structures as well as the formation of tracks in gravel locations, either from the dredge itself or plowed boulders (Caddy, 1973; Valentine and Lough, 1991). In addition, large, sessile, epifaunal organisms showed reductions in abundance, biomass, and diversity in dredged areas (Valentine and Lough, 1991; Collie et al., 1997, 2000; Veale et al., 2000). Studies also found that “bushy” taxa, such as bryozoans, hydroids, and tubes (amphipod or worm), were largely disrupted by dredging (Langton and Robinson, 1990; Collie et al.,

1997, 2000; Hill et al., 1999). Those species that were better adapted to the physical disturbance of dredging generally included larger molluscs, echinoderms, and predators such as starfish, crabs, and whelks (Collie et al., 1997; Hill et al., 1999; Murawski et al., 2000; Bradshaw et al., 2002).

Project Goals, Hypotheses, and Rationale

Project Justification

Biodiversity is an important area of research in ecology that will continue to be studied far into the future. E.O. Wilson (1997), who coined the term biodiversity, defines it as “all hereditarily based variation at all levels of organization, from the genes within a single local population, to the species composing all or part of a local community, and finally to the communities themselves that compose the living parts of the multifarious ecosystems of the world”, while Levington (1995) summarizes it as “a parameter describing, in combination, the species richness and evenness of a collection of species.” Nearly two million species have been identified on Earth, and many more will likely be identified as the search continues. The greatest numbers of unidentified species are likely to come from tropical rainforests as well as most of the ocean realm. The Ocean Studies Board has noted numerous locations around the world where 33-92% of species from a collected taxon are undescribed; a Georges Bank study found this to be true for 33% of marine polychaetes collected (NRC, 1995). With such species diversity comes a wide range of trophic interactions within the marine realm. Phytoplankton, filter feeders, carnivores, and detritivores, among other trophic groups, create additional levels of trophic interaction that form complex food webs, where only food chains may be present

on land (Ray, 1988). This suggests that though there are likely several species fulfilling any given niche within an area, if one of these trophic groups was removed, there would be repercussions throughout the environment.

One example of how the presence of certain species can greatly affect an environment as a whole can be seen in the kelp forest ecosystems of the Pacific Northwest. Sea otters were nearly exterminated by fur traders during the 19th century for their prized pelts. With the decrease of this trophic group, an increase in abundance of their prey, sea urchins, was bound to occur. Once the sea urchin, an herbivore, became prevalent, its preferred food source, kelp, became the target of increased predation. These echinoderms devour the holdfast at the base of the kelp stalk, letting the fronds float away to leave behind only a barren seafloor inundated with sea urchins (Primack, 1993; Levinton, 1995). Recently, however, a new level of interaction has been added to this ecosystem. Due to demand from the Asian seafood market, sea urchins have become targeted by fishermen and have decreased in abundance, thus allowing kelp forests to have the possibility of rebounding. The confounding factor, however, is that during the 1990s, killer whales had begun to prey upon sea otters due to the declining sea lion and whale populations, another anthropogenic holdover of 19th century hunting (Estes et al., 1998; Hatfield et al., 1998; Jackson et al., 2001). As one can observe, various factors that can affect just one species can have major implications upon an entire environment. With the removal of sea otters, the kelp forest ecosystem, which stretches from the benthic environment around their stalk holds to the fronds and gas-filled floats near the ocean surface, can undergo a ecosystem-wide state change due to the increasing number of herbivorous sea urchins. In addition, in some environments, e.g. the Northwest

Pacific, kelp forests are an important factor controlling coastal erosion, as these regions generally do not possess coastal buffers such as sand bars, barrier islands, etc.; one such example is a study by Martin (1996) that found a reduction in wave energy of 70-85% across a 258m-wide kelp bed.

One of the major factors currently affecting biodiversity is that of habitat degradation or destruction (Levinton, 1995). On Georges Bank, these anthropogenic effects are largely attributable to mobile fishing gears such as trawls and dredges. A variety of studies have examined this effect, either by comparing exploited versus unexploited areas or by the use of closed areas which create unfished, control locations. As stated previously, both gear types affect both the physical and biogenic structure of the habitat (NEFSC, 2002). With increased fishing effort, substrate morphology becomes temporarily smoothed, though natural events such as seasonal storms can reform these features or create new ones. Fishing intensity can cause reductions in macrobenthic infauna and epifauna. In general, small infaunal organisms, such as polychaetes and nematodes, are not significantly affected in either abundance or biomass, even though fishing gear can cause a “chumming effect” in that the meiofauna become suspended in the water column (Brylinsky et al., 1994; Drabsch et al., 2001; Jennings et al., 2002; NEFSC, 2002). The factor that allows for little to no change, or in some cases an increase, is the fact that meiofaunal organisms are largely opportunistic with fast life histories, and can retreat further into the sediment (Brylinsky et al., 1994; Hill et al., 1999). Additionally, mobile scavengers and opportunistic predators, such as crabs, whelks, and starfish, have shown no significant changes in abundance, biomass, or diversity (Freese et al., 1999; Hill et al., 1999; Jennings et al., 2002).

Most of these changes, however, have been found to generally enhance food supply for fish. This is because the passing of fishing gear over the benthos will damage, kill, and/or suspend prey items for fish, such as commercially important species like whitefish, flounders, and others (Kaiser and Spencer, 1994; Engel and Kvitek, 1998; Jennings et al., 2002). Groenewold and Fonds (2000) estimated that between 6-13% of the annual macrobenthic secondary production per unit area could be made available to scavengers by a single pass of fishing gear. The problem that must be considered, however, is that of the habitat being a nursery area for young, commercially important species. Studies have found that young fish require structurally complex habitat for foraging and protection from predators (Tupper and Boutilier, 1995; Auster, 1998; Engel and Kvitek, 1998; Lindholm et al., 1999). Thouzeau et al. (1991) found that juvenile sea scallops also show greater survivorship in more complex habitats, specifically a gravel-pebble substrate. With intensive fishing pressure present in many locations, these habitats may become of limited function to juvenile organisms. Without these nursery regions, commercially important fish stocks will come to a sort of “bottle neck” where there will be inadequate recruitment of mature fish as many of the juveniles will not survive due to the limited availability of structurally complex habitat (Tupper and Boutilier, 1995; Auster, 1998).

Regions that show little evidence of prior fishing effort, as well as newly closed grounds such as marine protected areas (MPAs), have shown that proper management may have great beneficial effects on currently exploited locations (Agardy, 1994; Brailovskaya, 1998; Auster and Shackell, 2000; Murawski et al., 2000). In relatively unexploited locations as well as closed areas, macrobenthic epifauna were more abundant

and tended to be less patchy when compared to fished areas (Engel and Kvitek, 1998; Freese et al., 1999; Collie et al., 1997, 2000; McConnaughey et al., 2000). Intensity and duration of previous fishing effort also plays a role, however. European waters have seen long-term periods of heavy fishing which has led to long-term changes in benthic communities (de Groot, 1984; Hill et al., 1999; Rumohr and Kujawski, 2000; Bradshaw et al., 2002). In areas such as the Georges Bank region and the North Sea, estimates are that from 6% to 450% of the area is trawled annually, with some areas having been dredged as well (Churchill, 1989; Gislason, 1994; Auster et al., 1996; Pilskaln et al., 1998). Much of this effort is targeted at specific locations where abundance of the target species is optimal. (Currie and Parry, 1996). The scale of the analysis is key, however, as Rijnsdorp et al. (1998) found that specific areas (blocks measuring 9 km²) within the North Sea were fished from 0-400 times were year. Watling and Norse (1998) equated this stress on the benthos to that of forest clearcutting which receives much greater criticism, but occurs at level two orders of magnitude less than benthic trawling and dredging. Though closed areas create locations where benthic assemblages can repopulate, one problem that is generated, however, is that fishing effort becomes displaced to regions previously less exploited.

Approach

The major approach used to determine changes in the benthic invertebrate assemblages within this study was the separation of stations by distance either inside or outside a closed area boundary present on Georges Bank. These stations were up to 20 km from the boundary, covering a range of depths, sediment types, and fishing efforts. In

addition to sampling the invertebrates collected by a scallop survey dredge, subsamples of scallops and their associated attached epifauna were also analyzed. To clarify terminology within this project, “fauna” will from here be defined as those invertebrates, both infaunal and epifaunal, retained using a scallop survey dredge; “scallop [shell] epifauna” will be defined as those invertebrates observed living attached to live *Placopecten magellanicus* shells. Data collected from this sampling was analyzed for differences in abundance and biomass, as well as species diversity and evenness. In addition, changes in the statistics of scavenger and opportunistic predator species, such as crabs, starfish, and whelks, are also discussed.

Another approach that was examined is whether sea scallop presence is an important factor for settlement and growth of sessile epifauna. This was done by removing the data representing scallops and any attached epifauna from the analysis. After doing so, the adjusted data was analyzed for differences in abundance and biomass, as well as species diversity and evenness.

Project Objectives

(1) To determine whether there is a difference in invertebrate species diversity, abundance, biomass, and/or species evenness between the inside and outside of closed area boundaries.

H₀: Invertebrate species diversity, abundance, biomass, and/or species evenness inside the boundary equals that found outside the boundary.

(2) To determine whether sea scallop presence is a factor controlling invertebrate species diversity, abundance, biomass, and/or species evenness between the inside and outside of closed area boundaries if one accounts for sea scallop presence.

H₀: Invertebrate species diversity, abundance, biomass, and/or species evenness inside the boundary equals that found outside the boundary without concern to the presence or abundance of sea scallops.

(3) To determine whether there is an increase in invertebrate scavenger and opportunistic predator (e.g. crabs, starfish, whelks) abundance and/or biomass due to the presence of fishing effort.

H₀: Invertebrate scavenger abundance and biomass are equivalent between the inside and outside of closed area boundaries.

(4) To determine whether distance from a closed area boundary and observed levels of fishing effort are factors controlling invertebrate species diversity, abundance, biomass, and/or species evenness within the open areas surrounding the closed area boundaries.

H₀: Invertebrate species diversity, abundance, biomass, and/or species evenness within the open areas surrounding the closed area boundaries do not vary due to distance from a closed area boundary and/or fishing effort.

MATERIAL AND METHODS

Invertebrate Assemblage Study

Survey Cruise

On July 15th, 2002, the National Marine Fisheries Service (NMFS) commenced its annual sea scallop survey aboard the R/V *Albatross IV*. Two cruise legs were undertaken, the first being in the Mid-Atlantic Bight from July 15 to July 26, while the second leg took place in the Georges Bank region from July 29 to August 13. Three hundred and nine stations were sampled within the Georges Bank region at depths ranging from 14 to 60 fathoms (25.6-109.7m). Fifteen minute tows were made at a speed of 3.8 knots using an 8-foot New Bedford style scallop dredge, providing a one nautical mile tow path (4,516 m² dredged). The dredge was outfitted with a 2-inch (51mm) ring bag and a 1-½ inch (38mm) mesh liner to retain smaller fauna. All scallops greater than 25mm in shell height as well as all fish and most large mobile invertebrates, such as *Cancer* crabs or squid, were quantified by the scientists and volunteers aboard the vessel.

Sampling for this study was undertaken during the second leg of the survey. A maximum of one hundred and seventy-one possible stations were selected by their proximity to a closed area boundary, with a maximum distance of 20 kilometers either inside or outside the border (Figures 3, 4a), with station locations being randomly selected prior to this selection process. Operational constraints as well as sampling problems reduced the coverage to 138 stations (Figure 4b). A total area of 623,208m² was covered for this project.

Subsampling and Preservation Methods

After the dredge's haul had been picked over twice for target survey species such as sea scallops, finfish, and *Cancer* sp. crabs, the remaining invertebrate "trash" was shoveled into orange (1.3 bushel) baskets. One orange basket translates into a volume of roughly 46 liters (Hart, *pers. com*). A basket was selected and its contents dumped into a square wooden frame measuring 67.3 cm (L) x 67.3 cm (W) x 12.7 cm (H), providing a surface area of 0.453 m². The invertebrate sample was then evenly spread out within the wooden frame. Using a large perforated coffee can with a surface area opening of roughly 0.0182 m², a 1/25 (1.84 liter) subsample was taken by pushing the can into the larger sample within the wooden frame. The frame was then lifted away to clear the remaining sample from around the coffee can. The subsample within the perforated coffee can was then taken to be washed thoroughly in order to remove excess sediment and marine slime. The remaining subsample was subsequently placed in a labeled Zip-Loc bag and frozen for later analysis.

Once the sea scallops from the station had been measured for length frequency data, up to three random scallops, if present, were selected from each of the following size classes, 1) <90mm, 2) 90-100mm, and 3) >100mm, providing up to nine scallops per station. The scallops were subsequently shucked with both shell valves then being placed in a labeled Zip-Loc bag and frozen for later analysis.

Laboratory Protocol

Samples were thawed prior to beginning the identification of the invertebrates collected, with each sample being worked up individually. Thawing times were 1.5 hours

for the scallop shell samples and 5 hours for the invertebrate samples. Samples were initially separated into general taxonomic groups, such as starfish, crabs, bryozoans, etc. These were then further separated to species level, when possible. Samples were worked up until completed, i.e. no samples were refrozen. Benthic samples and scallop shell samples were completed separately due to the difference in thawing times and lack of freezer organization, i.e. associated samples were generally in different boxes. Each taxa had the following metrics recorded: 1) number of individuals, 2) weight (in grams) of individuals, and for sea scallops 3) shell height measurements (in mm). Totals per taxa within a benthic sample were then calculated using the following expansion factor equation:

$$X_{\text{sample}/m^2} = \frac{X_{\text{sample}} \times B_{\text{single}} \times B_{\text{total}}}{\text{Area}_{\text{tow}}}$$

where “ X_{sample} ” is the count/weight value from the collected sample, “ B_{single} ” is the expansion of the sample to a single bushel, “ B_{total} ” is the expansion to the entire haul, and “ Area_{tow} ” is the total area the dredge swept ($4,516\text{m}^2$), providing values of the number of organisms or grams of organisms per m^2 (X_{sample/m^2}). Characteristic specimens of most taxa were placed in 5% buffered formalin and kept for later comparisons.

The expansion equation for the scallop shell epifauna required converting the scallop shell data collected into a number representative of the entire observed population at each station. Scallop length frequencies were collected at sea, but were generally only a subsample of those collected due to time constraints at each station. These values were converted into percentage length frequencies and were then multiplied by the total scallop

abundance at the station to achieve a total length frequency distribution for each station. Each size category in the length frequency was then converted into a surface area value by assuming the surface area of a scallop is equivalent to a circle. This assumption takes into account that 1) shell height, i.e. distance from shell hinge to gape, is longer than shell width and will lead to a small overestimate of area, and 2) the shell is three dimensional, not flat, and will lead to a small underestimate of area. As the two factors “approximately” cancel each other out, this assumption is reasonable for this measurement, and has been used by other researchers (Dadswell and Weihs, 1990; Cheng and DeMont, 1996; Cheng et al., 1996). These surface area values were then multiplied by the number of scallops within the given size class to determine the total surface area of scallops within the length frequency. These values were then summed to calculate the total surface area of scallops present at a given station. The following equation was then used to determine the count or grams per square meter of benthic area of epifaunal taxa attached to scallops:

$$X_{\text{sample/m}^2} = \frac{\sum \left(\left(\frac{X_i}{SA_i} \right) \left(\frac{SA_{\text{total}}}{Area_{\text{tow}}} \right) \right)}{n_{\text{shells}}}$$

where “ X_i ” is the count/weight value from the i^{th} collected scallop shell sample, “ SA_i ” is the surface area in cm^2 of the i^{th} collected scallop shell sample, “ SA_{total} ” is the total surface area in cm^2 of all scallops within a station (calculated above), “ $Area_{\text{tow}}$ ” is the total area the dredge swept ($4,516\text{m}^2$), and “ n_{shells} ” is the number of scallop shells sampled at the given station, providing mean values and standard deviations of the

number of organisms or grams of organisms per m^2 (X_{sample/m^2}). Characteristic specimens of most taxa were placed in 5% buffered formalin and kept for later comparisons.

Finally, it must be stated that the values calculated for the benthic samples as well as the scallop shell subsamples, both shown above as X_{sample/m^2} , were determined using a dredge efficiency of 100%. As the efficiency of the survey dredge is likely to be closer to 50%, the calculated values are likely underestimates and should be considered minimum swept area estimates (Hart, 2003).

Data Analysis

Due to the abundance of data collected, various ecological values were determined per station, including total biomass (g/m^2), total abundance ($\#/m^2$), species richness (number of taxa present), Pielou's evenness, and the Shannon-Wiener Index of biodiversity. These variables were tested using ANOVAs to determine whether there were any significant associations to various factors such as whether the station was within an open or closed area, distance from a closed area boundary (ranging from 0.01-20km), sediment type, and the depth of the station. Total abundance and biomass values were also considered for organism groups, such as decapods, asteroids, etc. A two-factor, three-covariate ANCOVA was employed to test for significant effects due to fishing region and sediment type. In addition, as sea scallop presence was controlled for in one hypothesis test, various tests including two-factor, four-covariate ANCOVAs, paired-sample t-tests, and independent sample t-tests were employed during the statistical analysis of this data. Finally, access to the scallop fleet's vessel monitoring system (VMS) data provided an opportunity to test the effects of fishing within a collection of

disturbed sites. As an additional factor, distance from the closed area boundary may show what effect its presence has on fishing effort and biodiversity. A multiple linear regression was used to test for significant effects using several independent variables such as fishing intensity provided by the VMS, distance from the closed area boundary, geographic location, and depth. Throughout these analyzes, tests of covariance and homogeneity of variance (Levene test) were conducted with the appropriate transformations being applied when necessary.

RESULTS

Faunal Composition

A total of 95 taxa representing 8 phyla (Bryozoa, Hydrozoa, and 10 other taxa undetermined) were identified over 138 stations on Georges Bank. Mean invertebrate density (Table 1a) was characterized by Echinoidea (30%), Asteroidea (20%), Ophiuroidea (12%), and Bivalvia (10%). Mean biomass, however, was dominated a single taxa: Bivalvia (71%). The most commonly occurring taxa present during the survey included Bryozoa, Hydrozoa, Polychaeta, Bivalvia, Decapoda, Echinoidea, and Asteroidea, which were present at a minimum of 78% of the stations. Additionally, Porifera and Gastropoda were regularly sampled in at least 50% of the stations (Table 1a).

The subset of 68 open area stations on Georges Bank included 87 taxa within 8 phyla (Table 1b). The main taxonomic groups observed in terms of mean density included Asteroidea (19%), Ophiuroidea (18%), Cirripedia (18%), and Echinoidea (13%). Mean biomass, though, was dominated by Bivalvia (58%) and Porifera (10%).

The most commonly sampled taxa included Bryozoa, Hydrozoa, Polychaeta, Bivalvia, Decapoda, and Asteroidea, which were sampled in at least 83% of open area stations. Porifera, Gastropoda, and Echinoidea were also commonly observed in at least 50% of samples (Table 1b).

Observations within the 70 closed area stations on Georges Bank covered 87 taxa from 8 phyla (Table 1c). Mean density was comprised largely of Echinoidea (44%), Asteroidea (20%), and Bivalvia (13%). Mean biomass was represented largely by Bivalvia (74%) and Echinoidea (11%). Within closed area stations, the most common taxonomic groups (greater than 77% presence) were Bryozoa, Hydrozoa, Polychaeta, Bivalvia, Decapoda, Echinoidea, and Asteroidea. Gastropoda was also commonly sampled in at least 50% of stations (Table 1c).

Mean density over all stations was composed largely of a small set of taxa: 3 echinoderms species, *Echinarachnius parma* (28.9%), *Asterias vulgaris* (18.9%), and *Ophiura sarsi* (10.0%), the barnacle *Balanus amphitrite niveus* (8.0%), and the bivalve *Placopecten magellanicus* (6.0%), which accounted for over 71% of mean density. Three of these species, however, *Placopecten magellanicus* (70.2%), *Echinarachnius parma* (8.7%), and *Asterias vulgaris* (5.6%), comprised over 84% of mean biomass (Table 2a).

Of the 68 open area stations, mean density was largely comprised of the following taxa: 3 echinoderms species, *Asterias vulgaris* (18.0%), *Ophiura sarsi* (15.4%), and *Echinarachnius parma* (11.8%), and the barnacle *Balanus amphitrite niveus* (17.5%). Mean biomass within open area stations exhibited the following dominant taxa: *Placopecten magellanicus* (57.5%), 2 echinoderm species, *Asterias vulgaris* (5.4%) and

Echinarachnius parma (4.9%), and 2 species of sponge, *Haliclona oculata* (4.6%) and *Suberites ficus* (3.7%), which encompassed over 76% of mean biomass (Table 2b).

Mean density of samples collected from the 70 closed area stations was typified by 2 echinoderm species, *Echinarachnius parma* (43.1%) and *Asterias vulgaris* (19.6%), and the bivalve *Placopecten magellanicus* (8.0%). Two of these species, *Placopecten magellanicus* (74.2%) and *Echinarachnius parma* (9.9%), comprised over 84% of the mean biomass within the closed area sites (Table 2c).

Geographic Distribution of Ecological Variables

The number of taxa per Georges Bank station ranged from 5 (Stations 235, 314) to 35 (Stations 245, 246). Mean density varied between 0.1 organisms/m² (Station 487) and 34.1 organisms/m² (Station 502); mean biomass ranged from 1.0 g/m² (Station 299) to 315.8 g/m² (Station 385). Mean values (\pm SD) were 18.7 ± 6.6 taxa, 306.7 ± 490 organisms/100m², and 4.5 ± 5.7 kg/100m² (Table 1a). Within open areas, species richness ranged from 7 (Stations 271, 300, 428) to 34 (Station 493), mean density from 0.2 organisms/m² (Stations 300, 469) to 34.1 organisms/m² (Station 502), and mean biomass from 1.0 g/m² (Station 299) to 161.1 g/m² (Station 516). Mean open area values (\pm SD) were 18.3 ± 6.5 taxa, 281.8 ± 550 organisms/100m², and 2.2 ± 3.0 kg/100m² (Table 1b). Within closed areas, species richness ranged from 5 (Stations 235, 314) to 35 (Stations 245, 246), mean density from 0.1 organisms/m² (Station 487) to 23.3 organisms/m² (Station 254), and mean biomass from 2.3 g/m² (Station 487) to 315.8 g/m² (Station 385). Mean closed area values (\pm SD) were 19.1 ± 6.7 taxa, 330.9 ± 420 organisms/100m², and 6.7 ± 6.7 kg/100m² (Table 1c).

Species richness was found to be highest (26-35 taxa) within the Great South Channel extending into the NE portion of the Nantucket Lightship Closed Area (NLCA) and SW portion of Closed Area I (CA1), the NE peak of Closed Area II (CA2), and the eastern portion of CA2 extending into Canada (Figure 5a). Intermediate values (16-25 taxa) buffered regions with the highest species richness, as well as included most of CA1 and the SW portion of CA2. These values also extended into the open areas west of CA2's NE peak as well as to the SW of CA2. The lowest densities of taxa were observed within the open areas: 1) east of NLCA, 2) NE of CA1, and 3) around the southern portion of CA2, as well as within: 1) the central portion of NLCA, and 2) the SE and western portions of CA2.

The highest abundance values (10-34 organisms/m²) were observed within central Great South Channel, the NE portion of NLCA and CA1 (extending into the open area), the SE portion of CA2, and a portion of the NE peak of Georges Bank, west of CA2 (Figure 5b). Midrange values (2-10 organisms/m²) were located around high density regions as well as sporadically throughout the Great South Channel region, NLCA, CA1, and western CA2. Low density stations (0-2 organisms/m²) were observed throughout the SE portion of Georges Bank extending into CA2 and intermittently throughout the Great South Channel region.

Biomass values were the highest (150-300 g/m²; wet weight) within the three Georges Bank closed areas as well as within Canadian waters of the NE peak (Figure 5c). Intermediate values (50-150 g/m²) extended throughout the closed areas as well as into the northern section of the Great South Channel. Low biomass stations (0-50 g/m²) were

largely located within the Great South Channel and other open areas, though some low biomass sites did occur within closed area boundaries.

Pielou's evenness values (J' , based on biomass) exhibited the largest values (0.5-0.7) within open areas, while closed areas were generally low (0.0-0.5). Some locations within the closed area boundaries displayed higher values, specifically within southern CA1 as well as stations along the western boundary of CA2 (Figure 5d). Pielou's evenness values (J' , based on density) were found to be greatest (0.6-0.9) within the open areas of the Great South Channel region and the NE peak of Georges Bank, as well as within the NE portion of the NLCA, central CA1, and N, E, and SW CA2 (Figure 5e). The lowest values (0.0-0.6) were observed in the open areas surrounding CA1, as well as within central NLCA, NE CA1, and W and SE CA2.

Shannon-Wiener Index scores (H' , based on density), were generally highest (1.5-3.6) within the Great South Channel and the open areas surrounding CA2, with scattered occurrences within the closed area boundaries (Figure 5f). Medium range values (1.0-1.5) generally buffered regions of greater diversity and expanded further into closed areas. Low Shannon-Wiener Index values (0.0-1.5) were mostly observed within the NE portion of the NLCA, central CA1, the NE peak of Georges Bank, as well as E and SW CA2.

Bathymetric Distribution

Mean number of taxa sampled throughout Georges Bank open area stations were noted as showing a significant change with depth (ANOVA; $F = 2.385$, $p = 0.039$), specifically between stations of 50-59m and 80-89m in depth (Tukey HSD test; $p =$

0.027). No clear pattern was observed, with the highest values at 50-59m; values decreased through 80-89m, with a slight increase at the deepest stations (Figure 6). Closed area stations, however, showed no significant variation with depth (ANOVA; $F = 1.729$, $p = 0.129$). Values generally decreased to 70-79m with the number of taxa increasing with further depth.

Mean density values (organisms/m²) of Georges Bank open area stations exhibited a significant change with depth (ANOVA; $F = 4.563$, $p = 0.001$) with values at 50-69m significantly greater than at 80-89m (Tukey HSD test; $p = 0.005$). Densities peaked at stations of greater than 100m and 50-59m in depth, with the lowest values at 80-89m (Figure 7). Closed area stations exhibited a significant difference in relation to depth (ANOVA; $F = 3.472$, $p = 0.005$) with values at 50-59m being significantly greater than at 80-89m and over 100m (Tukey HSD test; $p < 0.037$). Mean density increased from the shallowest sites to 50-59m, after which values decreased to 80-89m; values increased again at 90-99m and decreased at the deepest stations.

Mean biomass (g/m²; wet weight) of open area stations did exhibit a significant change associated with depth (ANOVA; $F = 5.171$, $p < 0.001$). Values were relatively steady from stations less than 50m to 60-69m, decreased to 80-89m, followed by a slight increase with depth (Figure 8). Mean biomass from sites at 50-69m was found to be significantly greater than at 80-99m (Tukey HSD test; $p < 0.027$). Within closed area samples, biomass showed no significant change with depth (ANOVA; $F = 0.576$, $p = 0.748$). Biomass increased from the shallowest sites to 50-59m, became highly variable through 90-99m, and then decreased at stations greater than 100m in depth.

Pielou's evenness (J' , based on biomass) was not significantly different with depth within open area stations (ANOVA; $F = 1.535$, $p = 0.182$). Evenness ranged from 0.4-0.5 at all depths except at 70-79m (0.34) and greater than 100m (0.31; Figure 9). Additionally, closed area stations did not vary significantly with depth (ANOVA; $F = 1.002$, $p = 0.432$). Evenness decreased from stations less than 50m in depth (0.38) to 80-89m (0.18), followed by an increase with depth (0.30 at greater than 100m).

Within open area stations, Pielou's evenness (J' , based on density) exhibited a significant change with bathymetry (ANOVA; $F = 2.438$, $p = 0.035$), specifically between stations at 50-59m and 60-69m in depth (Tukey HSD test; $p = 0.044$; Figure 10). Closed area sites, however, showed no significant variation in association with depth (ANOVA; $F = 1.498$, $p = 0.194$). Evenness showed a general increasing trend with depth after 50-59m, though the largest mean value was found at stations less than 50m deep.

Shannon-Wiener Index values for open area stations did not show a significant change with depth (ANOVA; $F = 2.052$, $p = .072$). Index values fluctuated with depth, but followed a general decreasing trend (Figure 11). In addition, no significant change with depth was recorded for closed area stations (ANOVA; $F = 1.367$, $p = 0.242$). Scores were largest at both less than 50m and greater than 100m locations (roughly 2.5) with intermediate depths fluctuating from 1.4-2.0.

Distribution by Sediment Type

Mean species richness throughout open area sites was shown to be significantly different according to sediment type (ANOVA; $F = 4.271$, $p = 0.004$). Species richness within GCB sediments was found to be significantly different from: 1) SFS (Tukey HSD

test, $p = 0.031$), 2), BSH (Tukey HSD test, $p = 0.032$), and 3) ISH (Tukey HSD test, $p = 0.025$); MCS were not significantly different from other sediment types (Figure 12). Closed area samples also varied significantly with sediment type (ANOVA; $F = 3.794$, $p = 0.008$). Within closed areas, GCB sediments significantly varied in comparison to: 1) SFS (Tukey HSD test, $p = 0.015$), 2) MCS (Tukey HSD test, $p = 0.043$), and 3) ISH (Tukey HSD test, $p = 0.006$), while BSH environments were not found to be significantly different from other sediment types.

Mean density (organisms/m²) over open area Georges Bank stations showed a significant variation in relation to sediment type (ANOVA; $F = 4.899$, $p = 0.002$). BSH sites had significantly greater mean densities when compared with: 1) SFS (Tukey HSD test; $p = 0.005$) and 2) GCB (Tukey HSD test; $p = 0.030$; Figure 13). Closed areas also showed a significant change with sediment type (ANOVA; $F = 7.079$, $p < 0.001$). SFS sediments were found to exhibit significantly higher densities than BSH and ISH environments (Tukey HSD test; $p < 0.047$) while MCS stations were observed to be significantly greater in abundance when compared to BSH regions (Tukey HSD; $p = 0.014$).

Mean biomass (g/m²; wet weight) within open area Georges Bank stations was determined to vary significantly by sediment type (ANOVA; $F = 9.211$, $p < 0.001$). GCB environments were significantly greater than MCS, BSH, and ISH (Tukey HSD, $p < 0.034$); SFS sediments did not significantly differ from other sediment types (Figure 14). Within closed areas, biomass was not found to be significantly different in association with sediment type (ANOVA; $F = 2.463$, $p = 0.054$). GCB and MCS environments were

observed to have the highest biomass, while BSH and ISH sediments comprised the lowest values.

Pielou's evenness (J' , based on biomass) was not significantly different in association to sediment type over with open area survey stations (ANOVA; $F = 1.915$, $p = 0.119$). Values were highest within MCS environments (0.52), while SFS sediments scored the lowest (0.30; Figure 15). Closed area station also did not vary significantly with bathymetry (ANOVA; $F = 0.573$, $p = 0.683$). Evenness scores were greatest in GCB environments (0.36), while all other sediment types had mean scores less than 0.31.

Pielou's evenness (J' , based on density) within open areas was determined to be significantly different in association with sediment (ANOVA; $F = 3.508$, $p = 0.012$). Both BSH and GCB environments were shown to have significantly higher evenness scores compared to SFS (Tukey HSD test; $p < 0.020$; Figure 16). Closed area stations also displayed a significant change with sediment type (ANOVA; $F = 6.569$, $p < 0.001$). GCB environments had significantly greater evenness values when compared to SFS and MCS (Tukey HSD test; $p < 0.039$); BSH sediments were found to vary significantly in comparison to SFS environments (Tukey HSD test; $p = 0.002$).

