Ecology of Deep-Sea Asteroidea from Atlantic Canada

by

© Katherine Sarah Petra Gale

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Abstract

Sea stars (Echinodermata: Asteroidea) from shallow-water habitats worldwide are known to influence local biodiversity and community structure through their feeding behaviours. Deep-sea (> 200 m) asteroids may have similar ecological roles, but there is little information available for most species. To better understand the roles of asteroids in communities on continental margins, I investigated the diets, distributions, habitat use, and species associations of about 30 subtidal and bathyal asteroid species from 37–2243 m off Newfoundland and Labrador (NL), Canada. Stomach content analysis, stable isotope analysis, and live animal observations of seven bathyal species revealed asteroids to be either top predators of megafauna or secondary consumers (mud ingesters, infaunal predators, suspension feeders). Two of the predatory species consume corals and sponges, whereas the other species feed mainly on crustaceans, molluscs, and organic matter in sediment. Using a data set covering ~600,000 km^2 and including over 350,000 individual asteroid records, I found most species to have wide depth ranges spanning > 1000 m. Using cluster analysis, I identified three different asteroid assemblages over the study area, including the Grand Banks, the Laurentian Channel, and the north-eastern Newfoundland shelf and slope. Multivariate analyses revealed asteroids associate with corals, sponges, bivalves, and other echinoderms, and that depth and local substrate influence assemblages. Most asteroids were found on silt or mud, while a few occurred mainly on hard substrates. This analysis contributes to the growing knowledge of benthic invertebrates in NL waters, providing baseline distribution and ecological information for many poorly-known bathyal asteroid species, and indicating that the feeding behaviours of some asteroids may affect deep-sea benthic communities.

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I am persuaded that the sea will be forever wild... here is one part of the natural world safely beyond our reach.

- David Pitt-Brooke, *Chasing Clayoquot*

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Co-Authorship Statement

The research in this thesis and all written work was carried out by Katie Gale under the guidance of Annie Mercier and Jean-François Hamel. The contributions for the data chapters are as follows:

Chapter 2: Annie Mercier conceived and supervised the project with input from Jean-François Hamel. Katie Gale collected and analyzed the data, and wrote the chapter with guidance and input from Annie Mercier and Jean-François Hamel.

Chapter 3: Annie Mercier supervised the project with input from Jean-François Hamel, Kent Gilkinson provided data from the Department of Fisheries and Oceans, and Katie Gale analyzed the data and wrote the article with guidance and input from the other three authors.

Chapter 1

General Introduction

1.1 **The deep sea**

The deep sea is the largest environment on Earth, with almost 90% of the oceans found deeper than the continental shelf break at an average depth of ~200 m worldwide (Gage and Tyler 1991). Given that these deep waters lack sufficient light for photosynthetic production, energy in non-chemosynthetic systems must be imported from surface waters in the form of phytodetritus, food falls (animal carcasses), and other material such as feces (Gage and Tyler 1991; Tyler 1995; Rex and Etter 2010). This import of organic material is often seasonal and localized, causing food limitation in most deep-sea ecosystems. The limited food, coupled with low temperatures and high pressure at depth, led early researchers to believe the deep sea could not support life (Gage and Tyler 1991). From early surveys such as the *Challenger* Expedition to recent initiatives such as the Census of Marine Life, it is now known that deep-sea biodiversity is substantial and in some cases may exceed that of shallow-water regions (Carney 1997; Levin et al. 2001). Advances in deep-sea technology have contributed to the discovery and cataloguing of many new species, but the ecological understanding of deep-sea organisms remains far behind that of their shallower water counterparts.

1.2 **Role of megafauna in the deep sea**

Mobile invertebrate megafauna, such as echinoderms and decapod crustaceans, are ecologically important components of deep-sea benthic ecosystems (Gage and Tyler 1991; Rex and Etter 2010). Megafauna can influence biodiversity by increasing environmental complexity through sediment modification (e.g., mounds; Kukert and Smith 1992) or by providing novel habitats for other species (e.g., sponges and corals; Buhl-Mortensen et al. 2010). Trophic interactions involving megafauna can also influence community structure. By ingesting or displacing large quantities of sediment during feeding, deposit- and infaunal-feeding megafauna are responsible for a substantial amount of bioturbation (Rhoads and Young 1970; Gallucci et al. 2008); this activity can influence the abundance and composition of other species through direct predation of infauna (Ambrose 1993; Gallucci et al. 2008), disruption of larval settlement (Rhoads and Young 1970), or redistribution of labile carbon and other nutrients (Miller et al. 2000; Iken et al. 2001). Scavenging megafauna are often the first to exploit large, localized food parcels (food falls, phytodetritus patches) at depth, facilitating the use of such carbon sources by lower trophic levels (Yeh and Drazen 2009; Jeffreys et al. 2011).

Echinoderms, including the classes Asteroidea, Ophiuroidea, Holothuroidea, and Echinoidea, are often the dominant mobile megafauna (numerically or by biomass) in many areas of the deep sea (Billett 1991; Gage and Tyler 1991). Their abundance and wide range of feeding behaviors, including suspension feeding, deposit feeding, and predation (Jangoux and Lawrence 1982), indicate that echinoderms occupy a range of ecological niches in deep-sea benthic communities. However, little is known about the ecology of individual species of echinoderm in most regions worldwide. In an effort to increase our understanding of these ubiquitous organisms, this thesis is focused on assessing the ecological roles of a subset of deep-sea asteroids (sea stars) from the northwest Atlantic.

1.3 **Study organisms: the Asteroidea**

1.3.1 *Diversity*

The class Asteroidea includes about 1900 species in 36 genera worldwide (Mah and Blake 2012). Species diversity is highest in cold- and deep-water habitats, with many families restricted to the deep sea (Mah and Blake 2012). The morphological and ecological variation among asteroid species is considerable. Different species can inhabit soft or hard bottom habitats and are found from the intertidal to the abyss (Grainger 1966; Mah and Blake 2012). The smallest known asteroids are only centimetres, with the largest species (*Pycnopodia helianthoides*) reaching almost 1 m wide (Lambert 2000; Benavides-Serrato et al. 2007). Asteroids feed on dissolved organic matter, detritus, fresh algae, carrion, or live animals by passive diffusion, opportunism, or active hunting (Jangoux 1982).

The feeding behaviors of asteroids are related to their morphology. Because most species cannot raise their arms very far vertically, most are benthic feeders (predators, deposit feeders, etc.; Sokolova 2000). However, suspension feeding occurs in the Brisingida and some species in the Forcipulatida (e.g., *Labidiaster annulatus* and *Rathbunaster californicus*), which have many long, flexible arms that can be raised into the water column to capture zooplankton and suspended organic material (Dearborn et al. 1991; Emson and Young 1994; Lauerman 1998). The suspension-feeding brisingid asteroids are functionally sessile (Lundsten et al. 2009), but most asteroids are mobile: the exceptional *Luidia ciliaris* can pursue prey at up to 5 cm s^{-1} (Brun 1972). The tube feet (podia) of asteroids are morphologically variable among taxa (Vickery and McClintock

2000). Suckered tube feet are found in many species and aid in attachment to substrate and prey manipulation, while pointed tube feet, found mostly in the order Paxillosida, are used to burrow in soft sediment and push food towards the mouth (Santos et al. 2005). Most asteroids have an extrudable stomach and feed extra-orally, allowing for feeding on encrusting organisms or those too large to swallow (Jangoux 1982; Lawrence 2012). A minority of asteroids, including those in the Paxillosida, feed intra-orally since they lack extrudable stomachs (Jangoux 1982). This constraint theoretically limits the size of prey that can be captured, since all items must fit inside the stomach; however, the elastic nature of the body wall allows copious amounts of sediment or fairly large, hard items (e.g., shelled animals) to be fully engulfed (Madsen 1961; Jangoux 1982).

1.3.2 *Ecological roles*

The tremendous diversity of asteroids contributes to their wide-ranging ecological roles. Many species of intertidal and subtidal (≲ 60 m) asteroids are well known for their predatory behaviors, which in some cases can shape local community structure (e.g. *Pisaster ochraceus*¸ Paine 1969*; Stichaster australis,* Paine 1971; *Odontaster validus*, Dayton et al. 1974). Many asteroids live or feed infaunally, which can lead to extensive bioturbation and disruption of sediments (Miller et al. 2000).

Although much is known about shallow-water asteroids, ecological research of deep-sea species lags far behind. Recent studies have begun to close this gap by including deep-sea asteroids in food web studies worldwide, such as in the northeast Atlantic (Iken et al. 2001; Howell et al. 2003), the Mid-Atlantic Ridge (Reid et al. 2012), cold seeps in the Gulf of Mexico (Carney 2010), and Arctic regions such as Svalbard (Renaud et al.

2011; Bergmann et al. 2011), the Chukchi Sea (Feder et al. 2010), and the Barents Sea (Tamelander et al. 2006). These studies indicate that asteroids occupy a range of trophic positions, from deposit feeder to predator, with some species being "top predators" in their systems (e.g., *Poraniomorpha tumida*; Tamelander et al. 2006; Bergmann et al. 2009). Asteroids in the northwest Atlantic have not yet been incorporated into a food web study.

1.4 Asteroids in Eastern Canada

The present study took place at depths of 37–2243 m over the continental shelf and slope of Newfoundland and Labrador (NL), including southern Labrador, the northern and southern Newfoundland shelf, the Grand Banks, and the eastern part of the Laurentian Channel. The deep-sea asteroid fauna of Atlantic Canada has been catalogued, with about 50 species having been documented in NL waters or having ranges that potentially include this area (Grainger 1966; Haedrich and Maunder 1985; Clark and Downey 1992). The NL asteroid fauna includes some Arctic species as well as species occurring in the temperate northwest Atlantic (i.e., the northeastern United States) (Grainger 1966; Franz et al. 1981; Haedrich and Maunder 1985). Ecological information for asteroids in NL is only available for those found at very shallow depths (Schneider et al. 1987; Himmelman and Dutil 1991) and for the circumpolar *Ctenodiscus crispatus* (Shick et al. 1981). The ecology of most, if not all, of the deep-sea asteroids from NL is completely unknown, but is of interest in light of the high biomass over the NL shelf and slope, particularly the Grand Banks (Nesis 1965), and the anthropogenic impact to the benthos from fishing and the emerging oil and gas industry (Hutchings and Myers 1995;

Aquarone and Adams 2008). Given their diversity and abundance in NL, information on the trophic ecology, geographic and bathymetric distributions, species associations and habitat utilization of deep-sea asteroids will aid in understanding the ecological processes and interactions of the benthic fauna of the region.

1.5 Goals of thesis and chapter structure

The objectives of this thesis are to elucidate the ecology of asteroids from the continental shelf and slope of Newfoundland and Labrador, Canada, with a focus on deep-sea taxa. This thesis contains four chapters: following this introduction (Chapter 1), I report on the diets and trophic ecology of some of the common deep-sea asteroid species (Chapter 2), determine distributions, assemblages, and habitats for a large number of species known to occur in the northwest Atlantic on the continental shelf and slope of Newfoundland and Labrador (Chapter 3), and provide general conclusions (Chapter 4).

In Chapter 2, I studied the diets and feeding behaviors of seven species of deep-sea asteroid to explore their potential ecological roles. I used stable isotope and stomach content analysis of preserved specimens, laboratory observations of live asteroids, and *in situ* ROV imagery to demonstrate that these focal species occupy several trophic niches. Two of the species are likely primarily predators of sponges and corals, which are known to be important biogenic habitats. Other species feed infaunally on molluscs, small crustaceans, and organic matter in the sediment, and one suspension feeding species ingests zooplankton.

In Chapter 3, I used a large dataset of invertebrate bycatch and remotely operated vehicle (ROV) video observations to determine the geographic and bathymetric ranges for many of the asteroid species found on the continental shelf and slope around NL. Additionally, I explored the patterns of asteroid assemblages, their preferred substrate types, and relationships with co-occurring benthic invertebrates to produce a framework for understanding the ecological roles of asteroids in the region. Both depth and substrate type appear to be important factors in organizing the assemblages of asteroids. Most asteroid species inhabit wide depth ranges, utilize soft-bottom habitats, and are found in close proximity to other epibenthic species including corals and sponges.

In Chapter 4, I summarize these results and discuss the potential importance of asteroids within the Newfoundland continental shelf and slope ecosystem.

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Chapter 2

Trophic ecology of deep-sea Asteroidea from eastern Canada*

2.1 **Abstract**

Asteroids (sea stars) can be important predators in benthic communities and are often present in ecologically important and vulnerable deep-sea coral and sponge habitats. However, explicit studies on the trophic ecology of deep-sea asteroids are rare. We investigated the diets of seven species of deep-sea asteroid from the bathyal zone of Newfoundland and Labrador, eastern Canada. A multifaceted approach including live animal observations, stomach content analysis, and stable isotope analysis, revealed the asteroids to be either top predators of megafauna or secondary consumers (mud ingesters, infaunal predators, suspension feeders). The stable isotope signatures of *Ceramaster granularis, Hippasteria phrygiana,* and *Mediaster bairdi* are characteristic of high-level predators, having $\delta^{15}N$ values 4.4 ‰ (more than one trophic level) above *Ctenodiscus crispatus, Leptychaster arcticus, Novodinia americana,* and *Zoroaster fulgens.* We present strong evidence that corals and sponges are common food items for two of the predatory species, *C. granularis* and *H. phrygiana*. During laboratory feeding trials, live *H. phrygiana* fed on several species of soft coral and *C. granularis* fed on sponges. Stomach content analysis of wild-caught individuals revealed sclerites from sea pens (e.g. *Pennatula* sp.) in the stomachs of both asteroid species; *H. phrygiana* also contained sclerites from at least two other species of octocoral and siliceous sponge spicules were

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present in the stomachs of *C. granularis.* The stomach contents of the secondary consumers contained a range of invertebrate material. *Leptychaster arcticus* and *Ctenodiscus crispatus* feed infaunally on bulk sediment and molluscs, *Zoroaster fulgens* is a generalist infaunal predator, and the brisingid *Novodinia americana* is a specialist suspension feeder on benthopelagic crustaceans. This study provides a foundation for understanding the ecological roles of bathyal asteroids, and suggests that some species may have the potential to be important modulators of deep-sea benthic communities.

2.2 **Introduction**

Non-chemotrophic deep-sea food webs depend on the surface production of organic material, including phytodetritus, particulate organic material (POM), and food-falls (animal carcasses), that is either seasonal or localized; hence, food limitation is common in deep-sea ecosystems (Gage and Tyler 1991; Sokolova 2000). With limited food input and low densities of organisms, most areas of the deep sea appear to promote opportunistic feeding behaviors. Predatory specialists are rare, whereas deposit-feeders are more common in deep than in shallow waters (Carey 1972; Gage and Tyler 1991).

Many species of sea star, or asteroid (Asteroidea: Echinodermata), are known to be important predators in benthic communities worldwide and in some cases can be integral to shaping food webs (Paine 1966; Menge 1982). The feeding behaviors of many polar and temperate shallow-water species have been shown to strongly influence local biodiversity. For example, the Northeast Pacific asteroid *Pisaster ochraceus* maintains space availability in the rocky intertidal by preying on mussel beds (Paine 1966), and the

Antarctic asteroid *Odontaster validus* feeds on the larvae of sponge predators, removing pressure on the sponges and allowing them to flourish (Dayton et al. 1974).

Asteroids occur throughout the world's oceans at bathyal and abyssal depths (Carey 1972; Howell et al. 2002; Hendrickx et al. 2011), but information on the biology of most deep-sea species remains scarce. Although the diets of some deep-sea asteroids have been described from stomach contents (e.g., Carey 1972; Mah 2007), the general and trophic ecology of most species have received little attention. Some species, particularly those in the family Goniasteridae, have been suggested to be important predators of cold-water corals (Krieger and Wing 2002; Mah et al. 2010), but it is still unclear whether deep-sea asteroids show specialized feeding behaviors that could influence local biodiversity such as those documented in their shallow-water relatives. Determining the specific diets and methods of food acquisition for deep-sea asteroids is an important step in understanding their broader ecological roles.

Previous work indicates that, like their shallow-water relatives, deep-sea asteroids exhibit a range of feeding strategies including suspension feeding, deposit feeding, predation, and scavenging (Carey 1972; Sokolova 2000; Howell et al. 2003). Suspension feeding in asteroids is observed primarily in the order Brisingida, which capture POM and zooplankton from the water column (Sokolova 2000). Deposit feeding asteroids are common and diverse, and can be broken into two groups: surface deposit feeders that feed on organic material including phytodetritus, POM, and biofilms (Sokolova 2000; Howell et al. 2003; Jeffreys et al. 2009), and mud ingesters that ingest bulk sediment and absorb heterotrophic bacteria or sedimentary organic matter (SOM) (Gage and Tyler 1991; Howell et al. 2003). Predatory or carnivorous asteroids, which feed on animal material, can be divided based on the size and type of their prey: megafaunal predator/scavengers feed on sessile, usually colonial, organisms like sponges, corals, and bryozoans (Carey 1972; Sokolova 2000; Mah et al. 2010) and utilize food-falls (Kemp et al. 2006; Yeh and Drazen 2009), while infaunal predators feed on subsurface macrofauna including molluscs, echinoderms, and crustaceans (Jangoux 1982). It has been suggested that there is little difference between predators, deposit feeders, and scavengers in the deep sea because most species feed opportunistically on any available organic matter (i.e., the "omnivores" of Carey, 1972 or "croppers" of Dayton and Hessler, 1972). However, sympatric asteroid species can span several trophic levels (Iken et al. 2001; Bergmann et al. 2009), indicating that dietary differences exist and may be influenced by differences in behavior, morphology, or habitat of co-occurring species.

Information on the trophic ecology of deep-sea asteroids has historically come from stomach content analysis (e.g., Carey 1972), and more recently from stable isotope or fatty acid analyses and *in situ* imagery (Iken et al. 2001; Howell et al. 2003). Stomach content analyses remain useful but provide an incomplete, short-term picture of diet, since there is a bias towards recently ingested items with hard parts, such as sediment and skeletal elements (Sheppard and Harwood 2005). Stable isotope analysis can supplement stomach-content studies by revealing longer-term trophic interactions, because the $\delta^{13}C$ and $\delta^{15}N$ signature of an individual or species represents its "trophic niche" within its community (Sherwood et al. 2008). Underwater photography and videography have provided insights into feeding behaviors of deep-sea asteroids, such as the specialized suspension-feeding postures of the Brisingida (Emson and Young 1994) and the scavenging behaviors of several species on dead fish and mammals (Kemp et al. 2006;

Yeh and Drazen 2009). Although laboratory studies of deep-sea asteroids have generally not been carried out, such studies on shallow-water asteroids have revealed trophic and competitive behaviors not otherwise apparent (Shick et al. 1981; McClintock et al. 2008).

On the continental slope of Newfoundland and Labrador, Canada, asteroids are among the most species-rich yet understudied group of echinoderms, with at least 25 species present (Haedrich and Maunder 1985; Chapter 3). The goal of the present study is to use stomach-contents, stable isotope analysis, *in situ* ROV observations, and feeding experiments with live individuals to examine the feeding behaviors and diet of seven species of deep-sea asteroid. Our study provides a foundation for understanding the ecological roles of asteroids in eastern Canada, and suggests that some species are potentially important predators, thereby shaping their local communities.

2.3 **Methods**

2.3.1 *Focal species*

Based on a preliminary assessment of video footage and field samples taken from the Newfoundland and Labrador shelf and slope, seven species were selected for the present study because they were among the most common and were presumed to represent a range of feeding behaviors: *Ceramaster granularis, Ctenodiscus crispatus, Hippasteria phrygiana, Leptychaster arcticus*, *Mediaster bairdi, Novodinia americana,* and *Zoroaster fulgens* (Table 2-1, Figure 2-1). In addition, the diet of most of these species is either completely unknown or unreported for this region. Many other asteroid species that co-occur with our focal species, such as *Porania pulvillus, Astropecten* *americanus, Pseudarchaster parelii,* and *Psilaster andromeda* may also be ecologically important but were not considered here for feasibility reasons.

2.3.2 *Collection and maintenance*

All asteroids were collected as bycatch during multispecies trawl surveys conducted by Fisheries and Oceans Canada (DFO) between 2005 and 2011 along the north-eastern continental shelf and slope of Newfoundland and Labrador (NL), Canada, at depths of 258–1418 m. Specimens analyzed for stomach contents and stable isotopes were immediately frozen and stored at -20 ºC until processing. Those used for live trials (*C. granularis* and *H. phrygiana*) were maintained in flow-through tanks aboard the ship then transported to the laboratory, where they were kept in darkened flow-through tanks supplied with unfiltered seawater at a temperature between -1 and 9 ºC to roughly match *in situ* temperatures (Stein 2007).

2.3.3 *Stomach contents*

Stomach contents were analyzed from asteroids collected on 35 surveys between 2005 and 2011 (Figure 2-2). Most specimens were collected in October – December, except for two *Ceramaster granularis* and four *Ctenodiscus crispatus* that were collected in June. Stomachs from 5–14 individuals of each species were examined (total n = 70; Table 2-1). For most species the aboral body wall was removed and the entire stomach was dissected out; for *Z. fulgens* and *N. americana,* which have heavily calcified discs, it was more efficient to extract the stomach contents with forceps and a pipette through the oral opening. Stomach contents were isolated from stomach tissue under a stereomicroscope (Nikon SMZ1500). After large contents were isolated, or if no material was visible in the stomach, half of the stomach tissue was dissolved in 5.25% sodium hypochlorite (household bleach) to isolate small hard structures present, such as sediment grains, sclerites, or spicules. The bleach solution was then decanted off and the remaining stomach material was rinsed, isolated, and photographed with a digital camera (Nikon DXM1200F) fitted to a microscope (Nikon Eclipse 80i) or the above-mentioned stereomicroscope. Specimens or structures were measured digitally using the freeware program ImageJ (Abràmoff et al. 2004).

2.3.4 *Stable isotopes*

A subset of 3–5 specimens per species (total n = 32; Figure 2-2) was selected for $\delta^{13}C$ and $\delta^{15}N$ stable isotope analysis. For most of the species, all samples used for analysis were collected in December 2011. For *M. bairdi,* only three samples were available from 2011, so two additional individuals collected in November 2006 and December 2010 were used. Similarly, scarcity of *N. americana* samples in our collection necessitated use of two samples from November 2005 and three from November 2006. All specimens used also had their stomach contents analyzed, except one *N. americana* sample which did not include an oral disc. Samples were prepared for analysis as per Sherwood et al. (2008). From each frozen individual a piece of body wall (0.5–1 g), sometimes including tube feet, was collected. Care was taken to exclude pieces of gonad or pyloric caeca. A small amount of 5% HCl was added and the sample was dried at ~70 ºC for 2–4 days. The dried samples were then ground using a mortar and pestle and treated with HCl for ~5 h to remove carbonates. The samples were washed with distilled water and were re-dried for 3–6 days. Powdered samples (1 mg) were packed into tin capsules and analyzed simultaneously for total C, total N, $\delta^{13}C$, and $\delta^{15}N$ at the CREAIT TERRA facility of Memorial University. Stable isotope values are presented using the conventional δ notation, expressed in ‰, using the equation

$$\delta X = [(R_{sample} / R_{standard}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Standards used were Vienna Pee Dee Belemnite (VPDB) for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$.

