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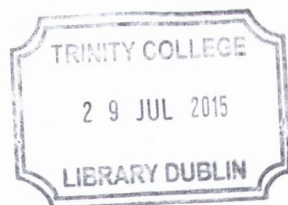
Deep-sea coral reef ecology:
Feeding mechanisms, community interactions, and habitat
associations of deep-sea echinoids

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A thesis submitted in partial fulfillment of the requirements of the award of Doctor of
Philosophy

September 2014

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Thesis 10646

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Angela Stevenson

01/09/2014 Dublin

Author contributions

Table 1. Chapter 2 author contributions

Contributor	Statement of contribution
Angela Stevenson (candidate)	Designed sampling protocol. Analyzed the data. Wrote the paper.
Dr. Carlos Rocha	Provided insight for the discussion. Edited the paper.

Table 2. Chapter 3 author contributions

Contributor	Statement of contribution
Angela Stevenson (candidate)	Conceived and designed methods. Analyzed the data. Wrote the paper.
Prof. Fraser J.G. Mitchell	Edited the paper.

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Prof. Fraser J.G. Mitchell	Provided insight for the discussion and results. Edited the paper.
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Prof. Fraser J.G. Mitchell	Provided insight for the discussion and results. Edited the paper.

In memory of a dear friend, Caoimhe Muldoon, who lived her life with so much compassion.

Summary

The ultimate aim of the thesis was to probe into the ecology of deep-sea echinoids in order to contribute newfound information to this topic, as well as develop tools to facilitate ecological work in deep-sea environments. This was achieved using a multifaceted approach, including analyses of gut content and stable isotope, as well as video and image analyses; data and samples for these came from field work in Ireland and France, in the NE Atlantic; and seamounts in Australia and New Zealand, in the SW Pacific.

Firstly, gut content analyses helped elucidate specific food sources consumed by echinoids. *E. affinis* and all echinothurids (except *A. fenestratum*) were sediment filled, which is the usual type of material found in the guts of deposit feeders. But those of *A. fenestratum*, *C. cidaris*, *G. elegans*, and *G. alexandri* unexpectedly held a wide range of materials. Their contents revealed spectacular feeding habits on highly desirable material such as the coral infrastructure and crinoids, suggesting that some deep-sea echinoids engage in carnivory on both sessile and highly mobile invertebrates. While stable isotope analyses (SIA) added very little to our understanding of specific food sources consumed, it did provide evidence suggesting that coral material might be an important source of organic nitrogen for somatic tissue growth in some echinoid taxa. And enriched $\delta^{15}\text{N}$ values suggest that echinoids incorporate foods with distinctly higher $\delta^{15}\text{N}$ values than that of POM and sediment. These results could be a consequence of opportunistic feeding as well as bioerosion of the live coral framework and consequent grazing of fauna attached to the dead coral infrastructure.

Secondly, SIA further contributed to our knowledge of deep-sea echinoid nutritional information as it provided valuable information regarding trophic positioning, and assimilation of nitrogen and carbon from food sources for somatic and reproductive growth. Sympatric echinoid taxa spanned three benthic trophic levels suggesting an expansion of echinoid taxa trophic niches. Evidence of nutrient partitioning among coexisting echinoid taxa was also found in the carbon data. Significant interspecific differences were found in the $\delta^{13}\text{C}$ signatures of the somatic and reproductive tissues suggesting that different sources of carbon are assimilated into all tissues after the deposition of phytodetritus has taken place on the deep sea floor. However, this pattern differed for the data obtained before the deposition of phytodetritus; similar sources of carbon were assimilated into somatic tissues

of different taxa, while some of these different taxa utilized significantly different sources of carbon to manufacture their reproductive tissues.

Seasonally deposited phytodetritus was incorporated into the reproductive tissues of the seasonal breeder, *G. alexandri*, but not those of continuous breeders, Cidaroida and Echinothurioida. The material however was also found to support somatic tissue growth in cidaroids. Hence seasonal breeders might utilize surface-derived phytodetritus to manufacture reproductive tissues, while continuous breeders might only utilize it for somatic tissue growth or not at all. Poor spatial repeatability compromise these results, thus requiring further investigation to better understand the role of phytodetritus in fuelling the growth and reproduction of deep-sea echinoids.