Shannon-Wiener Index scores displayed a significant variation associated with sediment type within open area survey sites (ANOVA; $F = 2.994$, $p = 0.025$) with GCB environments being significantly more diverse than SFS (Tukey HSD test; $p = 0.018$; Figure 17). Within closed areas, Shannon-Wiener Index scores also varied significantly (ANOVA; $F = 6.819$, $p < 0.001$). GCB environments had significantly higher scores in comparison to SFS, MCS, and ISH sediments (Tukey HSD test; $p < 0.020$); BSH

sediments were found to be significantly more diverse when compared to SFS environments (Tukey HSD test; $p = 0.004$).

Distribution of Dominant Taxonomic Groups

Bathymetric Distribution

Within open area stations, echinoderms were the most abundant at depths greater than 60m (41-98% relative abundance; 0.4-8.5 ind./m²) with no visible pattern associated with depth (Figure 18a). Shallow depths were dominated by crustaceans (less than 50m: 38%, 0.3 ind./m²; 50-59m: 61%, 2.9 ind./m²). Molluscs were generally found to decrease in abundance with depths greater than 50-59m (from 0.6 to 0.1 ind./m²). Anthozoan densities were observed to peak at depths of 90-99m (26%, 0.5 ind./m²)

Within closed area stations, echinoderm abundance dominated all depths (44-86%; 0.7-5.4 ind./m²) except for 80-89m (molluscs: 57%; 0.6 ind./m²) with no notable pattern associated with bathymetry (Figure 18b). Molluscs were the second-most numerous taxa at depths shallower than 80m (8-42%; 0.5-1.1 ind./m²) and generally showed a decrease with depth (1.1 ind./m² at less than 50m to 0.2 ind./m² at greater than 100m). Crustaceans showed low abundance (0.1-0.3 ind./m²) except at 90-99m (0.8 ind./m²). Anthozoans were found to be highly concentrated at depths of 90-99m (21%; 0.8 ind./m²).

In open area locations, molluscs were the dominant taxa from 50-99m (51-73% relative biomass; 2.3-25.5 g/m²), being replaced at depths less than 50m by sponges (74%; 25.2 g/m²) and at depths greater than 100m by echinoderms (74%; 10.2 g/m²). Sponge biomass exhibited a decrease with depth (25.2 g/m² at less than 50m to 0.03 g/m²

at greater than 100m). Echinoderms were found to have low biomass (0.5-4.7 g/m²) except at stations greater than 100m in depth (Figure 19a). Crustaceans did not exhibit large fluctuations in biomass (2-19%; 0.4-1.7 g/m²).

Within closed area sites, molluscs were the most common taxa in terms of biomass (50-93% relative biomass; 15.40-61.0 g/m²) with the largest measurements between 50-99m in depth (Figure 19b). Echinoderm biomass fluctuated with depth, but contributed much to the remaining biomass (4-30%; 2.3-23.8 g/m²). Polychaete and bryozoan biomass generally decreased in association to depth; these taxa provided substantial inputs to overall biomass at stations less than 50m in depth (bryozoans: 10%, 4.3 g/m²; polychaetes: 9%, 3.6 g/m²). Sponges were most prevalent at 90-99m (6%; 3.8 g/m²). Crustaceans did not display large changes in biomass with depth (1-4%; 0.6-1.3 g/m²).

Distribution by Sediment Type

Within open area sites, echinoderms were the most abundant taxa within SFS, BSH, and ISH sediments (71-82% relative abundance; 0.8-8.5 ind./m²), and were common on other bottoms as well (22-23%; 0.6-0.9 ind./m²; Figure 20a). MCS environments were found to be numerically dominated by ascidians (44%; 1.1 ind./m²) while crustaceans were the most abundant taxa with GCB regions (55%; 2.2 ind./m²). Molluscs played a prominent role in all environments except SFS bottoms (9-23%; 0.1-0.7 ind./m²). Anthozoans were most numerous within SFS (9%; 0.9 ind./m²) and ISH (6%; 0.1 ind./m²) locations. Ascidians were not observed within SFS and ISH sediments, while pycnogonids were absent from sampling within GCB bottoms.

The abundance of echinoderms dominated all closed area sediment types (47-83% relative abundance; 0.5-5.8 ind./m²) except for GCB bottoms (39%; 0.8 ind./m²; Figure 20b) in which molluscs were the most numerically abundant taxa (49%; 1.0 ind./m²). Molluscs were also an important component of abundance within MCS, BSH, and ISH environments (28-38%; 0.4-0.8 ind./m²). Crustaceans played a substantial role within all sediment types (7-11%; 0.1-0.5 ind./m²). Within SFS sediments, both anthozoans (6%; 0.4 ind./m²) and molluscs (5%; 0.3 ind./m²) played a small role in abundance. Ascidians were not found within SFS and ISH sediments, while pycnogonids were absent from sampling within GCB bottoms.

In open area locations, molluscs controlled biomass within all sediment types (41-73% relative biomass; 3.9-34.1 g/m²) except within SFS regions where echinoderms were dominant (76%; 15.1 g/m²; Figure 21a). Echinoderms were an important component of biomass within all other sediment types as well (6-22%; 1.4-3.0 g/m²). Crustaceans were a common component of biomass within MCS, BSH, and ISH regions (10-15%; 1.2-1.4 g/m²), while poriferans constituted a significant portion within MCS, BSH, and GCB sediments (10-13%; 1.2-4.9 g/m²). In addition, bryozoans played a small role within areas of BSH (5%; 0.5 g/m²) and GCB (5%; 2.2 g/m²). Within SFS environments, anthozoans were a notable component of biomass (5%; 1.1 g/m²). Additionally, ascidians were noted as important within MCS regions (8%; 1.1 g/m²).

Biomass within closed area sites was dominated by molluscs, regardless of sediment type (52-88% relative biomass; 29.3-82.6 g/m²; Figure 21b). Echinoderms were also observed to be an important component of biomass within SFS regions (44%; 26.5 g/m²), and were the second-most prevalent taxa in terms of biomass within all

other sediment types (8-12%; 2.7-11.0 g/m²). Bryozoans also were an important component of biomass within GCB regions (6%; 6.4 g/m²).

Statistical Analysis on Ecological Variables of the Benthic Invertebrate Community

Mean species richness varied significantly in relation to sediment type (ANCOVA; $F = 4.971$; $p < 0.001$) and open/closed area location ($F = 7.782$; $p = 0.006$) when the covariates of latitude ($p < 0.001$) and longitude ($p < 0.001$) were taken into account (Table 3). A significant difference was observed in mean density (individuals/m²) values in regard to sediment type (ANCOVA; $F = 14.139$; $p < 0.001$), when depth ($p = 0.031$) and longitude ($p = 0.013$) effects were kept constant. Mean biomass (g/m² wet weight) was found to be significantly different in association to sediment type (ANCOVA; $F = 3.505$; $p = 0.010$) and open/closed area location ($F = 33.313$; $p < 0.001$) when the covariates of depth ($p = 0.009$), latitude ($p = 0.017$), and longitude ($p = 0.039$) were accounted for in the analysis. Mean values for Pielou's Evenness Index (based on biomass) varied significantly with open/closed area location (ANCOVA; $F = 16.195$; $p < 0.001$). A significant change in mean Pielou's Evenness (based on density) was determined in association with sediment type (ANCOVA; $F = 10.925$; $p < 0.001$), when the latitude covariate ($p = 0.001$) was taken into account. Mean values of the Shannon-Wiener Index (based on density) displayed a significant variation with sediment type (ANCOVA; $F = 9.088$; $p < 0.001$) and open/closed area location ($F = 5.554$; $p = 0.020$) after the covariates of latitude ($p = 0.001$) and longitude ($p = 0.039$) were taken into account.

Distribution of Scallop Epifauna

Epifaunal Composition

A total of 35 invertebrate taxa of representing 8 phyla were observed living on live *Placopecten magellanicus* shells from sampling conducted at 120 stations on Georges Bank where scallops were present. Scallop shell fidelity was determined for each taxa over all Georges Bank stations as well as separately within open or closed areas (Table 4). Scallop shell fidelity is here defined as the percentage of the total biomass of a taxa that is present on live *Placopecten magellanicus* shells. Several taxa were rarely sampled ($n < 5$ stations); these included *Cuspidaria glacialis*, *Hiatella arctica*, *Crucibulum striatum*, and an unidentified white encrusting sponge. In addition, some taxa such as the stalked sea squirt, *Boltenia ovifera*, were only located within a given region such as the Great South Channel, which limited sampling to within certain fishing areas, i.e. closed area sampling of *Boltenia ovifera* was minimal ($n = 1$ station). Taxa from five phyla (Chordata: Ascidiacea, Bryozoa, Annelida, Mollusca, and Arthropoda: Cirripedia) displayed high levels of scallop shell fidelity with over 50% of observed biomass present on live scallop shells compared to the benthic environment. Some taxa such as *Haliclona oculata* and *Crepidula plana*, however, exhibited little, if any, requirement for scallop shell presence as less than 1% of their observed biomass was present on live *Placopecten magellanicus* shells.

Geographic Distribution

The largest observed epifaunal density per one hundred square centimeters of live *Placopecten magellanicus* shell (127.1 individuals/100cm² shell) occurred within a single

station in the central portion of the Great South Channel (Figure 22a). Medium densities (3.0-15.0 ind./100cm² shell) were recorded within the Great South Channel region, CA1, the NE peak of Georges Bank both inside and outside the CA2 boundary, as well as within the open area SE of CA2. The lowest values (0.0-3.0 ind./100cm² shell) were observed throughout the Georges Bank region, though values between 1.0-3.0 ind./100cm² were most common on the NE peak of Georges Bank.

The largest concentrations of epifaunal biomass per 100cm² of live scallop shell (20.0-77.8 g/100cm² shell) were noted within CA1 and on the NE peak of Georges Bank (Figure 22b). Intermediate values of biomass (5.0-20.0 g/100cm² shell) were recorded within the NE portion of the NLCA, CA1, and the NE peak of Georges Bank, as well as sparsely within the Great South Channel, the open area SW of CA2, and within Canadian waters. The lowest observed values (0.0-5.0 g/100cm² shell) were generally seen within the Great South Channel, the open area NE of CA1, and the SE portion of Georges Bank, both inside and outside of the CA2 boundary.

Epifauna living on the surface of live scallop shells was most abundant (1.0-25.3 individuals/m²) within the central portion of the Great South Channel (Figure 22c). Medium densities (0.5-1.0 ind./m²) were observed within the S, SE, and NE portions of CA2 extending into Canadian waters. The lowest values (0-0.5 ind./m²) were present throughout the open and closed area regions, though values from 0.2-0.5 ind./m² were more commonly present within closed area boundaries.

Mean biomass of scallop shell epifauna was observed to be greatest (10.0-14.6 g/m²) with the NE peak of Georges Bank, extending from CA2 into Canadian waters (Figure 22d). Intermediate values (1.5-10.0 g/m²) were recorded within the NE portion

of NLCA, CA1, S and NE CA2, and the open area NW of CA2. Minimum biomass (0.0-1.5 g/m²) was generally observed within the open areas, though all three closed areas did contain stations with low biomass observations.

Bathymetric Distribution

Open area stations did not exhibit a significant change in epifaunal density per one hundred square centimeters of live *Placopecten magellanicus* shell, in association with bathymetry (ANOVA; $F = 0.560$, $p = 0.760$). Densities per 100 cm² of scallop shell decreased from stations less than 50m in depth (5.4 organisms/100cm² shell) to 80-89m (0.4 organisms/100cm² shell), followed by a moderate increase with depth (1.4-2.2 organisms/100cm² shell; Figure 23a). Within closed areas, densities per 100 cm² scallop shell showed a significant variation with depth (ANOVA; $F = 3.882$, $p = 0.003$). Densities at depths greater than 100m were found to be significantly greater than at depths of 50-89m (Tukey HSD test; $p < 0.028$).

Within open area sites, epifaunal density on live *Placopecten magellanicus* shells did not show a significant variation with depth (ANOVA; $F = 0.522$, $p = 0.789$). Densities were highest at depths less than 50m (0.2 organisms/m²) and generally decreased with depth (Figure 23b). Closed areas stations also displayed no variation in scallop epifaunal density with depth (ANOVA; $F = 0.454$, $p = 0.839$); no clear bathymetric pattern was observed.

Biomass values per one hundred square centimeters of live *Placopecten magellanicus* shell did not vary significantly with depth within open area sites (ANOVA; $F = 0.309$, $p = 0.929$). No clear bathymetric pattern was observed, with values generally

lowest from 60-89m in depth (Figure 24a). Within closed areas, epifaunal biomass per 100 cm² scallop shell was found to be significantly different with depth (ANOVA; $F = 10.013$, $p < 0.001$). Values at depths greater than 100m were significantly greater than at depths between 60-99m (Tukey HSD test; $p < 0.002$); biomass from depths less than 70m were significantly greater than at stations between 80-89m (Tukey HSD test, $p < 0.017$); values at 70-79m were significantly less than at depths from 50-59m (Tukey HSD test; $p = 0.028$).

Scallop epifaunal biomass within open area stations was not found to be significantly different in association with bathymetry (ANOVA; $F = 0.538$, $p = 0.777$). Biomass decreased with depth after 50-59m, except between 90-99m (Figure 24b). Closed area scallop epifaunal biomass showed no significant variation with depth (ANOVA; $F = 0.950$, $p = 0.468$). No clear bathymetric pattern was observed; biomass decreased from 50-59m to 80-89m, followed by an increase with depth.

Distribution by Sediment Type

Epifaunal densities per one hundred square centimeters of live *Placopecten magellanicus* shell were not found to be significantly different with regard to sediment type within open area locations (ANOVA; $F = 0.566$, $p = 0.688$). Densities were highest (1.6-1.7 ind./100cm² shell) within BSH and GCB environments, and lowest (0.6 ind./100cm² shell) within ISH locations (Figure 25a). Closed area densities did not show a significant change with sediment type (ANOVA; $F = 1.835$, $p = 0.135$). Highest values were recorded within BSH environments (1.6 ind./100cm² shell), while the lowest

abundances (0.4-0.5 ind./100cm² shell) were observed within MCS and ISH sediment types.

Mean scallop epifaunal densities within open areas were not determined to be significant in relation to sediment type (ANOVA, $F = 0.578$, $p = 0.680$). Densities ranged from lows within SFS and MCS sediments (0.02 ind./m²) to BSH and ISH environments (0.04-0.05 ind./m²), with the largest densities observed within GCB regions (0.09 ind./m²; Figure 25b). Densities within closed area regions were determined to be not significant in association with sediment type (ANOVA; $F = 1.288$, $p = 0.286$). MCS locations had the highest mean scallop epifaunal densities (0.36 ind./m²), while SFS were observed to be the lowest (0.05 ind./m²); all other sediment types showed intermediate values (0.11-0.17 ind./m²).

Biomass of epifauna per 100cm² of live scallop shell was not found to be significantly different in association to sediment type within open area environments (ANOVA; $F = 0.281$, $p = 0.889$). Biomass values were highest within BSH regions (7.4 g/100cm² shell) and lowest within SFS environments (2.0 g/100cm² shell; Figure 26a). Within closed areas, epifaunal biomass per 100cm² scallop shell was determined to be significantly different between sediment types (ANOVA; $F = 3.056$, $p = 0.024$), specifically between SFS (8.6 g/100cm² shell) and ISH (2.5 g/100cm² shell) sediment types (Tukey HSD test; $p = 0.020$).

Mean epifaunal biomass on live scallop shells within open areas was not significantly different in relation to sediment type (ANOVA; $F = 0.824$, $p = 0.516$). Mean biomass within SFS regions was observed to have the lowest values (0.02 g/m²), while GCB environments were the highest (0.4 g/m²; Figure 26b). Closed area sites

showed a significant variation in epifaunal biomass with regard to sediment (ANOVA; $F = 3.707$, $p = 0.009$). MCS environments (3.0 g/m^2) were observed to have significantly greater scallop epifaunal biomass than regions of BSH (0.6 g/m^2 ; Tukey HSD test; $p = 0.048$) and ISH (0.4 g/m^2 ; Tukey HSD test; $p = 0.028$).

Statistical Analysis of Scallop Presence as a Factor Controlling Ecological Variables

No significant change was recorded in the density of organisms per 100cm^2 of live *Placopecten magellanicus* shell with regard to sediment type or open/closed area location; the covariate of latitude ($p = 0.011$) was found to be significant, however (Table 5). Biomass per 100cm^2 of live *Placopecten magellanicus* shell was not determined to be significant in relation to sediment type or open/closed area location, though the covariates of latitude ($p = 0.009$), longitude ($p = 0.005$), and average scallop shell length ($p = 0.043$) were significant. No significant change was noted for mean epifaunal density on live scallop shell with regard to sediment type or open/closed area location. Mean epifaunal biomass on live scallop shell showed a significant difference in relation to sediment type (ANCOVA; $F = 3.724$; $p = 0.007$) and open/closed area location ($F = 20.763$; $p < 0.001$), though no covariates were found to be significant.

To further analyze for changes associated with the presence of *Placopecten magellanicus*, scallop density and biomass values were removed from the data to test for biases linked to fishery removals of *Placopecten magellanicus*. Paired sample t-tests were run on all stations where scallops were present, with pairs being constituted of: 1) samples without the scallop epifauna included, versus 2) samples with the scallop epifauna included. This analysis was used to determine whether the taxa present on

scallop shells affected significant changes to ecological variables. Within open area sites, paired sample t-tests illustrated significant changes in species richness ($t = -16.445$; $p < 0.001$), biomass ($t = -3.226$; $p = 0.002$), density-based Pielou's Evenness ($t = 2.343$; $p = 0.023$), and the Shannon-Wiener Index ($t = -3.172$; $p = 0.002$), with no significant changes observed in density (Table 6a). Closed area stations showed significant variations in species richness ($t = -14.078$; $p < 0.001$), density ($t = -4.052$; $p < 0.001$), and biomass ($t = -4.092$; $p < 0.001$), while diversity indices such as Pielou's Evenness and the Shannon-Wiener Index were unremarkable (Table 6b).

Independent sample t-tests were also conducted to examine changes in ecological variables between open and closed area sites. In samples without scallop epifauna included, species richness was the single ecological variable found to be significantly different between the open and closed area locations ($t = -2.109$; $p = 0.037$; Table 6c) with values observed to be greater within closed areas. When samples including scallop epifauna data were analyzed, only biomass was determined to be significantly different, with values being greater within closed areas ($t = -2.300$; $p = 0.023$; Table 6d).

Distribution of Invertebrate Scavengers and Opportunistic Predators

Geographic Distribution

Invertebrate predator and scavenger densities (organisms/m²), including 9 species of decapods, 7 species of asteroids, and 5 species of Muricoidea whelk, were highest (3.0-7.9 organisms/m²) within central NLCA and NE CA1 as well as the open areas east of NLCA and on the NE peak of Georges Bank (Figure 27a). Intermediate densities (1.0-3.0 organisms/m²) were observed buffering high density areas, as well as within the Great

South Channel and the open area NE of CA1. The majority of low density (0.0-1.0 organism/m²) areas occurred within CA1, CA2, and within Canadian waters.

Biomass (g/m²; wet weight) of invertebrate predators and scavengers was highest (30-58 g/m²) within central NLCA and southern CA2 (Figure 27b). Intermediate values (5-30 g/m²) surrounded high biomass regions and further included N and E CA2, NE CA1, and the open areas NE and S of CA1. Low biomass values (0-5 g/m²) covered much of CA1 and CA2 as well as the open areas surrounding them, the Great South Channel, and NE NLCA.

Bathymetric Distribution

Open area stations showed a significant difference in invertebrate predator and scavenger abundance (organisms/m²) with depth (ANOVA; $F = 3.391$, $p = 0.006$). Abundance at depths greater than 100m was found to be significantly different than at depths of 50-69m and 90-99m (Tukey HSD test; $p < 0.030$). Densities greater than 1.0 organism/m² were observed between depths of 50-79m (Figure 28). Within closed area sites, no significant variation with depth was detected (ANOVA; $F = 0.781$, $p = 0.588$). Highest abundance was observed between 60-69m with a mean value of 1.5 organisms/m².

Open area sites displayed a significant change in biomass (g/m²; wet weight) with depth (ANOVA; $F = 4.654$, $p = 0.001$). Invertebrate predator/scavenger biomass at 60-69m was significantly greater than at stations below 70m in depth (Tukey HSD test; $p < 0.047$). Biomass increased from station less than 50m in depth to 60-69m, followed by a decrease with depth (Figure 29). Closed area biomass showed a weakly significant

variation with depth (ANOVA; $F = 2.253$, $p = 0.049$). Biomass ranged between 2.5-5.0 g/m^2 , except for stations at 70-79m (16.0 g/m^2) and greater than 100m in depth (0.9 g/m^2).

Distribution by Sediment Type

Within open areas, abundance of invertebrate scavengers and opportunistic predators (organisms/ m^2) was not observed to be significantly variable with sediment type (ANOVA; $F = 0.659$; $p = 0.623$). MCS and BSH environments had the lowest observed abundance (less than 0.7 organisms/ m^2), while all other sediments showed densities above 1.0 organisms/ m^2 (Figure 30). Closed area stations did not show a significant change associated with sediment type (ANOVA; $F = 1.533$; $p = 0.203$). The highest abundances (greater than 1.2 organisms/ m^2) were observed in MCS and ISH sediments, while BSH environments were lowest (0.3 organisms/ m^2).

Biomass within open areas displayed no significant change with sediment type (ANOVA; $F = 0.740$; $p = 0.568$). SFS environments were observed to have less than 1.0 g/m^2 of invertebrate scavenger and opportunistic predator biomass while all other environments were between 2.4-3.8 g/m^2 (Figure 31). Within closed area stations, a significant difference was recorded with sediment type (ANOVA; $F = 4.127$; $p = 0.005$). The lowest biomass values noted were within SFS and BSH sediments (2.1-2.2 g/m^2) and were found to be significantly less than MCS environments (11.2 g/m^2 ; Tukey HSD test, $p < 0.032$).

Statistical Analysis of Invertebrate Scavengers and Opportunistic Predators

Mean densities of invertebrate scavengers and opportunistic predators (organisms/m²) showed no significant change with sediment type or open/closed area location, though longitude covaried significantly ($p = 0.011$; Table 7). A significant difference in mean invertebrate scavenger and opportunistic predator biomass (g/m²) was shown in relation to sediment type (ANCOVA; $F = 4.054$; $p = 0.004$); latitude was found to be a significant covariate ($p = 0.034$).

Distribution of Commercial Scallop Fishing Effort

In 2000, peak scallop fleet fishing effort (200-250 hours bottom time per nm²) within the open areas of Georges Bank occurred within three regions: 1) the southern portion of Great South Channel between NLCA and CA1, 2) the region NE of CA1, and 3) the NE peak of Georges Bank west of CA2 (Figure 32). Intermediate fishing effort (100-200 hours bottom time per nm²) further extended regions of higher effort, and also included a portion of the Great South Channel NW of CA1. Lower values (20-100 hours bottom time per nm²) cover most of the Great South Channel region, as well as much of the area between the forty and fifty fathom depth contours between CA1 and CA2. The lowest values (0.2-10.0 hours bottom time per nm²) cover areas that connect regions of higher fishing effort and may likely be an artifact of the data. These results may be caused by vessels traveling between major fishing locations, vessels breaking down, periods of gear, dredge testing for new fishing grounds, etc.

Statistical Analysis of Fishing Effort and Distance from a Closed Area Boundary

A significant positive partial regression slope was found for species richness against longitude ($t = 4.298$; $p < 0.001$), with a $r^2 = 0.34$ (Table 8). A multiple linear regression of biomass showed a positive partial regression slope in relation to latitude ($t = 2.690$; $p = 0.009$), with a $r^2 = 0.23$. No significant partial regression slopes were found for the ecological variables of density ($r^2 = 0.09$), Pielou's Evenness Index (based on density; $r^2 = 0.10$), or the Shannon-Wiener Index (based on density; $r^2 = 0.13$).

No significant partial regression slopes were obtained for invertebrate scavenger and opportunistic predator densities (Table 9). The multiple linear regression provided a $r^2 = 0.15$. Biomass of invertebrate scavengers and opportunistic predators was determined to have three significant negative partial regression slopes: 1) latitude ($t = -2.161$; $p = 0.035$), 2) depth ($t = -2.897$; $p = 0.005$), and 3) fishing effort ($t = -2.751$; $p = 0.008$), providing a multiple linear regression with $r^2 = 0.26$.

DISCUSSION

A reasonable number of taxa were collected in comparison to previous studies on Georges Bank, with a total of 95 taxa over 138 stations. Collie et al. (1997) cataloged 91 species over 50 stations, while a study by Thouzeau et al. (1991) identified greater numbers (140 species in 65 stations). Both studies record high numbers of epifaunal species within their collections; Thouzeau et al. (1991) noted 76% of the recorded species were benthic epifauna. These findings closely resemble this study which collected 95 taxa over 138 stations, with 90% noted as epifaunal taxa. Other studies such as Maciolek and Grassle (1987), which reported 783 species, are not comparable to this study as only

9% of the benthic species identified were epifaunal taxa, largely associated with the type of gear used as well as the size of sieve mesh used in sample retention was 0.3mm, compared to the 38mm mesh dredge liner used in this study. Various factors, such as sampling gear, sieve size, bottom temperature, water depth, and sediment type, likely effected the number of taxa that were collected (Maciolek and Grassle, 1987; Theroux and Grosslein, 1987; Thouzeau et al., 1991).

Several caveats must be understood in reviewing the results of this study. The mesh-lined NOAA survey dredge is at best a semi-quantitative research device (Eleftheriou and Holme, 1984). As the efficiency of the survey dredge is assumed to be roughly 0.50, based on *Placopecten magellanicus* studies, values may be underestimates of true abundance and biomass (Hart, 2003). Dredge efficiency may also have varied in association to the sediment type at a particular station as sediment grain size varied from silts to gravel, interspersed with cobbles and boulders. The use of a NOAA survey dredge hindered the ability to quantitatively sample biogenic bottoms (a mixture of sand, gravel, cobble, and tubes of the polychaete *Filograna implexa*), as well as amphipod tubes, which have been observed in other studies in the region (Langton and Robinson, 1990; Thouzeau et al., 1991; Collie et al., 1997). Using differential GPS navigation, dredge hauls were one nautical mile in length, though this measurement may add imprecision to the data.

Environmental and Closed Area Boundary Effects on Invertebrate Fauna

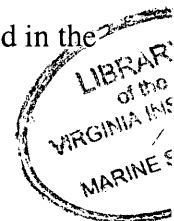
The covariates of latitude and/or longitude, used as a means of understanding geographic distributions on Georges Bank, were found to display significant variations in

mean species richness, density, biomass, Pielou's Evenness (density-based), and the Shannon-Wiener Index (\log_2 density-based; Table 3). Ecological variables were found to increase as latitude increased, largely associated with regions such as the northern portions of the Great South Channel, CA1, and CA2 which were the most productive and diverse (Figures 5a-f). Higher ecological values were also observed to be correlated with increasing longitude, generally with the greatest values found within the Great South Channel. These geographic findings are largely associated with regions of primarily gravel, cobble, and boulder sediment which provide three-dimensional structure for benthic species, in addition to limiting locations where fishing could be prosecuted (NEFSC, 2002). Both geographic variables illustrate a patchwork of productivity on Georges Bank, though these regions are largely associated with sand and gravel substrates.

Depth as a continuous covariate was also found to be an important variable influencing mean density and biomass with values decreasing with increasing depth (Table 3). Though most of the differences were not significant, general trends in the data were consistent with the highest values generally at depths less than 80m (Figures 7-8). Density values occasionally deviated from this finding with increases at depths greater than 90m, which is largely accounted for by the prevalence of silty-/fine-sand (SFS) environments at these depths within the regions sampled (Figures 7, 18a-b, 19a-b). These findings are similar to those of other general studies on macrofauna along the northwest Atlantic continental shelf (Theroux and Grosslein, 1987; Thouzeau et al., 1991; Theroux and Wigley, 1998). Other studies such as Collie et. al (1997) are not directly comparable as the regions sampled were predominantly composed of gravel substrates.

Once the covariates of latitude, longitude, and depth were taken into account, sediment type was determined to be a significant factor controlling ecological variables (Table 3). Gravel sediments interspersed with areas of cobbles and boulders (GCB) and medium-/course-sand (MCS) regions provided optimal physical environments for biodiversity, with the number of species, evenness, and Shannon-Wiener Index being significantly greater than the least structured environment of (SFS), a finding similar to a previous study (Thouzeau et al., 1991). Density values were significantly higher within SFS environments, largely due to the echinoderms *Asterias vulgaris*, *Echinarachnius parma*, and *Ophiura sarsi* (Table 2a, Figures, 20a-b). Few Georges Bank studies can be compared with this finding as (SFS) are generally overlooked in the literature as few commercial invertebrate species reside in this environment (Collie et al., 2000; Johnson, 2002). Mean biomass was characterized by the bivalve *Placopecten magellanicus* with the majority present in GCB and MCS environments (Table 2a, Figures 21a-b). As these sediment types are more commonly studied on Georges Bank, this finding is well founded in comparison to the literature (Thouzeau et al., 1991; Collie et al., 1997; Collie et al., 2000; Johnson, 2002; NEFSC, 2002; NRC, 2002).

Values for mean species richness, biomass, and the Shannon-Wiener Index (\log_2 , density-based) were observed to be significantly greater within closed areas when adjusted to account for the covariates (Table 3). Similar results have been noted in numerous studies (Collie et al., 1997; Collie et al., 2000; Drabsch et al., 2001; Jennings et al., 2001). In addition, Pielou's Evenness (biomass-based) was found to be significantly higher within open areas. Using biomass values to determine Pielou's Evenness allows for colonial organisms such as bryozoans, hydroids, and sponges to be included in the



result, but tends to give weight to species with larger individuals. This finding provides a similar result to other studies in that certain species (e.g. *Placopecten magellanicus*) proliferate within undisturbed areas and cause evenness values to decrease (Collie et al., 1997; NEFSC, 2002; NRC, 2002). Mean density values, however, did not vary between disturbed and undisturbed areas as has been noted in other studies (Collie et al., 1997; Collie et al., 2000). This finding may be associated with the limited number of sediment types studied in those projects.

In addition, biomass was the only ecological variable observed to have greater variability within closed areas in comparison to open fishing locations over all depths and sediment types (Figures 8, 14). This variability is largely associated with the abundance of large *Placopecten magellanicus* present within portions of the closed areas. This effect is evident within the values observed for Bivalvia; closed area sites contained an average of 5.0kg/100m² compared to 1.3kg/100m² within open area locations (Tables 1b, 1c). Other taxonomic groups such as Bryozoa, Echinoidea, and Asteroidea also showed large increases in prevalence within closed areas; within open area locations, only Porifera displayed a greater incidence in comparison to closed areas. Density showed some increased variability within open areas in comparison to closed area sites, though this was limited to certain depths and sediment types (Figures 7, 13).

Effects on Invertebrate Scavengers and Opportunistic Predators

Mean biomass of invertebrate scavengers and opportunistic predators showed significant variations with sediment type, while no factor was found to be significant in terms of mean density (Table 7). The largest individuals were found predominantly

within MCS substrates, which were shown to be significantly greater than predators/scavengers with SFS and BSH regions ($p < 0.030$; Figure 31). This finding may be an artifact of fishing effort as MCS substrates are commonly targeted by many commercial fisheries on Georges Bank. Change in fishing effort across the closed area boundaries, however, was not found to be a significant effect on the density or biomass of invertebrate scavengers and opportunistic predators. Other recent studies have made similar findings (Engel and Kvitek, 1998; Johnson, 2002). Collie et al. (1997) noted that mean sizes of *Pagurus acadianus* were larger in areas of disturbance, which may likely have been caused by migration into regions where prey had been damaged by scallop dredges. This study found similar results with the mean weight of *Pagurus acadianus* being greater within openly fished areas (5.63g compared to 4.23g), though not by a significant degree. In comparing the results for all noted invertebrate scavengers and opportunistic predators, closed areas were generally observed to have higher biomass, though these results were not significantly different (Figures 29, 31). Individual species exhibited less than 0.3g/m^2 variation in mean biomass between open and closed areas, except for *Asterias vulgaris* which displayed a 2.6g/m^2 increase in biomass within closed area sites, though this finding was not determined to be significant. The high variability in invertebrate scavenger and opportunistic predator populations, both between and within sediment types and depth ranges, further complicate these observations.