Trophic level estimates for each species were determined using the following equation (Sherwood and Rose 2005; Nilsen et al. 2008):

$$TL_{consumer} = [(\delta^{15}N_{consumer} - \delta^{15}N_{base}) / \Delta\delta^{15}N] + TL_{base}$$

where $TL_{consumer}$ and TL_{base} are the respective trophic levels of the organism in question and the chosen “base” of the food web, $\delta^{15}N_{consumer}$ and $\delta^{15}N_{base}$ are their respective $\delta^{15}N$ values, and $\Delta\delta^{15}N$ is the trophic fractionation for $\delta^{15}N$ (average 3.8‰ for polar and deep-sea studies, Iken et al. 2005). The $\delta^{15}N$ values for primary consumers, usually zooplankton, can be used to calculate the trophic levels of higher-level consumers when isotope values for the primary producer of a system are not known (Sherwood and Rose 2005; Nilsen et al. 2008). Zooplankton from the Newfoundland shelf edge was used as baseline consumer ($TL_{base} = 2.3$, $\delta^{15}N_{base} = 9.0$, Sherwood and Rose 2005).

2.3.5 *Laboratory feeding trials*

Laboratory feeding trials were carried out with *Ceramaster granularis* and *Hippasteria phrygiana* to test for predatory and scavenging behaviors. A first series of trials (referred to as “experimental trials”) were conducted in an enclosure (49 cm x 36 cm x 25 cm) positioned in a 1 m^3 tank filled with ~6 cm of fine silt sediment, based on

ROV observations of common field conditions for the asteroid species (Chapter 3). Temperatures in the tank ranged from 1.1–8.8 ºC over the course of the experiments (October 2010–March 2011), varying with local seawater conditions (consistent with *in situ* records from Stein, 2007). Because we were unable to maintain an even current in our tank, water flow was turned off for the duration of a trial to avoid potential differences in dispersal of prey effluent among trials. Although some asteroids have difficulties finding prey in still water (Drolet and Himmelman 2004), we confirmed that our test species were able to find food in the enclosure (mussel tissue, which they fed on during holding; see below). The asteroids and prey did not show any adverse reactions to being in still water, the tank being large enough to remain at a steady temperature throughout the trial. All asteroids were starved for at least two weeks (as per Rochette et al. 1994) prior to use in trials and were never exposed to air during transfers. Prey species were acclimated within the enclosure for > 20 minutes, or until they relaxed (i.e., tentacles fully extended), before predator introduction. For each trial, one asteroid was placed ~6 cm from a single prey. Noting that leading-arm preferences may exist in some species (Polls and Gonor 1975), the arm nearest to the madreporite was always pointed towards the prey. Individual asteroids were not used more than once in a 48-hour period. If no predation or contact occurred, a subsequent trial with a new asteroid was started immediately; if contact occurred, the prey was allowed to acclimate/relax as above prior to asteroid introduction.

Prey tested in the experimental trials included live individuals of the deep-sea corals *Duva florida* (Alcyonacea), *Flabellum alabastrum* (Scleractinia), *Pennatula* sp. (Pennatulacea), and *Stauropathes arctica* (Antipatharia), and the deep-sea anemone

Hormathia nodosa. Fresh tissue of subtidal mussel (*Mytilus* sp.) was used to test scavenging behavior. Given that both *C. granularis* and *H. phrygiana* were regularly observed feeding on mussel tissue during holding, these trials also confirmed the responsiveness of the asteroids in the experimental enclosure. An empty skeleton of the cup coral *F. alabastrum* (no animal tissue) was used to test the asteroids' response to novel, inert objects introduced in the same way as potential prey.

The experimental trials were documented with high resolution time-lapse imagery. Using a downward-facing DSLR camera (Nikon D5000) positioned directly above the tank, an image was taken every 8–10 seconds until the end of the trial. Trials (n = 6–14 individual *H. phrygiana* and 6–9 *C. granularis* per prey, total n = 146 trials) lasted 24 to 232 min and were ended under two conditions: (1) the asteroid exhibited one of the formal responses outlined below; or (2) the asteroid stopped moving for an hour. Still images from the trial were combined into 10–20 second long video clips using Quick-Time Pro v7.7 (Apple Inc., 2011). Videos were scored for one of three outcomes: (1) the asteroid did not move or moved within the enclosure but did not touch the prey ("no contact"), (2) the asteroid touched the prey but did not attempt to ingest it ("rejection"), or (3) the asteroid fed on the prey based on characteristic "humped" body posture and/or extrusion of its stomach over the prey ("predation"). Qualitative observations of any prey response were also taken.

A second set of trials ("informal trials"), which were not filmed or timed, were conducted in flow-through holding tanks. Freshly opened sea urchins *Strongylocentrotus droebachiensis* and eurybathic sponges *Isodactya palmata* were tested with both asteroid species, subtidal sponges *Halichondria panicea* were tested with *C. granularis*, and the pennatulacean *Anthoptilum grandiflorum* was tested with *H. phrygiana*. These trials lasted from 1–72 hours, and the outcomes scored only as “predation” or “no predation”.

2.3.6 In situ *observations*

In situ observations of asteroids were made from georeferenced video and images taken by the ROV ROPOS during a series of dives in 2007. These surveys were primarily designed for assessing coral and fish assemblages at different locations and are described in detail by Baker et al. (2012). Briefly, video transects (1 km long) were carried out along depth contours in three canyons on the southern continental slope of Newfoundland between 354–2243 m depth. Along the surveys, video was continuously recorded and opportunistic still images taken; time, depth, and location were recorded for all observations. From the videos and images, we collected data on potential feeding behaviors of our focal species and other asteroids of interest and their associations with other megafauna. For the asteroid species under study, we collected additional still images from dives in 2007 on the eastern Nova Scotia slope (43.682–44.478ºN, 57.141–61.489ºW) and at the Orphan Knoll off the northeastern Newfoundland slope (50.095ºN, 45.342ºW) in 2010.

2.4 **Results**

2.4.1 *Stomach contents*

Stomach contents were present in all species examined (summarized in Table 2-1). Most stomachs contained only small amounts of material, but only six individuals had totally empty stomachs (three *M. bairdi,* two *L. arcticus* and one *C. granularis*).

Hippasteria phrygiana often contained coral sclerites, which were found in 64% of individuals examined (Figure 2-3); the sclerites were present in large clumps (several hundred pieces) in about half the individuals (Figure 2-3b, insert). Five coral sclerite morphotypes were observed: white-pink bilobed rods (Figure 2-3b), red or clear 3-flanged rods (Figure 2-3b), clear spindle-type sclerites with tubercles (Figure 2-3a), and highly ornamented red club-type sclerites (Figure 2-3c). Other stomach contents for *H. phrygiana* included amphipods (27% of individuals; Figure 2-3e) and small numbers of sponge spicules (< 5 per stomach; 9% of individuals; Figure 2-3d). Sponge spicules were more common in *Ceramaster granularis* (Figure 2-4), with 38% of individuals containing < 5 spicules of several morphotypes, e.g. strongyle (Figure 2-4b and insert), acanthostyle (Figure 2-4c), curved oxea (Figure 2-4d) and tylostyle (Figure 2-4f). One individual had clumps containing hundreds of strongyle spicules (Figure 2-4a). *Ceramaster granularis* also contained benthic foraminiferans (8% of individuals; Figure 2-4f) and small numbers of clear and red 3-flanged coral sclerites (< 5 per stomach; 8% of individuals; Figure 2-4g). *Mediaster bairdi* contained only small amounts of sediment (< 12 grains per stomach; 86% of individuals) and benthic foraminiferans (29%). *Zoroaster fulgens* had the most varied stomach contents (Figure 2-5a-e), including copepods (40% of individuals), crustacean fragments (30%; appendages, heads, chitin pieces; mean length = 0.9 mm), mollusc shells (30%; 1 bivalve, width = 5.8 mm; 3 gastropods, mean width = 1.1 mm), benthic foraminiferans (20%), and diatoms (20%). *Novodinia americana* contained small crustaceans (Figure 2-5g) including copepods (80% of individuals) and various crustacean fragments (80%; mean length= 2.9 mm). Stomachs of *N. americana* contained 3-90 whole crustaceans and 3-46 fragments per individual. Several fish scales were also present (29% of individuals; mean width = 3 mm). *Leptychaster arcticus* contained benthic foraminiferans (20% of individuals, Figure 2-5b) and mollusc shells (20%; 1 bivalve, width = 4.6 mm; 1 gastropod, length=1.1 mm; Figure 2-5f). Sediment was found in 29–100% of individuals of each species; most individuals had only small amounts (< 12 grains), 10–45% of each species had moderate amounts (several hundred grains), and 20% of *L. arcticus* and 43% of *C. crispatus* had stomachs completely full of sediment such that material was extruding out of the oral opening.

2.4.2 *Stable isotopes*

Average $\delta^{13}C$ values for the seven asteroid species ranged from -12.8 to -18.0‰, while $\delta^{15}N$ values ranged from 11.6 to 17.0‰ (Table 2-1, Figure 2-6). Calculation of trophic levels revealed a lower trophic level for *C. crispatus, L. arcticus, N. americana,* and *Z. fulgens* (TL = 3.0 to 3.2), and a higher trophic level for the goniasterid asteroids *C. granularis, H. phrygiana,* and *M. bairdi* (TL = 4.1 to 4.4; Table 2-1). The $\delta^{13}C$ values did not significantly differ between the two groups ($F_{1,30} = 3.42$, $p = 0.074$), but the goniasterid asteroids had significantly higher $\delta^{15}N$ values (16.4 ± 0.9‰, n = 15) than individuals of the other four species (12.0 ± 0.9‰, n = 17) ($F_{1,30} = 195.28$, $p < 0.0001$). This 4.4‰ difference in $\delta^{15}N$ represents slightly more than one trophic level between the two groups, using an average 3.8‰ enrichment factor between trophic levels in polar and deep-sea studies (Iken et al. 2005). Most of our samples were collected in 2011, but a few were from previous years. We recognize that inter-annual differences in food type and quantity may influence isotope signatures. For *N. americana,* the $\delta^{13}C$ values from the 2005 sample were on average 3.5‰ higher than those from 2006, which may indicate annual differences in phytodetritus input. Seasonal effects are likely minimal, since all specimens used for stable isotope analysis were collected in November or December of each year. For *M. bairdi,* the 2006 sample had a δ^{13}C value slightly higher than those from 2011, but the 2010 sample fell within the 2011 range. Although there were some inter-annual differences seen in the δ^{13}C values, no differences were seen for the δ^{15}N values. The *N. americana* and *M. bairdi* samples from prior to 2011 had δ^{15}N values well within the δ^{15}N ranges of the lower and higher trophic levels, respectively; this indicates that while food quality might change among years, the trophic position of a species is fairly constant.

2.4.3 *Laboratory feeding trials*

In the experimental trials, *H. phrygiana* fed on most of the prey offered including deep-sea corals, sea anemone, and mussel tissue; *C. granularis* never fed on any of the sessile cnidarians but did feed on mussel tissue (Figure 2-7). Combining all experimental trials, the two species made contact with the potential prey in similar proportions (36% or 28/78 trials for *H. phrygiana* and 35%, 24/68, for *C. granularis*), whereas predation occurred in 18% of the trials (14/78) for *H. phrygiana* and only 3% (2/68) for *C. granularis*. Mussel tissue was most often fed on by both species, i.e. by 46% (6/13) of *H. phrygiana* and 22% (2/9) of *C. granularis*.

Hippasteria phrygiana fed on the corals *D. florida* (30% of trials, or 3/10)*, Pennatula* sp. (22%, 2/9)*, F. alabastrum* (14%, 2/14; Figures 2-7b, 2-8b)*,* and the sea anemone *H. nodosa* (8%, 1/13). *Hippasteria phrygiana* rejected prey it had touched in 8-38% of trials for each prey species, except those with *Pennatula* sp. where all contact resulted in predation. Predation by *H. phrygiana* occurred fastest with *F. alabastrum* (average 18 min after predator introduction) and slowest with *Pennatula* sp. (85 min). *Ceramaster granularis* fed on mussel tissue during the experimental trials but did not make contact with most of the other prey species (Figure 2-7). Although several individuals of both species made contact with the black coral *S. arcticus* and the skeleton of *F. alabastrum*, neither asteroid species attempted to eat those items.

In the informal trials, *H. phrygiana* fed on the pennatulacean *Anthoptilum grandiflorum* (7% of trials or 1/14, Figure 2-8a)*,* *C. granularis* fed on live sponges (*Halichondria panacea,* 66% of trials, 2/3; *Isodactya palmata,* 50%, 4/8; Figure 2-8c, d), and both species fed on sea urchin tissue often during routine feeding. *Hippasteria phrygiana* was never observed feeding on sponge tissue.

In most cases where the asteroids made physical contact with the prey but predation did not occur (“rejection”), the asteroids seemed unaffected. However, during some of the trials with *F. alabastrum* and *H. nodosa* both asteroid species appeared to react adversely when in contact with the tentacles of the prey: touching it with the tip of an arm, then retracting quickly and moving away. Overall, 50% of both *C. granularis* and *H. phrygiana* that made contact with *F. alabastrum* showed this behavior. Of those, all of the *C. granularis* and half of the *H. phrygiana* moved away from *F. alabastrum*; the remaining *H. phrygiana* fed on *F. alabastrum* despite the adverse reaction. Of *H. phrygiana* that touched *H. nodosa,* all initially retracted, 66% moved away, and 33% fed on it. A similar retraction behavior was observed in several individuals of *H. phrygiana* that rejected the black coral *S. arcticus:* the asteroid attempted to crawl on the coral but seemed to retract its tube feet quickly and position its body higher than normal, minimizing contact with the coral. But contrary to *F. alabastrum* and the anemone *H. nodosa*, *S. arcticus* was never preyed on. The prey species *H. nodosa* and *F. alabastrum* reacted in turn to the asteroids by retracting their tentacles and contracting their body. This response was observed in 100% of *H. nodosa* and 75% of *F. alabastrum* touched by *H. phrygiana* and 30% of *F. alabastrum* touched by *C. granularis,* regardless of whether predation ultimately occurred or not. The remaining prey species showed no obvious response to contact by the asteroids.

2.4.4 In situ *observations*

Four of our focal species, *C. granularis, H. phrygiana, M. bairdi,* and *N. americana,* were observed in the *in situ* images and video; the others were likely too small to be detected from the video or may have been buried in sediment. There was some evidence of predation on or utilization of corals and sponges as habitat by several species of asteroid (Figure 2-9). One *H. phrygiana* was observed feeding directly on a bamboo coral (Family Isididae) (Figure 2-9a), and another was seen in a likely feeding position on a coral *Acanthogorgia armata* (Figure 2-9b). *Hippasteria phrygiana* was observed in close proximity (0–300 cm) to sponges and corals in 71% and 77% of observations, respectively. No feeding events were observed for *C. granularis* or *M. bairdi,* although both species were often observed near sponges (37% and 57% of observations, respectively) and corals (81% and 77%). *Mediaster bairdi* was often seen on muddy substrates in dense sea-pen fields (predominately *Pennatula* spp. with individuals of *Halipteris finmarchica* and *Anthoptilum grandiflorum*; Figure 2-9c). *Novodinia americana* was often positioned on boulders or tall gorgonians, predominately

Keratoisis grayi (Figure 2-9d). Another asteroid species, *Tremaster mirabilis,* was observed feeding on the coral *A. armata* (Figure 2-9e); this is a novel observation as the feeding behaviors of *T. mirabilis* have not been previously reported.

2.5 **Discussion**

Based on stomach contents, stable isotopes, laboratory feeding trials, and *in situ* observations, we determined that the seven focal species studied here can be divided into a higher trophic-level grouping comprised of megafaunal predator/scavengers and a low trophic-level grouping that includes infaunal predators, mud ingesters, and suspension feeders.

Stomach contents were informative but were found in relatively small amounts in most of our asteroid specimens. Although regurgitation of stomach items has been reported for deep-sea organisms brought to the surface (e.g., fish; Feller et al. 1985), such occurrences were likely minimal for our specimens. Multiple stomachs contained large numbers of crustaceans (*N. americana*) or were engorged with sediment (*L. arcticus* and *C. crispatus*), indicating that stomach contents were often retained. The low numbers of items in the remaining species suggest rare feeding events, external feeding (extrusion of stomachs rather than ingestion of whole prey), or feeding on soft material that was not detected (Carey 1972; Fukuda and Naganuma 2001).

The number of experimental trials in which predation occurred was relatively low, even for the mussel tissue that both *C. granularis* and *H. phrygiana* regularly consumed during maintenance. We have no reason to believe the specimens were in poor physical condition, because they had been kept in the laboratory for over a year at the time of the trials and were regularly seen feeding (and breeding for some). It is possible that the still-water trials reduced the reaction times of the asteroids, which detect prey olfactorily, and that duration of monitoring was insufficient to detect all predatory behaviors. The data presented here therefore indicate that predation does occur on the given prey species, but predation rates may be underestimated compared to natural conditions.

2.5.1 *Megafaunal predator/scavengers*

Hippasteria phrygiana appears to be a generalist predator of sessile cnidarians including solitary corals, pennatulaceans (sea pens), gorgonians, soft corals, and sea anemones. In addition, *H. phrygiana* fed readily on freshly dead material in the laboratory, indicating that opportunistic feeding likely supplements predatory behaviors. The coral sclerites present in its stomach corroborate our laboratory and *in situ* observations of predation on corals. Some of the sclerites likely originated from pennatulaceans, although the exact species cannot be determined. Bilobed rods and red 3-flanged rods have been previously identified together from the pennatulacean *Pennatula* spp. in this region, and clear 3-flanged rods were found in the pennatulacean *Halipteris finmarchica* (English 2012). However, 3-flanged rod-type sclerites are found in many species of Pennatulacea (Dolan 2008), and a comprehensive study of the sclerites of Newfoundland species has not been completed. The spindle- and club-type sclerites found in the stomachs of *H. phrygiana* could be from many different corals; superficially, they resemble sclerites from several soft corals examined in our laboratory (*Drifa glomerata, Gersemia fruticosa,* and *Duva florida*; Z. Sun, unpublished data). The presence of amphipods in the stomachs of *H. phrygiana* indicates it may feed infaunally at times.

However, given that *H. phrygiana* has $\delta^{15}N$ values a full trophic level above the dedicated infaunal predators, small prey such as crustaceans likely make up a negligible portion of its diet.

Ceramaster granularis appears to feed primarily on sponges, supplemented by opportunistic scavenging on carrion. The siliceous spicules found in its stomach belong to demosponges, but the exact species are not known. That *C. granularis* fed on two species of subtidal sponge in the laboratory suggests its diet is not restricted to a specific deep-sea species, but that it is a generalist sponge-feeder. Unlike *H. phrygiana, C. granularis* did not display any corallivory in the laboratory. The retraction behavior by the asteroids observed upon contact with *F. alabastrum* may represent a nematocyst defense by the coral, which appeared to be successful in deterring predation by *C. granularis* but not by *H. phrygiana.* Nematocyst defenses by epibiotic sea anemones have been shown to reduce the feeding rate of asteroids, in turn influencing the survival of the sea anemone's host (Patton et al. 1991; Mercier and Hamel 2008). Although there may be underlying physiological differences (e.g. perception of nematocysts) between *C. granularis* and *H. phrygiana,* the differences in success of the *F. alabastrum* defense response could also be influenced by the relative size ratio of the prey and predators. *Ceramaster granularis* is a relatively small species with a radius of ~20 mm (Clark and Downey 1992), and were roughly the same size as the *F. alabastrum* used in this study. *Hippasteria phrygiana* are much larger than *C. granularis,* reaching a radius of 150 mm (Clark and Downey 1992); given that larger-bodied asteroids are generally able to exploit larger prey (e.g. Menge 1972; Van Veldhuizen and Phillips 1978), *H. phrygiana* may have a physical advantage over *C. granularis* for predation on similar-sized prey. While we did not observe *C.*

granularis feeding on cnidarians, the stomachs of members of this species did contain pennatulacean sclerites. It is possible that *C. granularis* feeds on some corals in nature, perhaps on smaller or less defensive species than those tested here, or that the observed sclerites were ingested during scavenging.

Based on the similarity of its isotopic signature to those of *C. granularis* and *H. phrygiana*, it is possible that *Mediaster bairdi* is also a predator of benthic megafauna, supplemented by scavenging. However, its specific diet remains unclear. Because no live individuals were available, the behavior of *M. bairdi* was not observed, and stomach-content analysis only revealed small amounts of sediment and benthic foraminiferans. The lack of informative stomach contents may indicate that *M. bairdi* ingests softer-bodied organisms, perhaps cnidarian species with few or no sclerites [e.g. the pennatulacean *Anthoptilum grandiflorum* (English 2012) or sea anemones] or that it relies on dead organic material. Given its high δ^{15}N value, it is unlikely that *M. bairdi* feeds only on detritus without also taking animal prey. *Mediaster bairdi* may be a generalist scavenger/predator, taking a range of mega- and macrofaunal prey that we were not able to detect.

2.5.1.1 Feeding strategies of the Goniasteridae

The feeding behaviors we observed in our high-trophic level species (*C. granularis, H. phrygiana,* and *M. bairdi*) are consistent with other reports of deep-sea asteroids in the family Goniasteridae, many of which are known to prey on corals (Mah et al. 2010). The diets of other *Hippasteria* and *Mediaster* species are fairly well known, particularly from the Northeast Pacific, while little is known about any *Ceramaster* species. *Hippasteria heathi* is a main predator of deepwater *Primnoa* coral in Alaska, sometimes causing extensive damage (Krieger and Wing 2002), and some populations of *H. spinosa* (= *H. phrygiana,* Foltz et al., 2013) and *M. aequalis* are specialists on shallow (< 50 m) populations of sea pens *Ptilosarcus gurneyi* in Puget Sound (Birkeland 1974). Records of goniasterids feeding on sponges are less common, but have been documented for *M. aequalis* and *M. elegans abyssi* in the Northeast Pacific (Mauzey et al. 1968; Carey 1972). Chu and Leys (2010) reported a *Ceramaster* sp. in close association with glass sponges in the Northeast Pacific, although feeding was not confirmed. In addition to predation, goniasterids display opportunistic behaviors: both *H. spinosa* (= *H. phrygiana*) and *M. aequalis* have been reported feeding on detritus, small invertebrates, and carrion (Mauzey et al. 1968; Birkeland 1974), and *M. ornatus* and *C. bowersi* have been observed scavenging on dead fish in Hawaii (Yeh and Drazen 2009). Based on stable isotope data, Carlier et al. (2009) consider the Mediterranean species *C. grenadensis* to be a secondary consumer that may feed on decayed organic material. Although dietary specialization has been seen in some *Hippasteria* species*,* we found no indication that *H. phrygiana* or any of the goniasterids is a specialist in Newfoundland and Labrador waters. Flexibility of feeding behaviors likely contributes to the success of the Goniasteridae, the most widely distributed and speciose family of asteroids spanning polar, temperate, and tropical waters (Mah and Blake 2012).