Thirdly, video analyses of echinoid interactions with predators and competitors (inter- and intraspecific) suggest that the coral infrastructure not only provides an important food source for deep-sea echinoids, but also protection from predators. Migration along the coral infrastructure may be a predator-driven behaviour as echinoids seek refuge from predators. Interspecific competition may influence species-specific hierarchy on nutritiously valuable substrates in the deep-sea, but the lack of statistical significance in these trends merit further investigation in order to disambiguate the role of competition in deep-sea coral habitats. Overall, predation risk might play a stronger -or more detectable- role than competition in structuring echinoid space and resource use in deep-sea coral habitats.

Lastly, despite the added benefit of food and shelter provided by coral habitats, habitat-associations reveal that not all taxa prefer these habitats. Some taxa had a random association with various habitats, while others displayed non-random associations; and two distinct habitat preferences were detected in the study: some echinoids had a much greater affinity for living types of habitats, while others were more widespread over different types of habitats suggesting a more generalist association for available habitats. Also, population structure was significantly affected by habitat-related variables; of these variables, interspecific competition, depth, and fishing history were the most influential factors in determining the distribution patterns of echinoids.

The study emphasizes the value of video and image data as a reliable, effective, and inexpensive tool for conducting ecological research in the deep sea, and with it's evolution will no doubt continue to elucidate processes taking place in these systems.

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Nudibranch captured on Madrepora oculata (BOBECO cruise 2011)

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A beautiful specimen of Histocidaris purpurata

General introduction

1. Ecology in the deep sea

A principal objective in ecology is to study the factors driving spatial distribution and abundance patterns of populations, ultimately leading to the understanding of the observed community structure (Paine, 1974). Such factors are clear for neritic habitats where spatial differences in patterns of abundance, distribution, and behaviour have been attributed to food availability, competition, and predation (Paine, 1974; Menge and Sutherland, 1976; Sammarco, 1980; McClanahan, 1988; Birkeland, 1989; Rochette and Himmelman, 1996; Privitera et al., 2008; Orrock et al., 2013). But for deep-sea habitats few studies have examined the underlying ecological processes structuring these communities.

Deep-sea ecosystems are important both from an ecological and economic point of view, but their protection remains sparse and existing conservation methods are ill designed for these systems (Koslow, 2007). The need to further understand these deep-sea coral habitats is made apparent from the extensive anthropogenic damage observed in these habitats. The problem originates from a combination of our latent understanding of their ecology and their silent suffering as they remain hidden in the deeper parts of this world where their troubles persist out of sight from those who might want to preserve them. Prior knowledge of interactions between species in a community is required in order to make informed management decisions that will protect vulnerable ecosystems such as deep-sea coral habitats.

While ecological research is relatively accessible in shallow-water habitats, high costs and technical difficulties render these same studies inapplicable to deep-sea environments. However, the recent introduction and refinement of submersibles for deep-sea scientific investigations have enabled deep-sea research to move beyond a purely exploratory nature, where paradigms were generated, to a more experimental phase where ecological hypotheses begin to be tested (Danovaro et al., 2014). Remotely operated vehicles (ROV), benthic landers and bottom crawlers have permitted the recent exploration of hydrothermal vents, seeps, coral reefs, and precise collections and manipulative experiments in such habitats (Danovaro et al., 2014).

1.1 Feeding mechanisms in the deep sea and links to growth and reproduction

Specialized feeding mechanisms allow deep-sea megabenthos to adapt to limited resources available in deep ecosystems (Jumars et al., 1990). It is clear that deep-sea echinoderms have adapted to restricted food conditions, but our understanding of these adaptations and their nutrition is limited. For example, nutrient partitioning has been demonstrated in deep-sea holothurians and is thought to reduce competitive interactions between coexisting taxa (Billett et al., 1988; Miller et al., 2000; Wigham et al., 2003; FitzGeorge-Balfour et al., 2010), but this same feeding selectivity has not been established for other classes of echinoderms.

Also, a strong seasonal deposition of phytodetritus occurs in pulses coupled to surface ocean productivity in the NE Atlantic (Billett et al., 1983; Lampitt, 1985; Jumars et al., 1990; Thurston et al., 1994; Duineveld et al., 2004). Holothurians, echinoids, and ophiuroids are thought to exploit these ephemeral sources of phytodetritus, but its contribution to the total spectrum of nutrients assimilated into the organism is unknown because evidence linking it to seasonal growth and reproduction remains circumstantial (Tyler et al., 1982; Tyler and Gage, 1984b; Billett et al., 1988; Tyler, 1988; Gooday and Turley, 1990; Campos-Creasey et al., 1994; Tyler et al., 1995). For example, this material is thought to be used in reproductive growth, especially to fuel the energetically expensive vitellogenesis (Tyler et al., 1982; Tyler, 1988; Gooday and Turley, 1990), but it is unclear how it affects growth and reproduction. Is this material used by echinoids to coordinate reproductive events, and/or does it contribute towards nutrients assimilated for somatic growth and reproduction in echinoids?