Effects of Fishing Effort and Distance from Boundaries on Ecological Variables

Following a multiple linear regression, the level of fishing effort outside of the closed area boundaries (in terms of scallop dredge bottom time, in hours per nm^2) was

determined to be significantly correlated to biomass of invertebrate scavengers and opportunistic predators; all other ecological variables were not observed to be significantly correlated (Tables 8-9). Though a comparison of invertebrate scavenger and opportunistic predator biomass across closed area boundaries did not show a significant difference (Table 7), increasing levels of fishing effort throughout open areas was found to decrease the amount of observed biomass (Table 9). While invertebrate scavengers and opportunistic predators displayed minimal increases with low levels of fishing effort (<20 hours dredge bottom time per nm²), higher levels were found to decrease biomass. This effect illustrates that changes in invertebrate scavengers and opportunistic predators occur on a localized level in close proximity to active fishing. Fishermen are alleged to “fish the line,” a term illustrating the attempt to harvest commercial species which may have migrated from within closed area boundaries. As commercial GPS and the computer mapping software used by fishermen is not without error, vessels generally avoid fishing within a half mile of the boundary. With this fishery-imposed buffer present on both the inside and outside of the closed area boundary, invertebrate scavengers and opportunistic predators are likely unable to take direct advantage of organisms damaged or killed by dredges and trawls within another fishing area. This finding expands on the general assumption that fishing indirectly increases invertebrate scavenger and opportunistic predator biomass as distance from an area of disturbance may play an important role (Collie et al., 1997; McConnaughey et al., 2000; Johnson, 2002; NEFSC, 2002).

Distance from a closed area boundary was not found to be significantly correlated to any ecological variable (Tables 8-9). This finding is largely associated with the

geographic variability in fishing effort (Figure 32). Further sampling along a transect of stations from at an arbitrary distance within the open areas to the closed area boundary may better serve to test this hypothesis. Such a survey would provide a range of fishing efforts along the transect from heavily impacted to undisturbed at the closed area boundary. In addition, variability associated with the patchiness of Georges Bank environments would be greatly reduced.

Effect of Sea Scallop Presence on Ecological Variables

The sea scallop *Placopecten magellanicus* may be a factor controlling many ecological variables on Georges Bank as they are known to provide a solid substrate for epifaunal species (Anderson et al., 1997). Values of epifaunal biomass per 100cm² of live *Placopecten magellanicus* shell were found to be positively correlated with increasing mean shell height (Table 5). As fishermen select scallops over 100mm in shell height, open area locations become depleted of larger animals. Swimming studies on *Placopecten magellanicus* have found that animals from 80-100mm in shell height generally begin to become encrusted with a variety of epifaunal taxa which continue to accumulate as the shell grows (Dadswell and Weihs, 1990; Cheng and DeMont, 1996; Anderson et al., 1997). Mean scallop epifaunal biomass (g/m²) showed significant variations in association to sediment type as well as location within an open or closed fishing region (Table 5). The largest values were noted within MCS and GCB regions, areas known for large abundances of *Placopecten magellanicus*. Effects on densities of epifaunal taxa are more difficult to ascertain as many are colonial organisms such as bryozoans, hydrozoans, and sponges (Table 4). To analyze for changes associated with

the presence of *Placopecten magellanicus*, scallop abundance and biomass values were removed from the data and were treated as though they were inanimate objects, such as cobbles, so that only their physical structure could be used as a factor. Paired sample t-tests were run on all stations where scallops were present (n=120), with pairs being constituted of: 1) samples without the scallop epifauna included, versus 2) samples with the scallop epifauna included. This analysis was used to determine whether the taxa present on scallop shells affected significant changes to ecological variables.

Except for density, all ecological variables showed a significant difference between values with and without scallop epifauna within open area locations (Table 6a). Species richness, biomass, and the Shannon-Wiener Index exhibited increased values when live *Placopecten magellanicus* shells were present for epifaunal organisms to inhabit. Pielou's Evenness (density-based) values were found to decrease with the presence of scallop epifauna. This effect is related to increased abundances in certain non-colonial epifaunal taxa (e.g. *Balanus amphitrite niveus*) on live *Placopecten magellanicus* shells which become numerically dominant and cause overall evenness of taxa to decrease (Table 2b). Within closed areas, species richness, density, and biomass values were significantly greater when scallop epifauna data was included (Table 6b). The significant difference in density, which was not observed within open areas, may be associated with the increased surface area of live *Placopecten magellanicus* shell per square meter within the closed areas. Biodiversity indices were not found to be significantly different within closed fishing regions. This finding may be associated with the increased prevalence of colonial epifaunal taxa (e.g. bryozoans, hydroids, and sponges) present on live *Placopecten magellanicus* shell within the closed areas (Auster

et al., 1996; Collie et al., 2000; NEFSC, 2002). Such findings suggest that the physical presence of *Placopecten magellanicus* plays a significant role in the biodiversity of Georges Bank.

To further test what role *Placopecten magellanicus* and the epifauna present on scallop shells perform within the biodiversity of Georges Bank, two independent-sample t-tests were conducted to test whether the fishery removals of *Placopecten magellanicus* were a factor causing overall ecological variables to vary between open and closed area stations (Table 3). Upon removing *Placopecten magellanicus* data (including scallop shell epifauna) from the analysis, a comparison of fishing areas found that only species richness was significantly greater within closed areas (Table 6c). When scallop shell epifauna data was included in the analysis (with *Placopecten magellanicus* data still absent), only mean biomass was determined to be significantly greater within closed areas in comparison to open fishing regions (Table 6d). Species richness became insignificant after scallop shell epifauna data were included in the analysis for a number of reasons. Taxa present on scallop shells within the closed areas were also present living on the benthic substrate as well, while some of these taxa showed higher scallop shell fidelity within open areas (Table 4). Once scallop shell epifauna were included in the analysis, taxa that had not been present at open area sites reappeared in the data. This finding suggests that while some taxa may be observed on live *Placopecten magellanicus* shells within both disturbed and undisturbed regions, closed areas provide additional shelter from bottom fishing where certain taxa are able to proliferate on the benthic substrate. Biomass was found to be insignificant when *Placopecten magellanicus* density and biomass was removed from the analysis. Biomass became significantly greater

within closed areas after the scallop epifauna data was included largely due to the increased surface area provided by the unfished scallop population. Additionally, under either analysis, absence of *Placopecten magellanicus* and/or their epifauna caused the data to exhibit no significant changes in abundance or the biodiversity indices of Pielou's Evenness (density-based) or the Shannon-Wiener Index (Tables 6c-d).

Conclusions

In summary, variations in overall ecological variables (Table 3) can be attributed to environmental factors such as depth, sediment type, and geographic location, as well as defined fisheries regions, all to varying degrees. These results agree with previous studies with regard to macrobenthic epifauna (Theroux and Grosslein, 1987; Thouzeau et al., 1991; Collie et al., 1997; Theroux and Wigley, 1998; Collie et al., 2000; Drabsch et al., 2001; Jennings et al., 2001; Johnson, 2002; NEFSC, 2002; NRC, 2002). Invertebrate scavenger and opportunistic predator data showed no significant change with regard to open or closed area location, though a partial negative correlation was noted with regard to increasing fishing pressure in open fishing regions. This finding expands on previous studies which found limited increases in these taxa with low levels of fishing effort (Johnson, 2002). Conversely, the decrease in invertebrate scavengers and opportunistic predators is likely associated with damage incurred from increasing fishing effort as many of these species are bycatch within various fisheries. In general, however, the amount of fishing effort and distance from the closed area boundary were not found to be significant indicators of ecological variables. In regard to future research, scientists

wishing to analyze these factors should conduct transect-based sampling patterns through regions of variable fishing effort to elicit improved results.

These results come with the caveat that fishery removals of *Placopecten magellanicus* within open areas were determined to be a significant cause of the variation observed in ecological variables within open and closed fishery sites (Tables 6a-d). These effects can be attributed to *Placopecten magellanicus* as well as epifauna present on scallop shells. To further compare open and closed area sites, scallops and their epifauna were artificially removed from the data; species richness was noted to be significantly greater within closed areas in comparison to open areas (Table 6c). This result is most likely associated with taxa being present on substrate within closed area locations, while only present as scallop epifauna in open fishing regions. Epifaunal taxa within open areas would be less likely to find a stable attachment site other than small *Placopecten magellanicus* shells (<100mm) due to active fishing pressure. Other ecological variables showed no significant change due to fishing effort within the open areas. These findings suggest that though fishing effort changes the benthic environment, these effects are minimal when one controls for the role played by the target commercial species, in this case *Placopecten magellanicus*. If the epifauna present on *Placopecten magellanicus* shells are returned to the system, both species richness and biomass notably change (Table 6d). Though scallop fisheries largely return scallop shell to the benthic environment by preparing their product at sea, epifaunal taxa are generally only observed on live scallop shells. This observation is likely associated with both the stability of *Placopecten magellanicus* as a permanent settlement site and the fact that dead scallop shells are affected by bottom currents which cause continuous damage to the epifaunal

species attached to the shell. Live scallops, on the other hand, keep their upper shell valve directed towards the water column when eliciting their escape response. Species richness becomes insignificant when scallop epifauna are included in the analysis because scallops within open areas add further to the taxa present than do scallops within closed areas. In addition, biomass is found to be significantly greater due to the increased proliferation and surface area of *Placopecten magellanicus* present within closed areas. These findings further suggest that the presence of *Placopecten magellanicus* is a major factor effecting ecological variables within closed areas. Fishery removals of this species will undoubtedly affect ecological studies performed when *Placopecten magellanicus* is a key species in the ecosystem.

One additional caveat must be considered in regard to the findings involving fishery removals, that being the recovery time of the benthic environment. The period of time elapsed from the last commercial fishing trip within a given closed area to the time at which this survey was conducted ranged from 18-24 months for regions opened briefly in 1999-2001 to nearly 10 years for locations which have not been fished since their closure in 1994. Estimates of benthic recovery time on Georges Bank range from several months to as long as 5-10 years (Collie et al., 1997; Collie et al., 2000; Johnson, 2002; NEFSC, 2002; NRC, 2002). Level of disturbance may also be a factor effecting recovery time as sections of Georges Bank are fished numerous times per year (Auster et al., 1996; Collie et al. 1997; Collie et al., 2000). These findings will provide scientists with a basis for future investigations on the role of bottom fishing on ecological variables as well as present an indication that investigators should consider what role fishery removals of

particular target species have on these variables. Annual surveys should be conducted to further understand and estimate the role of recovery time.

FIGURES & TABLES

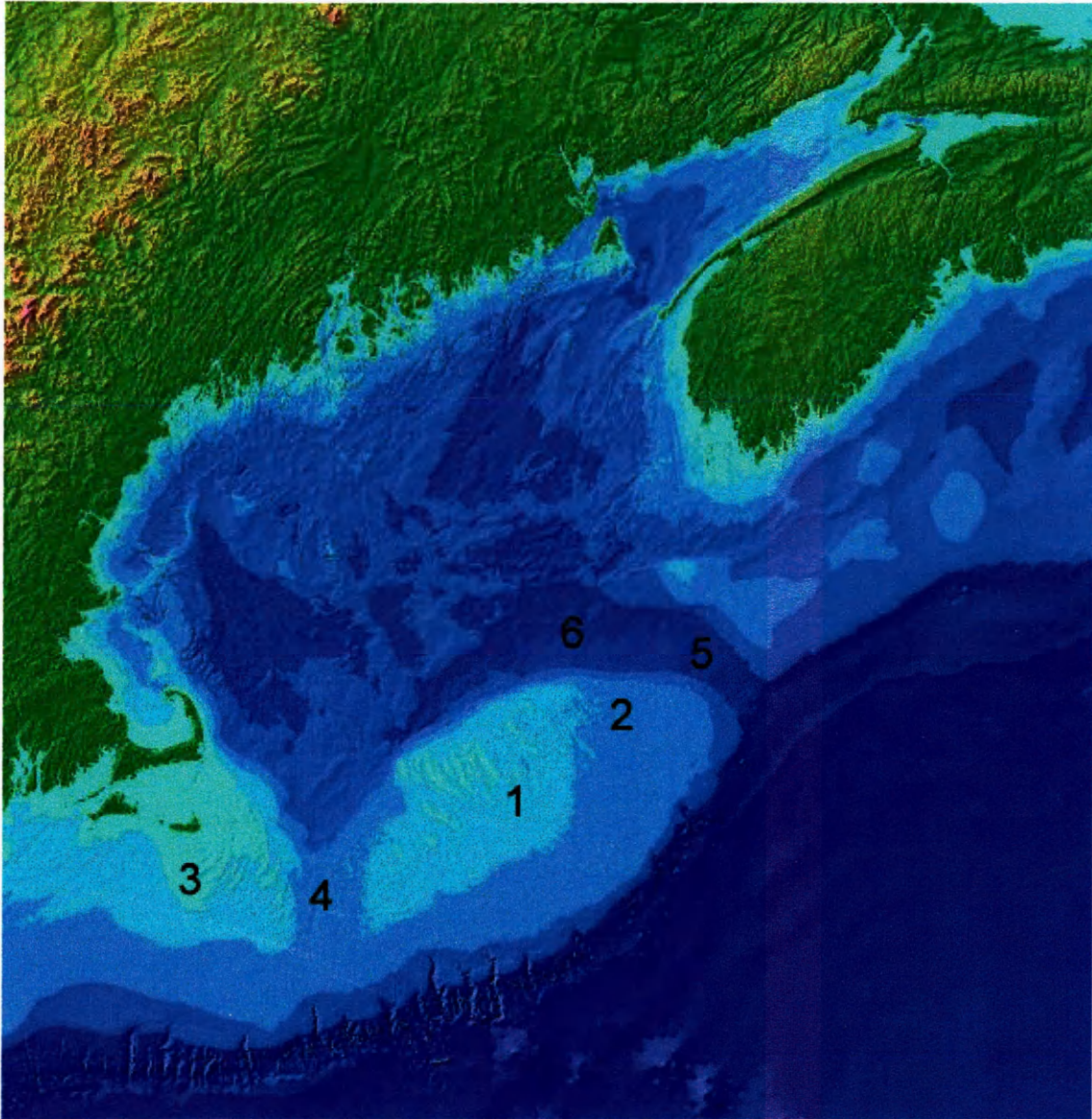


Figure 1. Georges Bank (1), east of Cape Cod, Massachusetts. Other locations of interest include: (2) the NE Peak of Georges Bank (largely in Canadian waters), (3) Nantucket Shoals, (4) Great South Channel, extending north-south of position indicated, (5) Northeast Channel, and (6) Georges Basin.

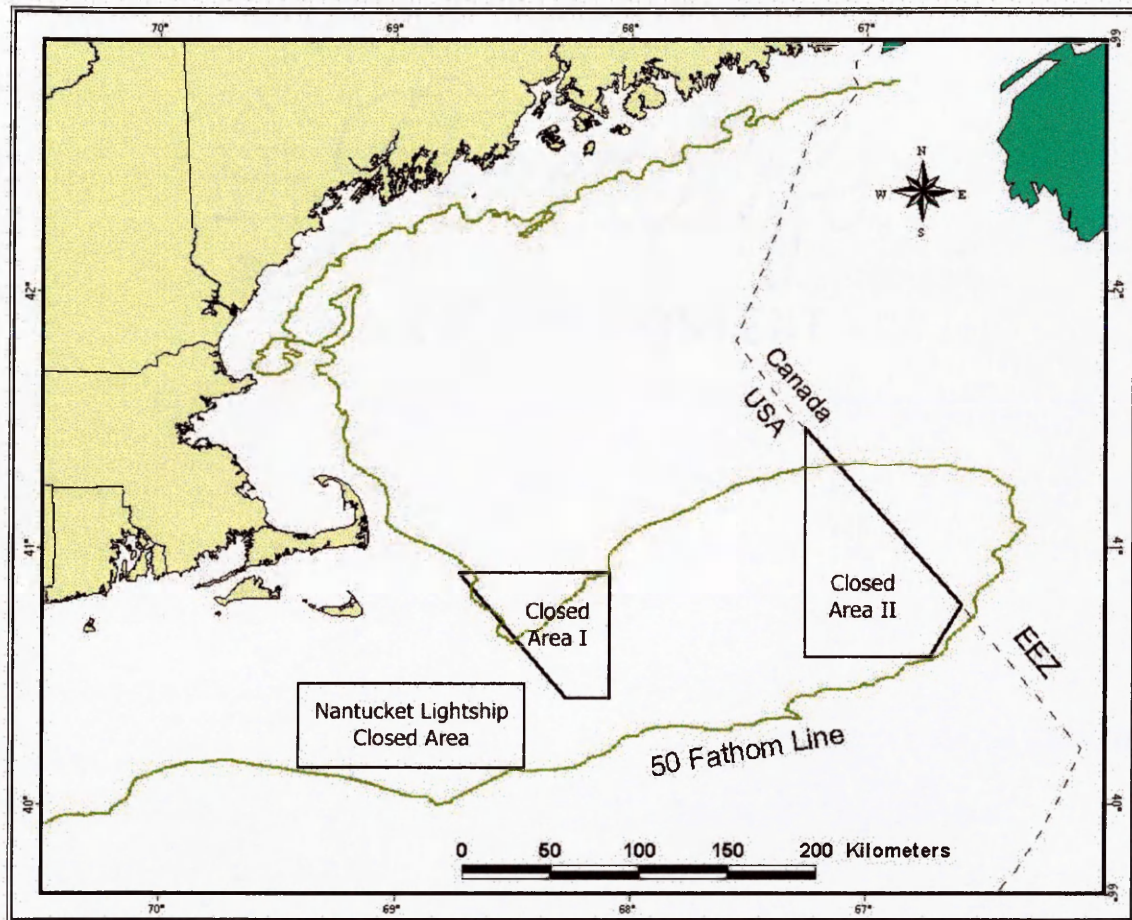


Figure 2. Georges Bank groundfish closed areas, initially closed in 1994. Also visible is the 50 fathom line showing the shape of Georges Bank, as well as the Economic Exclusion Zone (EEZ) of the United States and Canada.

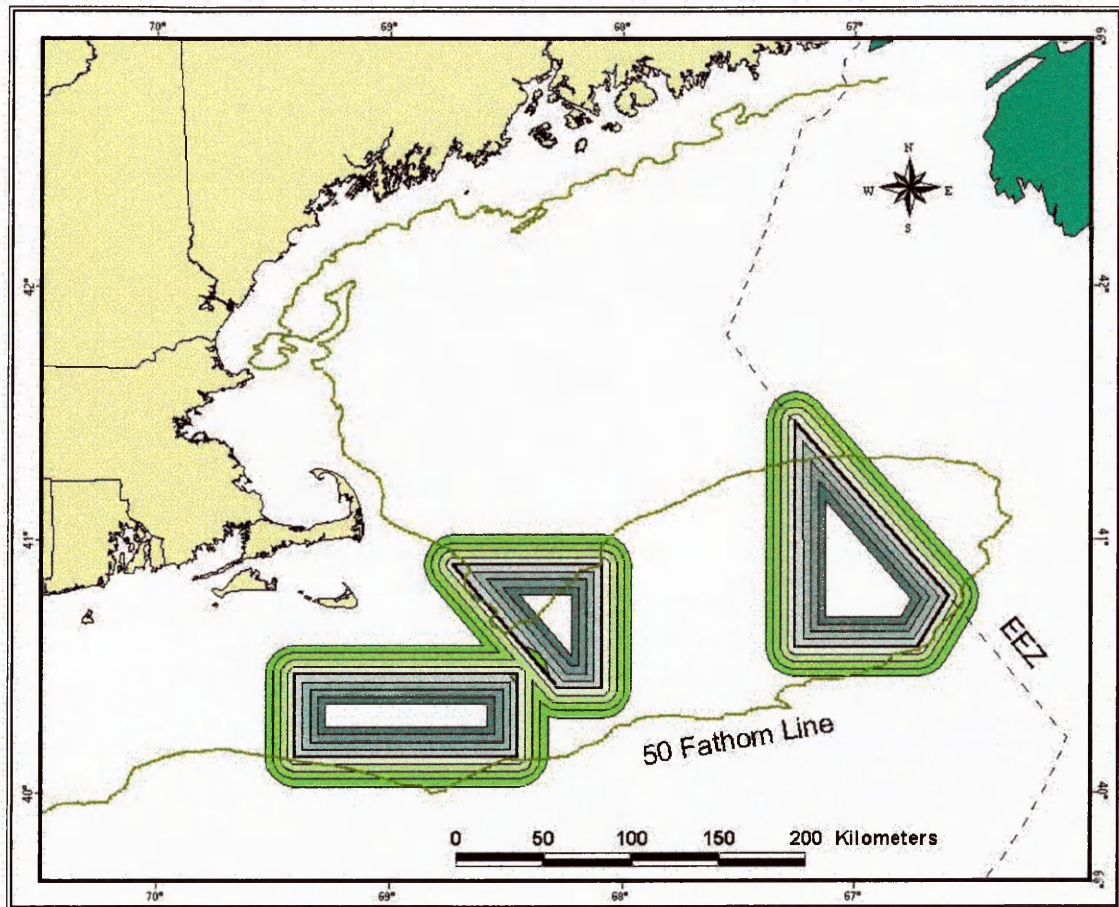


Figure 3. Five kilometer wide individual buffers inside and outside of the Georges Bank closed areas. Total buffer width is twenty kilometers both inside and outside of the closed area boundaries.

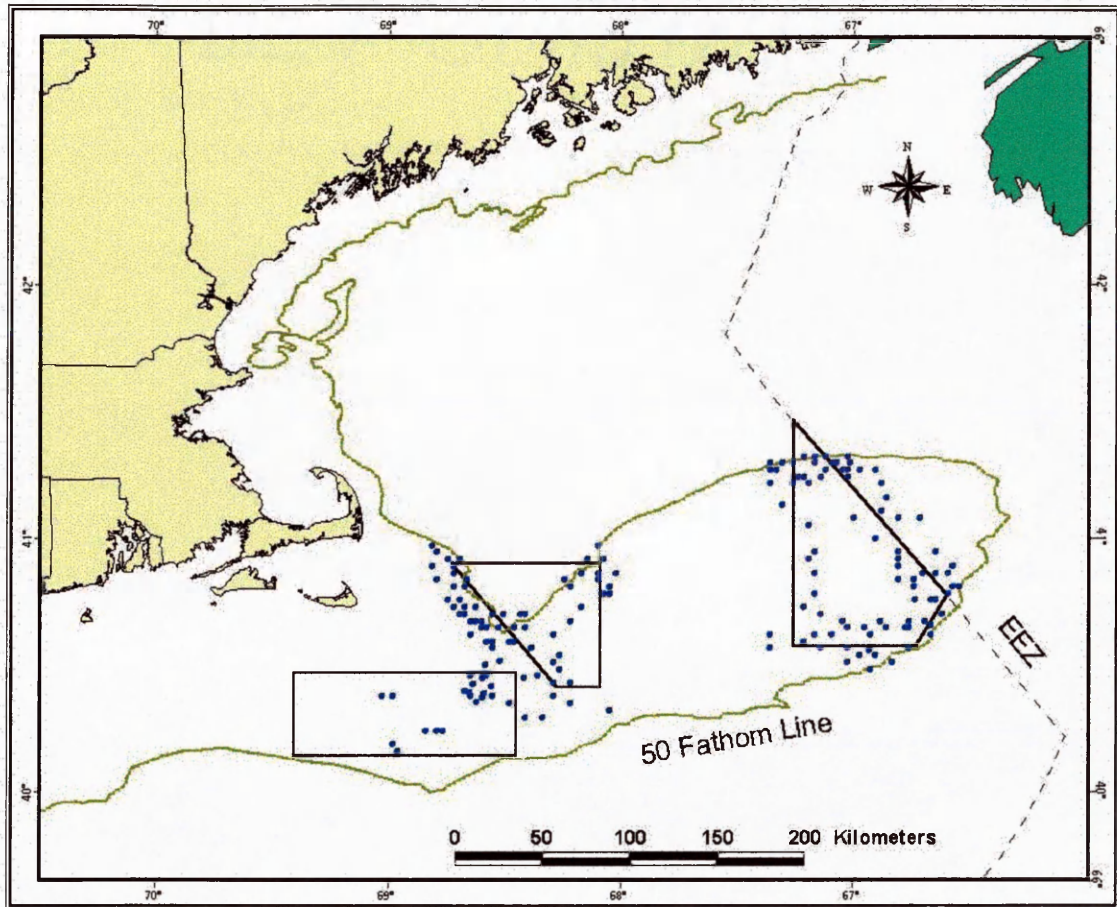


Figure 4a. One hundred and seventy-one stations selected using the buffers shown in Figure 3. These stations were to be sampled if conducted during the survey cruise.

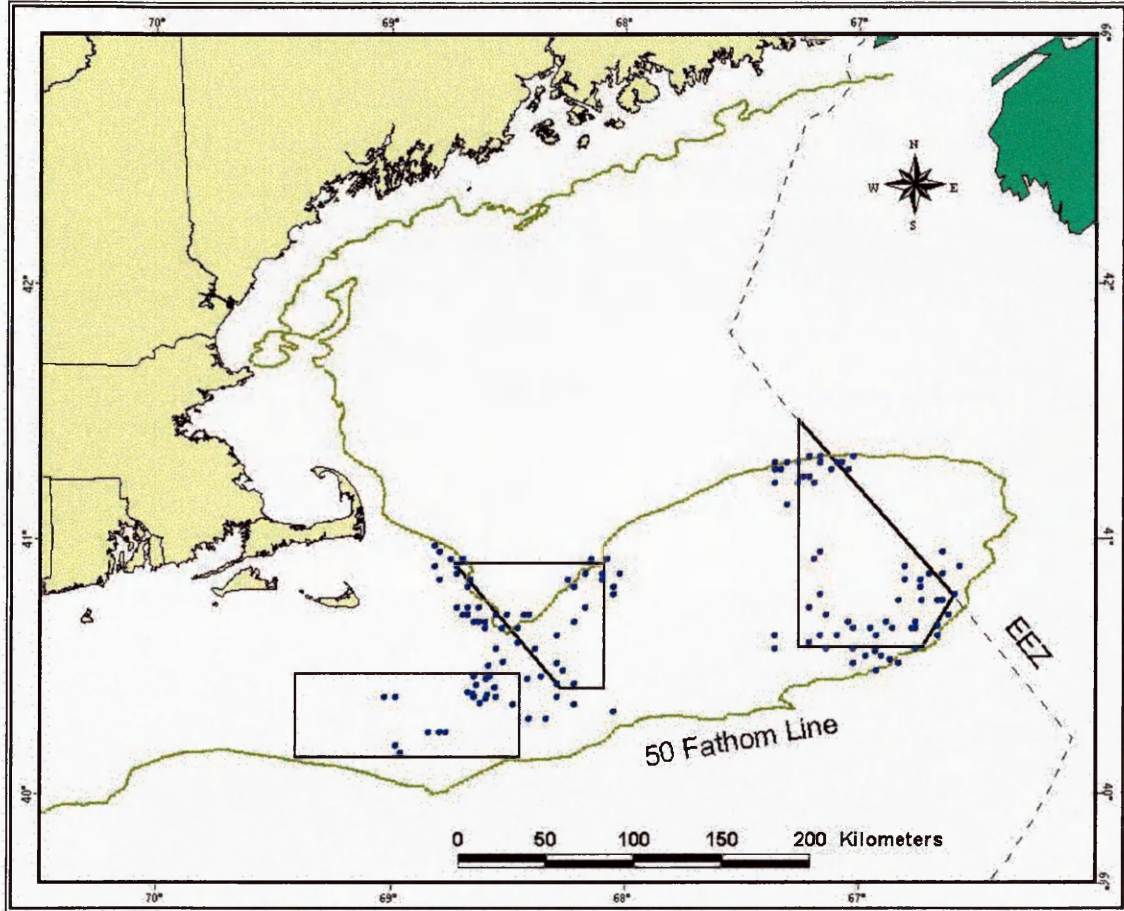


Figure 4b. The final one hundred and thirty-eight stations conducted during the survey cruise, with thirty-three selected stations removed due to operational constraints and sampling problems.

Taxonomic Groups	Density		Biomass		Number of Species		Frequency of Occurrence
	# 100m ²	Freq. (%)	g 100m ²	Freq. (%)	#	Freq. (%)	
Porifera	-	-	159.8	3.6	7	7.4	50.7
Ascidacea	9.8	3.2	20.9	0.5	4	4.2	15.2
Anthozoa	12.4	4.1	16.6	0.4	2	2.1	28.3
Bryozoa	-	-	124.9	2.8	6	6.3	95.7
Hydrozoa	-	-	14.8	0.3	13	13.7	93.5
Polychaeta	-	-	39.1	0.9	6	6.3	80.4
Bivalvia	29.8	9.7	3,139.9	70.5	13	13.7	95.7
Gastropoda	16.0	5.2	63.8	1.4	11	11.6	63.8
Scaphopoda	0.0	0.0	0.0	0.0	1	1.1	1.4
Opisthobranchia	0.2	0.1	0.2	0.0	1	1.1	7.2
Cephalopoda	0.0	0.0	2.1	0.0	3	3.2	9.4
Isopoda	0.1	0.0	0.0	0.0	1	1.1	2.2
Pycnogonida	0.3	0.1	0.0	0.0	2	2.1	8.7
Cirripedia	26.5	8.6	5.6	0.1	3	3.2	33.3
Decapoda	23.9	7.8	110.7	2.5	9	9.5	100.0
Holothuroidea	0.3	0.1	24.7	0.6	2	2.1	12.3
Echinoidea	91.4	29.8	436.3	9.8	2	2.1	78.3
Asteroidea	60.3	19.7	264.2	5.9	7	7.4	96.4
Ophiuroidea	35.7	11.6	27.2	0.6	2	2.1	37.7
Total	306.7	100.0	4,451.0	100.0	95	100.0	

Table 1a. Mean density (individuals/100m²), mean biomass (g/100m²; wet weight), number of taxa, percent composition, and frequency of occurrence of taxonomic groups of benthic invertebrates (except densities of sponges, bryozoans, hydroids, and polychaetes), as sampled from a total of 138 stations on Georges Bank.

Taxonomic Groups	Density		Biomass		Number of Species		Frequency of Occurrence
	# 100m ⁻²	Freq. (%)	g 100m ⁻²	Freq. (%)	#	Freq. (%)	
Porifera	-	-	212.7	9.9	6	6.9	55.9
Asciacea	19.5	6.9	42.1	2.0	3	3.4	22.1
Anthozoa	11.0	3.9	14.2	0.7	2	2.3	29.4
Bryozoa	-	-	83.9	3.9	6	6.9	94.1
Hydrozoa	-	-	15.2	0.7	13	14.9	88.2
Polychaeta	-	-	24.4	1.1	6	6.9	83.8
Bivalvia	18.0	6.4	1,256.2	58.3	11	12.6	100.0
Gastropoda	15.4	5.5	56.6	2.6	10	11.5	66.2
Scaphopoda	0.0	0.0	0.0	0.0	1	1.1	1.5
Opisthobranchia	0.2	0.1	0.2	0.0	1	1.1	4.4
Cephalopoda	0.0	0.0	4.1	0.2	3	3.4	10.3
Isopoda	0.0	0.0	0.0	0.0	0	0.0	0.0
Pycnogonida	0.3	0.1	0.0	0.0	2	2.3	7.4
Cirripedia	50.5	17.9	6.3	0.3	3	3.4	33.8
Decapoda	26.2	9.3	119.9	5.6	8	9.2	100.0
Holothuroidea	0.1	0.0	16.3	0.8	2	2.3	4.4
Echinoidea	35.5	12.6	135.8	6.3	2	2.3	69.1
Asteroidea	54.7	19.4	137.8	6.4	6	6.9	98.5
Ophiuroidea	50.2	17.8	29.4	1.4	2	2.3	44.1
Total	281.8	100.0	2,155.3	100.0	87	100.0	

Table 1b. Mean density (individuals/100m²), mean biomass (g/100m²; wet weight), number of taxa, percent composition, and frequency of occurrence of taxonomic groups of benthic invertebrates (except densities of sponges, bryozoans, hydroids, and polychaetes), as sampled from a total of 68 open area stations on Georges Bank.