2.5.2 *Infaunal predators and mud ingesters*

Zoroaster fulgens appears to be an infaunal predator, mostly taking crustaceans and molluscs. Based on lipid biomarkers, Howell et al. (2003) suggested that *Z.*

longicauda (=*Z. fulgens*) is a specialist on benthic or benthopelagic copepods in the Northeast Atlantic. Although our specimens of *Z. fulgens* did contain benthic copepods, the presence of molluscs leads us to believe *Z. fulgens* is a generalist rather than a specialist infaunal predator. Moreover, the diatoms found in its stomachs may indicate a phytodetrital component to its diet, so opportunistic behaviors cannot be ruled out. Differences in diet between the northeast and northwest Atlantic may be an artefact as *Z. fulgens* likely contains several cryptic species (Howell et al. 2004).

Ctenodiscus crispatus and *L. arcticus* are mud ingesters/infaunal predators that swallow bulk sediment often containing meio- and macrofauna. Individuals of both species were observed completely engorged with mud, which may be due to the highly expandable stomachs and flexible aboral surface common in mud ingesters (Shick et al. 1981). No information exists on the diets of any *Leptychaster* species, but *C. crispatus* is thought to be a non-selective feeder that sometimes ingests infaunal organisms (Shick et al. 1981). Lipid analysis of *C. crispatus* from inshore Newfoundland (170–300 m depth) suggests a strong bacterial and phytodetrital component to its diet (Parrish et al. 2009). Sedimentary organic material (SOM) and bacteria in sediments are likely the most important resources for mud ingesters (Sokolova 2000; Howell et al. 2003), and their acquisition of metazoans may be accidental (Sokolova 2000). However, the mollusc shells present in *L. arcticus* had no tissue remaining; if the molluscs were alive when ingested, then digestion occurred whether or not they were an intended food item. The trophic level (TL $\simeq$ 3) and stomach contents (molluscs, diatoms, foraminiferans) of these two species are similar to those of the infaunal predator *Z. fulgens*, suggesting that metazoan material likely contributes significantly to the diets of these mud ingesters.

Zoroaster fulgens and *C. crispatus* had the highest (most enriched) carbon signatures of the low-trophic level species in this study. Enriched $\delta^{13}C$ signatures have previously been observed in some ophiuroid and asteroid species (Hobson et al. 2002; Tamelander et al. 2006), which may be indicative of differences in metabolism among species/taxonomic groups (Tamelander et al. 2006). Alternatively, preferential selection of enriched particles (e.g., diatoms) during feeding could explain the enriched $\delta^{13}C$ values often seen in benthic consumers (Nadon and Himmelman 2006). The stomachs of *C. crispatus* and *Z. fulgens* both contained diatoms, which may be an important dietary resource for *C. crispatus* during reproduction (Parrish et al. 2009). A phytodetrital component to the diets of these species might explain the observed signatures.

2.5.3 *Suspension feeders*

Novodinia americana is a suspension feeder that ingests benthopelagic crustaceans, mostly copepods. The suspension feeding posture typical of the family Brisingidae (Emson and Young 1994) was evident in the ROV footage, with *N. americana* often positioned on tall corals or boulders (Figure 2-9d, Chapter 3). Most brisingids are presumed to suspension feed (Downey 1986), but there is not much specific diet information available; several species feed on crustaceans (Emson and Young 1994; Sokolova 2000; Howell et al. 2003), but some likely rely on suspended detritus, phytodetritus, and associated bacteria (Howell et al. 2003). We found no evidence that *N. americana* feeds on detrital material, and the abundance of crustaceans in the stomachs of members of this species indicates a fully carnivorous diet. *Novodinia americana* sits at TL $\simeq$ 3, similar to the infaunal predators studied here, suggesting a shared diet of primary consumers; however, *N. americana* has a lower (more depleted) $\delta^{13}C$ signature. This depleted signature could be explained by a diet consisting of benthopelagic or pelagic organisms instead of epi- or infauna, because pelagic-sourced diets are often $\delta^{13}C$-depleted compared to benthic-sourced diets (Fry and Sherr 1984).

2.6 **Conclusions**

This is the first published report of the trophic ecology of deep-sea asteroids in the northwest Atlantic. The seven species studied here, which represent a small portion of the known deep-water asteroid diversity of Newfoundland and Labrador (Haedrich and Maunder, 1985; Chapter 3), provide a glimpse of the diversified roles played by asteroids in the deep sea; they inhabit several different trophic niches and likely fulfill a range of ecological roles. Overall, the trophic groupings and feeding behaviors assigned to each species here agree well with published reports for conspecifics and congenerics found in other deep-sea regions worldwide. Apart from adding knowledge about the diets and potential ecological roles of the cosmopolitan species *Hippasteria phrygiana* and *Ctenodiscus crispatus,* we provide the first dietary records to our knowledge for *Ceramaster granularis, Leptychaster arcticus, Mediaster bairdi, Novodinia americana,* and *Tremaster mirabilis.*

Suspension-feeding asteroids like *N. americana* exploit pelagic resources (e.g., zooplankton) that would otherwise only be available to benthic feeders once they became carrion. Deposit-feeding species can influence the settlement, survival, and distribution of infauna and epifauna by destabilizing sediments and ingesting and re-distributing large proportions of available labile carbon (Rhoads and Young 1970; Miller et al. 2000).

Infaunal predators, which also disturb surface sediments, are known to affect infaunal diversity and community structure (e.g., Ambrose 1993). While little is known about local abundances of *L. arcticus* and *Z. fulgens, C. crispatus* is known to occasionally occur at high densities worldwide [e.g., to ~4000 ind ha^{-1} in the Beaufort Sea (Rand and Logerwell 2010); to ~6000 ind ha^{-1} in Newfoundland (Chapter 3) and likely has a considerable impact on soft-bottomed communities. The ecological roles and community impacts of the predatory and scavenging asteroids are difficult to quantify at present. The generalist corallivore *Hippasteria phrygiana,* which is among the most abundant deep-sea asteroids in Newfoundland (Chapter 3), likely exerts a strong influence on local coral communities. Predation by *H. phrygiana* or other predatory asteroids could hinder recovery of corals in areas impacted by anthropogenic disturbance (i.e., trawl damage), especially as there is inadequate protection for cold-water corals in the region (Baker et al. 2012).

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2.8 Tables and Figures

Table 2-1. Feeding type based on stable isotope values and stomach contents for asteroids collected from the shelf and slope of Newfoundland and Labrador. Feeding types: P/S = predator/scavenger, MI = mud ingester, SF = suspension feeder, IP = infaunal predator. The size of the asteroids is the major radius *R,* the average length from the centre of the disc to the tip of each arm. For *N. americana,* the size is given as the radius of the oral disc and is only available for 4/5 of the specimens used. TL = trophic level.

Species	Proposed feeding type	Sample depths (m)	N for isotopes (size ± SD, mm)	δ^{15}N (‰ ± SD)	δ^{13}C (‰ ± SD)	TL	N stomachs dissected	Stomach contents (N asteroids with that item present)
Brisingida								
Brisingidae								
Novodinia americana	SF	438-1375	5 (19.2 ± 2.6)	12.2 ± 1.0	-18.0 ± 2.3	3.1	5	Copepods (4) Crustacean fragments (4) Sediment traces (2)
Forcipulatida								
Zoroasteridae								
Zoroaster fulgens	IP	258-1230	5 (57.2 ± 27.2)	11.6 ± 1.0	-12.9 ± 1.9	3.0	10	Sediment traces (10) Copepods (4) Crustacean fragments (3) Mollusc shells (3) Diatoms (2) Benthic foraminiferans (2)
Paxillosida								
Astropectinidae								
Leptychaster arcticus	MI/IP	335-658	4 (18.3 ± 3.0)	12.1 ± 0.7	-17.2 ± 0.8	3.1	10	Sediment (trace to full) (7) Benthic foraminiferans (2) Mollusc shells (2)

Ctenodiscidae								
Ctenodiscus crispatus	MI/IP	305-353	3 (20.3 ± 3.6)	12.4 ± 1.0	-14.3 ± 2.2	3.2	7	Sediment (trace to full) (7) Benthic foraminiferans (3) Diatoms (2) Sponge spicules (1) Nematode (1)
Valvatida								
Goniasteridae								
Ceramaster granularis	P/S	304-1210	5 (30.8 ± 8.5)	17.0 ± 0.6	-13.2 ± 0.6	4.4	13	Sediment traces (11) Sponge spicules (6) Coral sclerites (1) Benthic foraminiferans (1)
Hippasteria phrygiana	P/S	304-992	5 (59.3 ± 28.2)	15.8 ± 1.1	-15.1 ± 1.1	4.1	11	Sediment traces (10) Coral sclerites (7) Amphipods (3) Sponge spicules (1)
Mediaster bairdi	Unknown P/S?	462-1418	5 (45.6 ± 13.7)	16.5 ± 0.4	-14.2 ± 1.0	4.3	14	Sediment traces (12) Benthic foraminiferans (4)

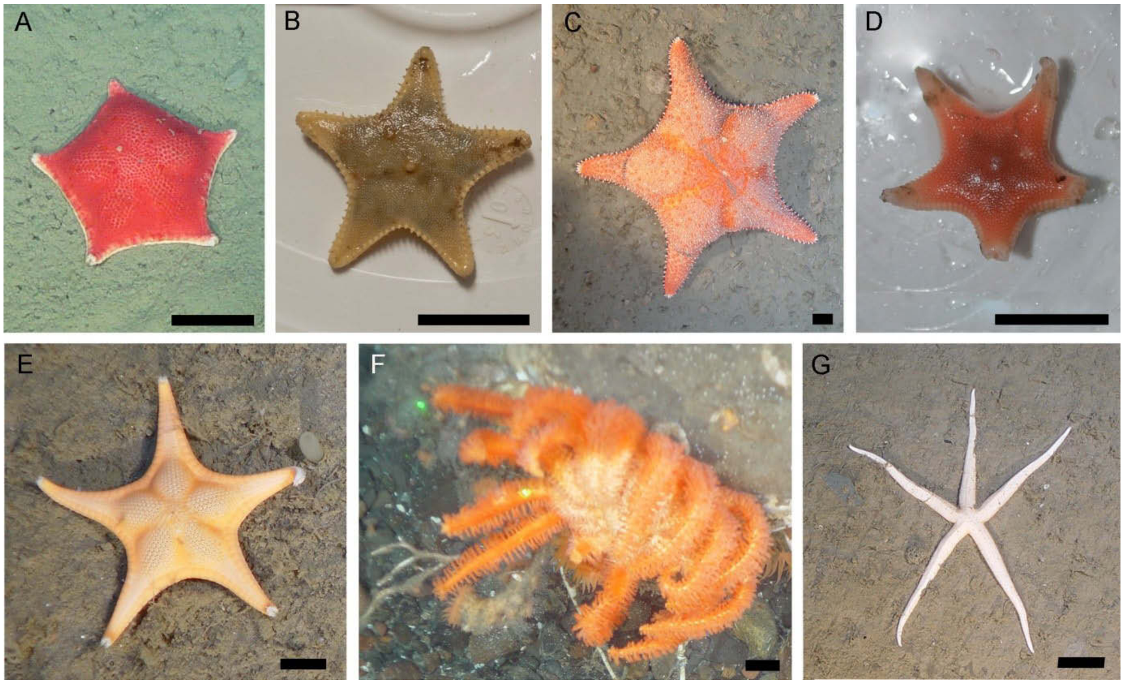

Figure 2-1. Focal asteroids studied. A) *Ceramaster granularis*, B) *Ctenodiscus crispatus*, C) *Hippasteria phrygiana*, D) *Leptychaster arcticus*, E) *Mediaster bairdi*, F) *Novodinia americana*, G) *Zoroaster fulgens*. Scale bars = 2 cm.

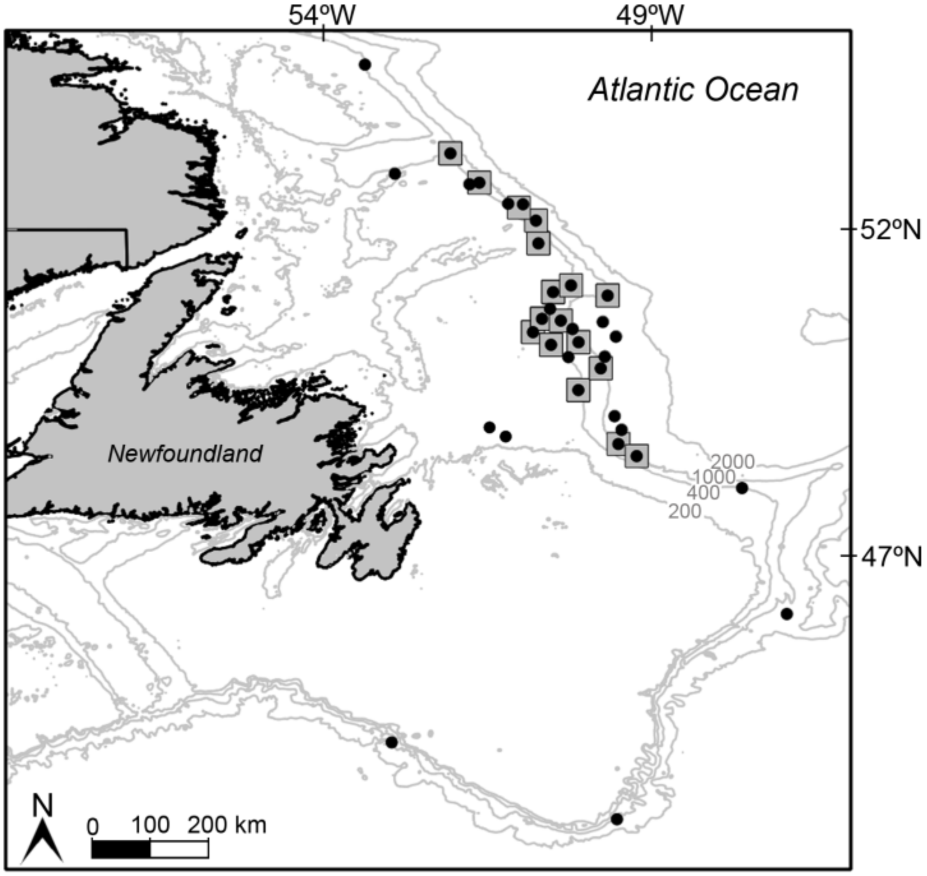

Figure 2-2. Geographic locations of asteroids collected along the coast of Newfoundland and Labrador (eastern Canada) for stable isotope analysis (grey squares) and stomach content analysis (black circles). Multiple specimens were used from most sites. Bathymetric contours (m) shown.

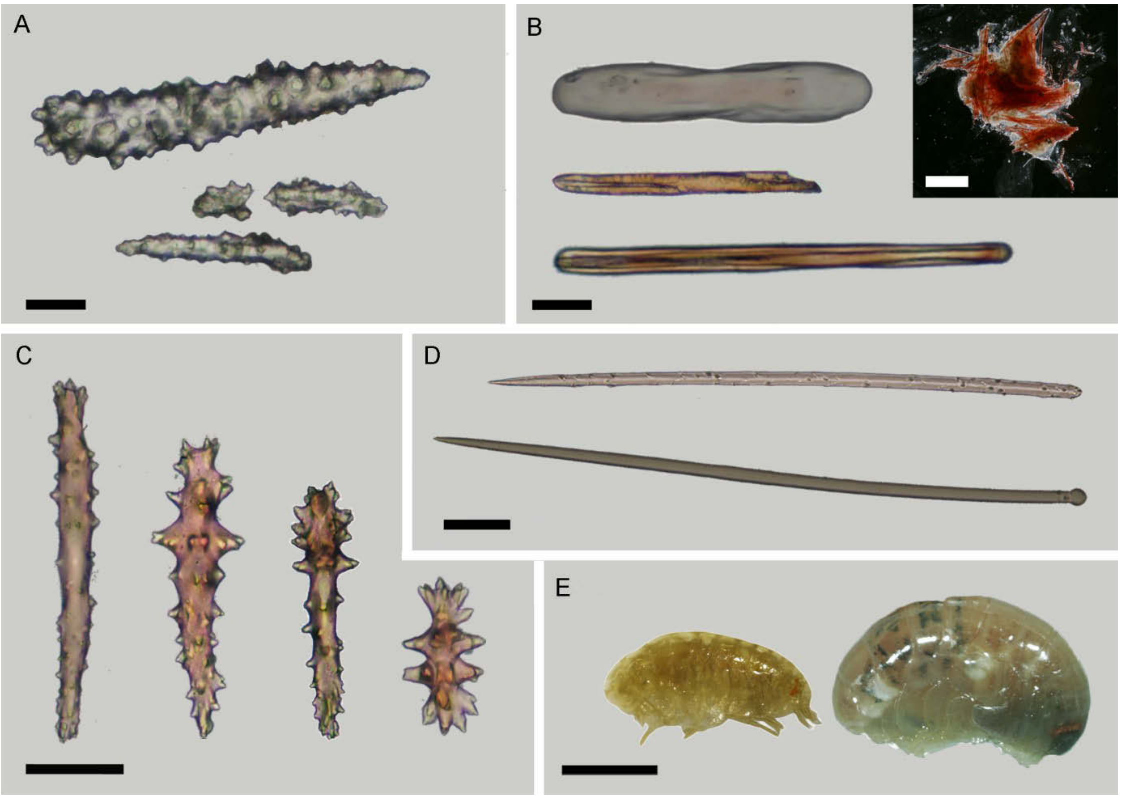

Figure 2-3. Stomach contents of *Hippasteria phrygiana*. A) Spindle-type coral sclerites, B) Pennatulacean-type sclerites including white-pink bilobed and red 3-flanged rods ranging in size from ~200 µm to > 1 mm; sclerites were found in a large mass in the stomach (inset), C) Red club-type sclerites, likely from a nephtheid coral, D) Sponge spicules (top = acanthostyle, bottom = tylostyle), E) Amphipods. Scale bars: A-D = 50 µm, B inset = 1 mm, E = 2 mm.

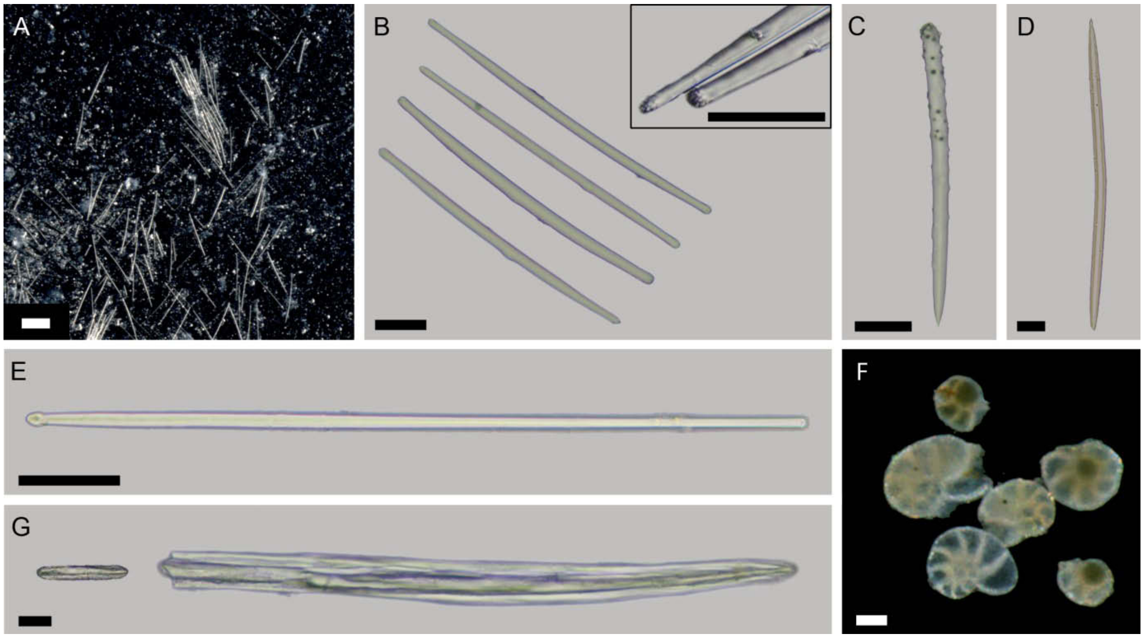

Figure 2-4. Stomach contents from *Ceramaster granularis.* A) Clump of sponge spicules, B) Strongyle spicules from A, with spiny heads (inset), C) Acanthostyle spicule, D) Curved oxea spicule, E) Tylostyle spicule, F) Benthic foraminiferans, G) Clear 3-flanged coral sclerites. Scale bars in A = 200 µm, B-G = 50 µm.

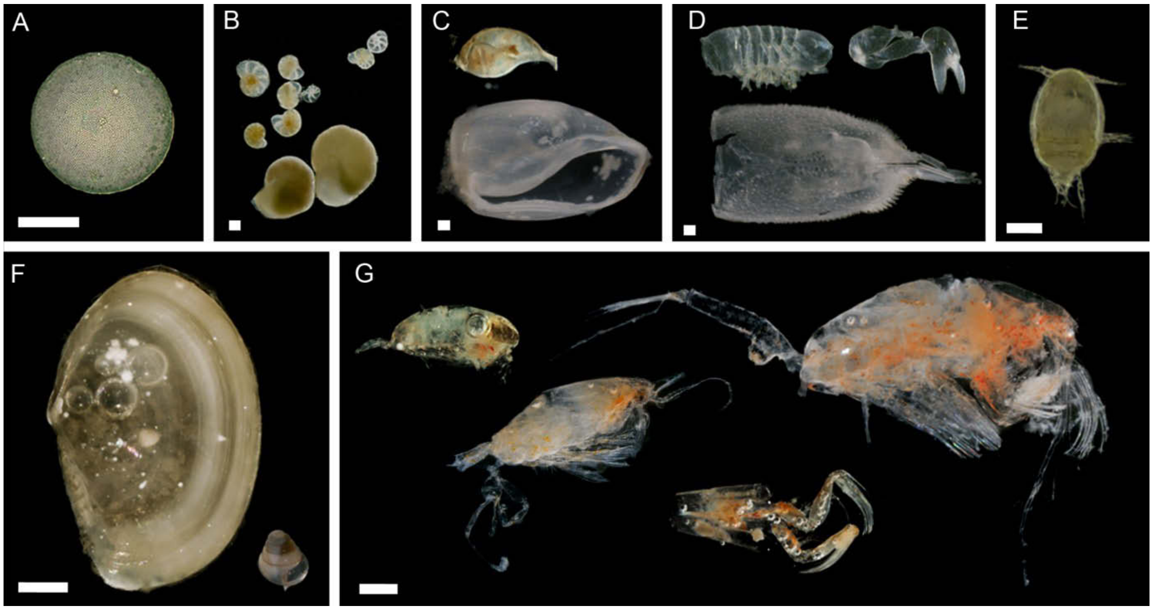

Figure 2-5. Stomach contents of deep-sea asteroids. A) Diatom and B) Benthic foraminiferans, both found in several species as per Table 2-1, C) Gastropod shells from *Z. fulgens*, D) Crustacean fragments from *Z. fulgens*, E) Typical copepod from *Z. fulgens*, F) Mollusc shells from *L. arcticus,* G) Representative copepods and fragments from *N. americana.* Scale bars in A-E = 100 µm, F-G = 1 mm.