1.1.1 Stable isotope ecology

Carbon and nitrogen stable isotope analyses (SIA) of tissues are a useful tool for investigating both the feeding habits of organisms (Peterson and Fry, 1987; Iken et al., 2001). Using these isotopes, ecological processes and activities can be traced and reconstructed (West et al., 2006). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures have provided valuable information on energy flow, nutrients consumed, and trophic relationships in estuaries, marine, and terrestrial systems (Koike et al., 1987; Peterson and Fry, 1987; Gage and Tyler, 1992; Ambrose and Norr, 1993; O'Reilly et al., 2002; Tayasu et al., 2002; Yatsuya and Nakahara, 2004; Michener and Lajtha, 2007). These allow for the measurement of carbon

and nitrogen assimilated by the organism and thus outline nutritionally important materials ingested (Melville and Connolly, 2003).

Shifts in $\delta^{15}\text{N}$ signatures are particularly useful in trophic positioning and $\delta^{13}\text{C}$ signatures are most useful in identifying the food source in an organisms diet (Suchanek et al., 1985; Mincks et al., 2008; van Oevelen et al., 2009). These can also provide a time-integrated measure of feeding history (Vander Zanden and Rasmussen, 2001; Tomas et al., 2006). Isotopic shifts can be seen in migratory birds, animals that undergo metamorphosis, and others changing diets due to shifts in food sources (Phillips and Eldridge, 2006). Due to varying turnover rates, isotopic enrichment differs between tissue types; looking at the isotopic composition of multiple tissues simultaneously can provide a more complete dietary history of the animal under investigation (Tieszen et al., 1983; Iken et al., 2001; Phillips and Eldridge, 2006). Blood plasma, liver, and gonads, for example, are known to have high turnover rates, so these tissues tend to reflect a more recent diet consumed during the shorter period of tissue formation (Tieszen et al., 1983; Iken et al., 2001; Phillips and Eldridge, 2006). ‘Long-lived’ tissues, such as muscle and bone, tend to have a lower turnover rate and thus provide an integrative measure of the food assimilated over a longer time span (Tieszen et al., 1983; Iken et al., 2001; Phillips and Eldridge, 2006; Tomas et al., 2006).

1.2 Species interactions and habitat associations

Over the past 10 years, refinement of ROVs and development of fiber optic communications and novel imaging tools have produced high quality deep-sea images suitable for ecological investigations (Danovaro et al., 2014). From these developments, it became possible to use imagery from deep-sea video transects to map habitats and quantitatively investigate megafaunal assemblages in deep-sea environments (Smith et al., 1993; Priede and Merrett, 1998; Lampitt et al., 2001; Solan et al., 2003, Jones et al., 2007; Howell et al., 2010). While video transects have proven to be a powerful tool to study these aspects of deep-sea megafaunal ecology, no study has yet exploited them to investigate ecological topics such as community interactions and habitat associations. Nevertheless, high definition video and image data from the deep sea have recently become readily

available and plentiful, making them an ideal resource to address ecological questions such as those concerning predator-prey and competitive interactions, for example.

1.2.1 Predation and competition in the deep sea

Predation pressures have a strong influence on the population structure, distribution, abundance, and behavioural adaptations of shallow-water echinoids (Carpenter, 1984; Scheibling and Hamm, 1991; Vadas and Elner, 2003). Predators of tropical coral and shallow-water temperate reef echinoids primarily consist of reef-fish species and decapods (Muntz et al., 1965; Birkeland, 1989; Scheibling, 1996; Barnes and Crook, 2001). Here, aggregative and flight responses have been proposed as prominent and effective mechanisms to reduce predation risk from such predators (see Scheibling, 1996; and Vadas and Elner, 2003).

Analytical work conducted on deep-sea communities has revealed significant positive correlations between gastropod predator diversity and overall infaunal diversity (Rex, 1976). Also, experimental work has shown that predation possesses a strong effect on the organization of infaunal assemblages (Thistle et al., 2008; Gallucci et al., 2008a, 2008b) and hydrothermal communities (Micheli et al., 2002), but the effect of predators on the behaviour of deep-sea megabenthos largely remains unknown. As well, feeding (Booolootian et al., 1959) and seasonal breeding (Young et al., 1992) aggregates have been documented among deep-sea echinoids, but there is no mention of defensive aggregates in the deep sea. It is likely, however, that behavioural adaptations coincide with those observed in their shallow-water counterparts.