Taxonomic Groups	Density		Biomass		Number of Species		Frequency of Occurrence
	# 100m ⁻²	Freq. (%)	g 100m ⁻²	Freq. (%)	#	Freq. (%)	
Porifera	-	-	108.5	1.6	6	6.9	45.7
Ascidacea	0.4	0.1	0.3	0.0	4	4.6	8.6
Anthozoa	13.8	4.2	18.8	0.3	2	2.3	27.1
Bryozoa	-	-	164.7	2.5	6	6.9	97.1
Hydrozoa	-	-	14.4	0.2	12	13.8	98.6
Polychaeta	-	-	53.5	0.8	5	5.7	77.1
Bivalvia	41.3	12.5	4,969.9	74.4	12	13.8	91.4
Gastropoda	16.6	5.0	70.7	1.1	11	12.6	61.4
Scaphopoda	0.0	0.0	0.0	0.0	1	1.1	1.4
Opisthobranchia	0.2	0.1	0.1	0.0	1	1.1	10.0
Cephalopoda	0.0	0.0	0.1	0.0	2	2.3	8.6
Isopoda	0.2	0.1	0.0	0.0	1	1.1	4.3
Pycnogonida	0.2	0.1	0.0	0.0	2	2.3	10.0
Cirripedia	3.2	1.0	4.9	0.1	3	3.4	32.9
Decapoda	21.6	6.5	101.7	1.5	8	9.2	100.0
Holothuroidea	0.5	0.2	32.9	0.5	2	2.3	20.0
Echinoidea	145.6	44.0	728.3	10.9	2	2.3	87.1
Asteroidea	65.7	19.9	387.1	5.8	5	5.7	94.3
Ophiuroidea	21.6	6.5	25.0	0.4	2	2.3	31.4
Total	330.9	100.0	6,681.1	100.0	87	100.0	

Table 1c. Mean density (individuals/100m²), mean biomass (g/100m²; wet weight), number of taxa, percent composition, and frequency of occurrence of taxonomic groups of benthic invertebrates (except densities of sponges, bryozoans, hydroids, and polychaetes), as sampled from a total of 70 closed area stations on Georges Bank.

Phylum	Species	Station Occurrence	Total Density (%)	Total Biomass (%)
Mollusca: Bivalvia				
	<i>Placopecten magellanicus</i>	130	6.0%	70.2%
	<i>Chlamys islandica</i>	4	0.0%	0.1%
	<i>Arctica islandica</i>	4	0.0%	0.1%
	<i>Modiolus modiolus</i>	20	0.3%	0.0%
	<i>Cyclocardia borealis</i>	10	0.0%	0.0%
	<i>Spisula solidissima</i>	8	0.1%	0.0%
	<i>Astarte castanea</i>	5	0.1%	0.0%
	<i>Anomia squamula</i>	97	2.9%	0.0%
	<i>Astarte undata</i>	5	0.0%	0.0%
	<i>Hiatella arctica</i>	4	0.1%	0.0%
	<i>Cerastoderma pinnulatum</i>	6	0.1%	0.0%
	<i>Macoma calcarea</i>	1	0.0%	0.0%
	<i>Cuspidaria glacialis</i>	1	0.0%	0.0%
Mollusca: Cephalopoda				
	Unidentified Cephalopod	2	0.0%	0.0%
	<i>Bathypolypus arcticus</i>	8	0.0%	0.0%
	<i>Illex illecebrosus</i>	3	0.0%	0.0%
Mollusca: Gastropoda				
	<i>Lunatia heros</i>	18	0.1%	0.6%
	<i>Buccinum undatum</i>	46	0.8%	0.4%
	<i>Crepidula plana</i>	47	3.5%	0.1%
	<i>Crepidula fornicata</i>	18	0.3%	0.1%
	<i>Colus pubescens</i>	13	0.2%	0.1%
	<i>Neptunea lyrata decemcostata</i>	1	0.0%	0.0%
	<i>Nassarius trivittatus</i>	13	0.1%	0.0%
	<i>Crucibulum striatum</i>	4	0.1%	0.0%
	<i>Lunatia triseriata</i>	6	0.0%	0.0%
	<i>Epitonium greenlandicum</i>	4	0.0%	0.0%
	<i>Colus pygmaea</i>	7	0.0%	0.0%
Mollusca: Opisthobranchia				
	Unidentified Opisthobranch	10	0.1%	0.0%
Mollusca: Scaphopoda				
	<i>Dentalium entale stimpsoni</i>	2	0.0%	0.0%
Echinodermata: Asteroidea				
	<i>Asterias vulgaris</i>	131	18.9%	5.6%
	<i>Crossaster papposus</i>	18	0.1%	0.2%
	<i>Henricia sanquinolenta</i>	30	0.4%	0.1%
	<i>Marthasterias glacialis</i>	4	0.2%	0.0%
	<i>Solaster endeca</i>	2	0.0%	0.0%
	<i>Astropecten americanus</i>	4	0.0%	0.0%
	<i>Asterias forbesii</i>	1	0.0%	0.0%
Echinodermata: Echinoidea				
	<i>Echinarachnius parma</i>	85	28.9%	8.7%
	<i>Strongylocentrotus droebachiensis</i>	38	0.8%	1.1%
Echinodermata: Holothuroidea				
	<i>Cucumaria frondosa</i>	6	0.0%	0.5%
	<i>Cucumaria pulcherrima</i>	12	0.1%	0.0%
Echinodermata: Ophiuroidea				
	<i>Ophiura sarsi</i>	18	10.0%	0.6%
	<i>Ophiopholis aculeata</i>	38	1.7%	0.0%

Table 2a. Rank order of all taxa sampled during the study within all areas of Georges Bank (138 stations), listed by the number of station occurrences, percentage of mean density, and percentage of mean biomass. Taxa are separated by taxonomic group and were identified to species level when possible. Continued on the following page.

Phylum	Species	Station Occurrence	Total Density (%)	Total Biomass (%)
Arthropoda: Pycnogonida				
	<i>Pycnogonum littorale</i>	10	0.1%	0.0%
	<i>Nymphon grossipes</i>	3	0.0%	0.0%
Arthropoda: Crustacea: Cirripedia				
	<i>Balanus hameri</i>	23	0.3%	0.1%
	<i>Balanus balanus</i>	18	0.4%	0.0%
	<i>Balanus amphitrite niveus</i>	12	8.0%	0.0%
Arthropoda: Crustacea: Decapoda				
	<i>Cancer borealis</i>	93	0.1%	1.3%
	<i>Pagurus acadianus</i>	104	3.4%	0.8%
	<i>Cancer irroratus</i>	68	0.1%	0.1%
	<i>Pagurus arcuatus</i>	39	3.4%	0.1%
	<i>Homarus americanus</i>	15	0.0%	0.1%
	<i>Hyas coarctatus</i>	21	0.3%	0.0%
	<i>Pelidnota mutica</i>	21	0.4%	0.0%
	<i>Pagurus pubescens</i>	1	0.0%	0.0%
	Unidentified Decapod Crab	2	0.0%	0.0%
Arthropoda: Crustacea: Isopoda				
	<i>Cirrolana sp.</i>	3	0.0%	0.0%
Annelida: Polychaeta				
	<i>Aphrodita hastata</i>	23	0.2%	0.3%
	<i>Filograna implexa</i>	27	-	0.3%
	Unidentified Scallop Boring Worm	90	-	0.2%
	<i>Terebellidae (Pista sp.?)</i>	12	-	0.1%
	<i>Hydroides dianthus</i>	4	-	0.0%
	<i>Spirorbis sp.</i>	58	-	0.0%
Porifera				
	<i>Suberites ficus</i>	44	-	1.8%
	<i>Haliclona oculata</i>	14	-	1.1%
	<i>Halichondria panicea</i>	26	-	0.6%
	<i>Polymastia mammillaris</i>	10	-	0.1%
	Unidentified Sponge	1	-	0.0%
	Unidentified White Encrusting Sponge	3	-	0.0%
	<i>Leucosolenia botryoides</i>	3	-	0.0%
Bryozoa				
	Unidentified Bryozoan 06	63	-	1.3%
	Unidentified Bryozoan 04	117	-	0.7%
	Unidentified Bryozoan 01	90	-	0.5%
	Unidentified Bryozoan 02	105	-	0.2%
	Unidentified Bryozoan 03	4	-	0.0%
	Unidentified Bryozoan 05	9	-	0.0%
Chordata: Ascidiacea				
	<i>Boltenia ovifera</i>	9	0.6%	0.3%
	Unidentified Tunicate	7	2.5%	0.2%
	<i>Dendrodoa carnea</i>	4	0.0%	0.0%
	<i>Molgula sp.</i>	3	0.0%	0.0%
Cnidaria: Anthozoa				
	<i>Epizoanthus americanus</i>	31	3.9%	0.4%
	<i>Tealia felina</i>	18	0.1%	0.0%
Cnidaria: Hydrozoa				
	Unidentified Hydroid 01	75	-	0.1%
	Unidentified Hydroid 04	112	-	0.1%
	Unidentified Hydroid 03	34	-	0.1%
	Unidentified Hydroid 09	64	-	0.0%
	Unidentified Hydroid 08	46	-	0.0%
	<i>Hydractinia echinata</i>	69	-	0.0%
	Unidentified Hydroid 12	35	-	0.0%
	Unidentified Hydroid 05	11	-	0.0%
	Unidentified Hydroid 02	31	-	0.0%
	Unidentified Hydroid 06	9	-	0.0%
	Unidentified Hydroid 07	2	-	0.0%
	Unidentified Hydroid 11	1	-	0.0%
	Unidentified Hydroid 10	2	-	0.0%

Phylum	Species	Station Occurrence	Total Density (%)	Total Biomass (%)
Mollusca: Bivalvia				
	<i>Placopecten magellanicus</i>	67	3.7%	57.5%
	<i>Chlamys islandica</i>	4	0.0%	0.4%
	<i>Arctica islandica</i>	2	0.0%	0.1%
	<i>Spisula solidissima</i>	5	0.1%	0.1%
	<i>Modiolus modiolus</i>	6	0.4%	0.1%
	<i>Cyclocardia borealis</i>	3	0.1%	0.0%
	<i>Astarte undata</i>	4	0.0%	0.0%
	<i>Anomia squamula</i>	46	1.5%	0.0%
	<i>Astarte castanea</i>	3	0.0%	0.0%
	<i>Hiatella arctica</i>	2	0.3%	0.0%
	<i>Cerastoderma pinnulatum</i>	3	0.2%	0.0%
	<i>Macoma calcarea</i>	0	0.0%	0.0%
	<i>Cuspidaria glacialis</i>	0	0.0%	0.0%
Mollusca: Cephalopoda				
	Unidentified Cephalopod	2	0.0%	0.2%
	<i>Bathypolypus arcticus</i>	5	0.0%	0.0%
	<i>Illex illecebrosus</i>	0	0.0%	0.0%
Mollusca: Gastropoda				
	<i>Buccinum undatum</i>	25	1.2%	1.1%
	<i>Lunatia heros</i>	4	0.1%	0.7%
	<i>Colus pubescens</i>	8	0.3%	0.3%
	<i>Crepidula fornicata</i>	5	0.2%	0.2%
	<i>Crepidula plana</i>	20	3.2%	0.2%
	<i>Lunatia triseriata</i>	3	0.0%	0.0%
	<i>Nassarius trivittatus</i>	4	0.1%	0.0%
	<i>Epitonium greenlandicum</i>	3	0.1%	0.0%
	<i>Crucibulum striatum</i>	3	0.2%	0.0%
	<i>Colus pygmaea</i>	4	0.0%	0.0%
	<i>Neptunea lyrata decemcostata</i>	0	0.0%	0.0%
Mollusca: Opisthobranchia				
	Unidentified Opisthobranch	3	0.1%	0.0%
Mollusca: Scaphopoda				
	<i>Dentalium entale stimpsoni</i>	1	0.0%	0.0%
Echinodermata: Asteroidea				
	<i>Asterias vulgaris</i>	65	18.0%	5.4%
	<i>Crossaster papposus</i>	10	0.2%	0.6%
	<i>Henricia sanquinolenta</i>	20	0.6%	0.2%
	<i>Marthasterias glacialis</i>	4	0.4%	0.1%
	<i>Solaster endeca</i>	2	0.0%	0.0%
	<i>Astropecten americanus</i>	2	0.1%	0.0%
	<i>Asterias forbesii</i>	0	0.0%	0.0%
Echinodermata: Echinoidea				
	<i>Echinarachnius parma</i>	33	11.8%	4.9%
	<i>Strongylocentrotus droebachiensis</i>	19	0.8%	1.4%
Echinodermata: Holothuroidea				
	<i>Cucumaria frondosa</i>	1	0.0%	0.8%
	<i>Cucumaria pulcherrima</i>	2	0.0%	0.0%
Echinodermata: Ophiuroidea				
	<i>Ophiura sarsi</i>	11	15.4%	1.3%
	<i>Ophiopholis aculeata</i>	21	2.3%	0.1%

Table 2b. Rank order of all taxa sampled during the study within the open areas of Georges Bank (68 stations), listed by the number of station occurrences, percentage of mean density, and percentage of mean biomass. Taxa are separated by taxonomic group and were identified to species level when possible. Continued on the following page.

Phylum	Species	Station Occurrence	Total Density (%)	Total Biomass (%)
Arthropoda: Pycnogonida				
	<i>Pycnogonum littorale</i>	4	0.1%	0.0%
	<i>Nymphon grossipes</i>	1	0.0%	0.0%
Arthropoda: Crustacea: Cirripedia				
	<i>Balanus hameri</i>	8	0.2%	0.2%
	<i>Balanus amphitrite niveus</i>	9	17.5%	0.0%
	<i>Balanus balanus</i>	7	0.1%	0.0%
Arthropoda: Crustacea: Decapoda				
	<i>Cancer borealis</i>	46	0.1%	2.4%
	<i>Pagurus acadianus</i>	51	4.9%	2.3%
	<i>Cancer irroratus</i>	28	0.1%	0.3%
	<i>Homarus americanus</i>	7	0.0%	0.2%
	<i>Pagurus arcuatus</i>	18	3.1%	0.2%
	<i>Hyas coarctatus</i>	8	0.5%	0.1%
	<i>Pelia mutica</i>	13	0.6%	0.0%
	<i>Pagurus pubescens</i>	1	0.0%	0.0%
	Unidentified Decapod Crab	0	0.0%	0.0%
Arthropoda: Crustacea: Isopoda				
	<i>Cirolana sp.</i>	0	0.0%	0.0%
Annelida: Polychaeta				
	<i>Aphrodita hastata</i>	9	0.3%	0.9%
	Unidentified Scallop Boring Worm	44	-	0.1%
	<i>Filograna implexa</i>	15	-	0.1%
	<i>Terebellidae (Pista sp.?)</i>	6	-	0.0%
	<i>Hydroides dianthus</i>	4	-	0.0%
	<i>Spirorbis sp.</i>	35	-	0.0%
Porifera				
	<i>Haliclona oculata</i>	11	-	4.6%
	<i>Suberites ficus</i>	18	-	3.7%
	<i>Halichondria panicea</i>	16	-	1.2%
	<i>Polymastia mammillaris</i>	7	-	0.4%
	<i>Leucosolenia botryoides</i>	3	-	0.0%
	Unidentified White Encrusting Sponge	2	-	0.0%
	Unidentified Sponge	0	-	0.0%
Bryozoa				
	Unidentified Bryozoan 06	31	-	2.6%
	Unidentified Bryozoan 02	53	-	0.6%
	Unidentified Bryozoan 01	40	-	0.4%
	Unidentified Bryozoan 04	55	-	0.3%
	Unidentified Bryozoan 05	5	-	0.0%
	Unidentified Bryozoan 03	1	-	0.0%
Chordata: Ascidiacea				
	<i>Boltenia ovifera</i>	8	1.4%	1.2%
	Unidentified Tunicate	6	5.5%	0.7%
	<i>Dendrodoa carnea</i>	2	0.0%	0.0%
	<i>Molgula sp.</i>	0	0.0%	0.0%
Cnidaria: Anthozoa				
	<i>Epizoanthus americanus</i>	14	3.8%	0.6%
	<i>Tealia feline</i>	8	0.1%	0.0%
Cnidaria: Hydrozoa				
	Unidentified Hydroid 01	35	-	0.2%
	Unidentified Hydroid 04	49	-	0.1%
	Unidentified Hydroid 03	14	-	0.1%
	Unidentified Hydroid 09	31	-	0.1%
	Unidentified Hydroid 08	24	-	0.1%
	<i>Hydractinia echinata</i>	29	-	0.0%
	Unidentified Hydroid 12	11	-	0.0%
	Unidentified Hydroid 05	7	-	0.0%
	Unidentified Hydroid 02	18	-	0.0%
	Unidentified Hydroid 06	5	-	0.0%
	Unidentified Hydroid 07	1	-	0.0%
	Unidentified Hydroid 11	1	-	0.0%
	Unidentified Hydroid 10	1	-	0.0%

Phylum	Species	Station Occurrence	Total Density (%)	Total Biomass (%)
Mollusca: Bivalvia				
	<i>Placopecten magellanicus</i>	63	8.0%	74.2%
	<i>Arctica islandica</i>	2	0.0%	0.1%
	<i>Astarte castanea</i>	2	0.1%	0.0%
	<i>Modiolus modiolus</i>	14	0.1%	0.0%
	<i>Cyclocardia borealis</i>	7	0.0%	0.0%
	<i>Anomia squamula</i>	51	4.2%	0.0%
	<i>Spisula solidissima</i>	3	0.0%	0.0%
	<i>Macoma calcarea</i>	1	0.0%	0.0%
	<i>Astarte undata</i>	1	0.0%	0.0%
	<i>Cerastoderma pinnulatum</i>	3	0.0%	0.0%
	<i>Hiatella arctica</i>	2	0.0%	0.0%
	<i>Cuspidaria glacialis</i>	1	0.0%	0.0%
	<i>Chlamys islandica</i>	0	0.0%	0.0%
Mollusca: Cephalopoda				
	<i>Illex illecebrosus</i>	3	0.0%	0.0%
	<i>Bathypolypus arcticus</i>	3	0.0%	0.0%
	Unidentified Cephalopod	0	0.0%	0.0%
Mollusca: Gastropoda				
	<i>Lunatia heros</i>	14	0.2%	0.6%
	<i>Buccinum undatum</i>	21	0.5%	0.2%
	<i>Crepidula plana</i>	27	3.7%	0.1%
	<i>Crepidula fornicata</i>	13	0.3%	0.1%
	<i>Colus pubescens</i>	5	0.1%	0.0%
	<i>Neptunea lyrata decemcostata</i>	1	0.0%	0.0%
	<i>Crucibulum striatum</i>	1	0.0%	0.0%
	<i>Nassarius trivittatus</i>	9	0.2%	0.0%
	<i>Colus pygmaea</i>	3	0.0%	0.0%
	<i>Lunatia triseriata</i>	3	0.0%	0.0%
	<i>Epitonium greenlandicum</i>	1	0.0%	0.0%
Mollusca: Opisthobranchia				
	Unidentified Opisthobranch	7	0.1%	0.0%
Mollusca: Scaphopoda				
	<i>Dentalium entale stimpsoni</i>	1	0.0%	0.0%
Echinodermata: Asteroidea				
	<i>Asterias vulgaris</i>	66	19.6%	5.7%
	<i>Crossaster papposus</i>	8	0.1%	0.1%
	<i>Henricia sanquinolenta</i>	10	0.1%	0.0%
	<i>Astropecten americanus</i>	2	0.0%	0.0%
	<i>Asterias forbesii</i>	1	0.0%	0.0%
	<i>Marthasterias glacialis</i>	0	0.0%	0.0%
	<i>Solaster endeca</i>	0	0.0%	0.0%
Echinodermata: Echinoidea				
	<i>Echinarachnius parma</i>	52	43.1%	9.9%
	<i>Strongylocentrotus droebachiensis</i>	19	0.9%	1.0%
Echinodermata: Holothuroidea				
	<i>Cucumaria frondosa</i>	5	0.1%	0.5%
	<i>Cucumaria pulcherrima</i>	10	0.1%	0.0%
Echinodermata: Ophiuroidea				
	<i>Ophiura sarsi</i>	7	5.4%	0.4%
	<i>Ophiopholis aculeata</i>	17	1.1%	0.0%

Table 2c. Rank order of all taxa sampled during the study within the closed areas of Georges Bank (70 stations), listed by the number of station occurrences, percentage of mean density, and percentage of mean biomass. Taxa are separated by taxonomic group and were identified to species level when possible. Continued on the following page.

Phylum	Species	Station Occurrence	Total Density (%)	Total Biomass (%)
Arthropoda: Pycnogonida				
	<i>Pycnogonum littorale</i>	6	0.0%	0.0%
	<i>Nymphon grossipes</i>	2	0.0%	0.0%
Arthropoda: Crustacea: Cirripedia				
	<i>Balanus hameri</i>	15	0.3%	0.1%
	<i>Balanus balanus</i>	11	0.6%	0.0%
	<i>Balanus amphitrite niveus</i>	3	0.1%	0.0%
Arthropoda: Crustacea: Decapoda				
	<i>Cancer borealis</i>	47	0.1%	0.9%
	<i>Pagurus acadianus</i>	53	2.2%	0.4%
	<i>Pagurus arcuatus</i>	21	3.7%	0.1%
	<i>Cancer irroratus</i>	40	0.1%	0.1%
	<i>Homarus americanus</i>	8	0.0%	0.0%
	<i>Hyas coarctatus</i>	13	0.2%	0.0%
	<i>Pelidnota mutica</i>	8	0.3%	0.0%
	Unidentified Decapod Crab	2	0.0%	0.0%
	<i>Pagurus pubescens</i>	0	0.0%	0.0%
Arthropoda: Crustacea: Isopoda				
	<i>Cirolana sp.</i>	3	0.1%	0.0%
Annelida: Polychaeta				
	<i>Filograna implexa</i>	12	-	0.3%
	Unidentified Scallop Boring Worm	46	-	0.3%
	<i>Aphrodita hastata</i>	14	0.1%	0.1%
	<i>Terebellidae (Pista sp.?)</i>	6	-	0.1%
	<i>Spirobranchia sp.</i>	23	-	0.0%
	<i>Hydroids dianthus</i>	0	-	0.0%
Porifera				
	<i>Suberites ficus</i>	26	-	1.2%
	<i>Halichondria panicea</i>	10	-	0.4%
	<i>Haliclona oculata</i>	3	-	0.0%
	<i>Polymastia mammillaris</i>	3	-	0.0%
	Unidentified Sponge	1	-	0.0%
	Unidentified White Encrusting Sponge	1	-	0.0%
	<i>Leucosolenia botryoides</i>	0	-	0.0%
Bryozoa				
	Unidentified Bryozoan 06	32	-	0.9%
	Unidentified Bryozoan 04	62	-	0.9%
	Unidentified Bryozoan 01	50	-	0.6%
	Unidentified Bryozoan 02	52	-	0.1%
	Unidentified Bryozoan 03	3	-	0.0%
	Unidentified Bryozoan 05	4	-	0.0%
Chordata: Ascidiacea				
	Unidentified Tunicate	1	0.0%	0.0%
	<i>Dendrodoa carnea</i>	2	0.0%	0.0%
	<i>Molgula sp.</i>	3	0.0%	0.0%
	<i>Boltenia ovifera</i>	1	0.0%	0.0%
Cnidaria: Anthozoa				
	<i>Epizoanthus americanus</i>	17	4.0%	0.3%
	<i>Tealia felina</i>	10	0.2%	0.0%
Cnidaria: Hydrozoa				
	Unidentified Hydroid 04	63	-	0.1%
	Unidentified Hydroid 01	40	-	0.0%
	Unidentified Hydroid 03	20	-	0.0%
	<i>Hydractinia echinata</i>	40	-	0.0%
	Unidentified Hydroid 09	33	-	0.0%
	Unidentified Hydroid 08	22	-	0.0%
	Unidentified Hydroid 12	24	-	0.0%
	Unidentified Hydroid 02	13	-	0.0%
	Unidentified Hydroid 05	4	-	0.0%
	Unidentified Hydroid 06	4	-	0.0%
	Unidentified Hydroid 07	1	-	0.0%
	Unidentified Hydroid 10	1	-	0.0%
	Unidentified Hydroid 11	0	-	0.0%

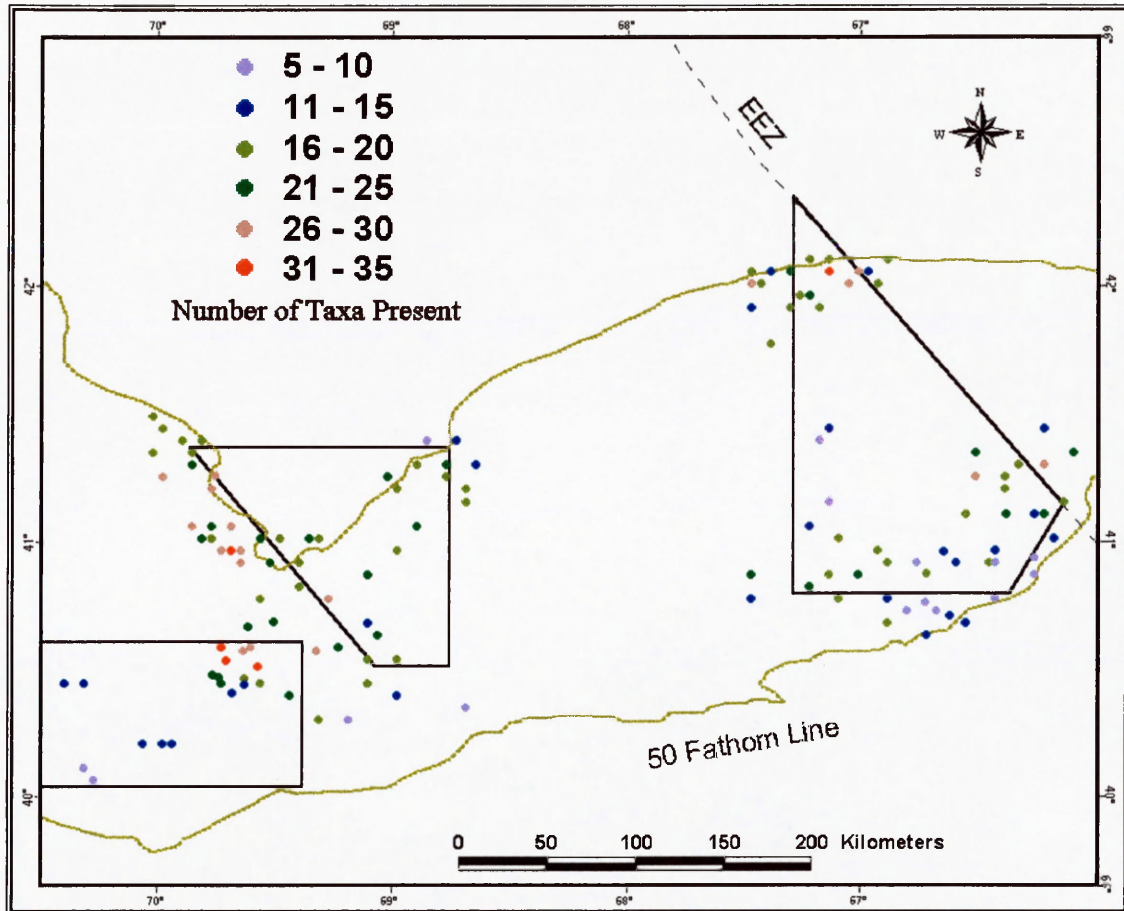


Figure 5a. Geographic distribution of benthic invertebrate species richness on Georges Bank.

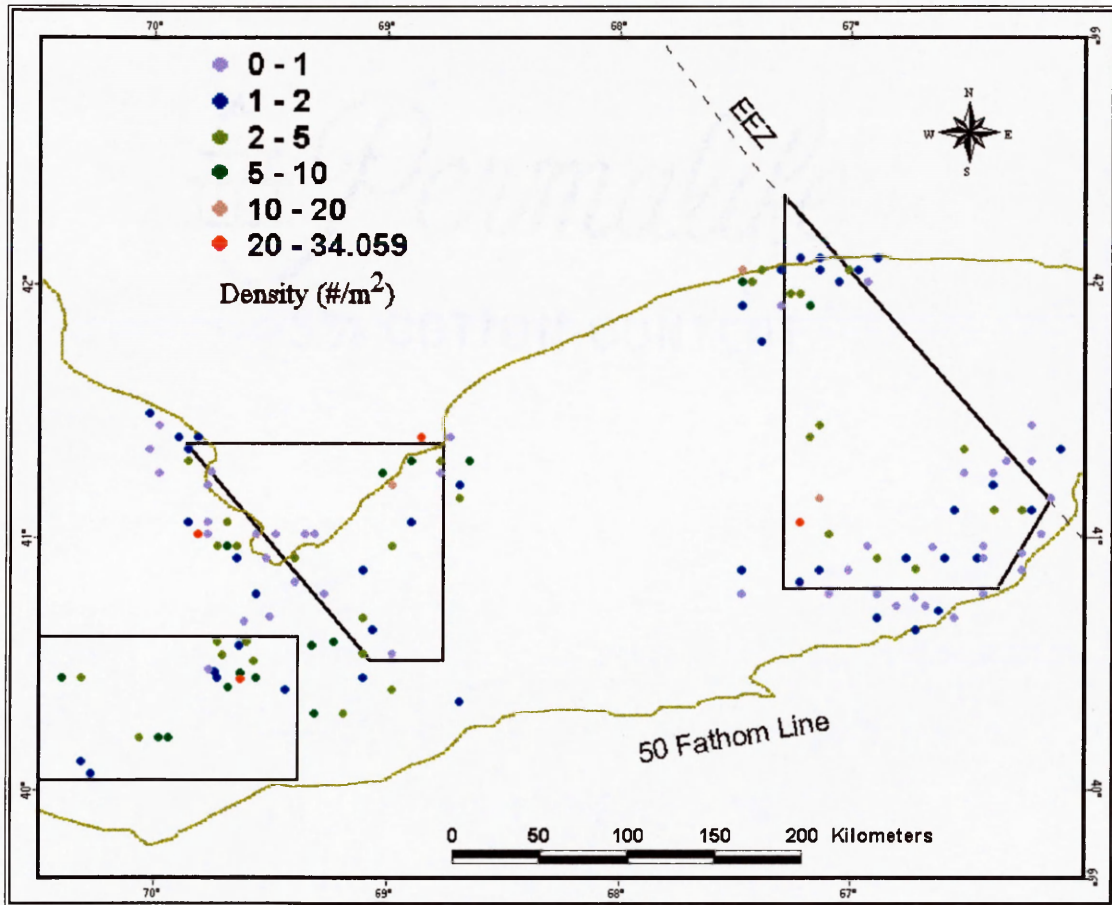


Figure 5b. Geographic distribution of benthic invertebrate density ($\#/m^2$) of all taxa combined (except densities of sponges, bryozoans, hydroids, and most polychaetes) on Georges Bank.