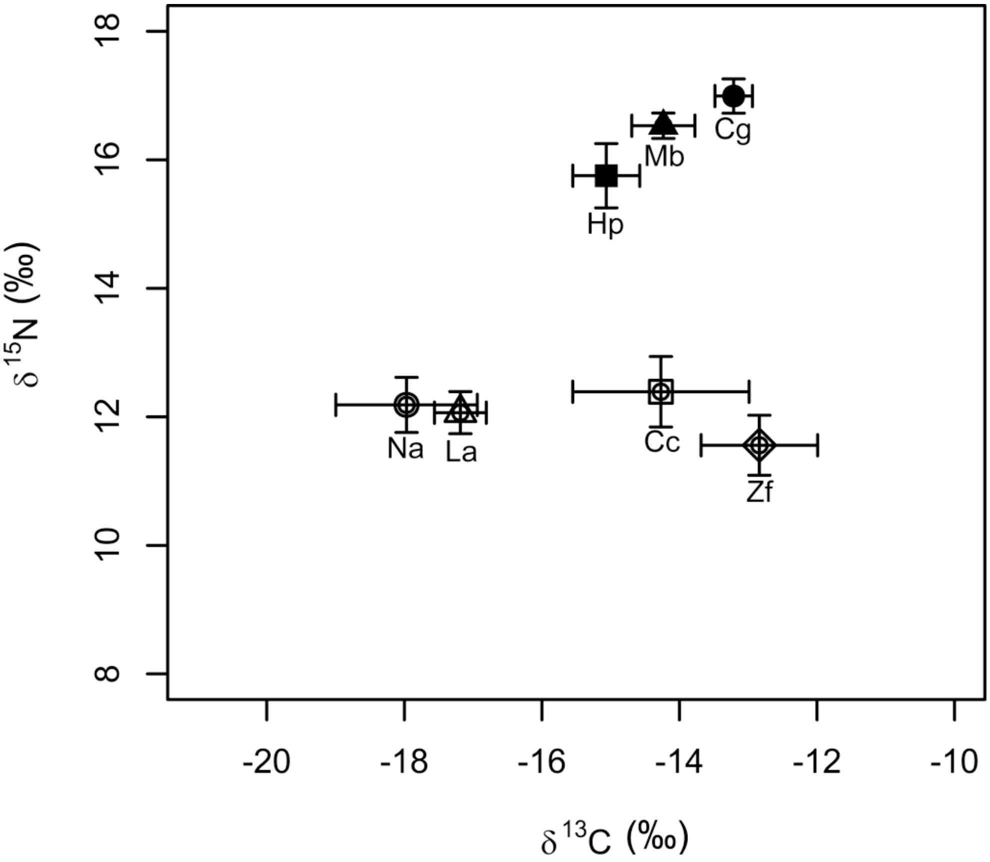

Figure 2-6. Stable isotope values (δ^{15}N and δ^{13}C) for seven species of deep-sea asteroid from the continental shelf and slope of Newfoundland (data are species mean ± standard error). Cc = *Ctenodiscus crispatus*, Cg = *Ceramaster granularis*, Hp = *Hippasteria phrygiana*, La = *Leptychaster arcticus*, Mb = *Mediaster bairdi*, Na = *Novodinia americana*, Zf = *Zoroaster fulgens*. N = 3-5 per species.

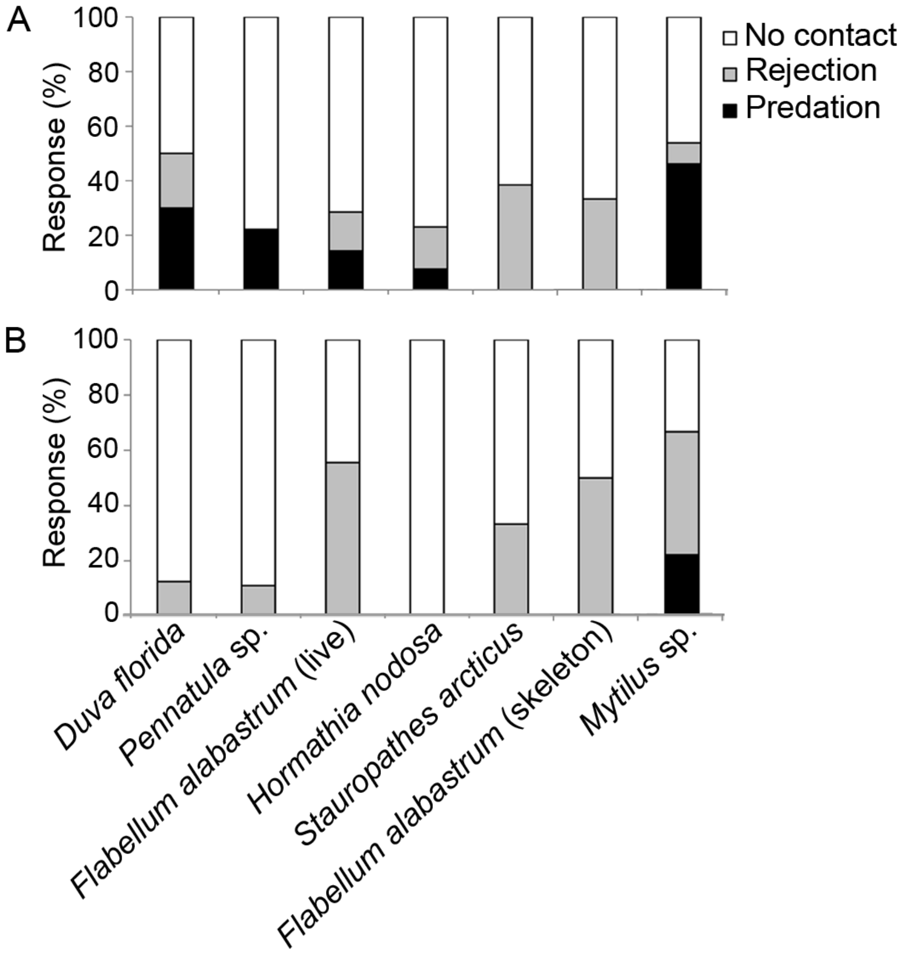

Figure 2-7. Feeding behaviors of A) *Hippasteria phrygiana*, and B) *Ceramaster granularis* during experimental trials. Data shown are proportion of responses scored in the trials (%): “no contact” (the asteroid never touching the prey), “rejection” (touching but no predation), or “predation” (feeding posture or extrusion of stomach observed). Total n = 146 trials (n = 6–14 individual *H. phrygiana* and 6–9 *C. granularis* per prey).

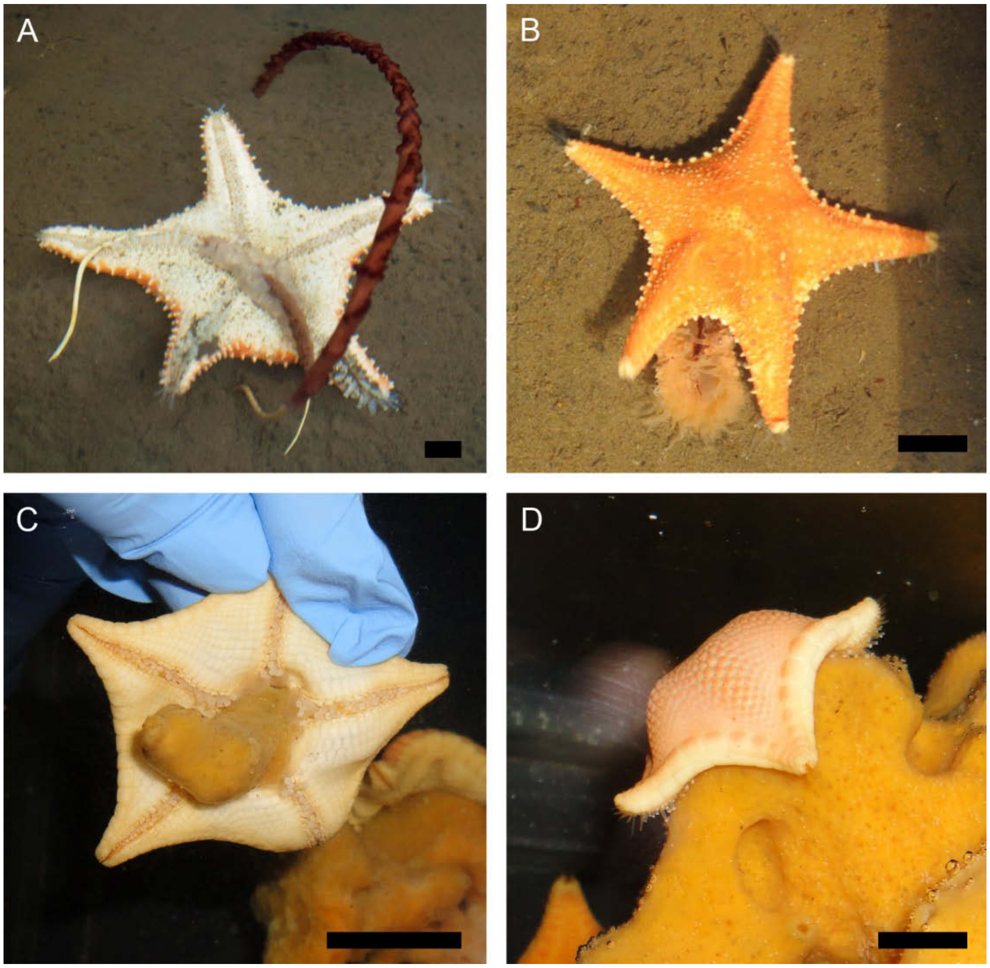

Figure 2-8. Examples of predation observed in laboratory conditions. A) *Hippasteria phrygiana* flipped over, showing stomach surrounding sea pen *Anthoptilum grandiflorum*, B) *H. phrygiana* preparing to feed on scleractinian coral *Flabellum alabastrum*, C) *Ceramaster granularis* with stomach everted around a sponge *Isodactya palmata*, D) characteristic "humped" feeding posture of *C. granularis* on sponge *I. palmata*. Scale bars = 2 cm.

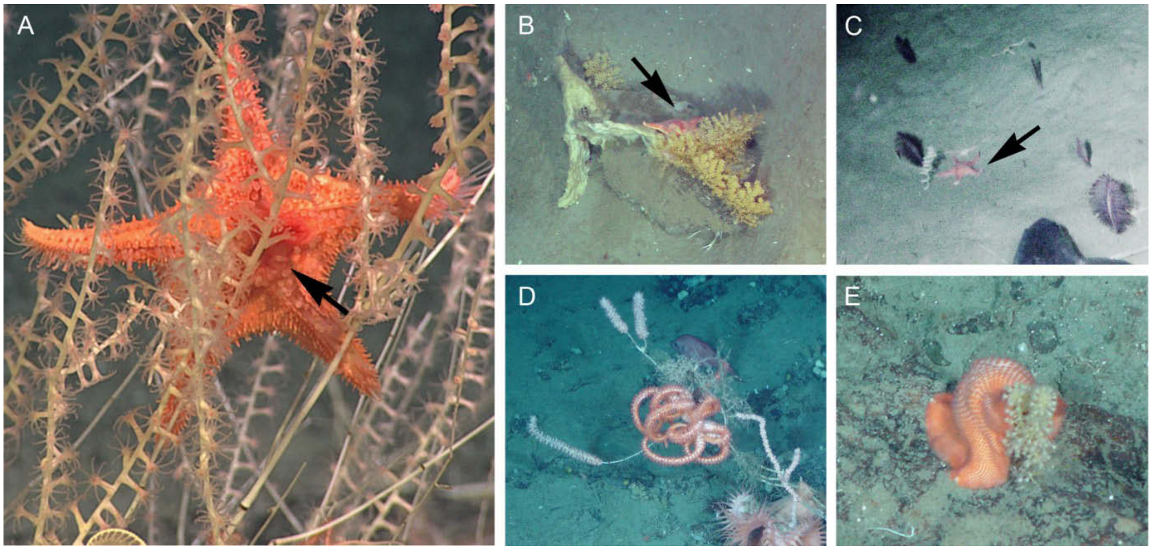

Figure 2-9. *In situ* images of deep-sea asteroids showing feeding and habitat associations with corals. A) *Hippasteria phrygiana* feeding on a bamboo coral (Family Isididae) at 2242 m; the asteroid's stomach can been seen everted around the coral's polyps (arrow), B) *H. phrygiana* (arrow) suspected to be feeding on a coral *Acanthogorgia armata* at 604 m, C) *Mediaster bairdi* (arrow) in a field of sea pens (mostly *Pennatula* spp.) at 1012 m, D) *Novodinia americana* in its characteristic feeding posture, sitting on a tall *Keratoisis grayi* at 543 m, E) *Tremaster mirabilis* feeding on a small coral *A. armata* at 572 m. Scale bars not available because tracking lasers on the ROV were off; refer to Figure 2-1 for typical sizes of asteroid species. All images courtesy ROPOS/DFO.

Chapter 3

Distribution, assemblages, and habitat use of Asteroidea from the continental shelf and slope of eastern Canada*

3.1 **Abstract**

Although continental shelf and slope environments typically exhibit high epifaunal biomass and have been subjected to increasing fishing pressure, ecological information on assemblages of non-commercial invertebrate species from subtidal and bathyal areas remains limited. Sea stars (Echinodermata: Asteroidea), which are known to influence communities through their feeding habits, have received less attention than structural taxa like corals and sponges. To better understand the ecological roles of asteroids on continental shelves, we investigated ~30 species and assessed their distributions and co-occurrence with other benthic invertebrates on the shelf and slope of eastern Canada. Using fisheries data and *in situ* video footage, we compiled a large data set covering ~600,000 km^2 that included over 350,000 individual asteroid records (37–2243 m depth). Multivariate analyses revealed geographically distinct asteroid assemblages, with maximal overall density at 400–500 m and highest diversity at 500–700 m. The most abundant and densely occurring species was *Ctenodiscus crispatus*. We found that asteroids associate with corals, sponges, bivalves, and other echinoderms, and that depth and substrate influence these assemblages. We identified species likely to affect coexisting organisms by their burrowing behavior that can disrupt epi- and infauna (*C. crispatus*) and through

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*A version of this chapter will be submitted to Marine Ecology with authors Katie S P Gale[1], Kent Gilkinson[2], Jean-François Hamel[3], Annie Mercier[1]

[1]Department of Ocean Sciences, Memorial University, St. John's, Newfoundland and Labrador, Canada A1C 5S7
[2]Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, St. John's, Newfoundland and Labrador, Canada, A1C 5X1
[3]Society for the Exploration and Valuing of the Environment, Portugal Cove-St. Philips, Newfoundland and Labrador, Canada A1M 2B7

predation on ecologically important corals (*Hippasteria phrygiana*). In addition to providing baseline distribution and ecological information for many bathyal asteroid species in the Northwest Atlantic, this work highlights the abundance and diversified roles of asteroids within continental shelf and slope ecosystems.

3.2 **Introduction**

For many subtidal and most deep-sea organisms, ecological information on feeding behaviors, species associations, and habitat use is poorly known. For numerous megafaunal taxa living below 200 m, even details of regional abundances and distributions are rare (Quijón and Snelgrove 2005; Soltwedel et al. 2009; Baker et al. 2012). Species lists, databases, and taxonomic descriptions generally document only geographic extent (or broad geographic region inhabited) and bathymetric minima and maxima. Although these descriptions can be useful for assessing regional biodiversity (e.g., Carr 2011), they do not consider areas of high abundance that correspond to geographic and depth optima (Howell et al. 2002). Identifying regions of high abundance, as well as ultimate geographic/bathymetric extent, is an important step in understanding biological, physical, and environmental conditions favorable for certain species. In addition, natural history information on habitat use, behaviors, species co-occurrences, and trophic interactions provide insight into the functional roles of species that influence higher-level ecosystem processes such as nutrient cycling and carbon sequestration, bioturbation and substrate modification, and habitat creation (Dayton 2003; Hewitt et al. 2008). Baseline distribution, abundance, and assemblage data is also important for tracking and responding to future range shifts, population declines, and species invasions that may result from changing ocean conditions, fishing and bycatch pressures, and other human activities (Ray 1996;

Buchsbaum and Powell 2008; Archambault et al. 2010). The development of effective marine conservation areas also depends on an understanding of local ecosystems (Ferrier and Drielsma 2010; Barrio Frojan et al. 2012).

Marine communities can be strongly influenced by the presence of predators (Dayton and Hessler 1972; Menge 1982) such as sea stars (Echinodermata: Asteroidea), which are among the most common mobile megafauna in benthic habitats (Gage and Tyler 1991). Shallow-water asteroids from polar, temperate, and tropical regions worldwide influence local biodiversity and community structure through their feeding behaviors (Paine 1966; Dayton et al. 1974; Menge 1982), and some evidence suggests that asteroids also play important ecological roles in deep-sea settings (Krieger and Wing 2002; Mah et al. 2010). Detailed distributions and habitat use have only been documented for a small number of shallow-water species in Atlantic Canada (Emerson 1973; Schneider et al. 1987; Himmelman and Dutil 1991). However, no studies have assessed small-scale geographic variability in presence or abundance, species associations, or habitats of deep-sea asteroids in the Northwest Atlantic, although trophic interactions for seven species were reported in Chapter 2 (Gale et al. 2013).

Newfoundland and Labrador, on the east coast of Canada, has an extensive continental shelf, covering an area of about 661,000 km^2 to the deepest shelf break (at ~ 400 m along the northern Newfoundland shelf), including the Grand Banks, which are of great ecological and economic importance. Known as one of the richest fishing grounds in the world, the area has been fished for hundreds of years; the introduction of trawlers in the mid-twentieth century marked the start of significant anthropogenic impact to benthic ecosystems (Hutchings and Myers 1995). The increased exploitation of shellfish (Sherwood and Rose 2005) and deep-sea fish (Haedrich et al. 2001; Devine et al. 2006), has raised concerns about potential impacts on non-target benthic organisms (Koslow et al. 2000; Barrio Frojan et al. 2012). Recent research has focused on cold-water corals and sponges, owing to their function as biogenic habitat (Wareham and Edinger 2007; Cogswell et al. 2009; Baillon et al. 2012; Baker et al. 2012; Kenchington et al. 2013). Other non-commercial invertebrate groups that may be indicative of vulnerable marine habitats, such as echinoderms (Barrio Frojan et al. 2012), have received less attention.

Almost 50 species of asteroid have been reported from shallow and deep waters off Newfoundland and the southern part of Labrador (Grainger 1964, 1966; Haedrich and Maunder 1985; Clark and Downey 1992; Mah et al. 2012). The NL shelf and slope share fauna with parts of the Arctic as well as the temperate northwest (NW) Atlantic biogeographic regions (Pocklington and Tremblay 1987; Spalding et al. 2007; Archambault et al. 2010). Arctic asteroid species have been recorded in southern Labrador (Grainger 1966), and many asteroid species found in Newfoundland also occur in Nova Scotia and the Gulf of Maine (Kindle and Whittaker 1917; Grainger 1966; Franz et al. 1981). The reported asteroid diversity indicates that, as in many cold-water regions (Mah and Blake 2012), asteroids have been quite successful in Atlantic Canada.

In this study, we use an extensive data set comprising over 350,000 individual asteroids collected from an area covering almost 600,000 km^2 of continental shelf and slope. Our goals were to assess the diversity of asteroid species present in Newfoundland and Labrador and determine the influence of environmental factors (depth, substrate) on their distributions and assemblages. Specifically, we investigated

1) bathymetric and geographic distributions, identifying areas of high abundance, 2) geographic patterns of asteroid assemblages, 3) habitat use (substrate type), and 4) interactions with co-occurring benthic invertebrates, such as corals.

3.3 **Methods**

3.3.1 *Multispecies surveys*

Asteroids and other benthic invertebrates were collected during multispecies research surveys conducted by Canada's Department of Fisheries and Oceans (DFO) using the vessels CCGS *Teleost*, CCGS *Templeman*, and CCGS *Needler* (Figure 3-1a). The surveys are primarily aimed at assessing commercial fish stocks, but since 2006 increased emphasis has been placed on identification of non-commercial invertebrate bycatch (Gilkinson 2013). The surveys occurred over most regions of the Newfoundland continental shelf, including the area bordering the Laurentian Channel, St. Pierre Bank, Grand Banks, and the northern Newfoundland shelf into Labrador to 57.5ºN (i.e., NAFO regions 2HJ and 3KLNOP) (Figure 3-1). Sampling was conducted using a Campelen 1800 shrimp trawl with rockhopper footgear. The area swept by each tow was calculated as the distance covered (given in nautical miles) converted to km (× 1.852) times the width of the net (16.9 m), multiplied by 100 for an area covered in hectares (ha). Average tow duration was ~16 minutes at a speed of ~3 knots, covering an average of 0.81 nautical miles (1.5 km) and an average area of 2.53 ha (0.025 km^2). Although ha is not a standard unit, it has been used to describe the abundances of megafauna that occur at relatively low densities (e.g., Howell et al. 2002; Jones et al. 2007). A combined total of 10,855 ha were surveyed from 2008 to 2011. Of the 4286 tows completed, 1899 were performed in fall (Sept–Dec) and covered the Grand Banks to Labrador; the remaining 2387 took place in spring

(April–June) and covered the Grand Banks and south coast to the Laurentian Channel. Sampling effort was not evenly distributed over the survey range: half of the tows (2150) were completed between 37 and 200 m, 37% (1584) between 201 and 500 m, and the remaining 13% (552) between 501 and 1480 m.

All invertebrates were identified, counted and weighed aboard the ship by trained DFO technicians. Catch data (count and biomass of each species) for each trawl tow was recorded, along with date and time, geographic location (start and end point of tow), tow distance and depth. All of the following analyses were carried out using both the count and biomass data; because the results were very similar, we used count data throughout. Asteroid records were classified into 15 taxa for analysis: *Asterias rubens*, *Astropecten americanus, Ceramaster granularis, Crossaster papposus, Ctenodiscus crispatus, Diplopteraster multiples, Henricia* spp. (mostly *H. sanguinolenta*), *Hippasteria phrygiana, Leptasterias* spp. (mostly *L. polaris*), *Porania pulvillus, Pseudarchaster parelii, Psilaster andromeda, Pteraster* spp., *Solaster* spp. (mostly *S. endeca*), and *Urasterias lincki*. A 16th grouping called “other Asteroidea” included unidentified asteroids, specimens identified at the level of family or order, and rare species (present in < 10 trawls; i.e., *Pedicellaster typicus*, *Poraniomorpha* spp., *Tremaster mirabilis,* and *Novodinia americana*). Additional species including *Leptychaster arcticus*, *Mediaster bairdi, Myxaster sol*, and Z*oroaster fulgens* were present in the DFO samples, but were not specifically recorded in the database because collection codes were not available for them. Therefore a full-scale analysis of the distribution of these species was not possible, but estimates of depth distributions were determined from specimens collected by the authors during the surveys since 2005.