Competitive interactions have also been deemed a crucial player in explaining deep-sea diversity patterns (Sanders, 1968; Slobodkin and Sanders, 1969; Grassle and Sanders, 1973). For example, a minimum distance found in the morphospace of deep-sea gastropod species suggests that these gastropod communities might be structured by competition (McClain, 2005). And megabenthic disturbance by mobile deposit feeders and scavengers near submarine canyon cliff faces reinforces the importance of habitat modifiers in the deep sea (McClain and Barry, 2010). Studies directly testing this hypothesis in the deep sea are lacking, but this paradox has been thoroughly tested in shallow water echinoids. Under food-limited conditions, inter- and intraspecific competition is frequently observed and

niche partitioning is common among shallow-water echinoids (Sammarco, 1980; McClanahan, 1988; McClanahan and Muthiga, 1988; Shulman, 1990; McClanahan, 1992; Privitera et al., 2008). The sympatrically occurring taxa, *Echinometra mathaei*, *Diadema savignyi*, and *Diadema setosum*, are spatially specialized to avoid competition with each other (McClanahan and Muthiga, 1988). They utilize different sized burrows and crevices when avoiding predators. In experimental trials, *Echinometra lucunter* and *Echinometra viridis* commonly engage in agonistic interactions between conspecifics and congeners, where encounters result in pushing, biting, and subsequent conquest of a location (Shulman, 1990).

Like *Echinometra* and *Diadema*, the two deep-sea echinoid taxa under observation in the present study, echinothurids and *C. cidaris*, co-occur in *Lophelia-Madrepora* reefs and surrounding habitats (Stevenson and Rocha, 2013). Where they co-occur within *Lophelia-Madrepora* reefs, these echinoids preferentially feed on the coral infrastructure (*i.e.*, dead and living reef) because it represents a potentially important and nutritious food source for echinoids (Stevenson and Rocha, 2013). While echinothurids and *C. cidaris* share these similarities in space and food resource use, it is unclear whether competition is taking place, but given that they depend on a similar food source within the same habitat then we assume that there is some degree of competition taking place for the coral resource as both food and refuge space.

1.2.2 Habitat associations

Understanding patterns of habitat use is an important aspect of animal ecology as it is the necessary first step towards understanding the ecological interactions between species and their predators, prey, competitors, and environment that shape these distributions (Heithaus et al., 2006). This is particularly important for ecologically important taxa like echinoids, which play a pivotal role in nutrient recycling and system engineering of shallow-water habitats (e.g., Bromely, 1978; Glynn et al., 1979; Sammarco, 1980; Koike et al., 1987; Jumars et al., 1990; Scheibling and Hamm, 1991; Bak, 1994; Glynn, 1997; Sauchyn and Scheibling, 2009).

Important species-specific reef interactions and habitat associations have been described for shallow-water systems, but relatively few studies have examined interactions

and associations in deep-sea coral habitats. Quattrini et al. (2012) documented habitat associations for fish and invertebrates on a deep-sea coral mound in California. The reef fauna was found to have high habitat specificity whereby fishes were shown to have a greater affinity for high vertical profile, degree of coral coverage, and topographic complexity and some megafaunal taxa associated with certain fine-scale factors while others had a more generalist association. Similarly, Marsh et al (2012) describe a consistent pattern of faunal zonation with distance from the hydrothermal vent source.

2. Aims of this study

The study broadly focuses on the feeding ecology, predator-prey and competitive interactions, as well as taxa-specific habitat associations of ten echinoid taxa in the NE Atlantic and six in the SW Pacific (Table 1).

Table 1. Echinoids investigated in each chapter and region.