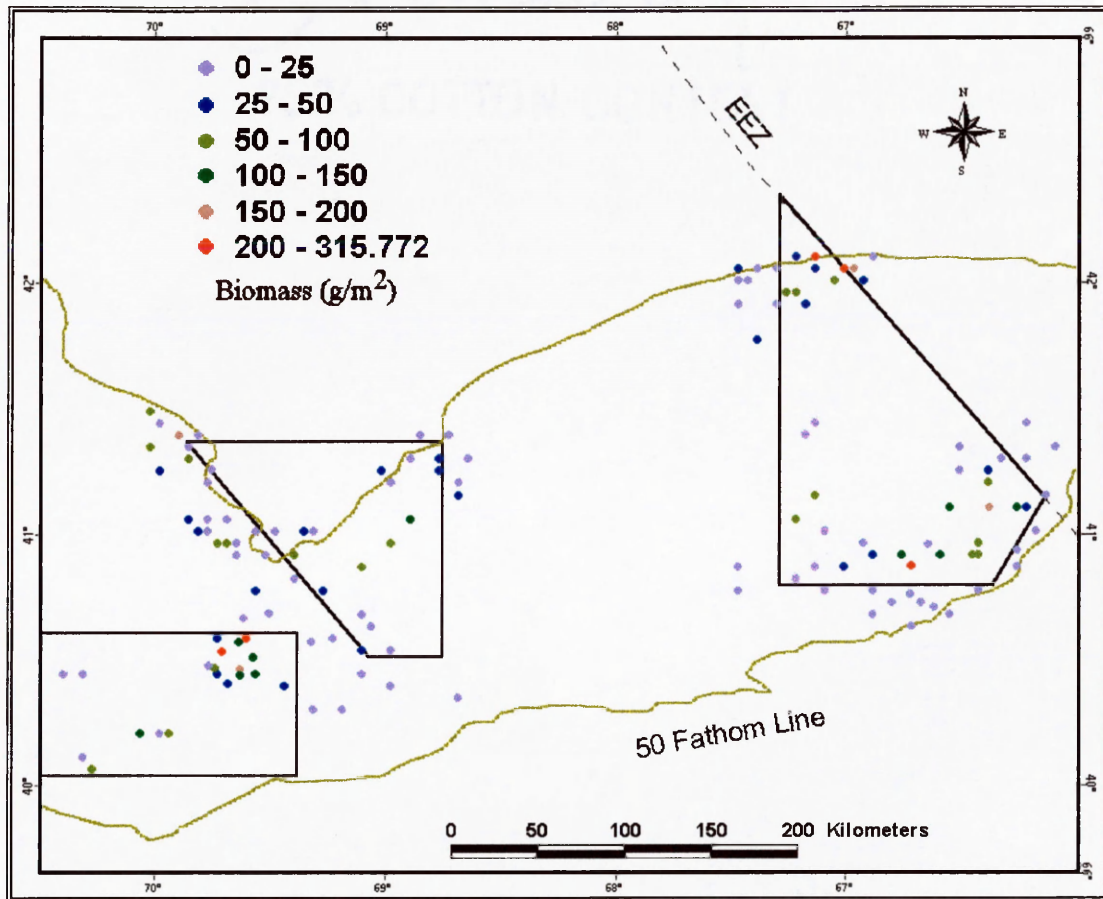


Figure 5c. Geographic distribution of benthic invertebrate biomass (g/m^2 ; wet weight) of all taxa combined on Georges Bank.

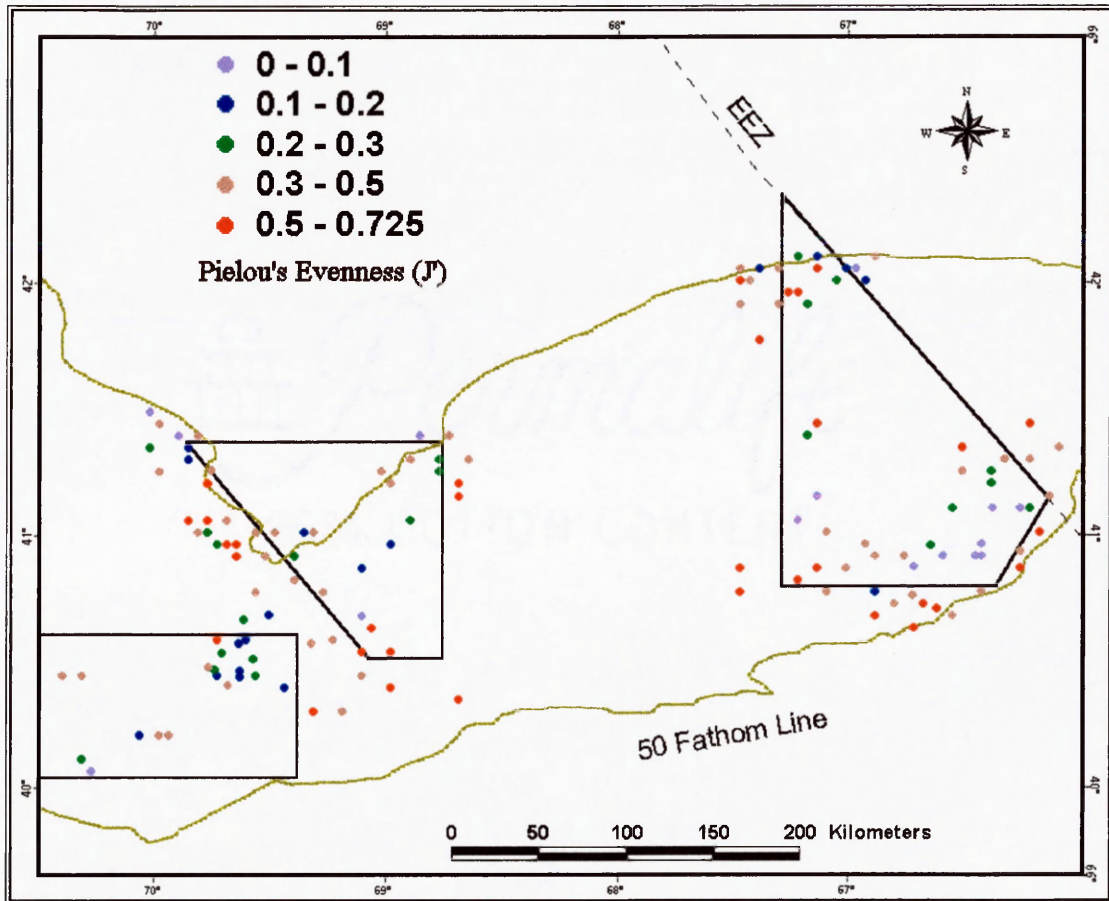


Figure 5d. Geographic distribution of Pielou's Evenness (J' based on biomass) of all taxa combined on Georges Bank.

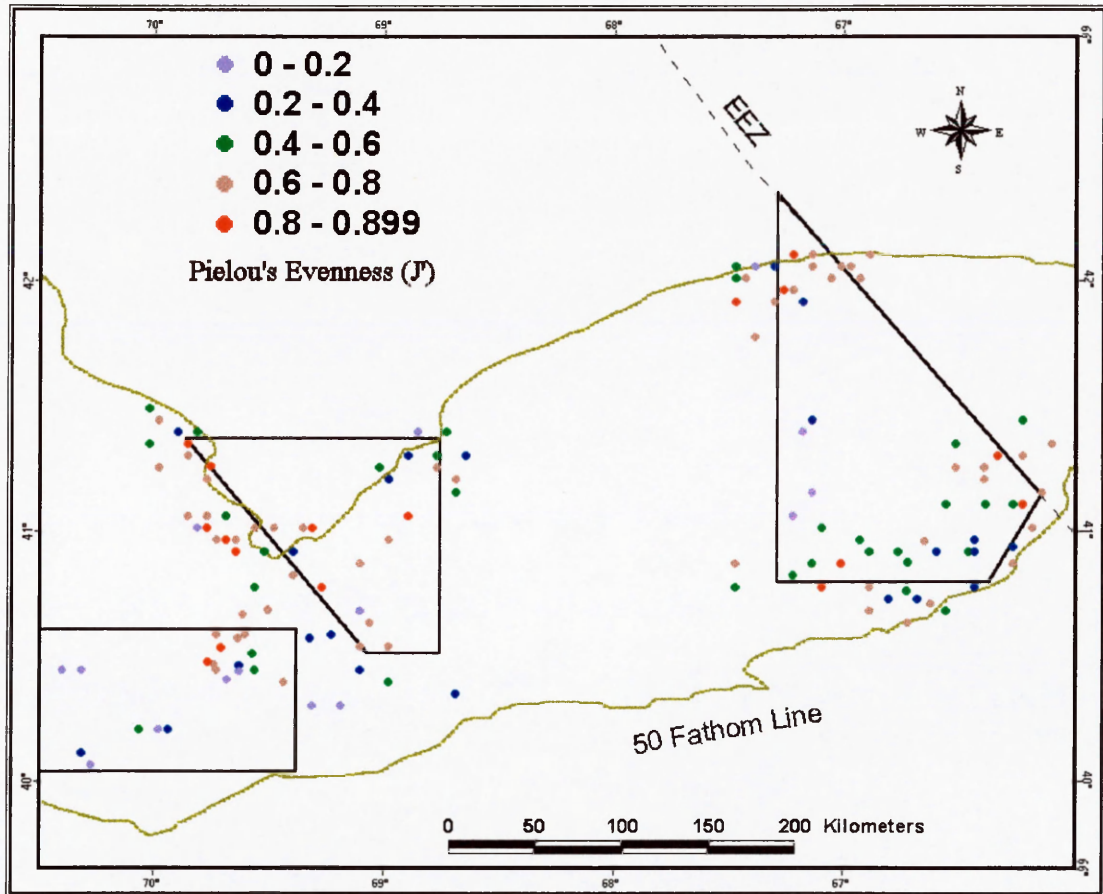


Figure 5e. Geographic distribution of Pielou's Evenness (J' based on density) of all taxa combined on Georges Bank.

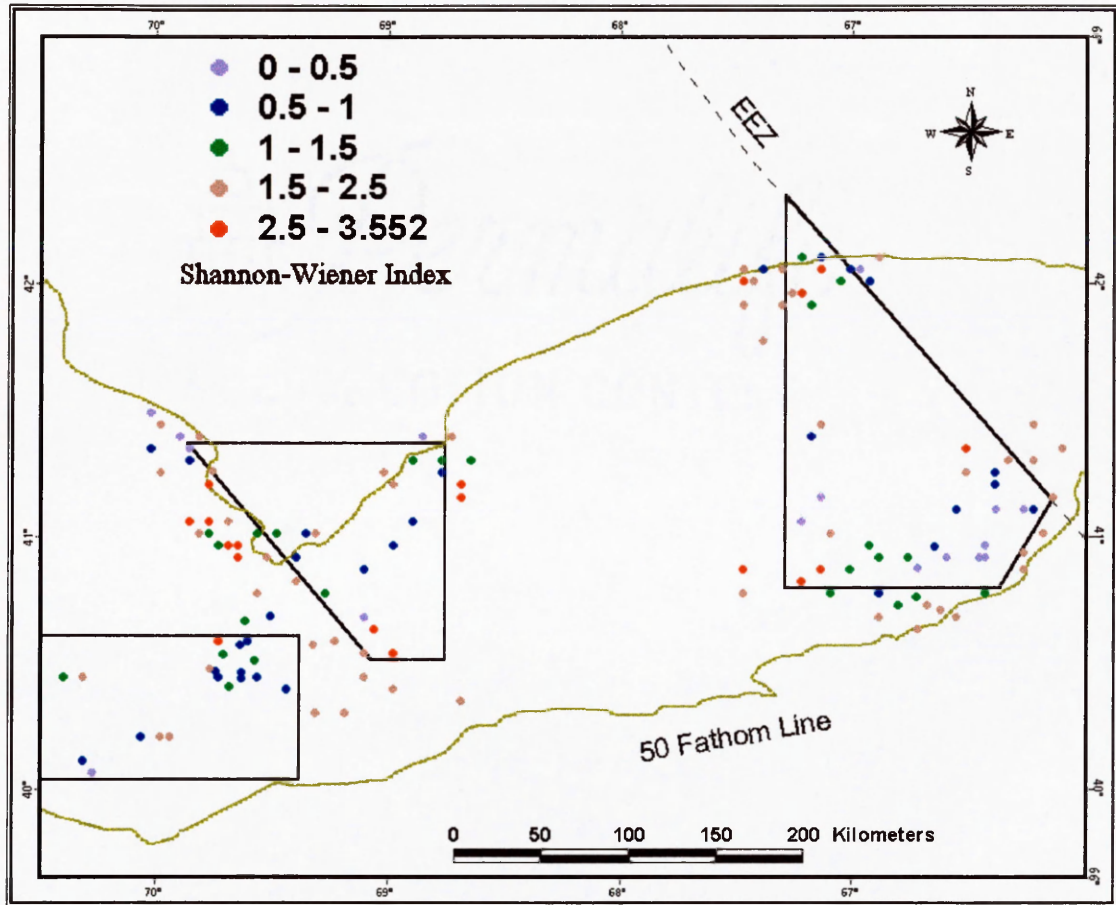


Figure 5f. Geographic distribution of the Shannon-Wiener Index (H' ; \log_2 , based on density) of all taxa combined on Georges Bank.

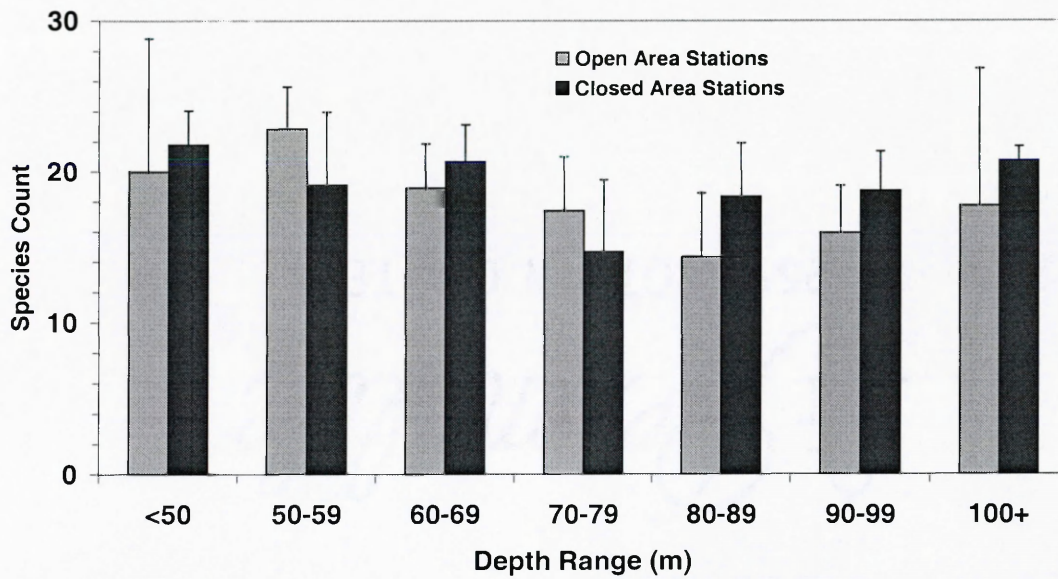


Figure 6. Mean taxa count, in relation to depth (95% confidence intervals shown).

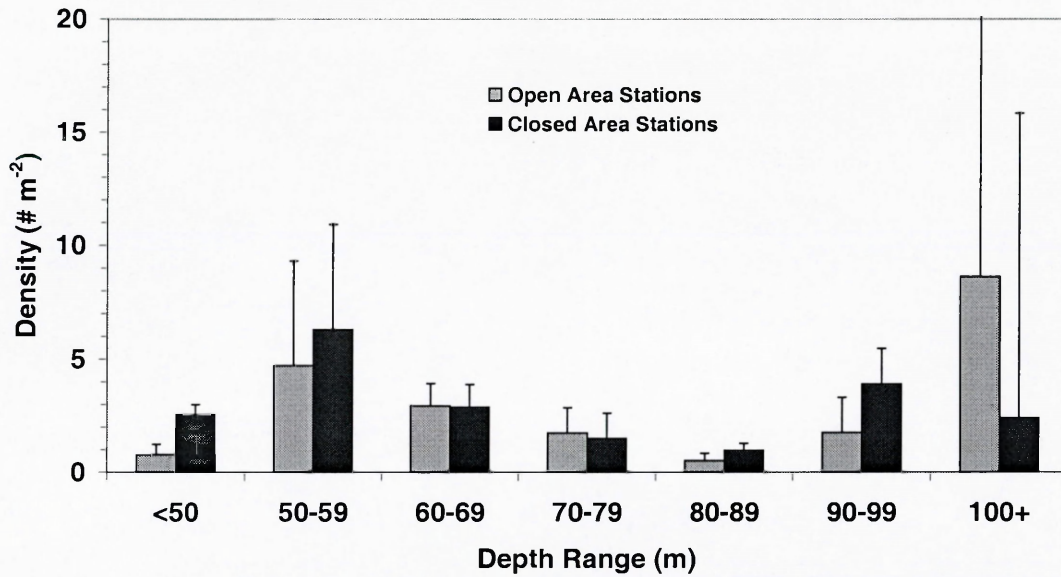


Figure 7. Mean density ($\#/m^2$) of all taxa combined (except densities of sponges, bryozoans, hydroids, and most polychaetes), in relation to depth (95% confidence intervals shown).

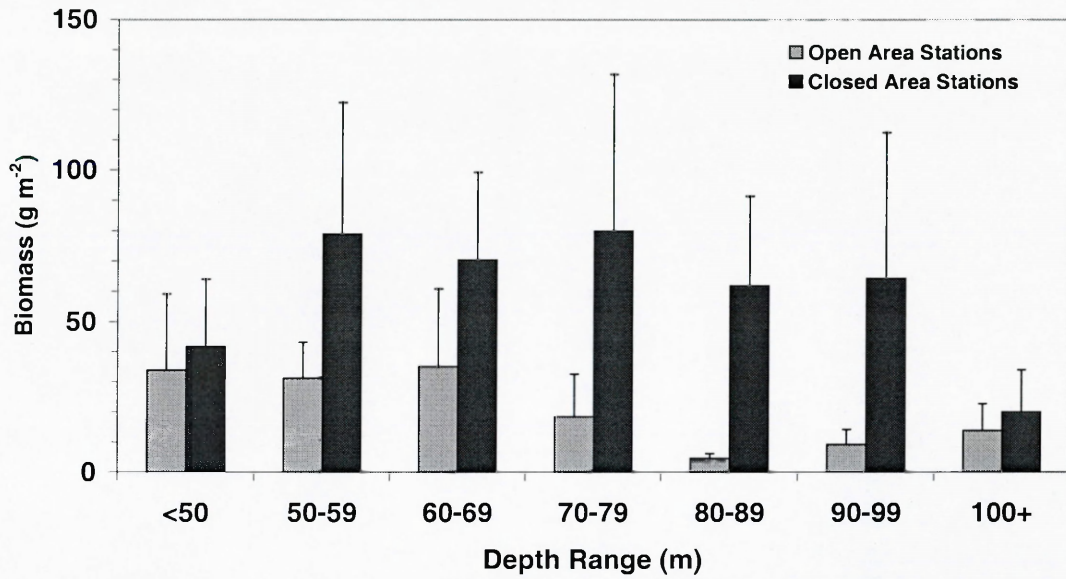


Figure 8. Mean biomass (g/m^2 ; wet weight) of all taxa combined, in relation to depth (95% confidence intervals shown).

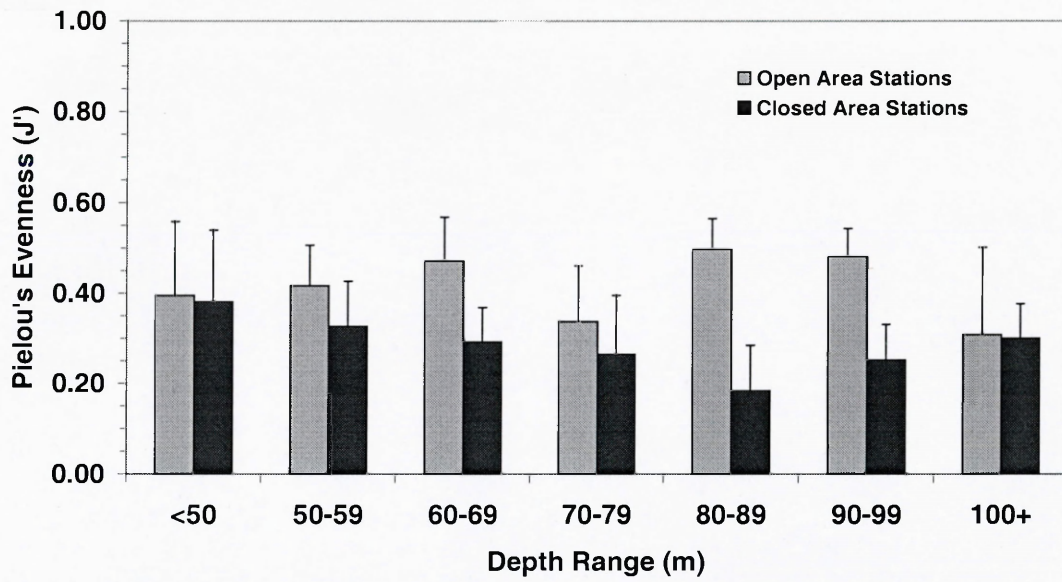


Figure 9. Pielou's Evenness (J' based on biomass), in relation to depth (95% confidence intervals shown).

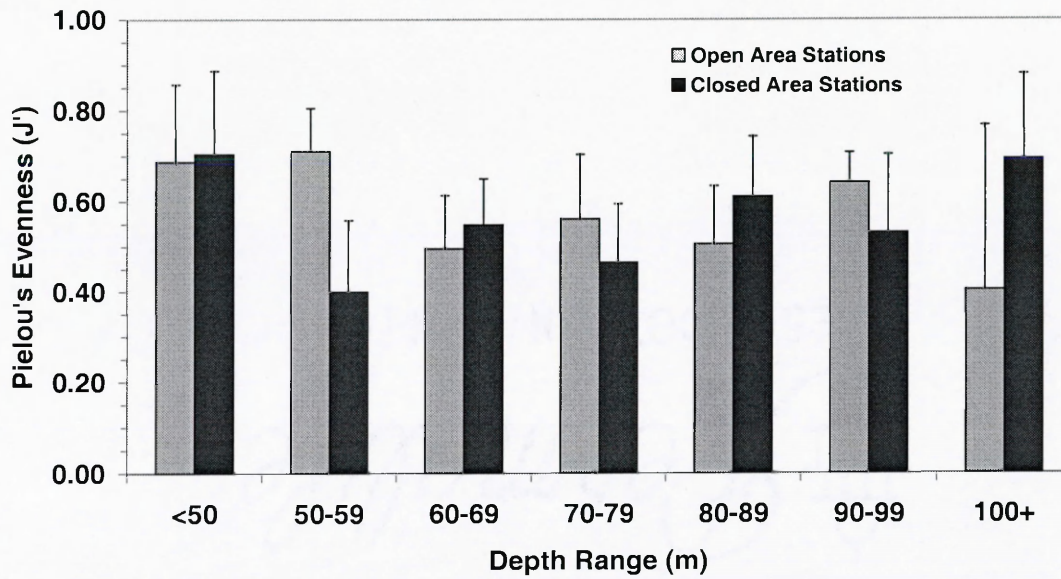


Figure 10. Pielou's Evenness (J' based on density), in relation to depth (95% confidence intervals shown).

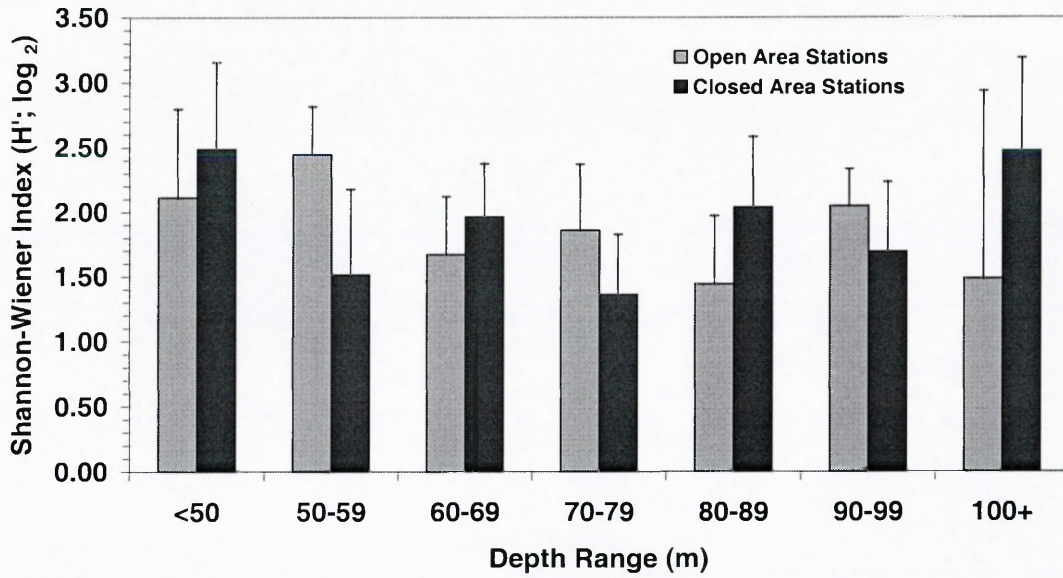


Figure 11. Shannon-Wiener Index (H' ; \log_2 , based on density), in relation to depth (95% confidence intervals shown).

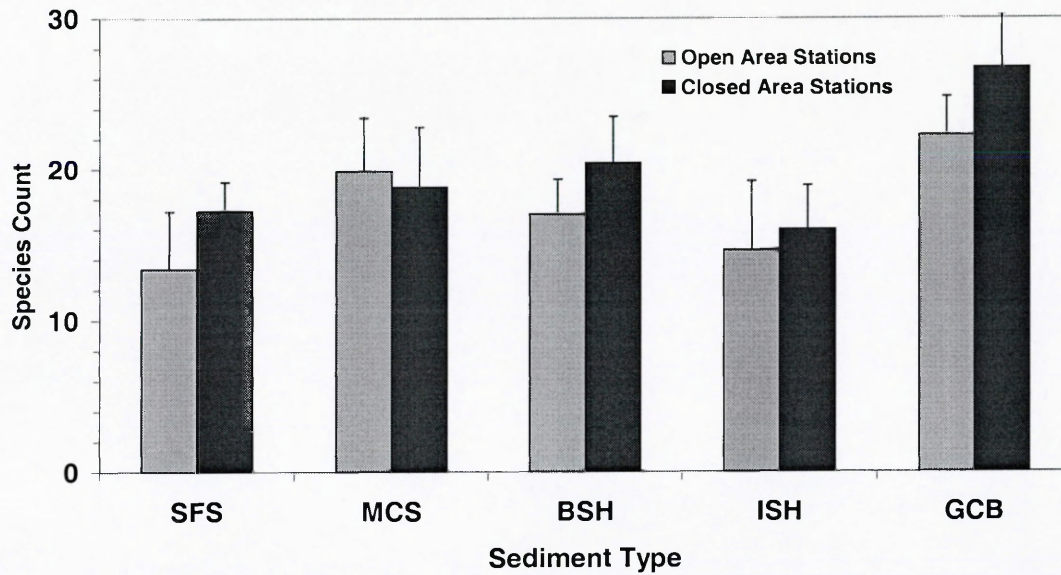


Figure 12. Mean taxa count, in relation to sediment type (95% confidence intervals shown). SFS – Silty/Fine Sand; MCS – Medium/Course Sand; BSH – Broken Shell Hash; ISH – Intact Shells; GCB – Gravel interspersed with Cobbles/Boulders.

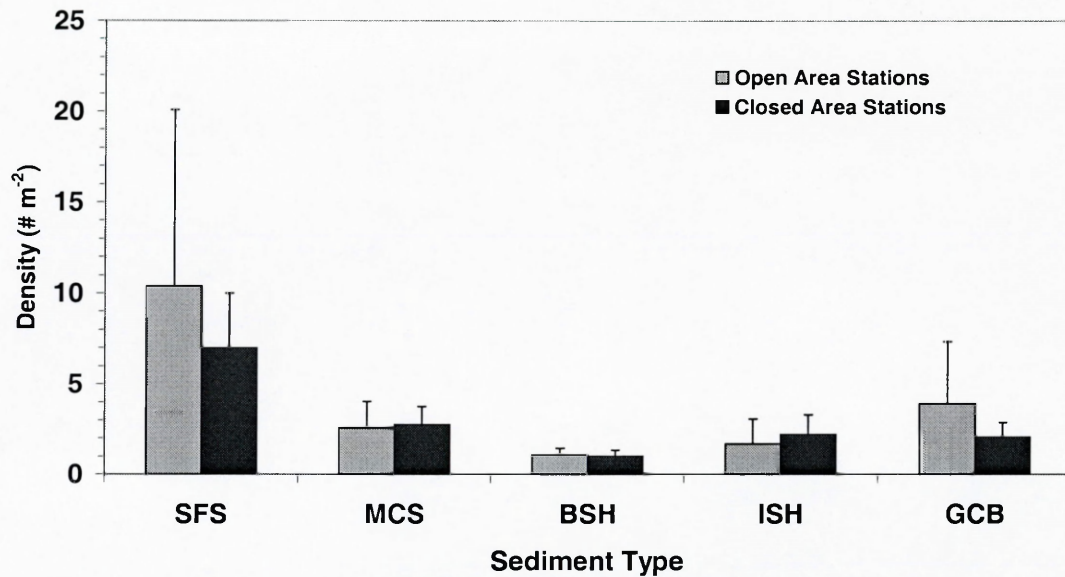


Figure 13. Mean density ($\#/m^2$) of all taxa combined (except densities of sponges, bryozoans, hydroids, and most polychaetes), in relation to sediment type (95% confidence intervals shown). SFS – Silty/Fine Sand; MCS – Medium/Course Sand; BSH – Broken Shell Hash; ISH – Intact Shells; GCB – Gravel interspersed with Cobbles/Boulders.

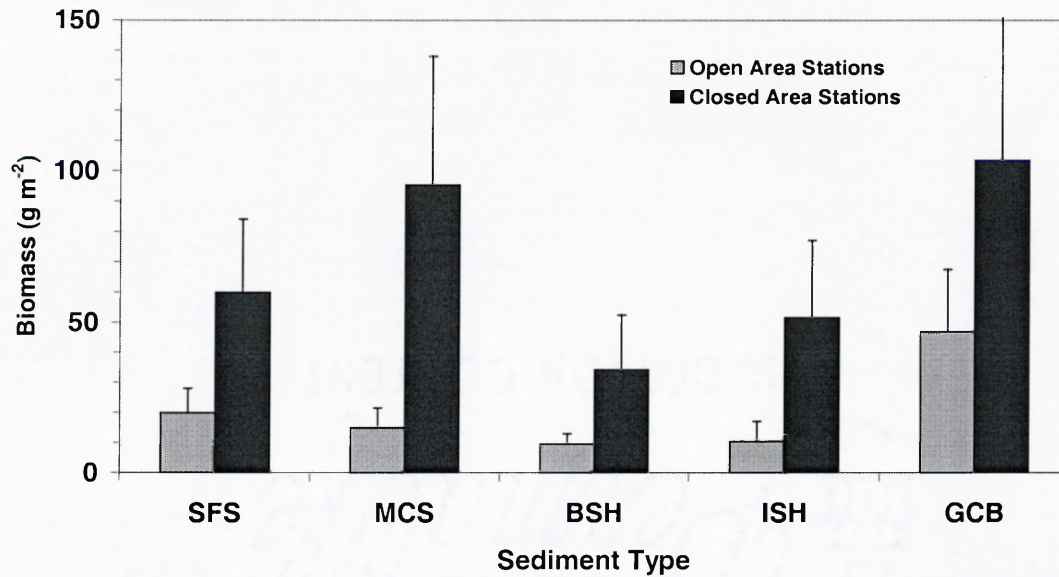


Figure 14. Mean biomass (g/m²; wet weight) of all taxa combined, in relation to sediment type (95% confidence intervals shown). SFS – Silty/Fine Sand; MCS – Medium/Course Sand; BSH – Broken Shell Hash; ISH – Intact Shells; GCB – Gravel interspersed with Cobbles/Boulders.