3.3.2 *Assessment of geographic patterns*

To assess potential geographic patterns of asteroids, the 4286 trawl tows were binned into 1222 geographic “blocks” (0.25º × 0.25º) by rounding the latitude and longitude of each tow to the nearest 0.25º. Each block included 1–22 trawl tows. Catch per unit effort (CPUE) for each asteroid taxon in each block was calculated as the number of individuals collected divided by the total area covered by all trawl tows in that block (ind ha^{-1}). Overall, 1046 blocks had asteroids present and were used to analyze asteroid assemblage patterns. After applying a Hellinger transformation to the CPUE data to make it appropriate for Euclidean-based routines (Legendre and Gallagher 2001), we conducted a cluster analysis using Euclidean distance with average grouping. We excluded “other Asteroidea” from this analysis because the group contained many species and would confound calculations of ecologically meaningful species groups. By examining the resulting dendrogram for natural breaks, three main clusters were identified and overlain on a map of the study area. Using the ‘vegan’ R package, an analysis of similarity (ANOSIM) was used to assess statistical differences of asteroid assemblages among clusters and a similarity percentage (SIMPER) analysis completed to determine the species that strongly contribute to those differences. Dominant species were also assessed using rank-abundance curves for each cluster and indicator species were identified using the *indval* function in the ‘labdsv’ R package.

To determine depth distributions and regions of highest density (i.e., depth optima) of each species, CPUE was calculated for each taxon within 100-m depth bands (number of individuals collected in all trawl tows within each depth band, divided by the total area covered by all tows in that band, ind ha^{-1}). We could not compare temperature and trawl-caught assemblage relationships because water temperature varied throughout the survey region, and different geographic areas were surveyed at different times of the year.

Species richness and diversity indices (Shannon-Weiner H’ and Pielou's evenness J’) were calculated for each block, cluster, and 100-m depth band, and were compared using ANOVA and post-hoc Tukey-Kramer tests where appropriate. All analyses were carried out in R and visualized in ArcMap 10.1.

3.3.3 *ROV surveys*

To assess asteroid habitat preference and fine-scale species co-occurrences (within ~3 m), we analyzed video surveys conducted with the remotely operated vehicle (ROV) ROPOS (Remotely Operated Platform for Ocean Science). In 2007 ROPOS completed a series of dives on the southern continental slope of Newfoundland, east of the Laurentian Channel (details in Baker et al. 2012). Three canyons were surveyed: Halibut Channel, Haddock Channel, and DesBarres Canyon. Seven dives covered depths of 354–2243 m and encompassed ~90 hours of bottom time (Figure 3-1b). Continuously recorded video comprised survey transects, supplemented with opportunistic still images. During the dives, the date, time, and positional data (latitude, longitude, and depth) of the ROV were recorded every second and overlain onto the video of the dive.

We scored occurrence of all asteroids in the videos along with positional data, the substrate the asteroid occupied, as well the percent cover of all substrates visible in the frame. Substrate types were assigned as per Baker et al. (2012): mud/sand, gravel (~ 0.2–5 cm), cobble (5–25 cm), boulder (> 25 cm), and outcrop (vertical structures of hard sediment and rock). Within all frames in which asteroids were observed, we also recorded the presence of other megafauna (e.g., corals and other anthozoans, echinoderms, sponges). Some sections of the video were not conducive to identifying asteroids to species, such as when the ROV was too high above the seabed or when individuals were not in the centre of the frame. In particular, *Hippasteria phrygiana* and *Mediaster bairdi* could not always be distinguished with confidence and questionable individuals were grouped together as "*Mediaster/Hippasteria*". Similarly, in some cases Brisingida species 1 and 2 (likely *Freyella elegans* and *Brisinga costata,* respectively) could not be distinguished in the videos and were grouped as "unidentified Brisingida".

3.3.4 *Analysis of species assemblages*

Assemblages comprising asteroids and other invertebrates were assessed from the trawl data. In addition to the 15 asteroid taxa, the analysis included 32 taxa of benthic megafauna (Table 3-1). Using presence/absence data of asteroids and invertebrates within the 0.25° blocks (n = 1221), we used nMDS with Jaccard distance to visualize associations. To determine the influence of depth on the assemblages, a redundancy analysis (RDA) was carried using Hellinger-transformed presence/absence data of all taxa using depth as an explanatory factor. The depth gradient was visualized on the nMDS plot using *envfit* in the 'vegan' package.

A similar analysis was carried out for the ROV data set with 31 invertebrate and 10 asteroid taxa; some asteroid taxa were excluded because of small sample sizes (< 6 observations: 6-armed species, *Pteraster* spp., and *Diplopteraster multiples*) or to avoid confounding effects of taxa that included potentially ecologically different species (unidentified Brisingida and *Mediaster/Hippasteria*). Using presence/absence data of asteroids and invertebrates within a frame of video that included an asteroid (n

= 620 frames), we used nMDS with Jaccard distance to visualize associations. To determine the influence of depth and substrate on the assemblages, RDA was carried using Hellinger-transformed presence/absence data of all taxa using depth and percent cover of substrates (mud, outcrop, gravel, and boulder) as explanatory factors. Because percent cobble was co-linear (redundant, highly correlated) with boulder, we excluded the cobble data from the analysis. The depth and substrate gradients were visualized using *envfit.* Significance of the canonical axes and explanatory factors was determined using a permutation test (*anova.cca* in package 'vegan'). Because this analysis includes only video frames containing an asteroid, it only considers species that co-occur with asteroids and is therefore not a comprehensive assemblage analysis. All analyses were completed in R.

3.4 **Results**

3.4.1 *Asteroid diversity*

Overall, we recorded 29 asteroid species from the trawl surveys and ROV videos. Abundance (number of individuals) and biomass were determined from 3102 (72%) of 4286 trawl tows from 2008 to 2011. A total of 351,974 individual asteroids belonging to 19 taxa were recorded (Table 3-2). In addition, we sampled a limited number of *Leptychaster arcticus* (20 individuals from 10 tows), *Mediaster bairdi* (62 from 28 tows)*, Myxaster sol* (6 from 5 tows), and Z*oroaster fulgens* (24 from 15 tows), allowing estimates of depth distributions for these species (Table 3-2)

The species richness (number of species) in the 0.25° blocks ranged from 1 to 10, Shannon-Weiner H' ranged from 0 to 1.96, and Pielou's J' ranged from 0 to 1. Blocks with high diversity occurred throughout the study area, mainly along the shelf break but also in patches on the Grand Banks, southern Newfoundland coast, and on the Labrador shelf (Figure 3-2). When depth was considered as a continuous variable (i.e., regression analysis), there was no significant relationship between any diversity index and depth (richness: $p = 0.7352$, $F_{(1,1045)} = 0.115$; H': $p = 0.691$, $F_{(1,1045)} = 0.691$; J': $p = 0.6116$, $F_{(1,821)} = 0.2581$). However, all indices differed significantly among 100-m depth bins (richness: $p < 0.001$, $F_{(1,1032)} = 5.391$; H': $p < 0.001$, $F_{(14,1032)} = 3.976$; J': $p < 0.001$, $F_{(14,1032)} = 3.343$). Species richness was highest between 400 and 700 m and H' was highest between 500 and 700 m; J' was more variable (Figure 3-3).

Thirteen species of asteroid were recorded from the ROV video, as well as two grouped taxa ("unidentified Brisingida" and "*Mediaster/Hippasteria*"). Seven of these species were also recorded from the trawl tows (Table 3-2). Of the six species observed on video but not recorded in the trawl surveys, four species (Brisingida species 1 and 2, *Plutonaster agassizi*, and the 6-armed species) were mostly found below the trawl survey depths (i.e., > 1480 m). One species (*Solaster earlli)* was present within the trawl survey range but had no individual collection code, so was probably recorded as *Solaster* sp. Similarly, we observed a *Pteraster* sp. that was distinct from those collected by trawls.

Overall, the most abundant and densely occurring species from the trawl tows were *Ctenodiscus crispatus* (289,729 individuals; 82% of total catch; maximum density 190 ind ha^{-1}), *Astropecten americanus* (13,928; 4%; 11.7 ind ha^{-1}), *Psilaster andromeda* (12,923; 4%; 9.4 ind ha^{-1}), *Leptasterias* spp. (8043; 3%; 2.2 ind ha^{-1}), *Crossaster papposus* (7891; 2%; 1.3 ind ha^{-1}), and *Henricia* spp. (7318; 2%; 3.2 ind ha^{-1}) (Table 3-1). The remaining taxa (apart from those in "other Asteroidea") occurred at densities below 1 ind ha^{-1}. Over the whole study area and considering all species, maximum asteroid density was recorded at 400–500 m with 213 ind ha^{-1}.

These abundances and densities are likely underestimates, especially for small or burrowing species, because trawls catch a only small proportion (< 1%) of available epifauna (Prena et al. 1999); although catch rates of large-bodied, non-burrowing asteroids have been reported as high as ~45% (Reiss et al. 2006).

We assessed the geographic extent of each asteroid species by determining their presence or absence within each of the 0.25° sampling blocks. *Henricia* spp., *Ctenodiscus crispatus*, *Crossaster papposus, Leptasterias* spp., and *Hippasteria phrygiana* were found in 360–510 of 1222 blocks, and comprised the most geographically widespread taxa (Figure 3-4). *Solaster* spp., *Asterias rubens*, *Porania pulvillus*, *Ceramaster granularis, Astropecten americanus*, and *Psilaster andromeda* were moderately widespread, each occupying between 102 and 227 blocks. *Pteraster* spp., *Diplopteraster multiples*, *Pseudarchaster parelii*, and *Urasterias lincki* were localized taxa found in only 14 to 31 blocks. *Poraniomorpha* spp., *Tremaster mirabilis, Novodinia americana,* and *Pedicellaster typicus,* which were rare taxa not included in the multivariate analysis, occurred in 1 to 9 blocks each.

3.4.2 *Bathymetric patterns*

Most of the asteroid taxa spanned wide depth ranges within the study region; 74% (17/23 species recorded from the trawl surveys) spanned depth ranges greater than 1000 m, and 96% (22/23) spanned depth ranges greater than 500 m (Table 3-2, Figure 3-5). One species, *Pedicellaster typicus*, was only recorded in one tow, precluding any depth range estimate. In general, there was no relationship between geographic coverage (number of blocks occupied by a taxon) and width of depth range determined from trawl tows; localized taxa depth ranges varied between 1188 and 1358 m, similar to widespread species that occupied depth ranges between 925 and 1405 m. Narrower ranges (504 to 1100 m) were evident in a few rare species. Most taxa were not evenly distributed throughout their depth distribution, but occurred at higher densities at certain depths (i.e., depth optima). The highest densities of *Asterias rubens, Crossaster papposus, Leptasterias* spp., and *Solaster* spp., for example, occurred at 0–100 m but these species were also present deeper than 900 m (Table 3-2, Figure 3-5). Fifteen asteroid species were recorded by trawl at subtidal depths (< 200 m), all of which also occurred > 200 m. Fourteen species were restricted to depths > 200 m, including those uncommon in the trawl records (*Leptychaster arcticus, Mediaster bairdi, Myxaster sol, Novodinia americana*, *Pedicellaster typicus, Tremaster mirabilis*, *Urasterias lincki,* and *Zoroaster fulgens*) and several from the ROV surveys (*Plutonaster agassizi*, *Pteraster* sp., *Solaster earlli*, 6-armed species, and Brisingida species 1 and 2).

For species observed in both types of survey, the depth distributions calculated from the ROV sightings generally fell within those determined from the trawl tows, although the ROV ranges were usually narrower (Table 3-2, Figure 3-6). The only exception was *Diplopteraster multiples,* which was sampled down to 1274 m by trawl and to 1822 m by ROV.

3.4.3 *Geographic patterns*

Cluster analysis revealed three distinct asteroid assemblages across the study region (Figure 3-7) that delineated fairly spatially coherent geographic regions (Figure 3-8). The species assemblages in the clusters differed statistically at $p < 0.001$ (ANOSIM) as did the average depth among the regions (NSS > LCNS > GB; $p < 0.001$). The Grand Banks region (mean depth 125 m) covers almost all of the Grand Banks and some shallow parts of the Labrador shelf. The northeast shelf/slope region

(NSS, mean depth 383 m) covers most of the northern Newfoundland shelf, stretching down towards the Flemish Cap, with patches on the southeast Newfoundland coast and the Labrador shelf. The Laurentian Channel/northwest shelf region (LCNS, mean depth 298 m) covers the Laurentian Channel, a strip of the southwest Grand Banks, and the eastern/central part of the northern Newfoundland shelf, with small patches on the Grand Banks and Labrador shelf. Of the initial 1046 blocks used for the cluster analysis, only 81 (< 8%) did not group with the three main clusters and were not considered further for analyses.

The SIMPER and *indval* analyses identified species that characterized each region, based on the density of each species in each block (CPUE) as well as the number of blocks in which each species occurred (Table 3-3). Rank-abundance curves (Figure 3-9) show that one or a few species comprise the majority of individuals in each region. High densities of *Leptasterias* spp. (mean = 1.8 ind ha^{-1}) and *Crossaster papposus* (1.6 ind ha^{-1}) and moderate numbers of *Henricia* spp., *Asterias rubens,* and *Solaster* spp. (< 0.4 ind ha^{-1} each) were present in the Grand Banks, the shallowest of all our sample regions. The *indval* analysis determined that *Leptasterias* spp., *C. papposus*, and *A. rubens* were indicator species for the Grand Banks ($p < 0.015$ for all). *Henricia* spp. characterized the NSS region (mean = 2.3 ind ha^{-1}, *indval* indicator species $p = 0.001$), along with *Hippasteria phrygiana, Ctenodiscus crispatus, Ceramaster granularis,* and *Porania pulvillus* (mean < 0.5 ind ha^{-1} each). The LCNS region was defined by high densities of *Ctenodiscus crispatus* (mean = 116.5 ind ha^{-1}, *indval* indicator species $p = 0.001$), with smaller numbers of *Hippasteria phrygiana* and *Henricia* spp. (< 0.4 ind ha^{-1} each). Most species occurred in all three regions except for *Urasterias lincki,* which was restricted to LCNS.

Diversity and evenness of asteroid taxa, but not richness, differed among regions (H’: $F_{(2,963)} = 40.925$, $p < 0.001$; J’:$F_{(2,963)} = 60.02$, $p < 0.001$; richness: $F_{(2,963)}= 2.5364$, $p = 0.080$; Table 3-3). Pairwise Tukey-Kramer post-hoc tests revealed significant differences among clusters for both H’ and J’ (GB > NSS > LCNS; $p < 0.001$).

3.4.4 *Substrate use by epibenthic species*

Most of the area covered during the ROV survey (> 350 m) had a mud/sand substrate; gravel, cobble and boulders were relatively common to ~800 m, and outcrops were rare, as described by Baker et al. (2012). Asteroids occurred mostly on mud and sand substrates (Figure 3-10). *Plutonaster agassizi* and Brisingida species 2 occurred only on mud/sand, whereas Brisingida species 1 was found either on mud/sand or outcrops. *Ceramaster granularis, Mediaster bairdi,* and *Solaster earlli* occurred mostly on mud/sand but sometimes on coarser substrates, and *Hippasteria phrygiana* and *Henricia* spp. were found roughly equally on all substrate types except outcrops. *Tremaster mirabilis* mostly occupied cobble and boulders, and never mud/sand. The brisingid *Novodinia americana* was always found on or near biogenic structures (the coral *Acanthogorgia armata*).

3.4.5 *Asteroid-megafauna assemblages*

RDA analysis determined the relationship between invertebrate assemblages from the trawl records and depth. Depth explained a total of 5.6% of the variation in assemblages of all invertebrates including asteroids. When only asteroids were considered, depth explained 6.7% of assemblage variation. The nMDS plot (Figure 3-11) shows associations among species from the trawl records. The deepest assemblages ($\gtrsim$ 800 m) included the asteroids *Pseudarchaster parelii*, *Psilaster* *andromeda*, *Astropecten americanus*, and *Urasterias lincki,* along with decapods (including *Lithodes* spp.), corals (pennatulaceans, *Flabellum* spp*., Anthomastus* spp*., Acanthogorgia armata, Acanella arbuscula*) and spatangoid echinoids. The shallowest grouping (< 200 m) included the asteroids *Leptasterias* spp., *Crossaster papposus*, *Asterias rubens*, and *Solaster* spp., along with bivalves *Chlamys islandica*, sea urchins *Strongylocentrotus* spp. (see note on Table 3-1), Clypasteroidea (sand dollars), Paguridae (hermit crabs), and crabs *Hyas* spp. At intermediate depths (~300–400 m), the asteroids *Henricia* spp. and *Ctenodiscus crispatus* were associated with nephtheid corals, sea anemones, brachiopods, and sponges. Between about 400 and 800 m the asteroids *Porania pulvillus*, *Hippasteria phrygiana*, *Diplopteraster multiples*, *Ceramaster granularis*, and *Pteraster* spp. did not show strong associations with other invertebrates in the analysis.

RDA analysis to relate invertebrate assemblages containing asteroids observed by ROV with depth and substrate type showed that depth and relative substrate cover explained 23.1% of the variation in assemblages (Table 3-4). Depth explained about half of the total variance; of the substrate factors, mud/sand explained 26% of the variance, outcrop and gravel explained 12–13% each, and boulder/cobble explained only 1%. Of all the factors, only the latter was not statistically significant (*anova.cca* permutation test, 999 iterations, p = 0.086).

The nMDS plot (Figure 3-12) shows associations among species from the ROV observations. The deepest (≳ 1000 m) asteroids, i.e., Brisingida species 1 and 2, were associated with the pennatulacean corals *Protoptilum carpenteri* and *Umbellula* sp., the gorgonian coral *Chrysogorgia agassizii*, the echinoid *Phormosoma placenta,* an unidentified echinoid species, stalked crinoids, a holothuroid, and burrowing sea anemones *Cerianthus* sp. *Plutonaster agassizi* separated from the deep group because of co-occurrence with a single large holothuroid. Most deep species associated with mud/sand substrates except Brisingida species 1*,* which, along with the shallower coral species *Desmophyllum dianthus,* associated mostly with outcrops. Gravel, when present, averaged about 12% cover and was usually mixed with mud/sand. Mud/sand and gravel-associated species included *Mediaster bairdi,* pennatulacean corals (*Pennatula* spp., *Halipteris finmarchica*, and *Anthoptilum grandiflorum*), ball-type sponges, and the bamboo coral *Acanella arbuscula*. Boulder and cobble-associated species (sometimes with small amounts of gravel) included the asteroids *Solaster* spp., *Henricia* spp., *Hippasteria phrygiana* and *Tremaster mirabilis*, the corals *Keratoisis grayi* and *Anthomastus* spp., nephtheid corals, and some sea anemones and sponges. *Novodinia americana* was associated with both boulders and outcrops, as well as with the boulder-associated fauna.

3.5 **Discussion**

This multivariate analysis of by-catch data and ROV video surveys provides baseline information for many dominant and less common asteroids in the northwest (NW) Atlantic and highlights trends in maximal overall density (400–500 m) and diversity (500–700 m) of asteroids, as well as geographically coherent assemblages. We identified several species likely to strongly influence their communities as they are associated with ecologically important corals and sponges, as well as bioturbating species*,* which occur in very high densities in soft-bottomed habitats. These data expand our understanding of benthic communities over vast continental shelf and slope habitats that are under significant anthropogenic pressure.

3.5.1 *Bathymetric and zonation patterns*

Marine fauna generally exhibit zonation along a gradient from the intertidal to the deepest parts of the ocean, with species having predictable bathymetric distributions (Carney et al. 1983). Rather than rigid assemblages at certain depths, a pattern of gradual turnover with depth is often seen as species with overlapping distributions gradually replace one another (Alton 1966; Carney et al. 1983; Howell et al. 2002). We did not detect clear depth restrictions or species replacement within the Asteroidea from the trawl records, as most species had depth ranges > 1000 m. This apparent eurybathy may indicate that asteroid recruitment can occur in a range of environmental conditions, possibly related to the uniformly cold water column deeper than ~ 60 m (< 4–5 °C throughout the year) that characterize the study sites (Department of Fisheries and Oceans 2009). Relatively high productivity and food availability at depth, relative to other parts of the world where zonation is documented, has been suggested to explain indistinct zonation patterns in fish in this region (Snelgrove and Haedrich 1985); adequate food availability may similarly contribute to the success of asteroids at a range of depths.

Although the trawl records did not reveal strong zonation patterns, we observed several species in the deepest ROV video (~1500–2200 m) that were absent in shallower dives or trawls. Two of these deepest species were brisingid asteroids, which generally have deep bathyal and abyssal distributions (Downey 1986). *Plutonaster agassizi* was also only seen at the deepest survey depths and was often partially buried in the very fine silty sediment abundant at depth; the coarser sediment or other environmental conditions in shallower water may limit the upward range of *P. agassizi.* The distinct set of species we observed > 1500 m is consistent with the work of Haedrich and Maunder (1985), who found a group of asteroids confined to > 1300 m in a canyon east of the Grand Banks (NL; Figure 3-13). Interestingly, Haedrich and Maunder (1985) reported several deep species we did not, including *Plinthaster dentatus, Benthopecten simplex,* and *Bathybiaster vexillifer*; this discrepancy may be related to the more southerly location of our ROV surveys compared to their study, or our lack of trawl surveys > 1480 m.

Depth zonation of asteroid species may be more evident when greater depths are considered. Howell et al. (2002) sampled to 4950 m in the NE Atlantic and found strong species turnover by depth for 47 species of asteroid; however, zonation was less evident considering only species from 200 to 1500 m. Haedrich and Maunder (1985) suggest that greatest faunal change for echinoderms in NL occurs at ~1200–1400 m and at 1800 m. Our data support this interpretation. Additional species not recorded here were reported by Nesis (1965) at 2150 m off the southwestern Grand Banks, including *Porcellanaster ceruleus* and *Pectinaster filholi* (as *Pontaster forcipatus*). A standardized sampling technique across the deep (> 1500 m) slope and adjacent abyssal plains would clarify bathymetric zonation patterns of asteroids, and would likely reveal novel species records for this region.

Although we observed considerable overlap in bathymetric distributions of asteroids, depth optima (depth of peak abundance) did show a shift from predominately shallow to predominately deep species. *Asterias rubens, Crossaster papposus, Leptasterias* spp., and *Solaster* spp. were most abundant at depths < 200 m, reflecting the shallow depths of the Grand Banks where they mainly occurred. A number of species peaked in abundance at intermediate depths: *Ctenodiscus crispatus* between 300 and 600 m, *Astropecten americanus* at 400 to 500 m, and *Psilaster* *andromeda* between 400 and 700 m. The overall maximum abundance and diversity of asteroids was also recorded in the 400–700 m stratum. This depth corresponds to the approximate location of the shelf break and upper continental slope around NL, and may represent a transition zone where shallow and deeper species co-occur. Peak abundance of asteroids at intermediate depths may indicate that food is also plentiful there, and is mirrored in the high abundance and biomass of corals at 400–900 m around the NL shelf (Murillo et al. 2011; Baker et al. 2012). The increased meio- and macrofaunal diversity associated with coral aggregations (Henry and Roberts 2007, Bongiorni et al. 2010) could help support a more diverse asteroid fauna. Some NL asteroids also feed directly on corals (Gale et al. 2013; Chapter 2) and may benefit from higher prey densities at these depths.