Geographic region	Echinoid	Chapter
Northeast Atlantic	<i>Gracilechinus elegans</i>	Ch 2, 3
	<i>Gracilechinus alexandri</i>	Ch 2, 3
	<i>Gracilechinus affinis</i>	Ch 3
	<i>Cidaris cidaris</i>	Ch 2, 3, 4, 5
	<i>Histocidaris purpurata</i>	Ch 3
	<i>Tromikosoma uranus</i>	Ch 3
	<i>Phormosoma placenta</i>	Ch 3
	<i>Sperosoma grimaldii</i>	Ch 3
	<i>Hygrosoma petersii</i>	Ch 3
	<i>Araeosoma fenestratum</i>	Ch 2, 3, 4, 5
Southwest Pacific	<i>Dermechinuds horridus</i>	Ch 5
	<i>Caenopedina porphyrogigas</i>	Ch 5
	<i>Gracilechinus multidentatus</i>	Ch 5
	<i>Poriodidaris purpurata</i>	Ch 5
	<i>Caenopedina otagoensis</i>	Ch 5
	Echinothuriidae	Ch 5

The study specifically aimed to:

(1) Elucidate the feeding mechanisms of deep-sea echinoids to further illustrate processes of resource exploitation by deep dwelling megabenthos under limited food resources by investigating, via gut content, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ stable isotope analyses:

- (i) potential food sources for echinoids (Chapter 2 & 3),
- (ii) comparing the history of food sources assimilated by coexisting taxa to see if nutrient partitioning is taking place to reduce interspecific competition (Chapter 3),
- (iii) examining how seasonal dietary shifts linked to the deposition of surface productivity might affect tissue formation in seasonal and continuous breeders (Chapter 3)

(2) Chapter 4 investigated the effects of predator-prey and competitive (*i.e.*, inter- and intraspecific) interactions on space and resource use by deep-sea echinoids in coral habitats.

(3) Chapter 5: “Species-specific coral habitat associations of echinoids in the deep sea” aimed to:

- (i) document the distribution of echinoids in deep-sea coral habitats,
- (ii) determine whether echinoids are associated with specific deep-sea coral habitats,
- (iii) explore relationships between echinoid distribution and six habitat-related predictor variables,
- (iv) determine if the patterns of distribution differ with taxonomic resolution.

(4) Evaluate video and image analyses as a potential tool to probe into the ecology of deep-sea megabenthos (Chapters 4 & 5).

The hypotheses tested were as follows:

(1) Chapter 3 tested the null hypothesis that deep-sea echinoids

- (i) feed at similar trophic levels ($\delta^{15}\text{N}$ signatures compared across similar tissues),
- (ii) on similar food sources ($\delta^{13}\text{C}$ signatures compared across similar tissues),
- (iii) and their tissue formation is not affected by seasonal dietary shifts linked to the seasonal deposition of surface productivity (achieved by comparing $\delta^{13}\text{C}$ signatures of tissues in spring and late summer; before and after deposition, respectively).

(2) Chapter 4 tests the null hypothesis that predation and competition have no effect on echinoid aggregation patterns and space use, such as positioning on the coral infrastructure (*i.e.*, live and dead reef structure) and substrate use.

(3) Chapter 5 specifically tests the null hypotheses

- (i) of a random association between echinoid distribution and habitats in which they occur,
- (ii) echinoid population structure within habitats is not significantly affected by habitat-related variables such as water depth, distance to nearest seamount, fishing intensity, the presence of other echinoids, geomorphology, and predator activity in the area,
- (iii) patterns of habitat association observed at a broad taxonomic scales do not differ from those at a more refined level.

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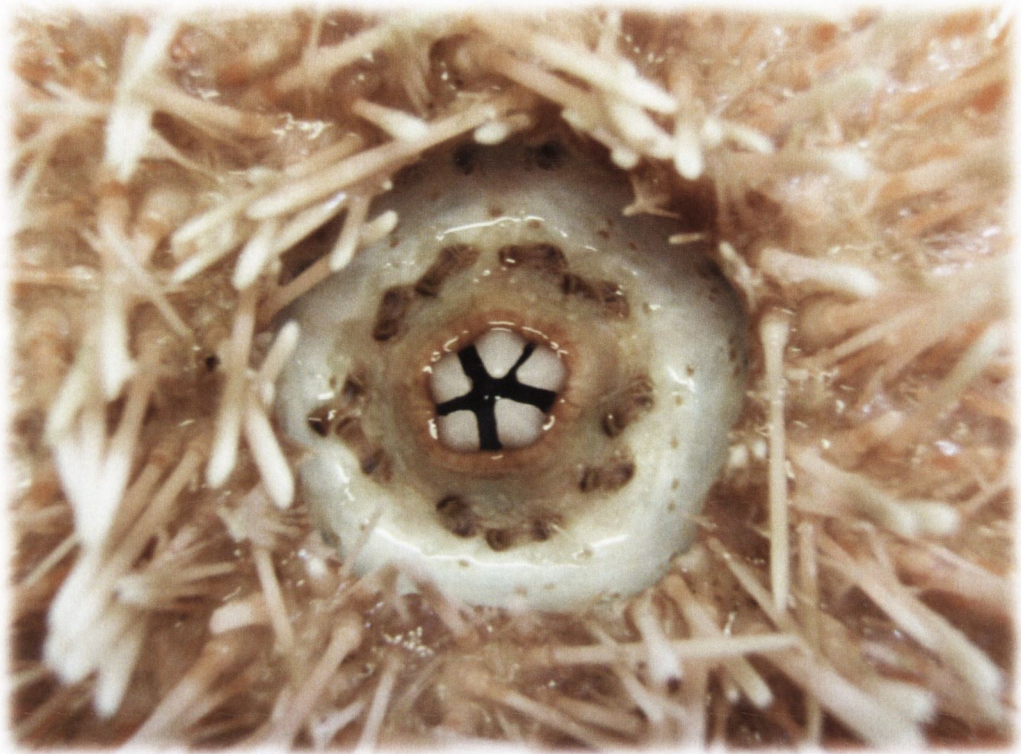
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Powerful teeth of Aristotle's Lantern from Gracilechinus elegans