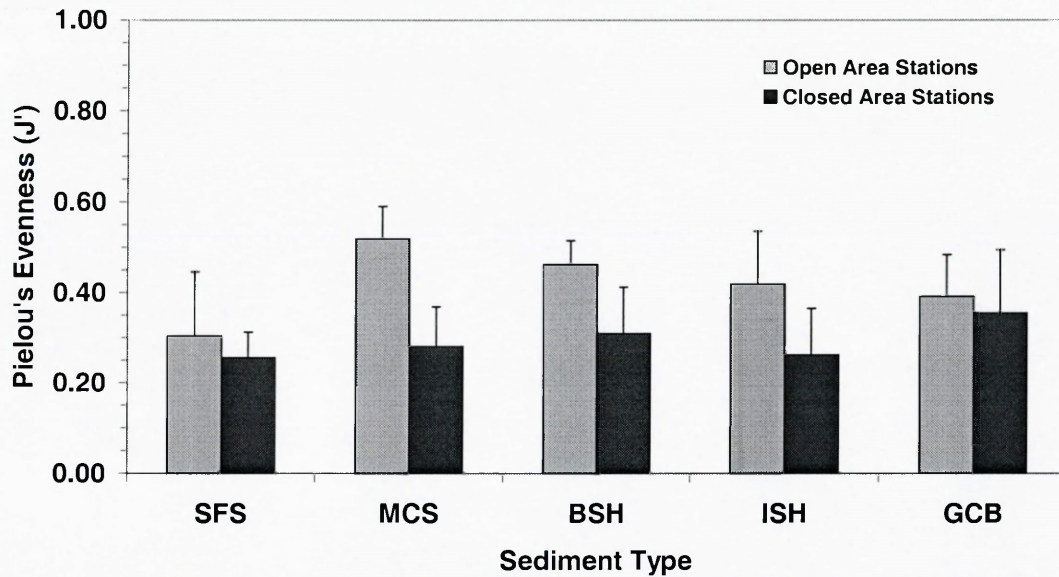


Figure 15. Pielou's Evenness (J' based on biomass), in relation to sediment type (95% confidence intervals shown). SFS – Silty/Fine Sand; MCS – Medium/Course Sand; BSH – Broken Shell Hash; ISH – Intact Shells; GCB – Gravel interspersed with Cobbles/Boulders.

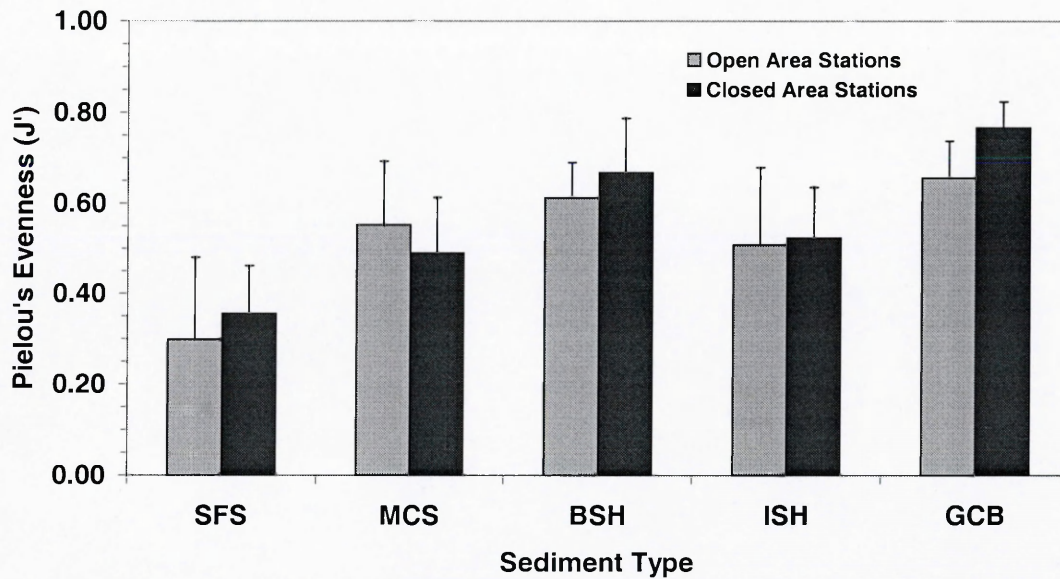


Figure 16. Pielou's Evenness (J' based on density), in relation to sediment type (95% confidence intervals shown). SFS – Silty/Fine Sand; MCS – Medium/Course Sand; BSH – Broken Shell Hash; ISH – Intact Shells; GCB – Gravel interspersed with Cobbles/Boulders.

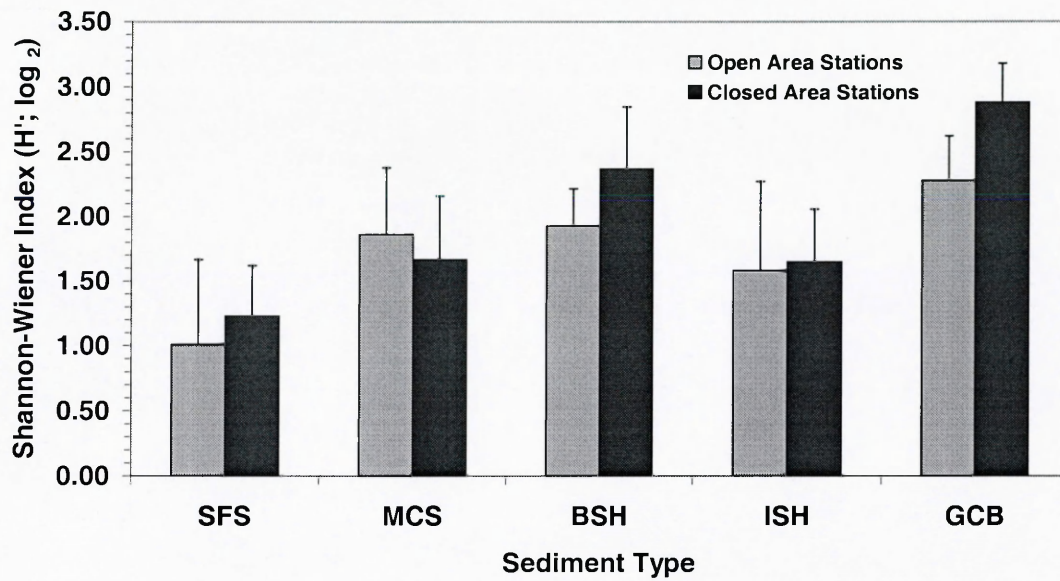


Figure 17. Shannon-Wiener Index (H' ; \log_2 , based on density), in relation to sediment type (95% confidence intervals shown). SFS – Silty/Fine Sand; MCS – Medium/Course Sand; BSH – Broken Shell Hash; ISH – Intact Shells; GCB – Gravel interspersed with Cobbles/Boulders.

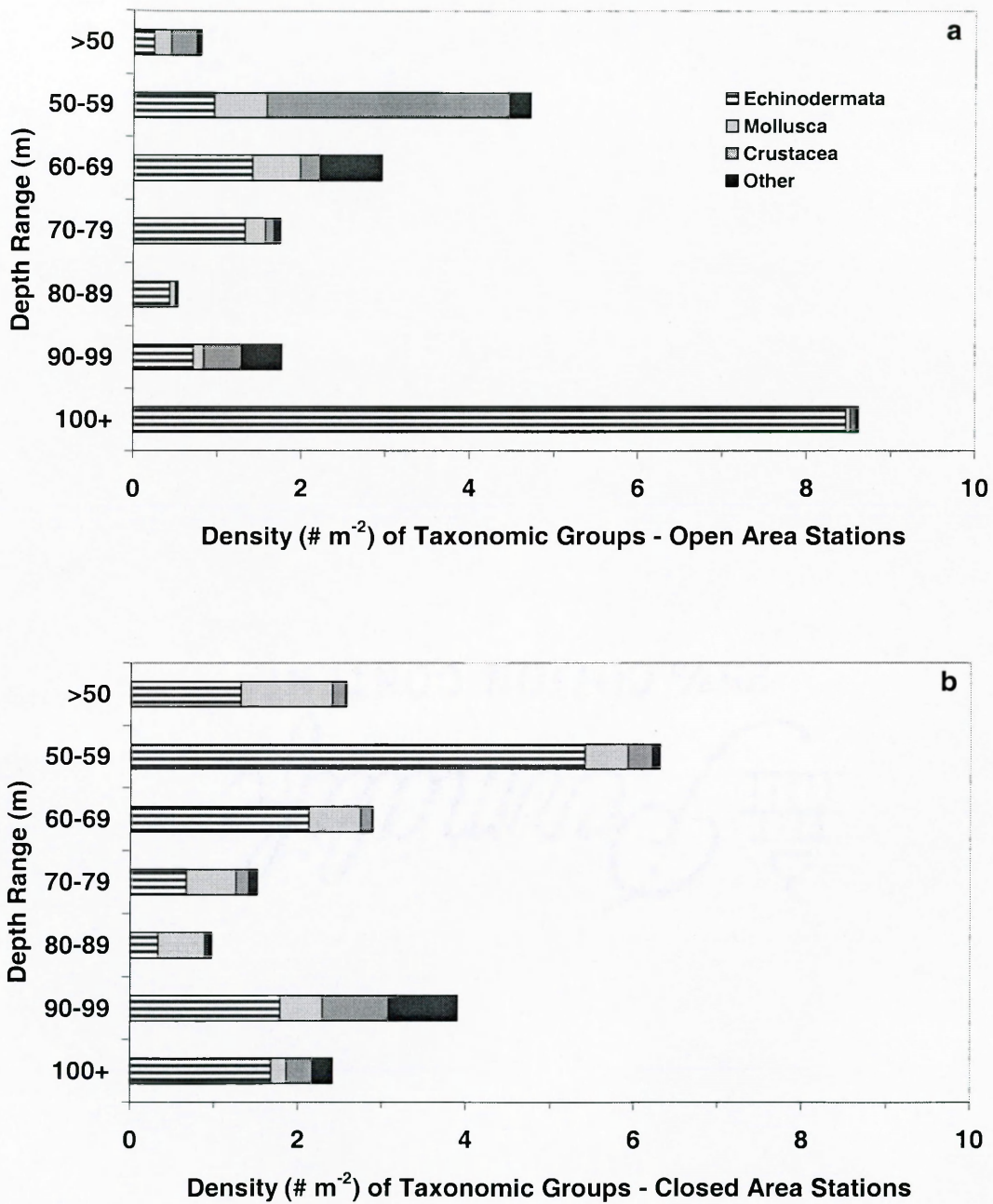


Figure 18a-b. Mean density ($\#/m^2$) of the major taxonomic invertebrate groups (except densities of porifera, bryozoa, hydrozoa, and most annelida), in relation to depth. Fig. 18a – Open Stations; Fig. 18b – Closed Stations

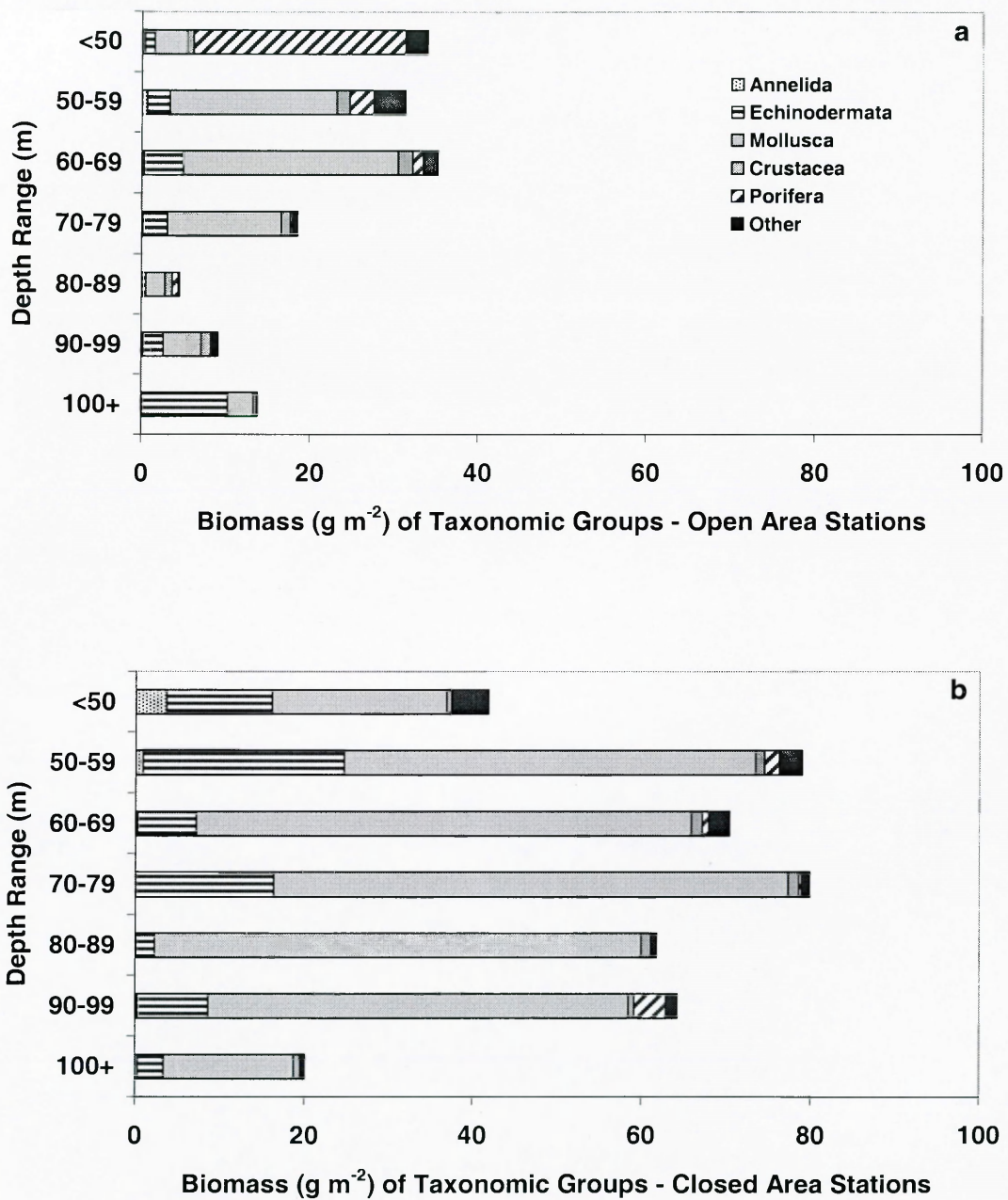


Figure 19a-b. Mean biomass (g/m^2 ; wet weight) of the major taxonomic invertebrate groups, in relation to depth. Fig. 19a – Open Stations; Fig. 19b – Closed Stations

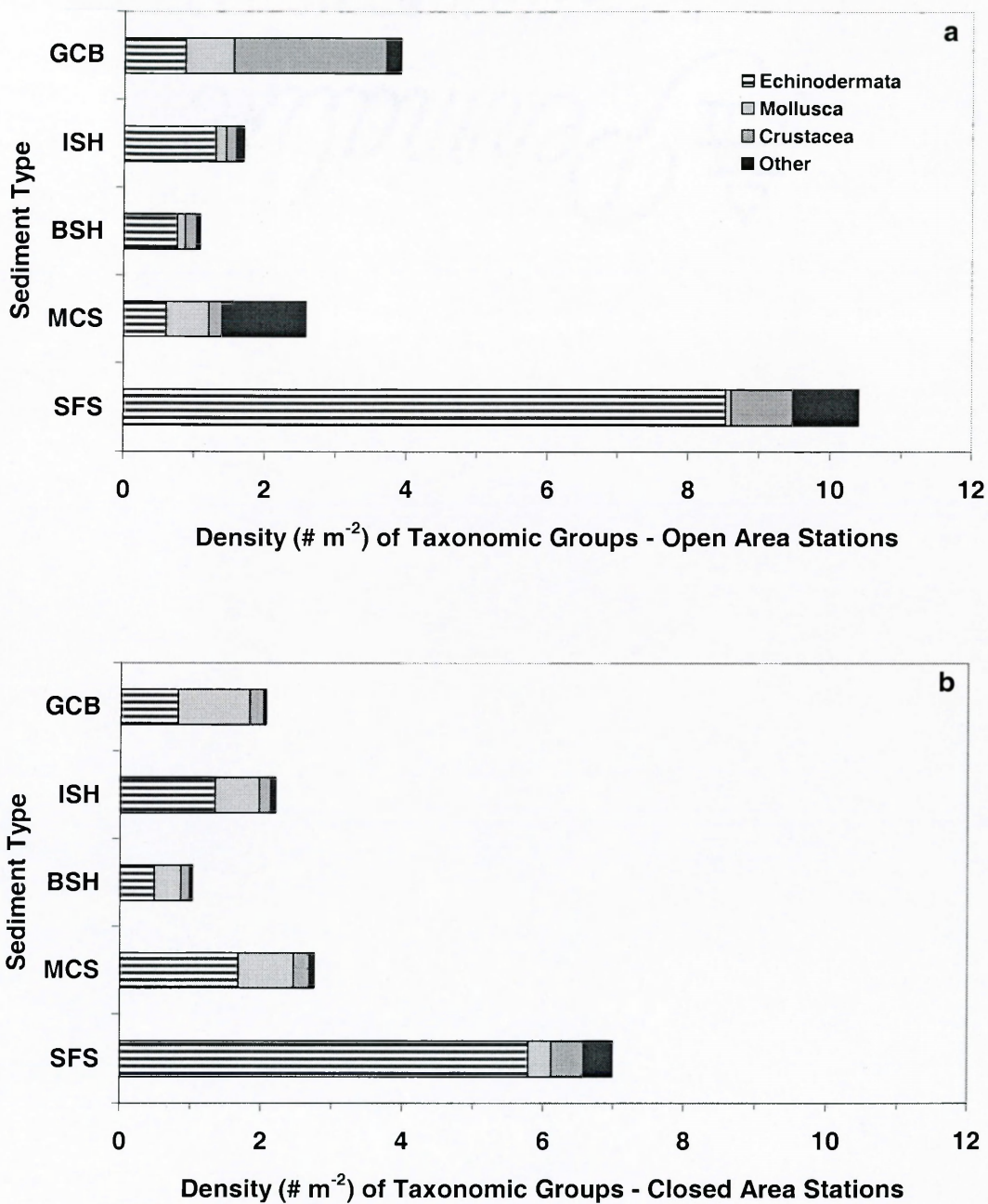


Figure 20a-b. Mean density ($\#/m^2$) of the major taxonomic invertebrate groups (except densities of porifera, bryozoa, hydrozoa, and most annelida), in relation to sediment type. SFS – Silty/Fine Sand; MCS – Medium/Course Sand; BSH – Broken Shell Hash; ISH – Intact Shells; GCB – Gravel interspersed with Cobbles/Boulders. Fig. 20a – Open Stations; Fig. 20b – Closed Stations

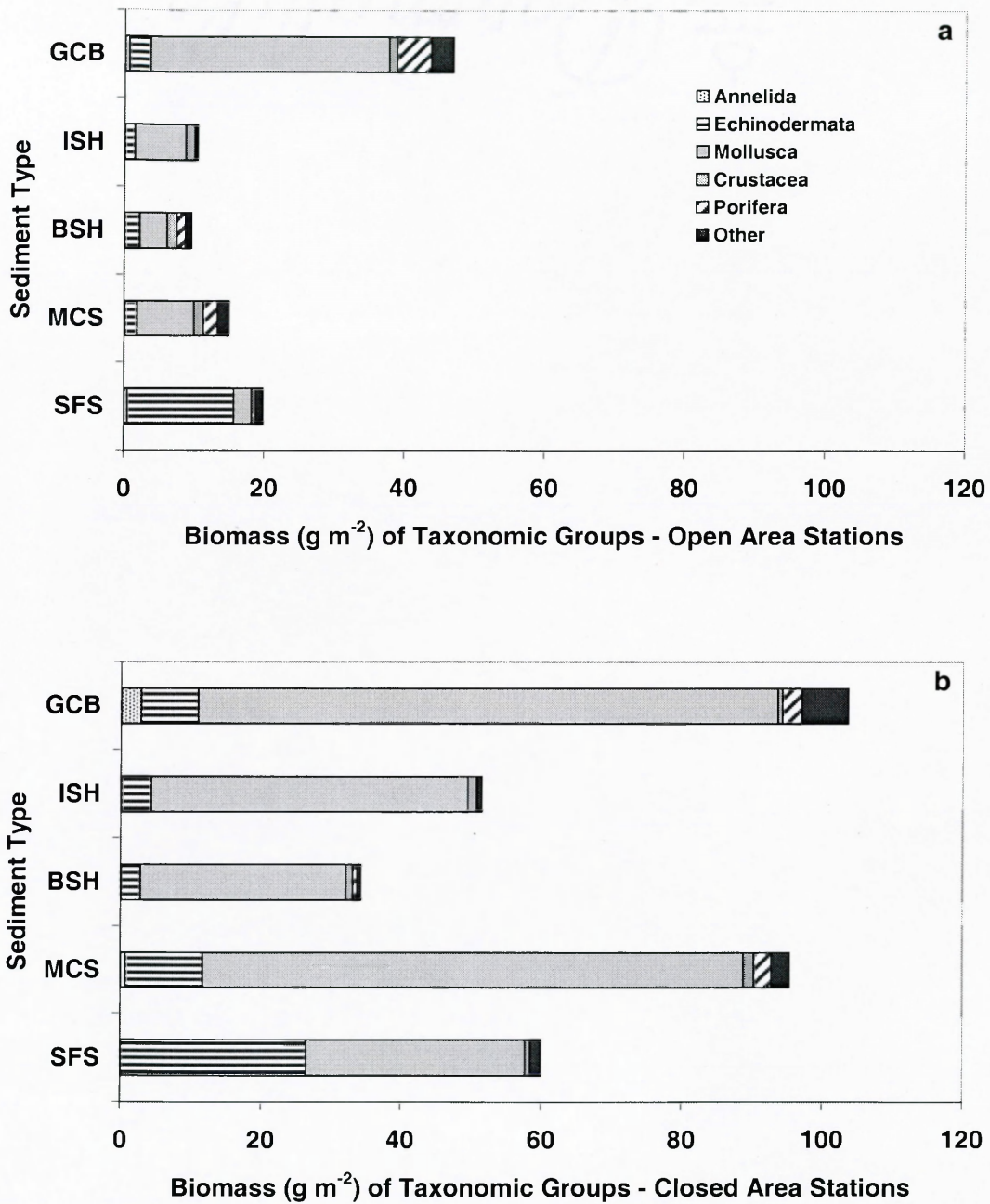


Figure 21a-b. Mean biomass (g/m^2 ; wet weight) of the major taxonomic invertebrate groups, in relation to sediment type. SFS – Silty/Fine Sand; MCS – Medium/Course Sand; BSH – Broken Shell Hash; ISH – Intact Shells; GCB – Gravel interspersed with Cobbles/Boulders. Fig. 21a – Open Stations; Fig. 21b – Closed Stations

Dependent Variable: Species Count following a log ₁₀ transformation					
		$r^2 = 0.31$	MSE = 0.023		
Source	df	Type III SS	F	p	
Depth	1	0.008	0.344	0.559	
Latitude	1	0.349	15.157	0.000	
Longitude	1	0.447	19.403	0.000	
Sediment	4	0.458	4.971	0.001	
Open/Closed Area	1	0.179	7.782	0.006	
Sediment x Open/Closed Area	4	0.196	2.125	0.082	

Dependent Variable: Density (ind./m ²) following a 4th root transformation					
		$r^2 = 0.41$	MSE = 0.075		
Source	df	Type III SS	F	p	
Depth	1	0.3588	4.7609	0.0310	
Latitude	1	0.0005	0.0071	0.9330	
Longitude	1	0.4832	6.4126	0.0126	
Sediment	4	4.2617	14.1386	0.0000	
Open/Closed Area	1	0.0132	0.1752	0.6763	
Sediment x Open/Closed Area	4	0.1954	0.6484	0.6291	

Dependent Variable: Biomass (g/m ²) following a 1/(4th root) transformation					
		$r^2 = 0.47$	MSE = 0.015		
Source	df	Type III SS	F	p	
Depth	1	0.108	7.095	0.009	
Latitude	1	0.090	5.892	0.017	
Longitude	1	0.066	4.349	0.039	
Sediment	4	0.214	3.505	0.010	
Open/Closed Area	1	0.508	33.313	0.000	
Sediment x Open/Closed Area	4	0.036	0.583	0.675	

Dependent Variable: Pielou's Evenness Index based on biomass					
		$r^2 = 0.23$	MSE = 0.029		
Source	df	Type III SS	F	p	
Depth	1	0.044	1.493	0.224	
Latitude	1	0.003	0.118	0.731	
Longitude	1	0.009	0.314	0.576	
Sediment	4	0.118	1.013	0.403	
Open/Closed Area	1	0.473	16.195	0.000	
Sediment x Open/Closed Area	4	0.133	1.138	0.342	

Dependent Variable: Pielou's Evenness Index based on density					
		$r^2 = 0.34$	MSE = 0.041		
Source	df	Type III SS	F	p	
Depth	1	0.070	1.706	0.194	
Latitude	1	0.491	11.981	0.001	
Longitude	1	0.014	0.343	0.559	
Sediment	4	1.790	10.925	0.000	
Open/Closed Area	1	0.129	3.161	0.078	
Sediment x Open/Closed Area	4	0.146	0.890	0.472	

Dependent Variable: Shannon-Wiener Index (log ₂) based on density					
		$r^2 = 0.32$	MSE = 0.634		
Source	df	Type III SS	F	p	
Depth	1	0.866	1.367	0.244	
Latitude	1	8.043	12.695	0.001	
Longitude	1	2.755	4.349	0.039	
Sediment	4	23.029	9.088	0.000	
Open/Closed Area	1	3.519	5.554	0.020	
Sediment x Open/Closed Area	4	3.120	1.231	0.301	

Table 3. Summary of 2-factor, 3-covariate ANCOVAs of ecological variables calculated from survey dredge samples collected on Georges Bank. Total observations = 138. MSE = mean squared error; df = degrees of freedom; SS = sum of squares

Taxonomic Group	Species	All Stations	Open Area Stations	Closed Area Stations
Porifera	Unidentified White Encrusting Sponge	33.3%	50.0%	0.0%
	<i>Suberites ficus</i>	16.2%	17.2%	15.5%
	<i>Halichondria panicea</i>	6.8%	1.3%	15.5%
	<i>Haliclona oculata</i>	0.0%	0.0%	0.0%
Ascidiacea	<i>Dendrodoa carnea</i>	75.1%	100.0%	50.3%
	<i>Boltenia ovifera</i>	11.1%	12.5%	0.0%
Hydrozoa	Unidentified Hydroid 01	32.2%	15.5%	46.9%
	Unidentified Hydroid 02	22.6%	22.2%	23.1%
	Unidentified Hydroid 04	12.6%	7.6%	16.6%
	<i>Hydractinia echinata</i>	7.1%	0.8%	11.8%
	Unidentified Hydroid 12	6.1%	9.2%	4.7%
	Unidentified Hydroid 08	4.0%	0.0%	8.3%
Bryozoa	Unidentified Bryozoan 03	100.0%	100.0%	100.0%
	Unidentified Bryozoan 04	98.0%	99.5%	96.6%
	Unidentified Bryozoan 02	44.6%	44.9%	44.4%
	Unidentified Bryozoan 01	13.3%	16.2%	10.9%
	Unidentified Bryozoan 05	4.6%	1.2%	8.0%
	Unidentified Bryozoan 06	0.3%	0.0%	0.6%
Anthozoa	<i>Tealia feline</i>	40.7%	37.5%	43.2%
Annelida	Unidentified Scallop Boring Worm	95.8%	98.3%	93.5%
	<i>Terebellidae (Pista sp.?)</i>	58.6%	50.0%	67.3%
	<i>Spirorbis sp.</i>	51.5%	61.6%	36.2%
	<i>Filograna implexa</i>	11.6%	20.0%	1.0%
Mollusca	<i>Cuspidaria glacialis</i>	100.0%	-	100.0%
	<i>Anomia squamula</i>	70.7%	69.2%	72.0%
	<i>Crepidula fornicata</i>	67.9%	96.6%	56.9%
	<i>Hiatella arctica</i>	25.0%	50.0%	0.0%
	<i>Crucibulum striatum</i>	25.0%	33.3%	0.0%
	<i>Modiolus modiolus</i>	11.1%	0.0%	15.9%
	<i>Crepidula plana</i>	0.5%	0.0%	0.9%
Pycnogonida	<i>Pycnogonum littorale</i>	10.0%	0.0%	16.7%
Cirripedia	<i>Balanus hameri</i>	64.7%	62.3%	66.0%
	<i>Balanus balanus</i>	61.1%	57.1%	63.6%
	<i>Balanus amphitrite niveus</i>	58.8%	67.1%	34.2%
Ophiuroidea	<i>Ophiopholis aculeata</i>	6.0%	4.8%	7.5%

Table 4. Ranked station percentage values (based on biomass) of benthic epifaunal species present only in association with the sea scallop, *Placopecten magellanicus*, for a given station category: 1) All Stations, 2) Open Area Stations, and 3) Closed Area Stations.

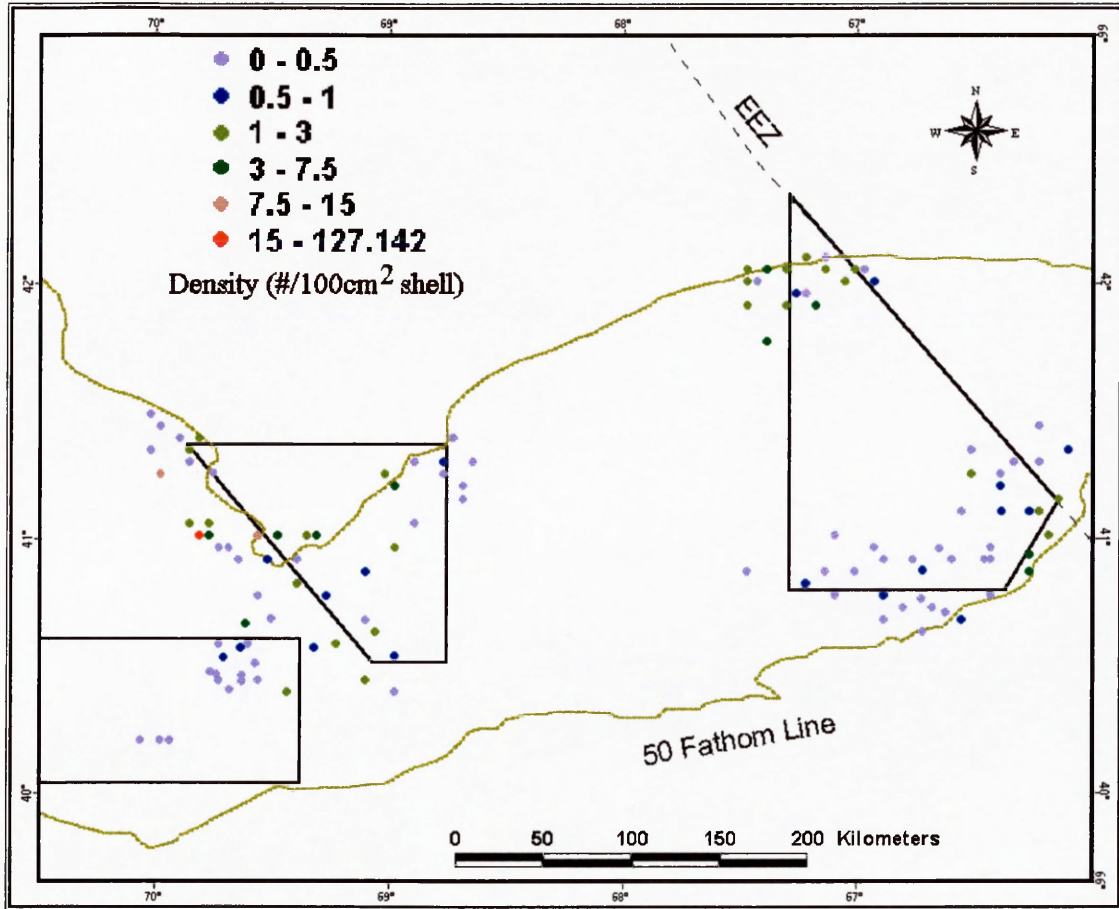


Figure 22a. Geographic distribution of mean scallop shell epifaunal density per 100cm² scallop shell surface area on Georges Bank.