Some species in our study also occur in the northeast (NE) Atlantic where their depth distributions and optima were described by Howell et al. (2002); important contrasts emerge when comparing the two basins. The distributions we recorded for *Zoroaster fulgens* and *Psilaster andromeda* included records 700–800 m shallower and optima 450–550 m shallower than those from the NE Atlantic, and our ROV observations of *F. elegans* (likely our Brisingid species 1) were ~2000 m shallower than the shallowest records for this species provided by Howell et al. (2002). Differences in water mass properties, particularly the temperature, likely drive faunal differences between the NE and NW Atlantic. The Arctic or sub-Arctic bioregion extends much further south along the North American coast (to Newfoundland) than it does along the European coast, largely because of the influence of the cold Labrador Current (Nesis 1965). The colder water temperatures in polar regions allow typically abyssal species to extend into shallower bathyal depths (Gage and Tyler 1991).

3.5.2 *Species assemblages and relationship to substrate*

Overall, depth explained only a small proportion of the observed variance in asteroid assemblages from the trawl surveys, indicating that many other factors likely influence epi-megafaunal distributions and co-occurrences. Although substrate data was not available for the trawl surveys, the ROV analyses (restricted to epibenthic species) indicate that local substrate can be important in structuring communities. Water currents can affect which sediments are exposed, particularly at shallow depths (Barrie et al. 1984), thereby influencing the habitat types available for benthic organisms. Food availability likely influences distributions and assemblages of deep-sea megafauna strongly, varying with phytodetritus input and depth (Soltwedel et al. 2009; Fanelli et al. 2013), although temperature, currents, and substrates are also important (Nesis 1965; Howell et al. 2002).

The shallow-water asteroids in our assemblage analysis (*Asterias rubens, Crossaster papposus,* and *Leptasterias* spp.) clustered with common invertebrate species from the Grand Banks, including echinoids *Echinarachnius parma* and *Strongylocentrotus* spp.*,* ophiuroids *Ophiura sarsi*, holothuroids *Cucumaria frondosa*, and bivalves *Mesodesma arctatum* and *Mytilus edulis*. Many of these invertebrates are known to be prey of asteroids (Himmelman and Dutil 1991, So et al. 2010). Hence, the abundance of asteroids on the Grand Banks may be explained by the very high biomass of potential epifaunal prey species there (Nesis 1965).

In the NSS region, *Henricia* spp., *Hippasteria phrygiana*, and *Ctenodiscus crispatus* were the most abundant asteroids recorded. *Ctenodiscus crispatus,* which dwells and feeds infaunally (Shick et al. 1981; Gale et al. 2013; Chapter 2), coexists with the echinoid *Brisaster fragilis*, the holothuroid *Psolus phantapus,* and several species of polychaete in the sandy-silt areas of the north and northeast Newfoundland shelf (Nesis 1965). Our epifaunal species assemblage analysis showed associations of *C. crispatus* with actiniarians, sponges, and brachiopods; the nature of potential interaction remains unknown, since the burrowing behavior of *C. crispatus* prevented observations in the ROV video. We determined that that *Henricia* spp. co-occurred with many suspension-feeding invertebrates including sponges, sea anemones, nephtheid corals, and brachiopods. *Henricia sanguinolenta* has been reported to feed on dissolved organic matter (Anderson 1960) as well as on sponges (Sheild and Witman 1993); its association with these species may be indicative of local environmental conditions amenable for capturing suspended or dissolved matter (e.g., adequate currents). Although *Hippasteria phrygiana* did not cluster strongly with any species in the trawl analysis, the ROV analysis indicated it associates at small scales with boulders and species such as sponges and certain sea anemones, which may be under-represented in trawl tows given the difficulty in sampling animals from rough terrain.

Of our regions, the LCNS had the lowest species diversity of asteroids as a result of the dominance of *C. crispatus*, a species previously reported in high numbers in the Laurentian Channel (Nesis 1965; Lévesque 2009). High abundances of pennatulaceans have also been reported in the Laurentian Channel (Cogswell et al. 2009; Baillon et al. 2013), but we did not confirm any association between pennatulaceans and *C. crispatus* there. Because we grouped all pennatulacean species together in the trawl analysis, their co-occurrence with *C. crispatus* may have been masked by stronger associations in other regions, such as those observed with pennatulaceans and soft corals at deeper depths. Alternatively, *C. crispatus* and pennatulaceans may not co-occur at a fine scale, perhaps because of the potentially disruptive burrowing behavior of *C. crispatus.* The large aggregations of mud-ingesting *C. crispatus* occurring in the Laurentian Channel likely process and redistribute immense amounts of labile carbon, thus shaping epi- and infaunal communities (Rhoads and Young 1970, Norling et al. 2007). Understanding the potential impacts of *C. crispatus* on pennatulacean corals is of interest, given recent evidence that pennatulaceans in the Laurentian Channel act as nursery habitat for commercially important redfish (*Sebastes* spp.) (Baillon et al. 2012).

While Labrador (north of the Strait of Belle Isle, ~52ºN) is sometimes considered a separate biogeographic region (Briggs 1995), we did not observe a unique asteroid assemblage or any endemic species in that region. The area north of 52ºN mostly clustered as NSS along with the adjacent northern Newfoundland shelf, although there were patches that grouped with the Grand Banks and LCNS regions. Despite the absence of a unique assemblage, the asteroids *Porania pulvillus*, *Hippasteria phrygiana, Henricia* spp*., Ceramaster granularis, Pseudarchaster parelii,* and *Urasterias lincki* were more common and more abundant in Labrador. South of 52ºN, *Leptasterias* spp*., Crossaster papposus, Asterias rubens, Solaster* spp*., Psilaster andromeda, Astropecten americanus,* and *Ctenodiscus crispatus* were more common and abundant. Depth alone cannot explain differences in species abundances between Newfoundland and Labrador: the Newfoundland section of the shelf has a slightly greater area, proportionally, at the shallowest depths (< 200 m) than the Labrador section (53% of the shelf to 1500 m vs. 48%), but this difference is reduced when areas < 300 m are considered (69% vs. 71%). Cooler waters north of 52ºN may contribute to higher abundances of some species in Labrador; however, some of those species also occur in relatively shallow waters (35–350 m) in the warmer waters of the Gulf of Maine (Franz et al. 1981). The Newfoundland-Labrador region has been variously placed in the Arctic bioregion (Pocklington and Tremblay 1987; Spalding et al. 2007) or the temperate NW Atlantic (Archambault et al. 2010); the southern part of Labrador and the majority of Newfoundland likely constitute a transitional faunal region between the two.

3.5.3 *Habitat use*

Habitat type influences the species and functional groups in a community, since different biological traits (size, mobility, feeding behaviors) thrive in different environmental conditions (Hewitt et al. 2008). The asteroids observed with the ROV in this study occurred mainly on mud or sand, with some species preferring harder substrates (cobble, boulder, or outcrops) and others occurring on many substrates. Hard substrates in the deep sea often have communities that differ from the surrounding soft sediments; e.g. some species such as corals require hard structures for attachment (Baker et al. 2012). Our observations of *Novodinia americana* occurring on biogenic substrates (tall corals) is consistent with previous records for suspension-feeding asteroids in the family Brisingidae (Downey 1986, Emson and Young 1994). The high occurrence of *Tremaster mirabilis* on cobble and boulder may be related to the habitat of its prey: *T. mirabilis* has been observed feeding on a coral *Acanthogorgia armata* (Gale et al. 2013; Chapter 2), which also mainly occurs on hard substrates (Baker et al. 2012). *Hippasteria phrygiana,* a habitat generalist, is known to feed on many sessile cnidarians including corals and sea anemones (Gale et al. 2013; Chapter 2), perhaps exploiting available prey depending on local conditions. Relating the habitat use of asteroids to their trophic ecology is hindered by a lack of diet information for most deep-sea species. In the absence of specific trophic data, small-scale habitat interactions can provide useful ecological information. For example, observations that a species occurs in muddy mixed substrate habitats may indicate deposit or infaunal feeding, while species recorded from hard substrate “islands” amidst mud may be feeding on other rock-dwelling or encrusting species. Information on habitat use, distributions, and species interactions is essential for understanding the roles of asteroids in benthic communities. Although our sampling methods account only for a fraction of epibenthic organisms and we have thus underestimated the abundance of asteroids in eastern Canada, the data in this study highlight the diversity, ubiquity, and ecological importance of this often overlooked group of deep-sea organisms.

3.6 **References**

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3.7 **Tables and Figures**

Table 3-1. List of non-asteroid invertebrate species included in trawl and ROV RDA analyses.

Taxon	Trawl	ROV
Porifera	Porifera	Porifera (cloud-type)
		Porifera (encrusting)
		Porifera (ball-type)
Echinodermata	Crinoidea (all species)	Crinoidea (stalked)
		Crinoidea (unstalked)
	Holothuroidea (all)	Holothuroidea (large, flat)
		Holothuroidea (other)
	Ophiuroidea (other)	Ophiuroidea (all)
	Gorgonocephalus arcticus	
	Echinoidea (other)	Echinoidea (other)
	Strongylocentrotus spp.*	*Phormosoma placenta*
	Clypasteroidea	
	Spatangoidea	
Anthozoa	Coral (other)	Coral (other)
	Acanella arbuscula	*Acanella arbuscula*
	Acanthogorgia armata	*Acanthogorgia armata*
	Anthomastus spp.	*Anthomastus* spp.
	Flabellum spp.	*Flabellum* spp.
	Keratoisis grayi	*Keratoisis grayi*
	Nephtheidae	Nephtheidae
	Paragorgia arborea	Antipatharia
	Paramuricea sp.	*Chrysogorgia agasszii*
		Desmophyllum dianthus
Pennatulacea	Pennatulacea (all)	*Anthoptilum grandiflorum*
		Halipteris finmarchica
		Pennatula spp.
		Protoptilum carpenteri
		Umbellula sp.
		Pennatulacea (other)
Actiniaria	Actiniaria (all)	Sea anemone (*Bolocera* sp. or *Urticina* sp.)
		Sea anemone (*Actinauge* sp.)
		Sea anemone (*Cerianthus* sp.)
		Sea anemone (other)

Decapoda	Paguridae	
	Lithodes spp.	
	Hyas spp.	
	Chionoecetes opilio	
	Decapoda (other species)	
Mollusca	Buccinidae	
	Gastropoda (other species)	
	Nudibranchia	
	Chlamys islandica	
	Bivalvia (other species)	
Other taxa	Ascidiacea	Bryozoa (erect forms)
	Brachiopoda	

* Includes both *Strongylocentrotus droebachiensis* and *S. pallidus*. Most *Strongylocentrotus* deeper than ~60 m are *S. pallidus* (Gagnon and Gilkinson 1994), but shipboard identification to species level is not feasible.

Table 3-2. Asteroid distribution data established from trawl surveys over the NL continental shelf and slope (2008–2011) and from *in situ* video taken by the remotely operated vehicle ROPOS on the southern NL shelf (2007).

	Trawl (depth range 37–1480 m)				ROV (depth range 354–2243 m)			
Species	Number of trawls with taxa present (number of ind recorded)	Maximum average density (ind ha^{-1})	Depth at maximum density or mean collection depth (m)	Depth distribution (m)	Number of observations	Depth distribution (m)	Mean depth (m)	Width of depth range (m)
Asterias rubens	231 (2010)	0.44	0-100	38-963				925
Astropecten americanus	165 (13928)	11.65	400-500	68-1412				1344
Ceramaster granularis	241 (957)	0.47	1100-1200	58-1422	27	335-1179	637	1364
Crossaster papposus	921 (7891)	1.33	0-100	37-1422				1385
Ctenodiscus crispatus	765 (289729)	190.06	400-500	45-1404				1359
Diplopteraster multiples	29 (129)	0.03	400-500	69-1343	4	604-1822	992	1753
Henricia spp.	840 (7318)	3.18	1200-1300	37-1442	119	355-821	594	1405
Hippasteria phrygiana	686 (2795)	0.96	500-600	50-1396	31	354-795	549	1346
Leptasterias spp.	830 (8043)	2.21	0-100	37-1134				1097
*Leptychaster arcticus***	10 (20)		530	335-1405				902
*Mediaster bairdi***	28 (62)		975	258-1418	56	537-1316	752	1160
Mediaster/Hippasteria					147	401-1020	703	619
*Myxaster sol***	5 (6)		1137	471-1404				933
*Novodinia americana**	3 (8)	0.03	1400-1500	319-1429	20	539-805	655	1100
*Pedicellaster typicus**	1 (18)	0.02	400-500	438				-
Plutonaster agassizi					28	1231-1869	1621	638

Porania pulvillus	199 (865)	0.56	500-600	47-1311				1264
Poraniomorpha spp.*	9 (38)	0.03	400-500	158-662				504
Pseudarchaster parelii	18 (167)	0.53	700-800	122-1480				1358
Psilaster andromeda	167 (12923)	9.40	400-500	43-1438				1395
Pteraster spp.	34 (99)	0.02	200-300	73-1285				1213
Pteraster sp. 1					3	647-795	722	722
Solaster earlli					35	398-899	600	501
Solaster spp.	331 (1419)	0.26	0-100	38-1182				1144
*Tremaster mirabilis**	4 (16)	0.02	1200-1300	347-1210	16	521-802	597	863
Urasterias lincki	14 (52)	0.05	1400-1500	241-1429				1188
*Zoroaster fulgens***	15 (24)		848	201-1405				1228
Brisingida species 1					46	1481-2243	1818	762
Brisingida species 2					92	1759-2242	2109	483
Unidentified Brisingida					25	1637-2242	2144	605
6-armed species					6	2032-2238	2154	206
Other asteroids	342 (3649)			45-1448				1403
Total	3102 (351794)				656			

* These rare species are included in the “other asteroids” tally and were not used for community analysis.

** Data are from samples collected by the authors that were not recorded by DFO staff, and which came from a limited survey area and may not be representative. Depths shown are mean collection depths. Not included in total.

Table 3-3. Regions determined by cluster analysis of asteroid CPUE. Diversity metrics (Shannon-Weiner H' and Pielou's J') are averages for all blocks in each region. SIMPER species are those that define the regions to 98% cumulative similarity. CPUE (ind ha^{-1}) is shown for each species, with proportion of blocks with each species in brackets. Species in bold are indicator species resulting from *indval.* Data provided as mean ± sd.

Region	Grand Banks (GB, 400 blocks)	Northeast Shelf/Slope (NSS, 281 blocks)	Laurentian channel/northwest shelf (LCNS, 284 blocks)
Depth	125 ± 111 m	383 ± 269 m	298 ± 198 m
Richness	3.15 ± 1.76	2.83 ± 1.79	3.04 ± 1.81
H'	0.74 ± 0.47	0.64 ± 0.52	0.41 ± 0.41
J'	0.63 ± 0.32	0.54 ± 0.37	0.34 ± 0.31
SIMPER species	***Leptasterias* spp. 1.81 (0.76)** ***Crossaster papposus* 1.59 (0.78)** *Henricia* spp. 0.40 (0.43) ***Asterias rubens* 0.46 (0.32)** *Solaster* spp. 0.21 (0.34)	***Henricia* spp. 2.30 (0.80)** *Hippasteria phrygiana* 0.53 (0.59) *Ctenodiscus crispatus* 0.85 (0.37) *Ceramaster granularis* 0.17 (0.25) *Porania pulvillus* 0.16 (0.23)	***Ctenodiscus crispatus* 116.49 (0.97)** *Hippasteria phrygiana* 0.42 (0.40) *Henricia* spp. 0.33 (0.31)

Table 3-4. Results from RDA analysis of species assemblages (presence-absence) from the ROV video, explained by substrate type and depth. P-values were determined by permutation test (*anova.cca* in R).

Explanatory variables	Canonical eigenvalues	% of total variance explained	p
% mud/sand	0.0606	26.2	0.001 *
% outcrop	0.0284	12.3	0.001 *
% gravel	0.0295	12.8	0.001 *
% boulder/cobble	0.0019	0.8	0.086
depth	0.1110	48.0	0.001 *
sum of canonical eigenvalues (total variance explained by all factors)	0.2360	100	

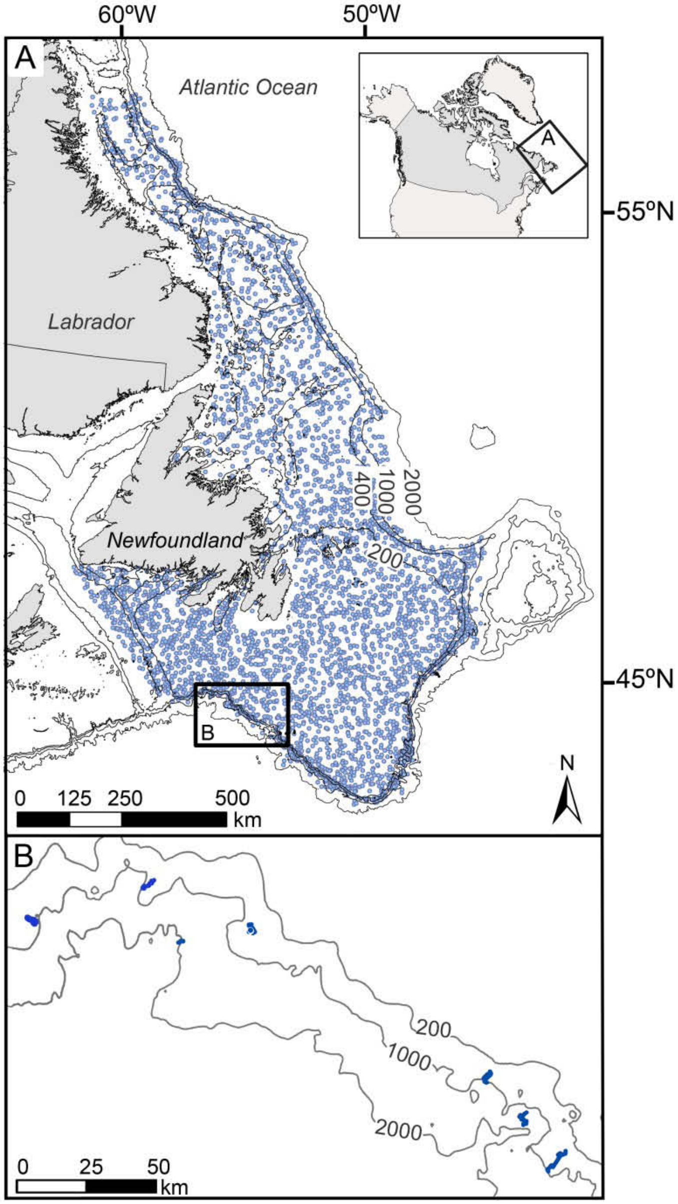

Figure 3-1. Map of study area. A) Locations of 4286 trawl tows (blue points) completed by DFO between 2008 and 2011, and B) 8 ROV dives completed in 2007.

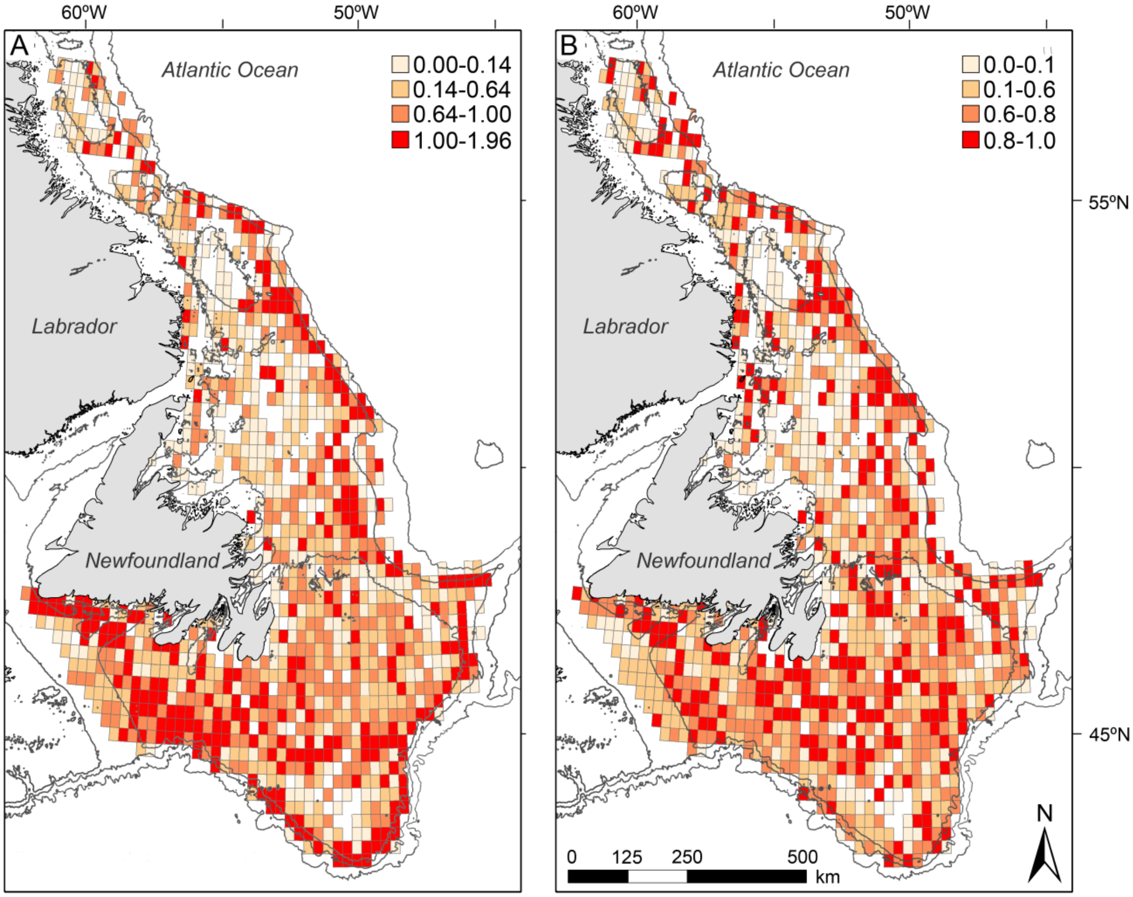

Figure 3-2. Diversity patterns of asteroids in 0.25 x 0.25° blocks through the study region. A) Shannon-Weiner H', and B) Pielou's evenness J'. Levels were split by quantiles.