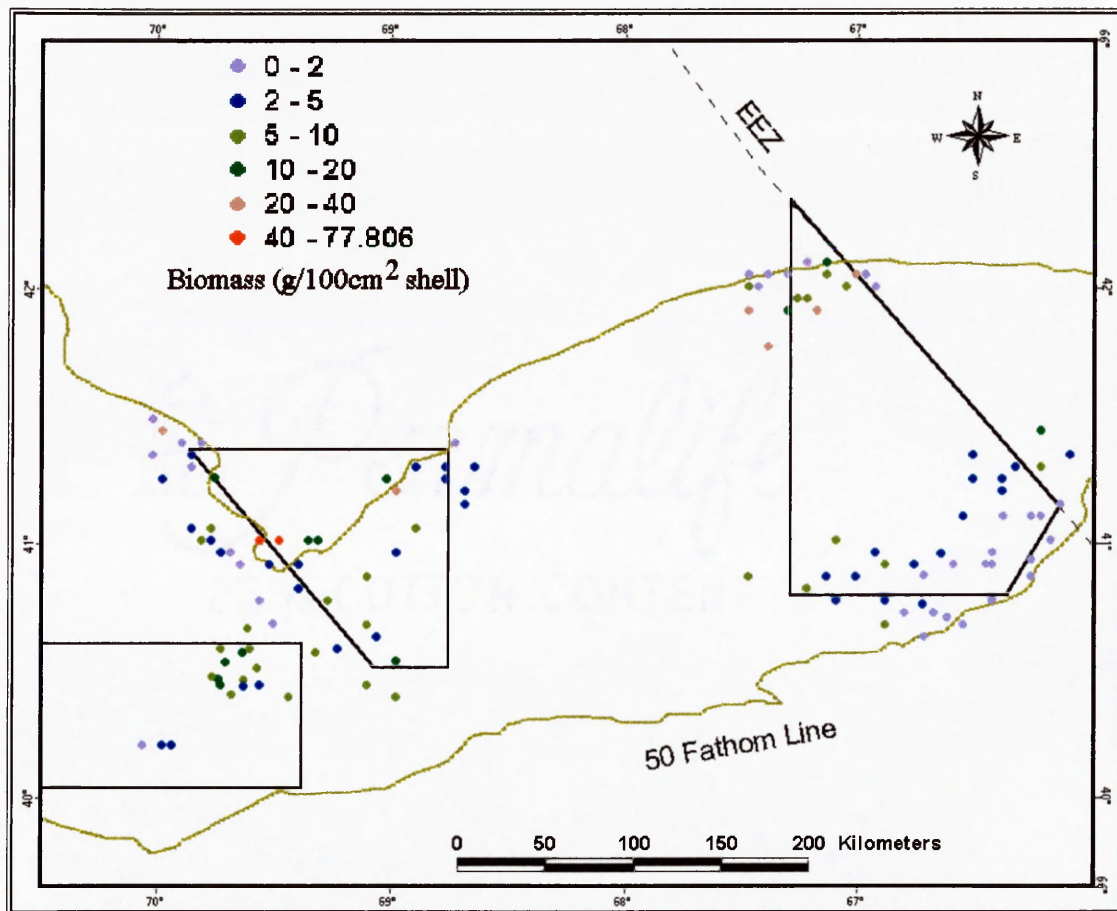


Figure 22b. Geographic distribution of mean scallop shell epifaunal biomass (grams wet weight) per 100cm² scallop shell surface area on Georges Bank.

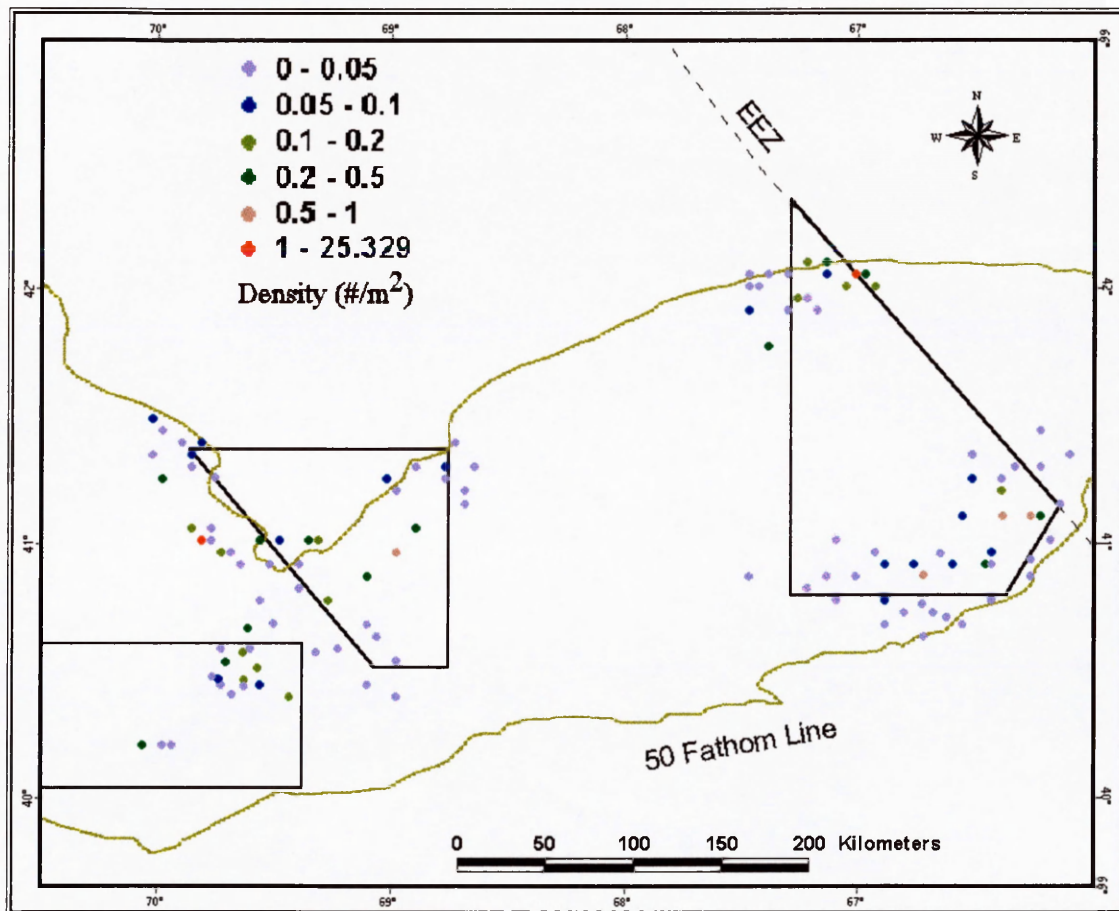


Figure 22c. Geographic distribution of mean scallop shell epifaunal density ($\#/m^2$) on Georges Bank.

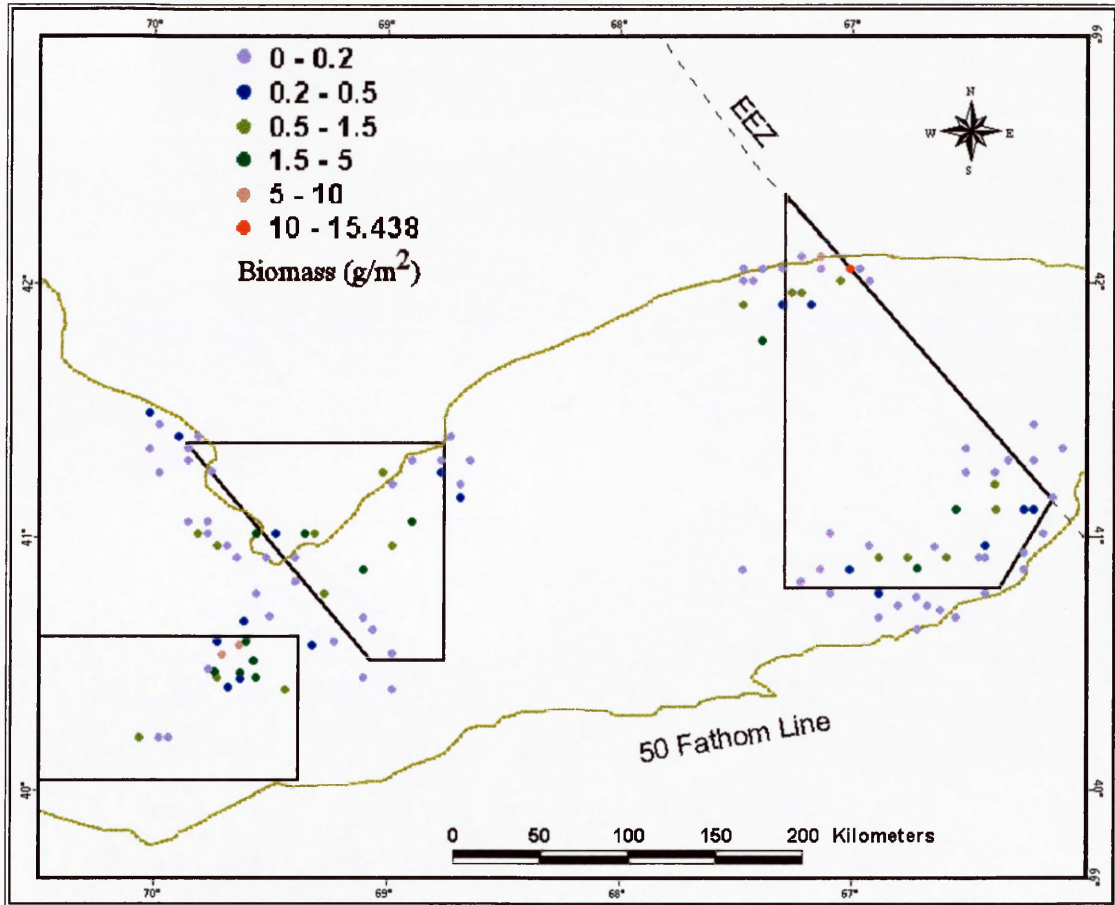


Figure 22d. Geographic distribution of mean scallop shell epifaunal biomass (g/m^2 ; wet weight) on Georges Bank.

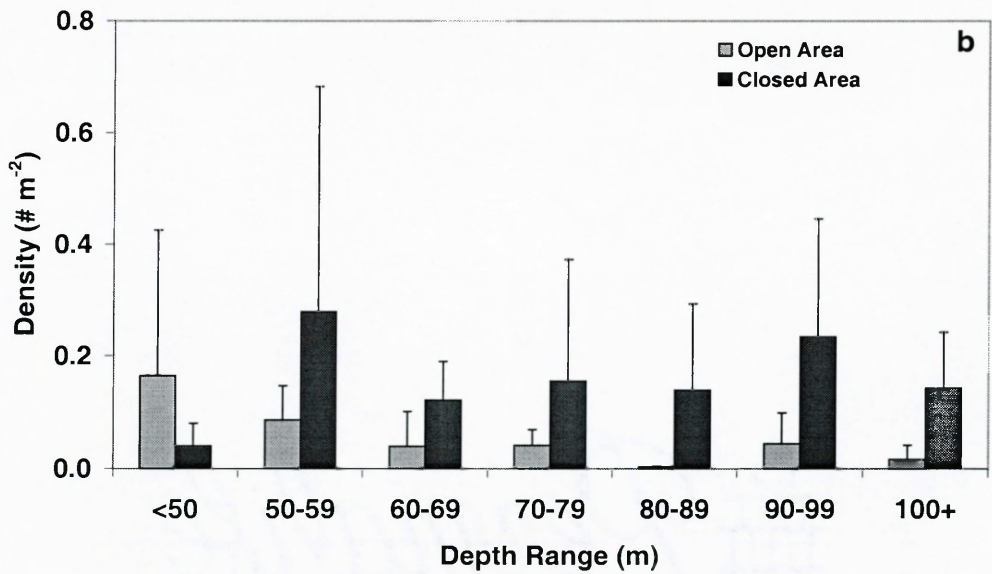
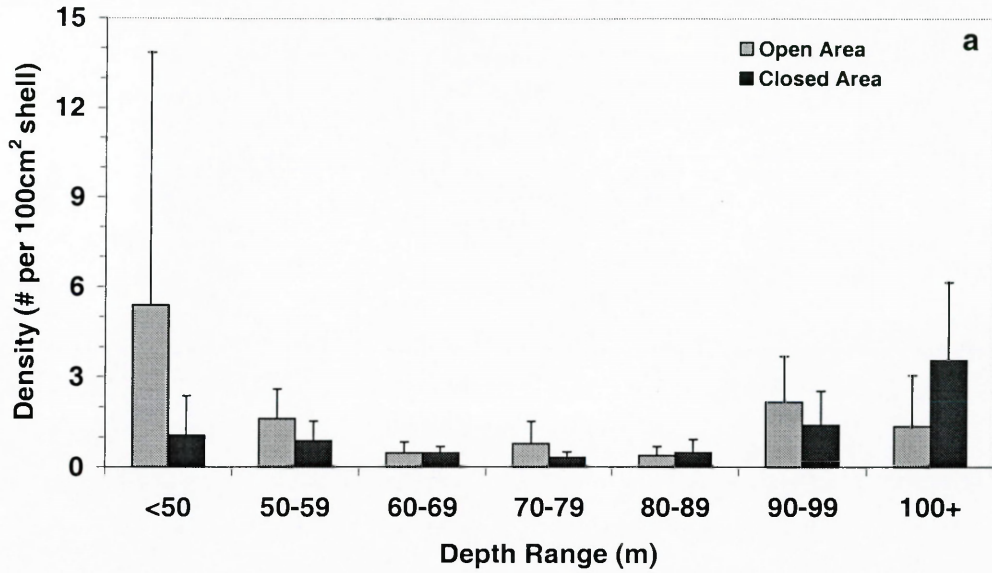


Figure 23a-b. A comparison of mean density between open and closed area stations, in relation to depth (95% confidence intervals shown). Fig. 23a – Mean scallop epifaunal density per 100cm² scallop shell surface area; Fig. 23b – Mean scallop epifaunal density per square meter bottom area

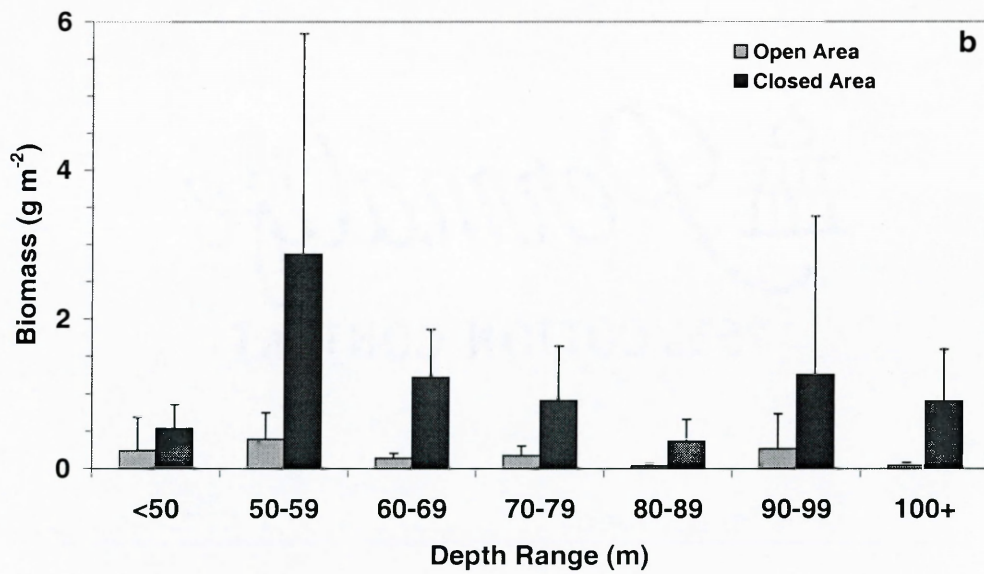
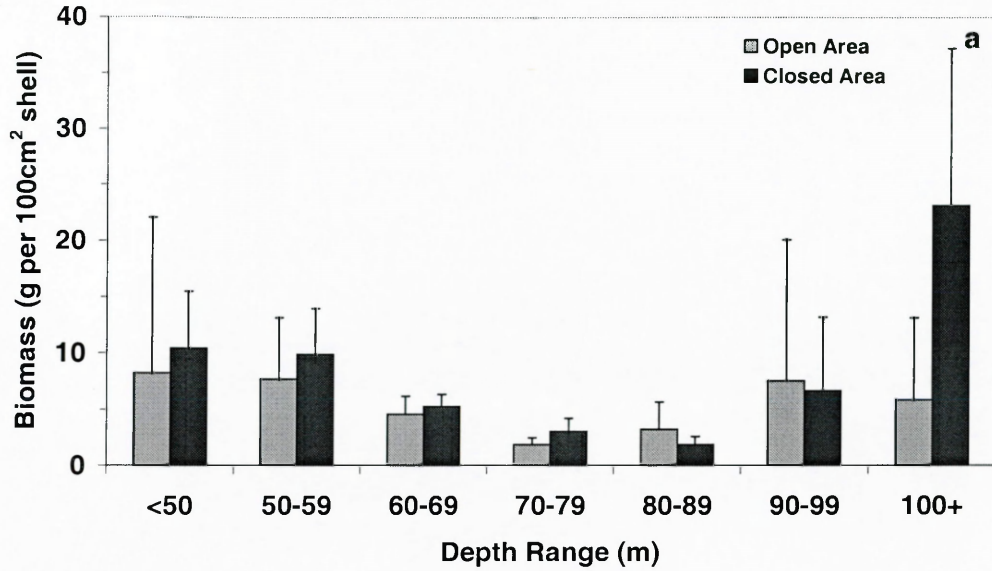


Figure 24a-b. A comparison of mean biomass (grams wet weight) between open and closed area stations, in relation to depth (95% confidence intervals shown). Fig. 24a – Mean scallop epifaunal biomass per 100cm² scallop shell surface area; Fig. 24b – Mean scallop epifaunal biomass per square meter bottom area

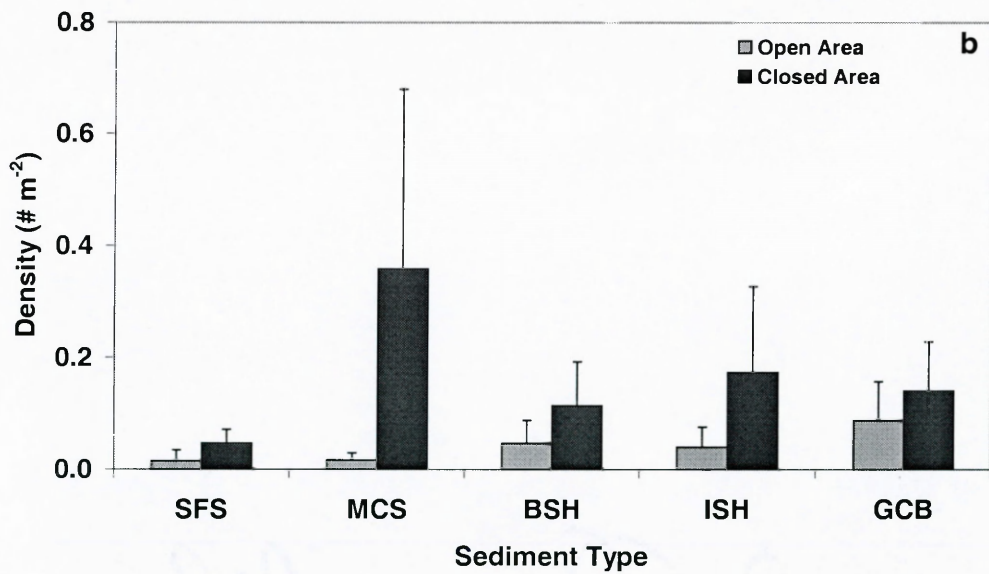
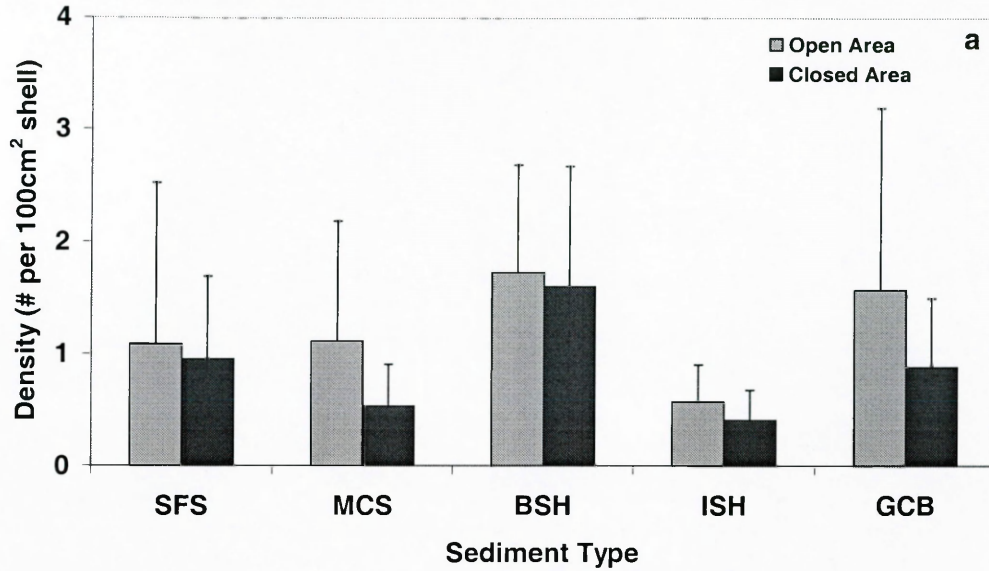


Figure 25a-b. A comparison of mean density between open and closed area stations, in relation to sediment type (95% confidence intervals shown). SFS – Silty/Fine Sand; MCS – Medium/Course Sand; BSH – Broken Shell Hash; ISH – Intact Shells; GCB – Gravel interspersed with Cobbles/Boulders. Fig. 25a – Mean scallop epifaunal density per 100cm² scallop shell surface area; Fig. 25b – Mean scallop epifaunal density per square meter bottom area

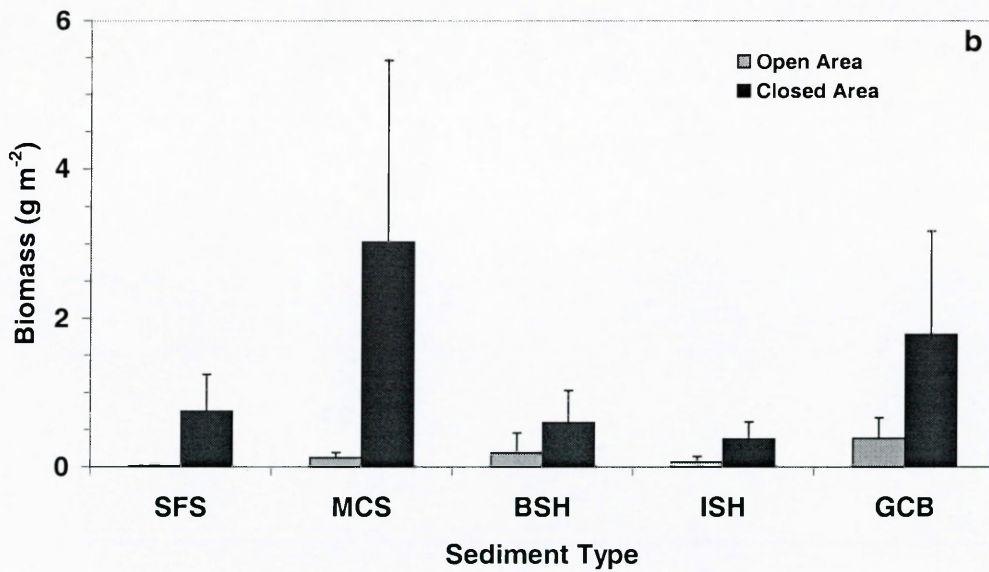
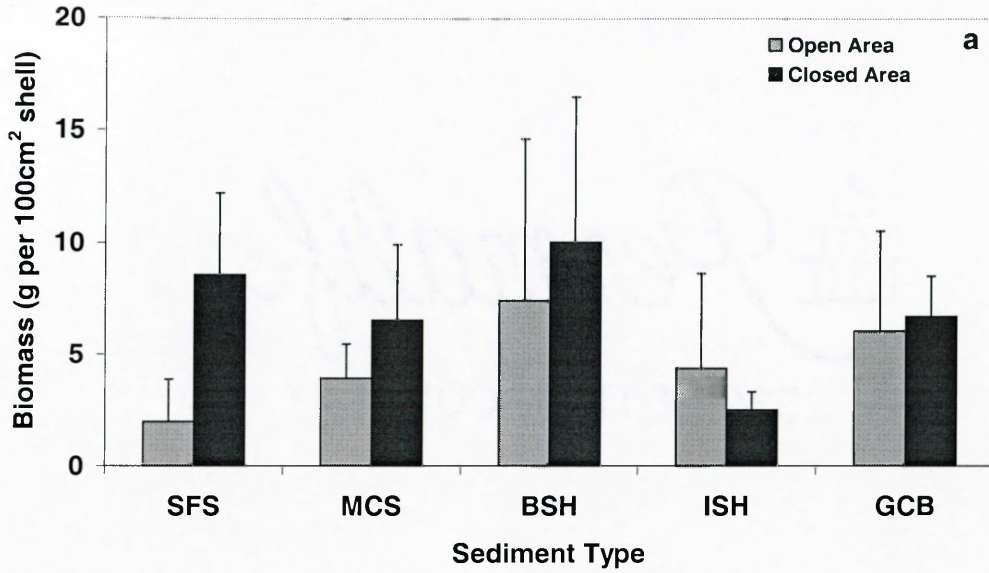


Figure 26a-b. A comparison of mean biomass (grams wet weight) between open and closed area stations, in relation to sediment type (95% confidence intervals shown). SFS – Silty/Fine Sand; MCS – Medium/Course Sand; BSH – Broken Shell Hash; ISH – Intact Shells; GCB – Gravel interspersed with Cobbles/Boulders. Fig. 26a – Mean scallop epifaunal biomass per 100cm² scallop shell surface area; Fig. 26b – Mean scallop epifaunal biomass per square meter bottom area

Dependent Variable: Density (organisms) per 100cm ² of live <i>Placopecten magellanicus</i> shell following a 4th root transformation					
$r^2 = 0.14$		MSE = 0.266			
Source	df	Type III SS	F	p	
Depth	1	0.314	1.181	0.280	
Latitude	1	1.765	6.631	0.011	
Longitude	1	0.327	1.229	0.270	
Average Scallop Shell Length	1	0.972	3.652	0.059	
Sediment	4	2.002	1.880	0.119	
Open/Closed Area	1	0.689	2.586	0.111	
Sediment x Open/Closed Area	4	0.456	0.428	0.788	

Dependent Variable: Biomass (g) per 100cm ² of live <i>Placopecten magellanicus</i> shell					
$r^2 = 0.20$		MSE = 84.223			
Source	df	Type III SS	F	p	
Depth	1	151.917	1.804	0.182	
Latitude	1	594.981	7.064	0.009	
Longitude	1	703.803	8.356	0.005	
Average Scallop Shell Length	1	352.128	4.181	0.043	
Sediment	4	472.043	1.401	0.239	
Open/Closed Area	1	18.891	0.224	0.637	
Sediment x Open/Closed Area	4	241.902	0.718	0.581	

Dependent Variable: Total Density (organisms/m ²) on live <i>Placopecten magellanicus</i> shell following a square root transformation					
$r^2 = 0.08$		MSE = 0.260			
Source	df	Type III SS	F	p	
Depth	1	0.001	0.006	0.941	
Latitude	1	0.171	0.656	0.420	
Longitude	1	0.106	0.408	0.524	
Average Scallop Shell Length	1	0.187	0.721	0.398	
Sediment	4	0.475	0.457	0.767	
Open/Closed Area	1	0.531	2.043	0.156	
Sediment x Open/Closed Area	4	0.513	0.493	0.741	

Dependent Variable: Total Biomass (g/m ²) on live <i>Placopecten magellanicus</i> shell following a 4th root transformation					
$r^2 = 0.45$		MSE = 0.077			
Source	df	Type III SS	F	p	
Depth	1	0.033	0.433	0.512	
Latitude	1	0.075	0.974	0.326	
Longitude	1	0.280	3.634	0.059	
Average Scallop Shell Length	1	0.295	3.838	0.053	
Sediment	4	1.146	3.724	0.007	
Open/Closed Area	1	1.597	20.763	0.000	
Sediment x Open/Closed Area	4	0.283	0.920	0.455	

Table 5. Summary of 2-factor, 4-covariate ANCOVAs of ecological variables of organisms living on live *Placopecten magellanicus* shell, calculated from survey dredge samples collected on Georges Bank. Total observations = 138. MSE = mean squared error; df = degrees of freedom; SS = sum of squares

Dependent Variable: Species Count					
Group (OPEN AREA)	Mean	N	Std. Deviation	Std. Error Mean	
Species Count (w/o Scallop Epifauna)	13.776	58	5.921	0.777	
Species Count (w/ Scallop Epifauna)	17.466	58	6.070	0.797	
Paired Differences					
Mean	Std. Deviation	Std. Error Mean	t	df	Sig. (2-tailed)
-3.690	1.709	0.224	-16.445	57	0.000
Dependent Variable: Density (organisms/m ²)					
Group (OPEN AREA)	Mean	N	Std. Deviation	Std. Error Mean	
Density (w/o Scallop Epifauna)	1.829	58	2.419	0.318	
Density (w/ Scallop Epifauna)	2.317	58	4.763	0.625	
Paired Differences					
Mean	Std. Deviation	Std. Error Mean	t	df	Sig. (2-tailed)
-0.488	3.320	0.436	-1.119	57	0.268
Dependent Variable: Biomass (g/m ²)					
Group (OPEN AREA)	Mean	N	Std. Deviation	Std. Error Mean	
Biomass (w/o Scallop Epifauna)	8.794	58	10.807	1.419	
Biomass (w/ Scallop Epifauna)	9.012	58	10.792	1.417	
Paired Differences					
Mean	Std. Deviation	Std. Error Mean	t	df	Sig. (2-tailed)
-0.217	0.513	0.067	-3.226	57	0.002
Dependent Variable: Pielou's Evenness Index based on density					
Group (OPEN AREA)	Mean	N	Std. Deviation	Std. Error Mean	
Pielou's Evenness, density based (w/o Scallop Epifauna)	0.643	58	0.230	0.030	
Pielou's Evenness, density based (w/ Scallop Epifauna)	0.626	58	0.220	0.029	
Paired Differences					
Mean	Std. Deviation	Std. Error Mean	t	df	Sig. (2-tailed)
0.017	0.056	0.007	2.343	57	0.023
Dependent Variable: Shannon-Wiener Index (log ₂) based on density					
Group (OPEN AREA)	Mean	N	Std. Deviation	Std. Error Mean	
SWI, log ₂ density based (w/o Scallop Epifauna)	1.783	58	0.762	0.100	
SWI, log ₂ density based (w/ Scallop Epifauna)	1.851	58	0.777	0.102	
Paired Differences					
Mean	Std. Deviation	Std. Error Mean	t	df	Sig. (2-tailed)
-0.069	0.165	0.022	-3.172	57	0.002

Table 6a. Summary of paired sample (total sample without *Placopecten magellanicus* data or the organisms living on its shells vs. total sample without *Placopecten magellanicus* data) t-tests of ecological variables calculated from survey dredge samples collected at open area sites on Georges Bank. Total observations = 58. df = degrees of freedom

Dependent Variable: Species Count					
Group (CLOSED AREA)	Mean	N	Std. Deviation	Std. Error Mean	
Species Count (w/o Scallop Epifauna)	15.984	62	5.547	0.704	
Species Count (w/ Scallop Epifauna)	19.419	62	5.835	0.741	
Paired Differences					
Mean	Std. Deviation	Std. Error Mean	t	df	Sig. (2-tailed)
-3.435	1.922	0.244	-14.077	61	0.000
Dependent Variable: Density (organisms/m ²)					
Group (CLOSED AREA)	Mean	N	Std. Deviation	Std. Error Mean	
Density (w/o Scallop Epifauna)	2.453	62	3.679	0.467	
Density (w/ Scallop Epifauna)	2.616	62	3.632	0.461	
Paired Differences					
Mean	Std. Deviation	Std. Error Mean	t	df	Sig. (2-tailed)
-0.163	0.318	0.040	-4.052	61	0.000
Dependent Variable: Biomass (g/m ²)					
Group (CLOSED AREA)	Mean	N	Std. Deviation	Std. Error Mean	
Biomass (w/o Scallop Epifauna)	14.353	62	18.973	2.410	
Biomass (w/ Scallop Epifauna)	15.609	62	19.187	2.437	
Paired Differences					
Mean	Std. Deviation	Std. Error Mean	t	df	Sig. (2-tailed)
-1.256	2.417	0.307	-4.092	61	0.000
Dependent Variable: Pielou's Evenness Index based on density					
Group (CLOSED AREA)	Mean	N	Std. Deviation	Std. Error Mean	
Pielou's Evenness, density based (w/o Scallop Epifauna)	0.593	62	0.251	0.032	
Pielou's Evenness, density based (w/ Scallop Epifauna)	0.578	62	0.228	0.029	
Paired Differences					
Mean	Std. Deviation	Std. Error Mean	t	df	Sig. (2-tailed)
0.015	0.107	0.014	1.103	61	0.274
Dependent Variable: Shannon-Wiener Index (log ₂) based on density					
Group (CLOSED AREA)	Mean	N	Std. Deviation	Std. Error Mean	
SWI, log ₂ density based (w/o Scallop Epifauna)	1.808	62	0.831	0.106	
SWI, log ₂ density based (w/ Scallop Epifauna)	1.874	62	0.871	0.111	
Paired Differences					
Mean	Std. Deviation	Std. Error Mean	t	df	Sig. (2-tailed)
-0.066	0.267	0.034	-1.958	61	0.055

Table 6b. Summary of paired sample (total sample without *Placopecten magellanicus* data or the organisms living on its shells vs. total sample without *Placopecten magellanicus* data) t-tests of ecological variables calculated from survey dredge samples collected at closed area sites on Georges Bank. Total observations = 62. df = degrees of freedom

Dependent Variable: Species Count					
Group (WITHOUT SCALLOP EPIFAUNA)	Mean	N	Std. Deviation	Std. Error Mean	
Open Area	13.776	58	5.921	0.777	
Closed Area	15.984	62	5.547	0.704	
Mean Difference	Std. Error Difference	t	df	Sig. (2-tailed)	
-2.208	1.047	-2.109	118	0.037	
Dependent Variable: Density (organisms/m ²)					
Group (WITHOUT SCALLOP EPIFAUNA)	Mean	N	Std. Deviation	Std. Error Mean	
Open Area	1.829	58	2.419	0.318	
Closed Area	2.453	62	3.679	0.467	
Mean Difference	Std. Error Difference	t	df	Sig. (2-tailed)	
-0.624	0.573	-1.089	118	0.278	
Dependent Variable: Biomass (g/m ²)					
Group (WITHOUT SCALLOP EPIFAUNA)	Mean	N	Std. Deviation	Std. Error Mean	
Open Area	8.794	58	10.807	1.419	
Closed Area	14.353	62	18.973	2.410	
Mean Difference	Std. Error Difference	t	df	Sig. (2-tailed)	
-5.558	2.845	-1.954	118	0.053	
Dependent Variable: Pielou's Evenness Index based on density					
Group (WITHOUT SCALLOP EPIFAUNA)	Mean	N	Std. Deviation	Std. Error Mean	
Open Area	0.643	58	0.230	0.030	
Closed Area	0.593	62	0.251	0.032	
Mean Difference	Std. Error Difference	t	df	Sig. (2-tailed)	
0.050	0.044	1.141	118	0.256	
Dependent Variable: Shannon-Wiener Index (log2) based on density					
Group (WITHOUT SCALLOP EPIFAUNA)	Mean	N	Std. Deviation	Std. Error Mean	
Open Area	1.783	58	0.762	0.100	
Closed Area	1.808	62	0.831	0.106	
Mean Difference	Std. Error Difference	t	df	Sig. (2-tailed)	
-0.025	0.146	-0.173	118	0.863	

Table 6c. Summary of two independent-samples (open area data vs. closed area data, in relation to total sample without *Placopecten magellanicus* data or the organisms living on its shells) t-tests of ecological variables calculated from survey dredge samples collected on Georges Bank. Total observations: Open area = 58; Closed area = 62. df = degrees of freedom

Dependent Variable: Species Count					
Group (WITH SCALLOP EPIFAUNA)	Mean	N	Std. Deviation	Std. Error Mean	
Open Area	17.466	58	6.070	0.797	
Closed Area	19.419	62	5.835	0.741	
Mean Difference	Std. Error Difference	t	df	Sig. (2-tailed)	
-1.954	1.087	-1.798	118	0.075	
Dependent Variable: Density (organisms/m ²)					
Group (WITH SCALLOP EPIFAUNA)	Mean	N	Std. Deviation	Std. Error Mean	
Open Area	2.317	58	4.763	0.625	
Closed Area	2.616	62	3.632	0.461	
Mean Difference	Std. Error Difference	t	df	Sig. (2-tailed)	
-0.299	0.770	-0.389	118	0.698	
Dependent Variable: Biomass (g/m ²)					
Group (WITH SCALLOP EPIFAUNA)	Mean	N	Std. Deviation	Std. Error Mean	
Open Area	9.012	58	10.792	1.417	
Closed Area	15.609	62	19.187	2.437	
Mean Difference	Std. Error Difference	t	df	Sig. (2-tailed)	
-6.597	2.868	-2.300	118	0.023	
Dependent Variable: Pielou's Evenness Index based on density					
Group (WITH SCALLOP EPIFAUNA)	Mean	N	Std. Deviation	Std. Error Mean	
Open Area	0.626	58	0.220	0.029	
Closed Area	0.578	62	0.228	0.029	
Mean Difference	Std. Error Difference	t	df	Sig. (2-tailed)	
0.048	0.041	1.169	118	0.245	
Dependent Variable: Shannon-Wiener Index (log ₂) based on density					
Group (WITH SCALLOP EPIFAUNA)	Mean	N	Std. Deviation	Std. Error Mean	
Open Area	1.851	58	0.777	0.102	
Closed Area	1.874	62	0.871	0.111	
Mean Difference	Std. Error Difference	t	df	Sig. (2-tailed)	
-0.023	0.151	-0.152	118	0.880	

Table 6d. Summary of two independent-samples (open area data vs. closed area data, in relation to total sample without *Placopecten magellanicus* data) t-tests of ecological variables calculated from survey dredge samples collected on Georges Bank. Total observations: Open area = 58; Closed area = 62. df = degrees of freedom

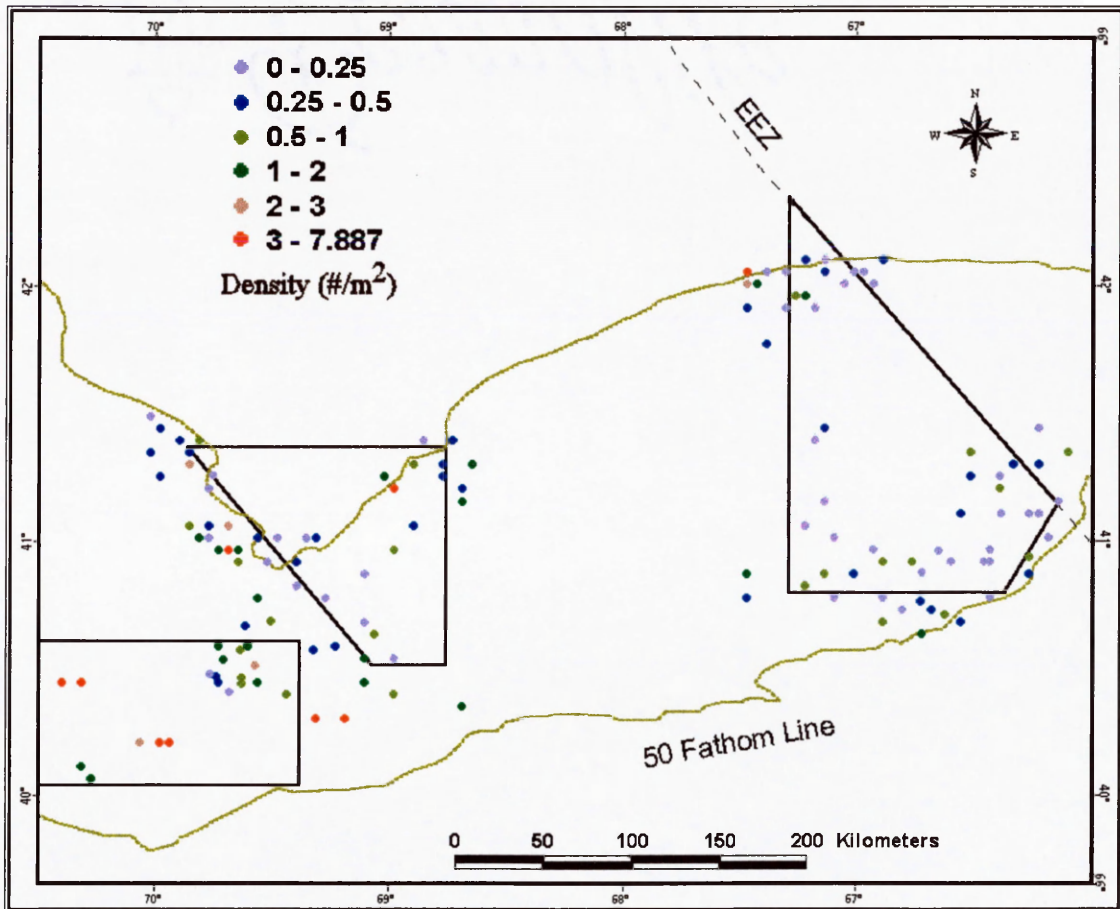


Figure 27a. Geographic distribution of invertebrate scavenger and opportunistic predator (9 species of decapods, 7 species of starfish, and 5 species of whelk) density (#/m²) on Georges Bank.

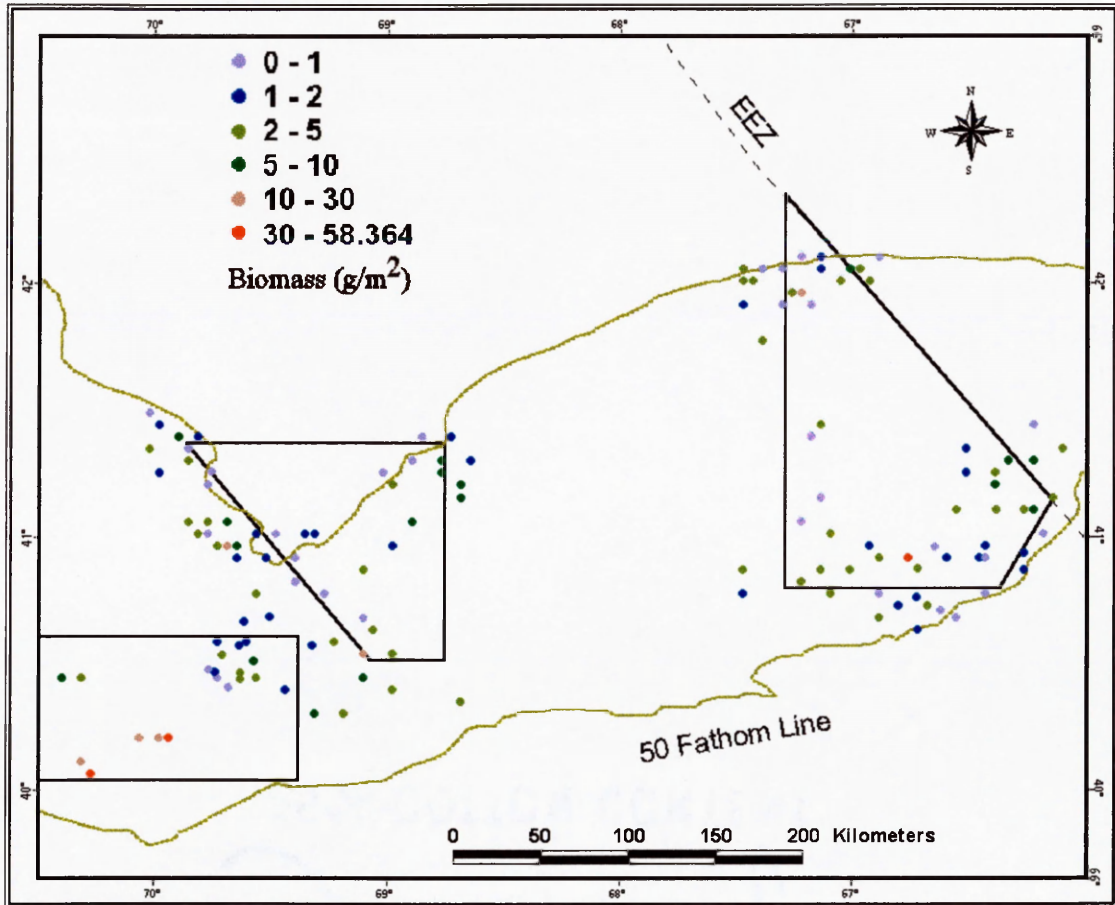


Figure 27b. Geographic distribution of invertebrate scavenger and opportunistic predator (9 species of decapods, 7 species of starfish, and 5 species of whelk) biomass (g/m^2 ; wet weight) on Georges Bank.

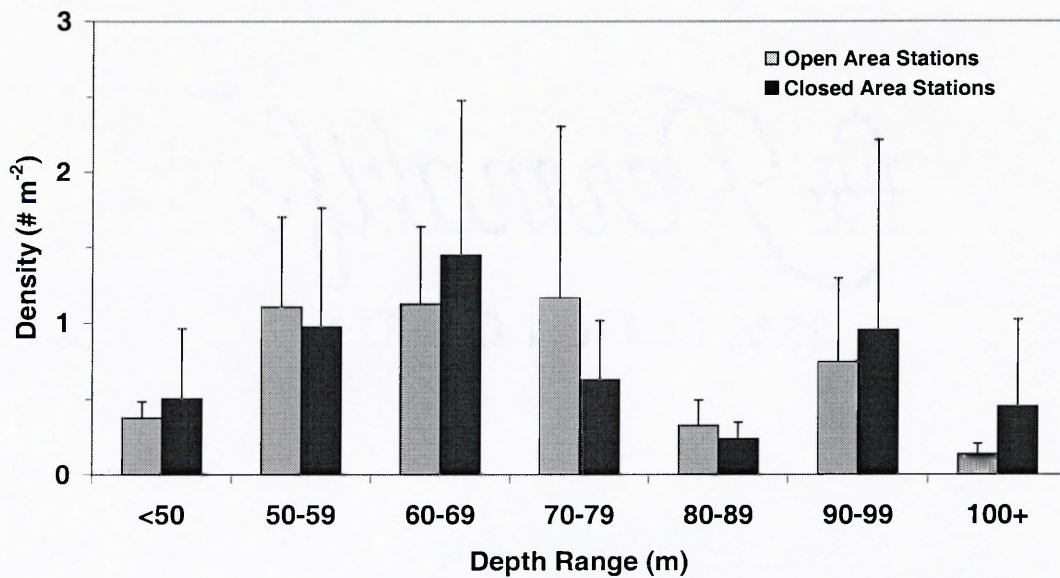


Figure 28. Mean density ($\#/m^2$) of invertebrate scavengers and opportunistic predators (9 species of decapods, 7 species of starfish, and 5 species of whelk), in relation to depth (95% confidence intervals shown).

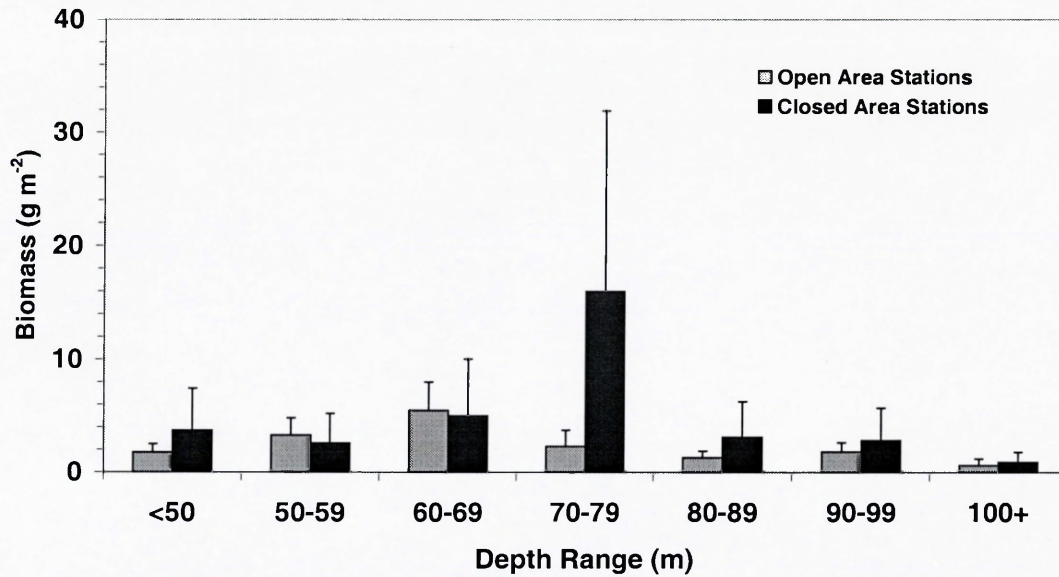


Figure 29. Mean biomass (g/m^2 ; wet weight) of invertebrate scavengers and opportunistic predators (9 species of decapods, 7 species of starfish, and 5 species of whelk), in relation to depth (95% confidence intervals shown).

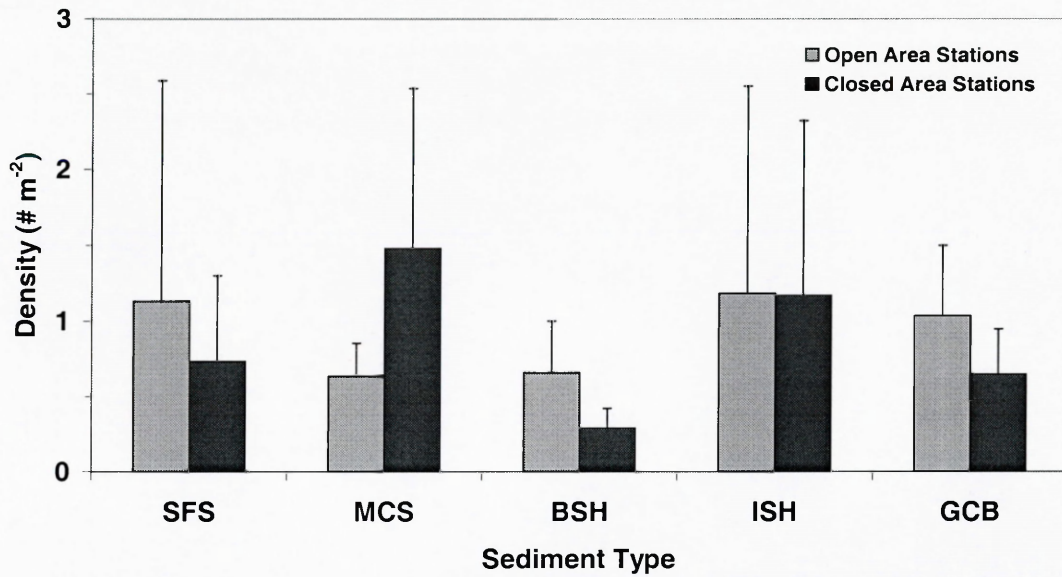


Figure 30. Mean density ($\#/m^2$) of invertebrate scavengers and opportunistic predators (9 species of decapods, 7 species of starfish, and 5 species of whelk), in relation to sediment type (95% confidence intervals shown). SFS – Silty/Fine Sand; MCS – Medium/Course Sand; BSH – Broken Shell Hash; ISH – Intact Shells; GCB – Gravel interspersed with Cobbles/Boulders.

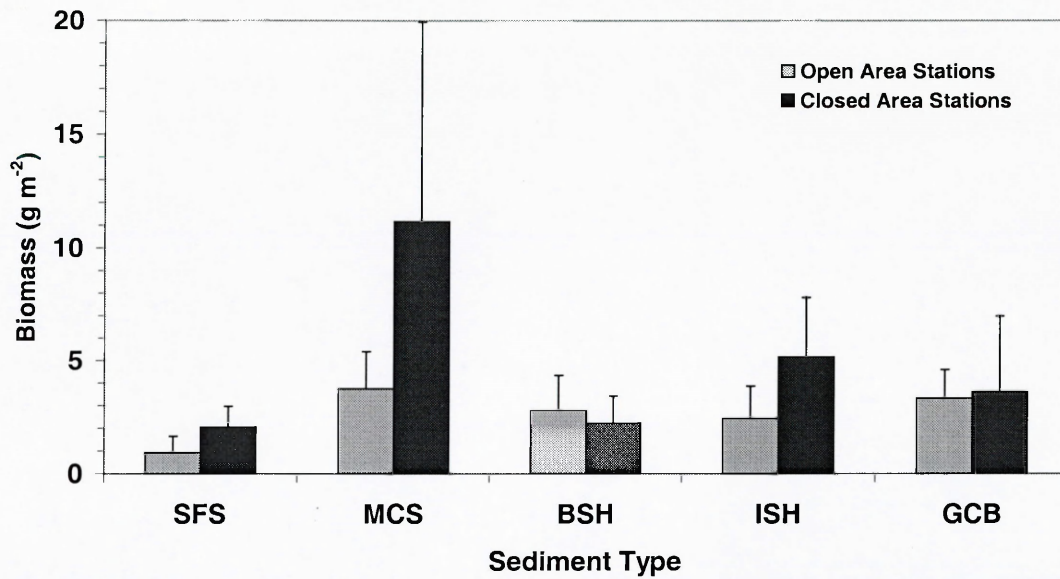


Figure 31. Mean biomass (g/m^2 ; wet weight) of invertebrate scavengers and opportunistic predators (9 species of decapods, 7 species of starfish, and 5 species of whelk), in relation to sediment type (95% confidence intervals shown). SFS – Silty/Fine Sand; MCS – Medium/Course Sand; BSH – Broken Shell Hash; ISH – Intact Shells; GCB – Gravel interspersed with Cobbles/Boulders.

Dependent Variable: Density (organisms/m ²) of invertebrate scavengers & opportunistic predators					
$r^2 = 0.21$		MSE = 1.618			
Source	df	Type III SS	F	p	
Depth	1	0.303	0.187	0.666	
Latitude	1	6.235	3.853	0.052	
Longitude	1	10.707	6.616	0.011	
Sediment	4	9.267	1.432	0.227	
Open/Closed Area	1	0.646	0.399	0.529	
Sediment x Open/Closed Area	4	6.199	0.958	0.433	

Dependent Variable: Biomass (g/m ²) of invertebrate scavengers & opportunistic predators following a 4th root transformation					
$r^2 = 0.24$		MSE = 0.118			
Source	df	Type III SS	F	p	
Depth	1	0.126	1.064	0.304	
Latitude	1	0.547	4.622	0.033	
Longitude	1	0.009	0.074	0.786	
Sediment	4	1.919	4.054	0.004	
Open/Closed Area	1	0.079	0.671	0.414	
Sediment x Open/Closed Area	4	0.444	0.939	0.444	

Table 7. Summary of 2-factor, 3-covariate ANCOVAs of ecological variables of invertebrate scavengers and opportunistic predators calculated from survey dredge samples collected on Georges Bank. Total observations = 138. MSE = mean squared error; df = degrees of freedom; SS = sum of squares

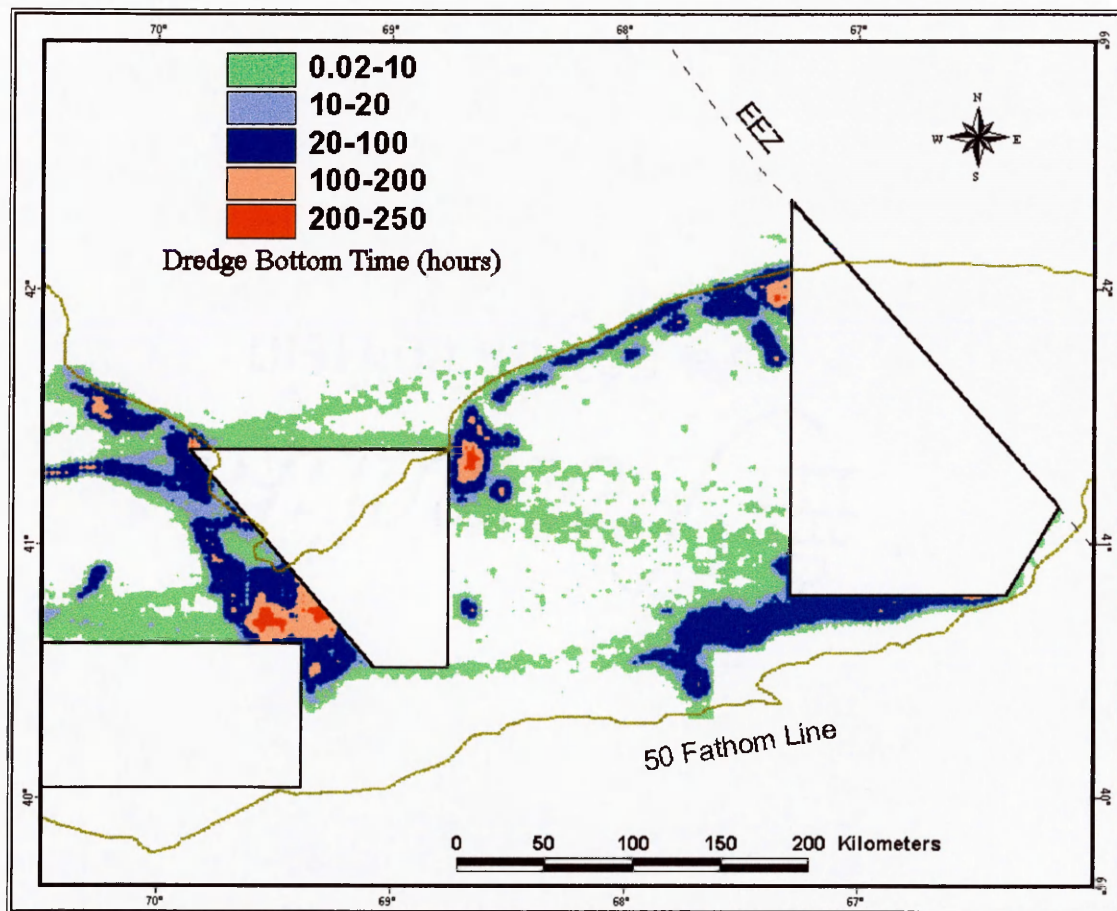


Figure 32. Geographic distribution of the scallop fleet fishing effort (in hours bottom time) from 2000 based on vessel monitoring system (VMS) data, with values within the closed areas set to zero to approximate 2001-2002 data.

Dependent Variable: Species Count					
Source	Beta	Std. Error	t	p	
Intercept	-313.250	94.262	-3.323	0.001	
Latitude	3.056	1.636	1.868	0.066	
Longitude	3.066	0.713	4.298	0.000	
Depth	-0.048	0.046	-1.047	0.299	
Fishing Effort	0.000	0.000	-0.736	0.465	
Distance from Closed Area Boundary	0.048	0.146	0.329	0.743	
<hr/>					
Dependent Variable: Density (ind./m ²)					
Source	Beta	Std. Error	t	p	
Intercept	-179.019	94.503	-1.894	0.063	
Latitude	1.947	1.640	1.187	0.240	
Longitude	1.399	0.715	1.956	0.055	
Depth	0.063	0.046	1.380	0.173	
Fishing Effort	0.000	0.000	-0.100	0.921	
Distance from Closed Area Boundary	0.206	0.146	1.410	0.163	
<hr/>					
Dependent Variable: Biomass (g/m ²)					
Source	Beta	Std. Error	t	p	
Intercept	-1277.755	470.833	-2.714	0.009	
Latitude	21.980	8.172	2.690	0.009	
Longitude	6.210	3.563	1.743	0.086	
Depth	-0.385	0.227	-1.692	0.096	
Fishing Effort	0.000	0.002	-0.192	0.849	
Distance from Closed Area Boundary	-0.320	0.727	-0.440	0.661	
<hr/>					
Dependent Variable: Pielou's Evenness Index based on density					
Source	Beta	Std. Error	t	p	
Intercept	-2.240	3.755	-0.596	0.553	
Latitude	0.092	0.065	1.404	0.165	
Longitude	-0.011	0.028	-0.370	0.713	
Depth	-0.003	0.002	-1.690	0.096	
Fishing Effort	0.000	0.000	0.119	0.906	
Distance from Closed Area Boundary	-0.002	0.006	-0.374	0.710	
<hr/>					
Dependent Variable: Shannon-Wiener Index (log2) based on density					
Source	Beta	Std. Error	t	p	
Intercept	-25.364	14.187	-1.788	0.079	
Latitude	0.463	0.246	1.881	0.065	
Longitude	0.129	0.107	1.203	0.234	
Depth	-0.008	0.007	-1.144	0.257	
Fishing Effort	0.000	0.000	0.000	1.000	
Distance from Closed Area Boundary	-0.008	0.022	-0.383	0.703	

Table 8. Summary of multiple linear regressions run on ecological variables calculated from survey dredge samples collected on Georges Bank. Total observations = 68. df = degrees of freedom

Dependent Variable: Invertebrate Predator and Opportunistic Scavenger Density (ind./m²)				
	r = 0.38		r² = 0.15	
Source	Beta	Std. Error	t	p
Intercept	2.159	18.581	0.116	0.908
Latitude	-0.367	0.322	-1.137	0.260
Longitude	0.204	0.141	1.454	0.151
Depth	-0.004	0.009	-0.419	0.676
Fishing Effort	0.000	0.000	-1.072	0.288
Distance from Closed Area Boundary	0.040	0.029	1.387	0.170

Dependent Variable: Invertebrate Predator and Opportunistic Scavenger Biomass (g/m²)				
	r = 0.51		r² = 0.26	
Source	Beta	Std. Error	t	p
Intercept	60.234	50.076	1.203	0.234
Latitude	-1.878	0.869	-2.160	0.035
Longitude	0.399	0.379	1.052	0.297
Depth	-0.070	0.024	-2.897	0.005
Fishing Effort	0.000	0.000	-2.751	0.008
Distance from Closed Area Boundary	-0.143	0.077	-1.843	0.070

Table 9. Summary of multiple linear regressions run on ecological variables of invertebrate scavengers and opportunistic predators calculated from survey dredge samples collected on Georges Bank. Total observations = 68. df = degrees of freedom

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