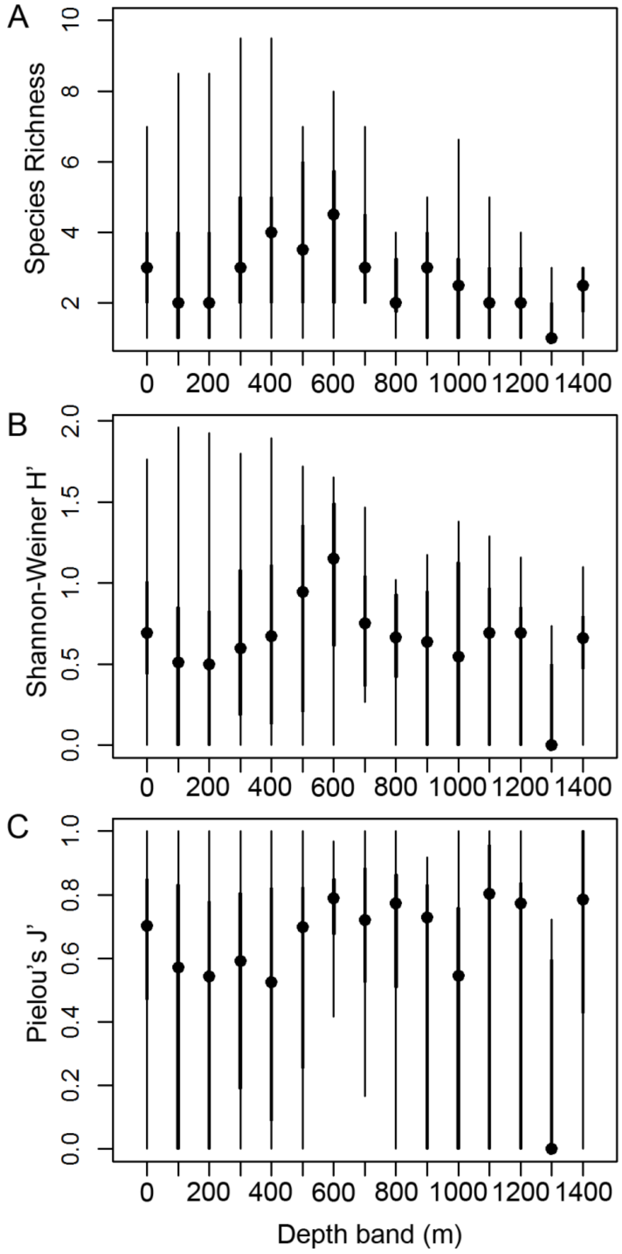

Figure 3-3. A) Species richness (number of species), B) diversity (Shannon-Weiner H') and C) evenness (Pielou's J') of asteroid species by 100-m depth band. Dots show means of blocks within each band, bold line delimits 25th and 75th quartiles, and thin line shows extent of values. Data from trawl surveys only.

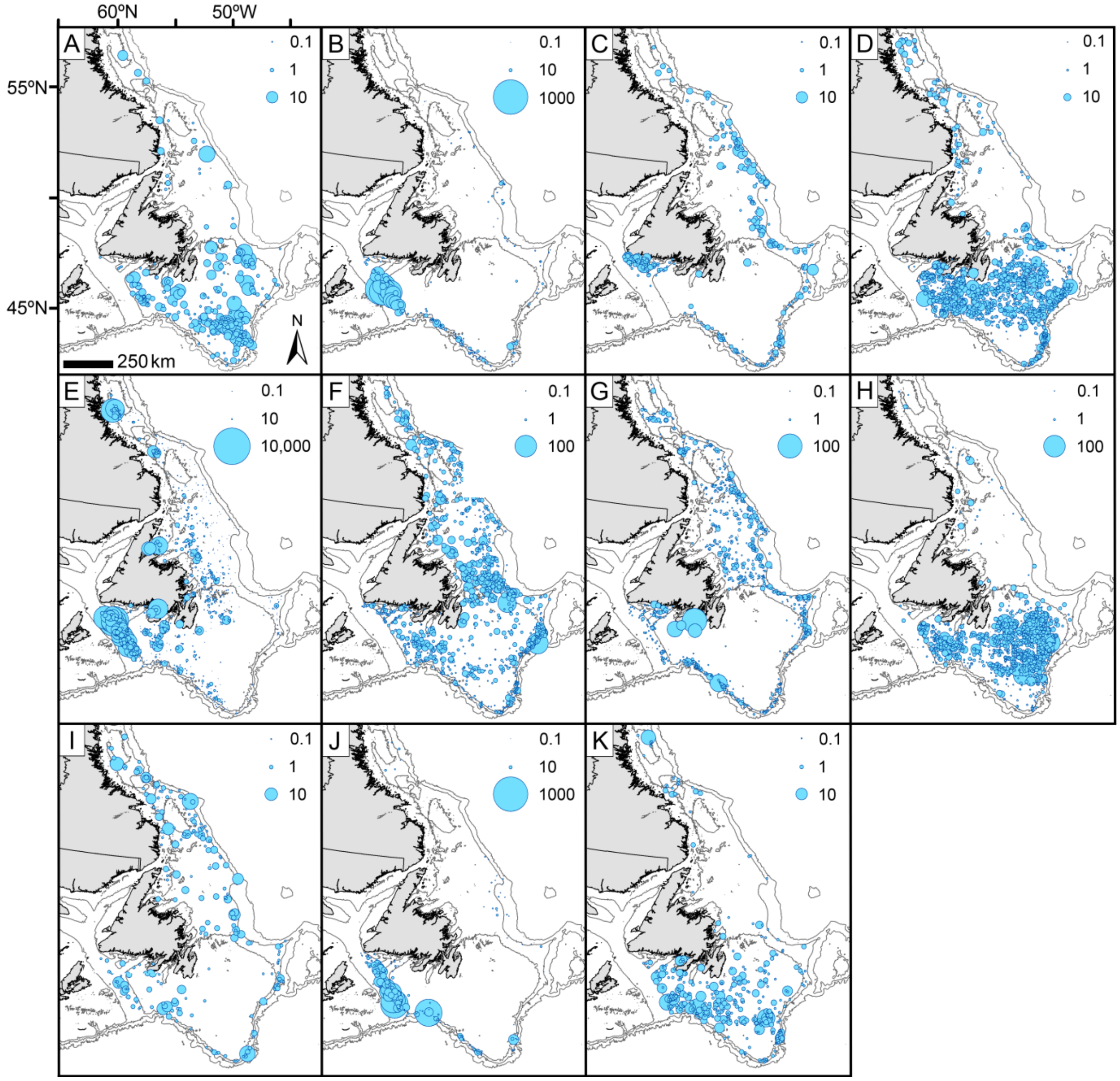

Figure 3-4. Geographic distribution of the 11 most widespread asteroid species collected from trawl surveys over the Newfoundland and Labrador shelf and slope. Size of the blue circles represents the CPUE (ind ha^{-1}) for individual trawl tows. Contour lines as for Fig 1. A) *Asterias rubens*, B) *Astropecten americanus,* C) *Ceramaster granularis,* D) *Crossaster papposus*, E) *Ctenodiscus crispatus,* F) *Henricia* spp., G) *Hippasteria phrygiana*, H) *Leptasterias* spp. (mostly *L. polaris*), I) *Porania pulvillus,* J) *Psilaster andromeda*, K) *Solaster* spp. (mostly *S. endeca*).

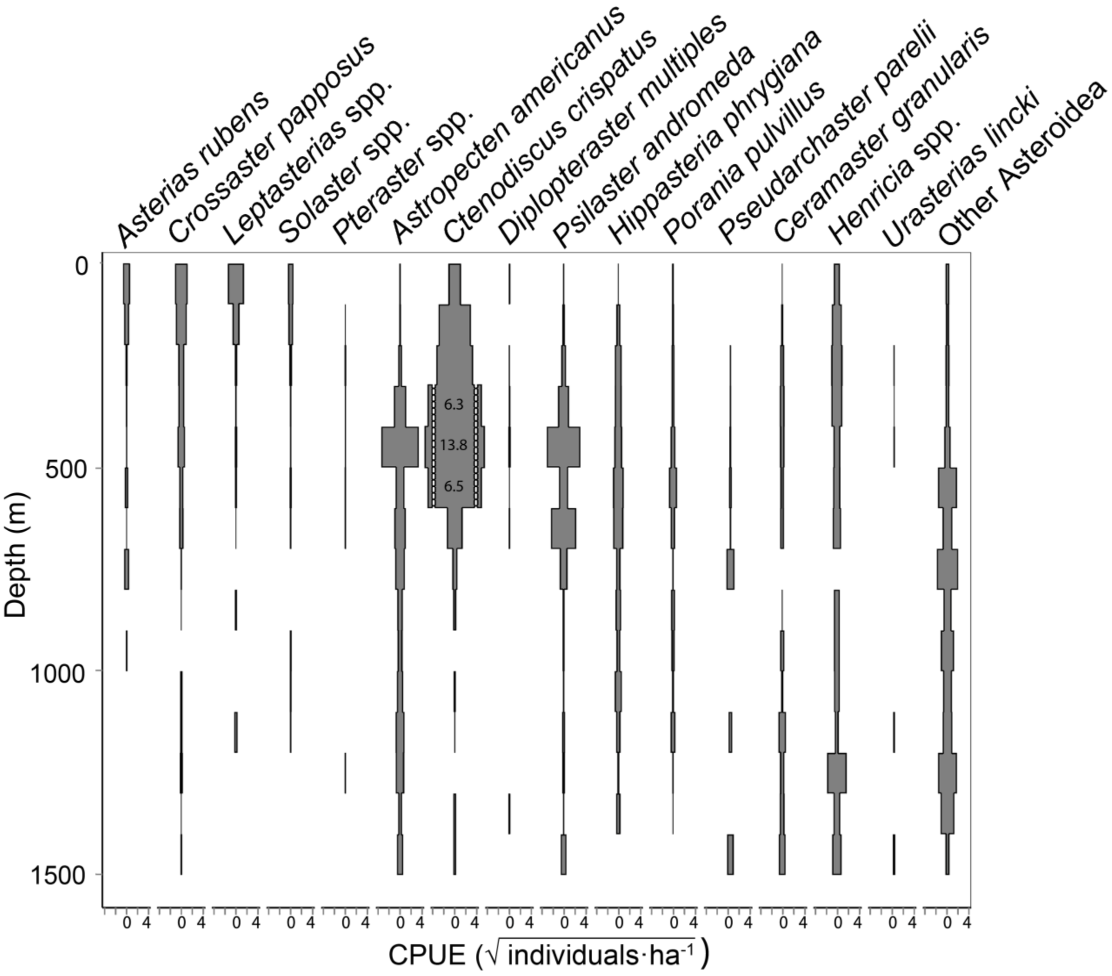

Figure 3-5. Depth distribution of 15 asteroid species plus “other Asteroidea” collected from 4286 trawls on the continental shelf and slope of Newfoundland and Labrador, Canada. Depth distribution of 15 asteroid species plus “other Asteroidea” collected from 4286 trawls on the continental shelf and slope of Newfoundland and Labrador, Canada. . Data from trawl surveys only. Width of bars indicates square-root of catch per unit effort (CPUE; ind ha^{-1}) averaged within 100-m depth bands. Species are shown in descending order of depth of maximum CPUE.

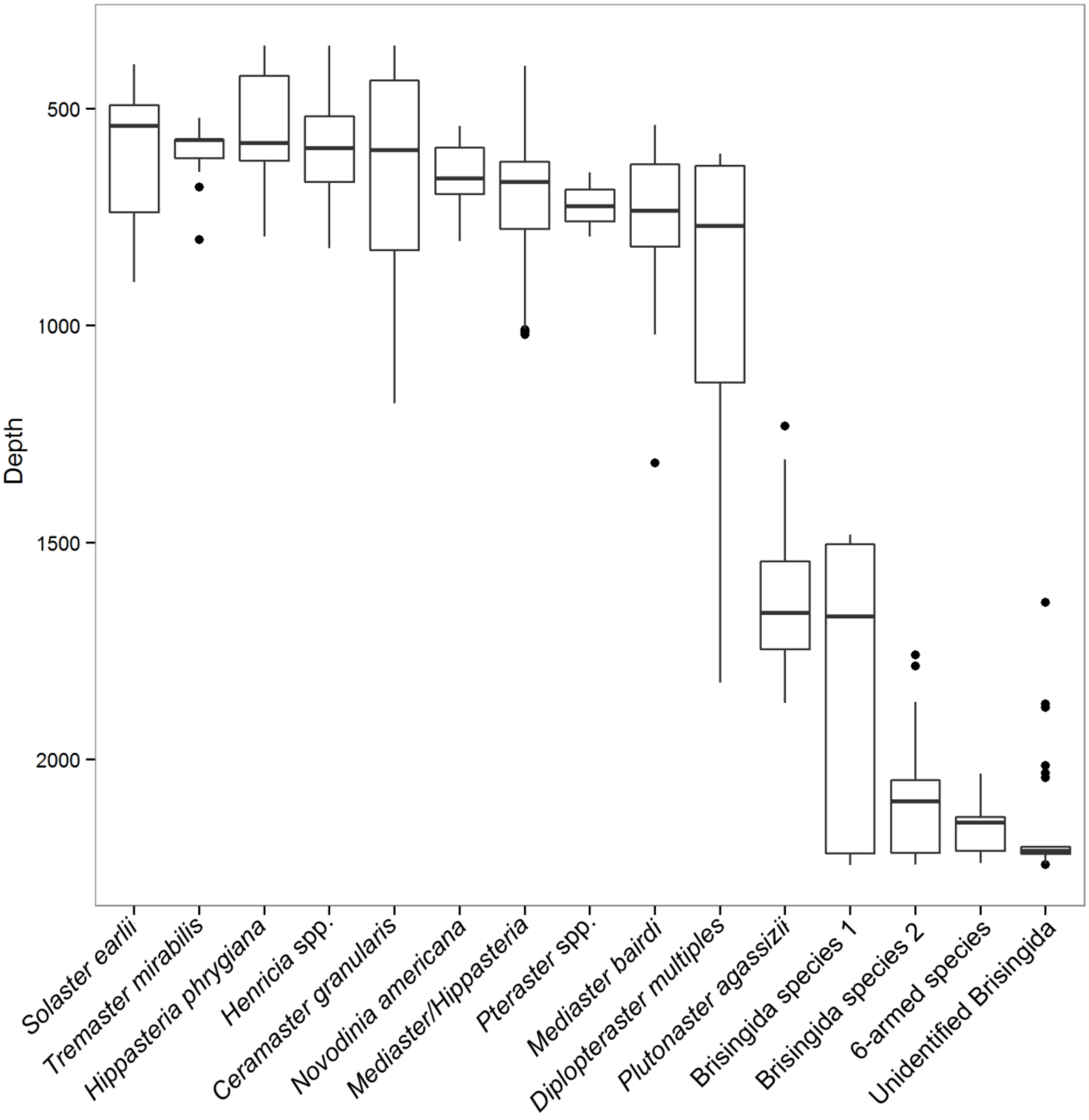

Figure 3-6. Depth distribution of asteroid species recorded from the ROV ROPOS on the southern shelf of Newfoundland in 2007, arranged in order of descending median depth. Dark horizontal lines indicate median, vertical lines indicate range, bounding boxes are 25th and 75th quartiles, and points are outliers. Data from ROV surveys only.

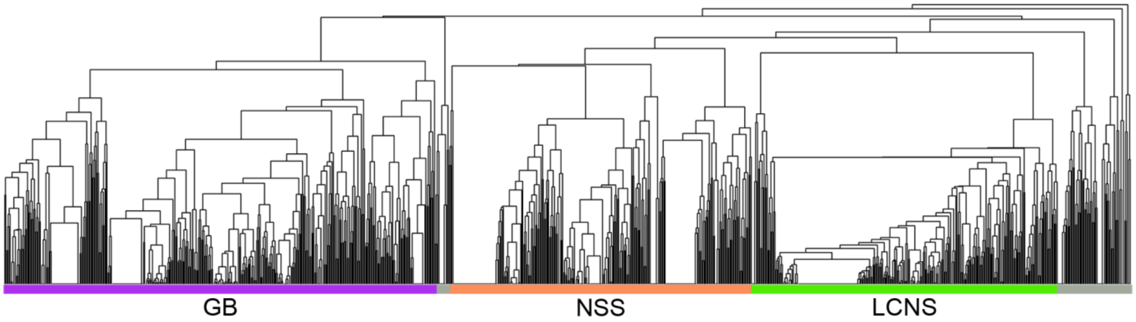

Figure 3-7. Cluster diagram (average grouping), using Hellinger-transformed Euclidean distances of CPUE data of asteroids in 1046 0.25º by 0.25º blocks. Data from trawl surveys only. GB = Grand Banks; LCNS = Laurentian Channel/northwest shelf; NSS = Northeast shelf/slope.

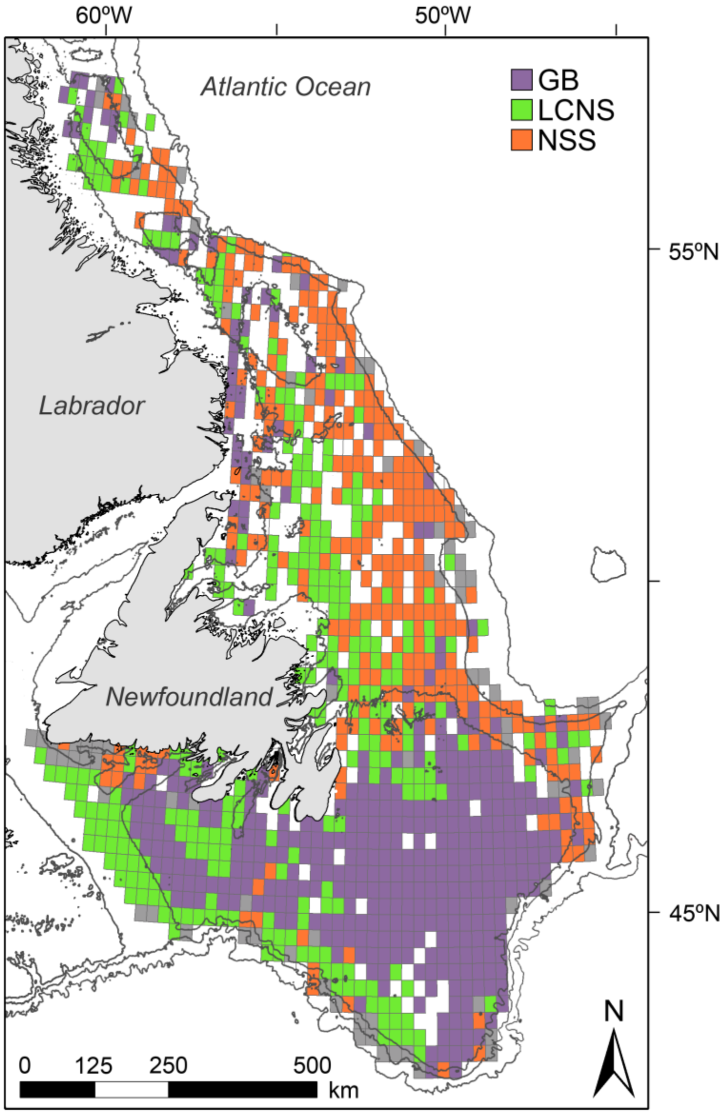

Figure 3-8. Geographic patterns of asteroid assemblages determined by cluster analysis of CPUE. Colored rectangles represent the 0.25° by 0.25° blocks assigned to each of the three geographic regions. White spaces indicate either that no asteroids were present or that area was not surveyed; grey blocks did not fall into any of the three main clusters. GB = Grand Banks; LCNS = Laurentian Channel/northwest shelf; NSS = Northeast shelf/slope. Color coding as in Fig 3-7.

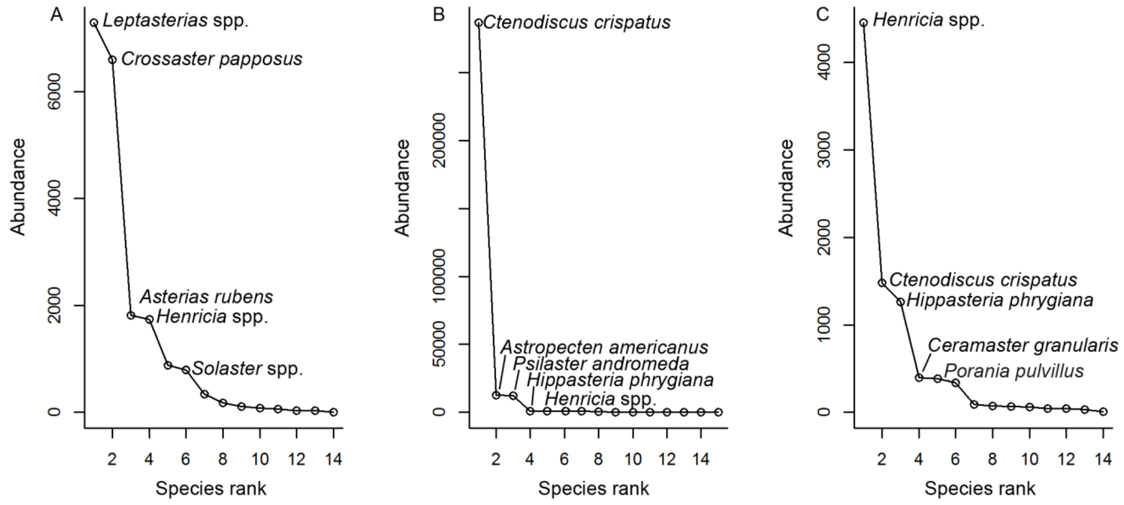

Figure 3-9. Rank-abundance curves for the three main regions determined by cluster analysis. Data from trawl surveys only. A) Grand Banks (GB), B) Laurentian Channel/northwest shelf (LCNS), C) Northeast shelf/slope (NSS). Y axes are number of individuals of each species.

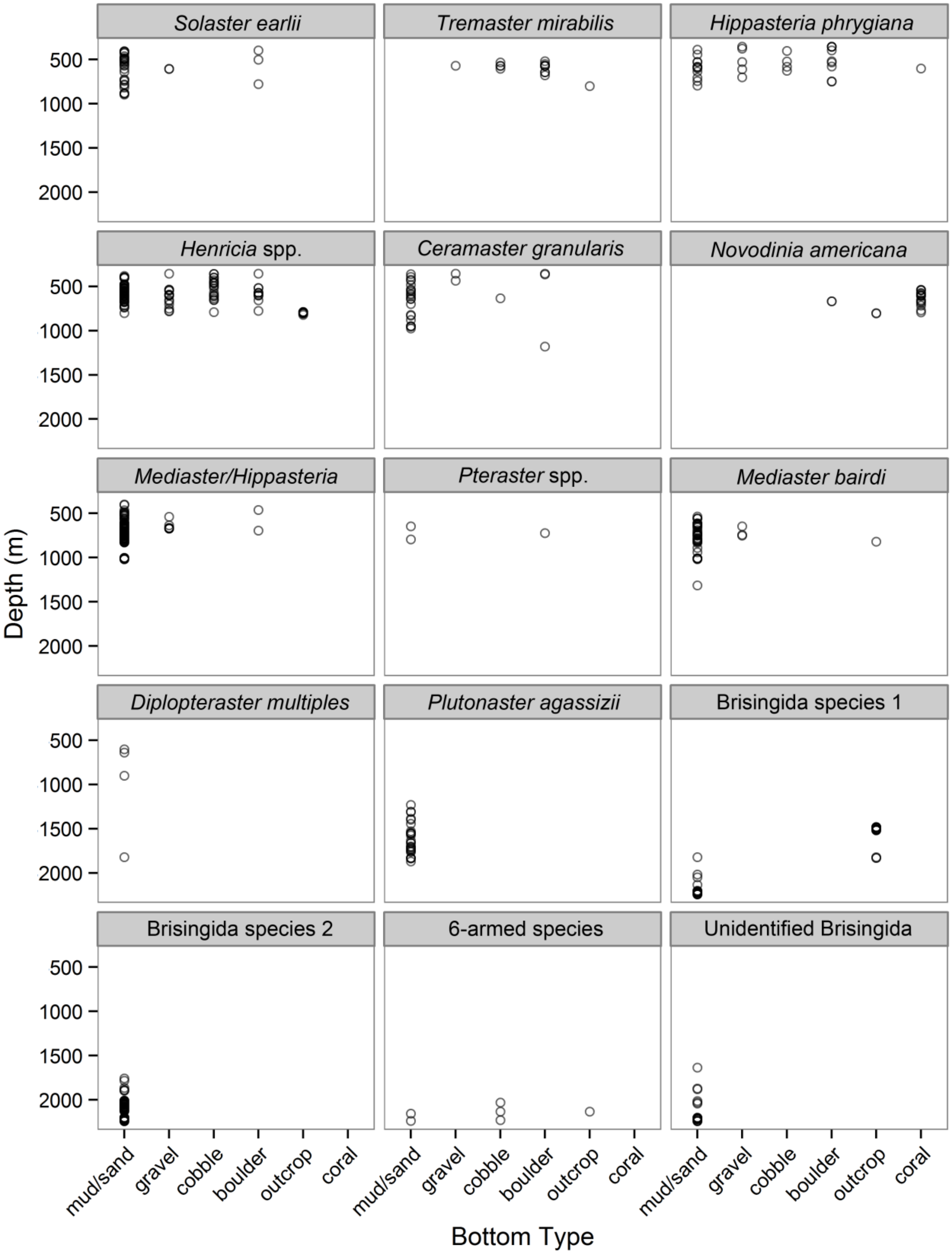
Solaster earlii
Tremaster mirabilis
Hippasteria phrygiana
Henricia spp.
Ceramaster granularis
Novodinia americana
Mediaster/Hippasteria
Pteraster spp.
Mediaster bairdi
Diplopteraster multiples
Plutonaster agassizii
Brisingida species 1
Brisingida species 2
6-armed species
Unidentified Brisingida
Depth (m)
500
1000
1500
2000
Bottom Type
mud/sand
gravel
cobble
boulder
outcrop
coral

Figure 3-10. Depth distribution of asteroid species recorded from the ROV ROPOS on the southern slope of Newfoundland in 2007, arranged according to the substrate that the asteroid was observed on. *Mediaster/Hippasteria* includes asteroids which are either *Mediaster bairdi* or *Hippasteria phrygiana* that could not be distinguished with confidence due to poor video quality; similarly, unidentified Brisingida includes individuals of either Brisingida species 1 or 2.

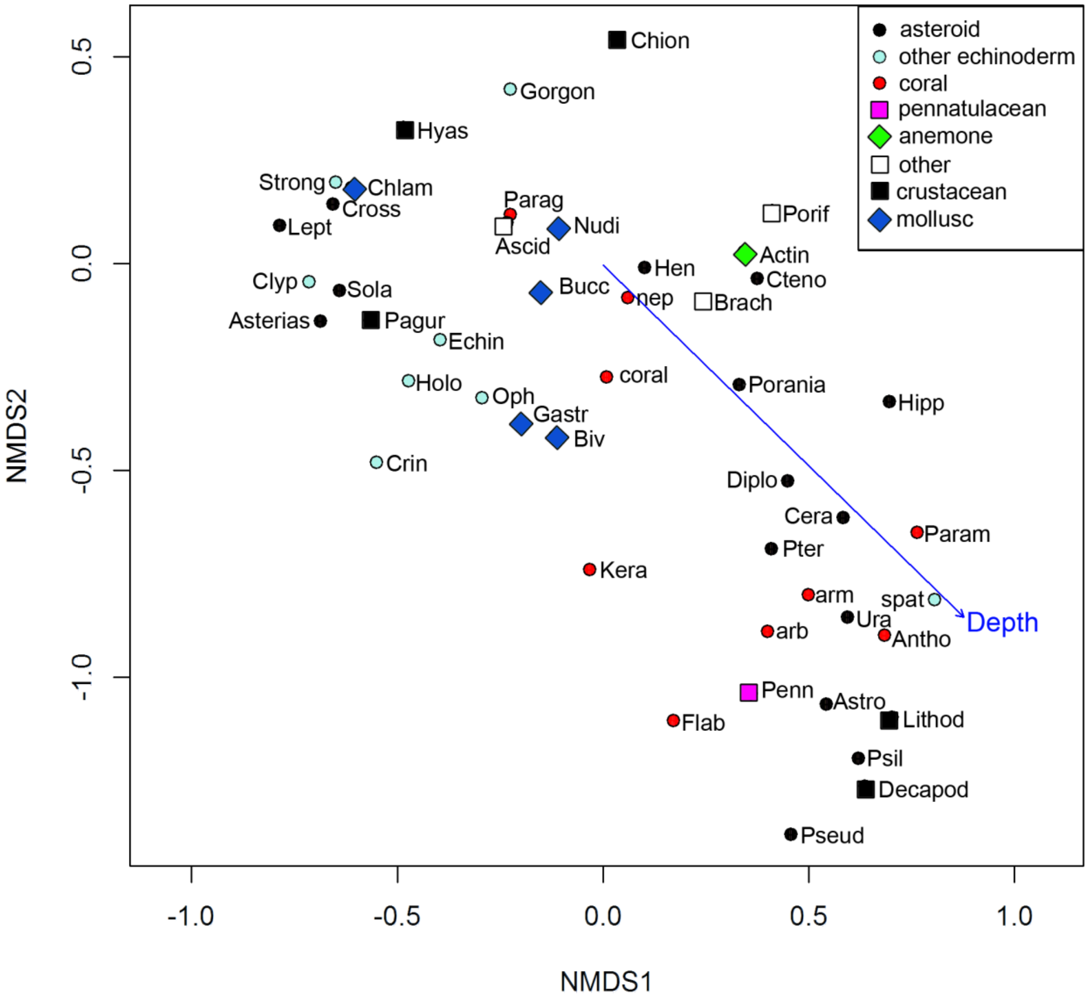

Figure 3-11. nMDS plot of species associations from the trawl surveys (n = 1221 blocks). Environmental vectors are the result of the envfit function in R and represent the depth gradient. Stress = 0.234. Asteroids: Asterias= *Asterias rubens*, Astro= *Astropecten americanus*, Cera= *Ceramaster granularis,* Cross= *Crossaster papposus*, Cteno= *Ctenodiscus crispatus*, Diplo= *Diplopteraster multiples*, Hen= *Henricia* spp., Hipp= *Hippasteria phrygiana*, Lept= *Leptasterias* spp., Sola= *Solaster* spp., Porania= *Porania pulvillus*, Pseud= *Pseudarchaster parelli*, Psil= *Psilaster andromeda*, Pter= *Pteraster*

spp., Ura= *Urasterias lincki*. Other echinoderms: Clyp= Clypasteroidea, Crin= Crinoidea, Echin= other Echinoidea, Gorgon= *Gorgonocephalus arcticus*, Strong= *Strongylocentrotus* spp., Holo= Holothuroidea, Oph= other Ophiuroidea. Corals: Antho= *Anthomastus* spp., arb= *Acanella arbuscula*, arm= *Acanthogorgia armata*, coral= other coral, Flab= *Flabellum* spp., kera= *Keratoisis gray*i, nep= Nephtheidae, Parag= *Paragorgia arborea*, Param= *Paramuricea* sp. Pennatulacea: penn= Pennatulacea. Anemone: Actin= all anemones. Other: Ascid= Ascidacea, Brach = Brachiopoda, Porif= Porifera. Crustaceans: Chion= *Chionoecetes opilio*, Decapod= other decapods, Hyas= *Hyas* spp., Lithod= *Lithodes* spp., Pagur= Paguridae. Molluscs: Biv= other Bivalvia, Bucc= Buccinidae, Chlam= *Chlamys islandica*, Gastr= other gastropods, Nudi= Nudibranchia.

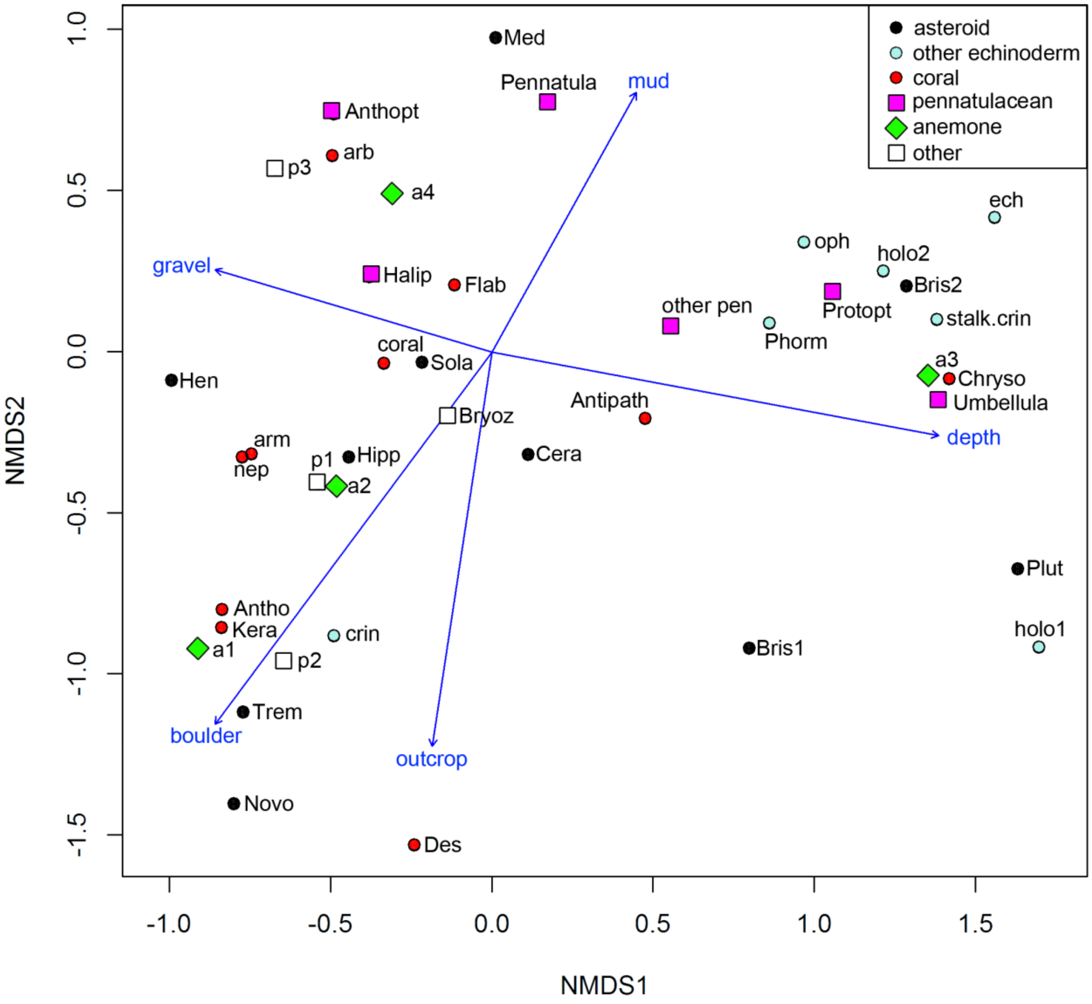

Figure 3-12. nMDS plot of species associations from the ROV data set (n = 620 video frames). Environmental vectors are the result of the envfit function in R and represent gradients of depth and substrate percent cover. Stress = 0.09. Asteroid codes: Bris1= Brisingida species 1, Bris2= Brisingida species 2*,* Cera= *Ceramaster granularis*, Hen= *Henricia* spp., Hipp= *Hippasteria phrygiana*, Med= *Mediaster bairdi*, Novo= *Novodinia americana*, Plut= *Plutonaster agassizi*, Sola= *Solaster earlli*, Trem= *Tremaster mirabilis*. Other echinoderms: crin= Crinoidea (unstalked), stalk.crin= Crinoidea (stalked), holo1=

Holothuroidea (large, flat), holo2= Holothuroidea (other), oph= Ophiuroidea, Phorm= *Phormosoma placenta*, ech= unidentified Echinoidea. Corals: Antipath= Anthipatharia, Antho= *Anthomastus* spp., arb= *Acanella arbuscula*, arm= *Acanthogorgia armata*, Chryso= *Chrysogorgia agassizii*, coral= other coral, Des= *Desmophyllum dianthus*, Flab= *Flabellum* spp., kg= *Keratoisis grayi*, nep= Nephtheidae, Pennatulaceans: Anthopt= *Anthoptilum grandiflorum*, Halip= *Halipteris finmarchica*, other pen= Pennatulacea (other), Pennatula= *Pennatula* spp., Protopt= *Protoptilum carpenteri*, Umbellula= *Umbellula* sp. Sea anemones: a1: *Bolocera* sp. or *Urticina* sp., a2= *Actinauge* sp., a3= *Cerianthus* sp., a4= other anemones. Other: Bryo= Bryozoa (erect forms), p1= Porifera (cloud-type), p2= Porifera (encrusting), p3= Porifera (ball-type).

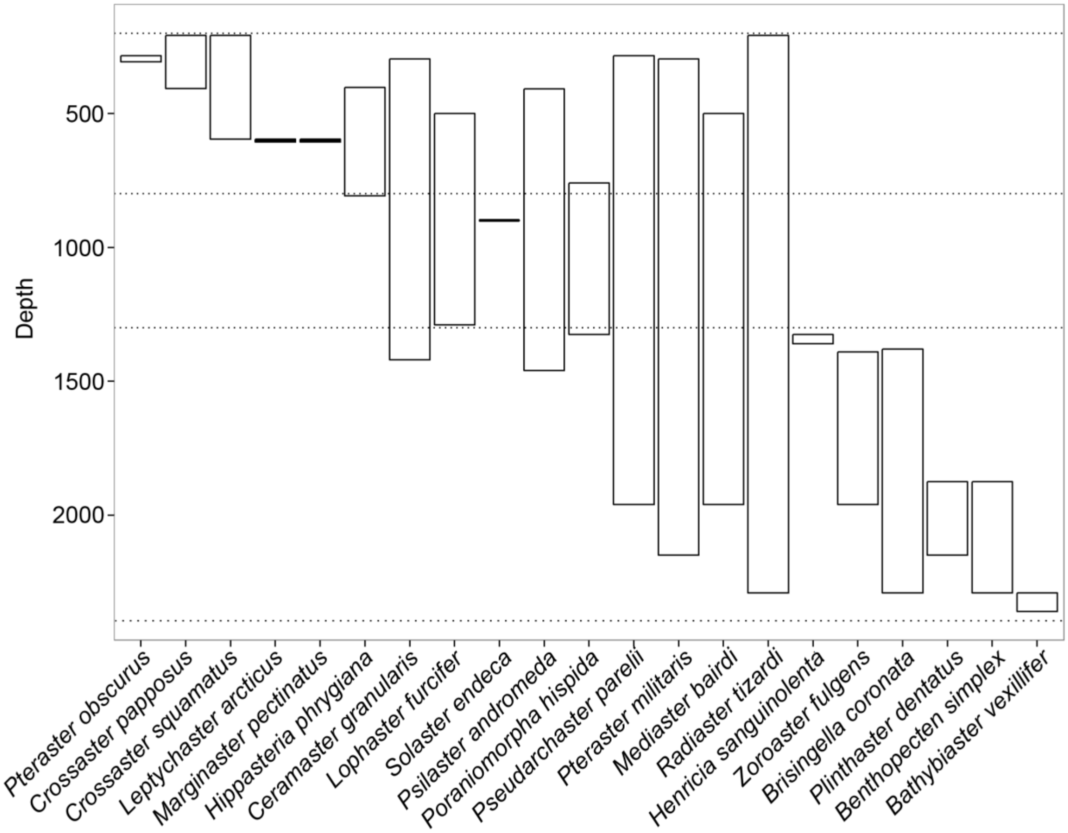

Figure 3-13. Depth distributions of asteroid species collected from Carson Canyon, Newfoundland, showing some evidence of zonation by depth. Data from Haedrich and Maunder (1985). Bars indicate minimum and maximum depth records for each species. Dashed lines are shown at 200, 800, 1300, and 2400 m.

Chapter 4

General conclusions

4.1 **Thesis summary**

In this thesis, I provide ecological information including trophic interactions, species assemblages, geographic and bathymetric distributions, and habitat use for many species of asteroid from the continental shelf and slope of Eastern Canada. In Chapter 2, I show that seven of the most common deep-water asteroid species in Newfoundland and Labrador occupy two trophic positions in the benthic food web – one that feeds on macrofauna in the sediment or water column, and one that feeds primarily on larger organisms, including corals and sponges. Within a trophic level, species exhibit different feeding behaviors and exploit different prey. The low trophic-level species included *Novodinia americana,* a suspension feeder that captures benthopelagic copepods, and *Ctenodiscus crispatus, Leptychaster arcticus,* and *Zoroaster fulgens,* infaunal feeders that feed on molluscs, crustaceans, and other organic material in the sediment. The high trophic-level species included *Ceramaster granularis*, which feeds on sponges, and *Hippasteria phrygiana,* which feeds on corals. The specific diet of *Mediaster bairdi*, which I also identified as a high trophic-level species based on its stable isotope signature*,* remains unresolved. In Chapter 3 I provide distribution data on almost 30 asteroid species found to ~2200 m, as well as their habitats and associations with other megafauna. Most asteroid species occupy wide depth ranges and utilize soft-bottom habitats, although this usage varies by species. *Tremaster mirabilis* and Brisingida species 1*,* for example, primarily occupied hard substrates like boulders and outcrops, whereas *Hippasteria phrygiana* and *Henricia* spp. showed no substrate preference. Differences in habitat use influence the suite of species that an asteroid species interacts with, and also affects its potential geographic extent. Given that soft sediments characterize most benthic habitats, species that utilize hard substrates may be geographically limited; conversely, mud-dwelling species could adapt to many locations. Asteroid species often associated with potential prey organisms such as corals, sponges, molluscs and other echinoderms. Asteroids that strongly associated with corals included *Novodinia americana,* which uses tall corals (*Keratoisis grayi*) as habitat, and *M. bairdi,* which often occurred in dense fields of pennatulacean corals. Within the Grand Banks, a distinct group of shallow-water asteroids associated with bivalves and echinoids. Deep-water assemblages included the poorly known species *Pseudarchaster parelii, Psilaster andromeda, Plutonaster agassizi,* and two unknown species in the Brisingida, which generally associated with soft substrates and some pennatulacean coral species.

The results from these two chapters indicate that asteroids in the northwest Atlantic are not an ecologically homogeneous group. Species-level differences in behaviors and adaptations likely contribute to the observed geographic and bathymetric distribution patterns and lead to wide-ranging ecological roles for asteroids in benthic communities. Differences in species' biological and ecological traits are important because functional diversity (the different roles that species play) may be more influential on ecosystem processes than taxonomic diversity or species richness (Giller et al. 2004). Without this ecological information for each species in a system, traits of related species or higher taxonomic groupings may be used instead. Although closely related species may share certain characteristics, intra-taxon differences in morphology, feeding behaviors, and habitat use do exist. Food web studies, which link individual species and biodiversity to ecosystem functioning

(Thompson et al. 2012), can be confounded by grouping or averaging organisms with dissimilar life histories. Considering all asteroids as predators, for example, can obscure understanding of trophic dynamics given that prey type and trophic level varies by species.

Benthic organisms, particularly those that utilize soft sediments as habitat and feed infaunally, bioturbate the sediment by moving over and through the substrate and by sorting food and sediment particles (Rhoads and Young 1970; Norling et al. 2007). Feeding and respiration of sediment-dwelling species also influences oxygen and organic nutrient transport throughout the sediment (Norling et al. 2007). The large aggregations of the burrowing asteroid *Ctenodiscus crispatus* (average ~200 ind ha^{-1}, up to ~6000 ind ha^{-1}) in the Laurentian Channel will process and redistribute large amounts of labile carbon by working through the sediment, which likely impacts co-occurring benthic species. Canada's Department of Fisheries and Oceans has identified the Laurentian Channel to be an Area of Interest for creation of a Marine Protected Area, due in part to its importance for the reproduction and feeding of many species (Department of Fisheries and Oceans 2011). Characterizing the influence of the abundant *C. crispatus* will contribute to a full understanding of this region. Other sediment-dwelling and infaunal feeding asteroid species, such as *Leptychaster arcticus* and *Plutonaster agassizi,* are also likely to influence local sediment and nutrient conditions, but are not known to form the dense aggregations seen in *C. crispatus*. Nonetheless, our understanding of the behaviors of most infaunal species remains limited.

Areas with large numbers of asteroids will experience strong predation pressures. *Hippasteria phrygiana* and *C. granularis,* which feed on corals and sponges, span wide geographic and bathymetric distributions. They are particularly abundant along the northeast NL shelf and slope, an area known to support diverse corals (Wareham and Edinger 2007) and abundant sponges (NAFO 2008; Fuller 2011). *Hippasteria phrygiana,* which I observed to feed on many coral species, is one of the largest-bodied and most abundant asteroids in this region; it likely ingests large volumes of material and could damage vulnerable coral communities already impacted by anthropogenic activities. Although aggregations of *H. phrygiana* have not been observed, individuals may form pairs during reproductive events in June and July (Baillon et al. 2011) that could lead to localized seasonal increases in *H. phrygiana* abundance and predation pressure. Predation by asteroids may constitute an important predator-prey relationship not been addressed in the northwest Atlantic. In Newfoundland, the asteroid *Solaster endeca* preys on recently settled sea cucumbers (So et al. 2010), but whether *H. phrygiana, C. granularis,* or other asteroid species prey on juvenile corals and sponges remains unknown. If predation on newly recruited sponges and corals exacerbates predation on adult populations, asteroids may strongly influence the distribution and abundance of these habitat-forming species more than previously recognized.

4.2 Future directions

This thesis contributes to the growing understanding of the ecology of the benthos of the continental shelf and slope around Newfoundland and Labrador and in eastern Canada. Previous studies of this area describe the distributions and associations of corals (Wareham and Edinger 2007; Baker et al. 2012a), sponges (NAFO 2008; Fuller 2011), other benthic species (Barrio Frojan et al. 2012), and fish (Baker et al. 2012b; Kenchington et al. 2013), and provide information on trophic interactions of fish and benthic invertebrates (Sherwood and Rose 2005) and corals (Sherwood et al. 2008). Collectively, these studies help inform how each species affects its community and how each will, in turn, be affected by changes to the environment and to biodiversity.

Although I have identified two species likely to be important predators of habitat-forming organisms and several others that contribute to bioturbation and sediment disruption, further work is required to assess the true functional diversity of Asteroidea in eastern Canada. For logistical reasons I only analyzed the diets of seven species in Chapter 2; the diets of at least 20 additional asteroid species remain unknown. Given that most species occur on soft sediments, many are likely infaunal or deposit feeders; however, niche partitioning amongst co-occurring benthic feeders remains to be addressed. Additionally, habitat use remains unknown for many species not observed in my ROV video analysis. Areas that would benefit from additional ROV surveys include: deep areas (> 1500 m) of the NL shelf and slope, where distinct species assemblages exist; areas along the shelf break, where asteroid diversity is high; hard-substrate areas inhabited by distinct fauna; and coral- and sponge-rich areas that could be impacted by asteroid predation. Laboratory experiments and observations can provide insight into the behaviors of deep-water species that are difficult or impossible to observe *in situ.* Ideally, future studies of the NL benthos will provide additional ecological information on under-studied asteroids and other non-commercial species, given that each species contributes to the functioning of the continental shelf and slope ecosystem.

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