Evidence for the bioerosion of deep-water corals by echinoids in the Northeast Atlantic

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Abstract

In situ video observations of echinoids interacting with deep-sea coral are common in the deep-sea, but paradoxically the deep-sea literature is devoid of reports of bioerosion by extant echinoids. Here we present evidence of contemporary bioerosion of cold-water coral by four species of deep-sea echinoids, *Gracilechinus elegans*, *Gracilechinus alexandri*, *Cidaris cidaris*, and *Araeosoma fenestratum*, showing that they actively predate on the living framework of reef building corals, *Lophelia pertusa* and *Madrepora oculata*, in the NE Atlantic. Echinoid specimens were collected in six canyons located in the Bay of Biscay, France and two canyons on the north side of the Porcupine Bank and Goban Spur, Ireland. A total of 44 live specimens from the four taxa (9 of *G. elegans*, 4 of *G. alexandri*, 21 of *C. cidaris* and 10 of *A. fenestratum*) showed recent ingestion of the coral infrastructure. Upon dissection, live coral skeleton was observed encased in a thick mucus layer within the gastrointestinal tract of *G. elegans* and *G. alexandri* while both live and dead coral fragments were found in *C. cidaris* and *A. fenestratum*. Echinoid bioerosion limits the growth of shallow-water reefs. Our observations suggest that echinoids may also play an important role in the ecology of deep-water coral reefs.

Keywords: Echinoid; bioerosion; gut content; deep-sea coral; *Lophelia pertusa*; *Madrepora oculata*; NE Atlantic; Bay of Biscay ; Porcupine Bank

1. Introduction

Bioerosion is an essential process regulating the degradation of carbonate skeletal material in marine habitats and an important aspect of reef ecology that is often overlooked (Wisshak et al., 2005). In deep-sea coral reefs, bioerosion has received little attention despite a wealth of recent studies carried out in an effort to gather evidence supporting conservation strategies for these environments (*e.g.*, Bromley, 2005; Mah et al., 2010). Cold-water coral habitats constitute refuge for a host of mega- and macroinvertebrates, but interactions, trophic or otherwise, between them and the host are not fully understood. Research conducted on *Lophelia* skeleton bioerosion to date has largely focused on endolithic (boring and encrusting) forms, such as the sponges *Alectona millari* and *Aka labyrinthica*; the foraminifer *Hyrrokin sarcophaga*; the fungus *Dodgella*; and the sabellid worm *Perkinsiana socialis* (Rogers 2004; Beuck and Freiwald, 2005; Bromley, 2005; Wisshak et al., 2005; Beuck et al., 2007).

Among known extant epilithic bioeroders, asteroides, such as the Hippasterinae, are accepted as the main predators of deep-sea coral (Krieger and Wing, 2002). These echinoderms are known to erode gorgonians, alcyonaceans, antipatharians and other deep-sea cnidarians (Krieger and Wing, 2002; Mah et al., 2010). Other predators of the alcyonacean *Primnoa* include nudibranchs and snails (Krieger and Wing, 2002). The rare gastropods, “*Coralliophila*” *richardi* and *Babelomurex sentix* (Coralliophilinae), are known bioeroders of *Lophelia* and *Madrepora* in Mediterranean deep-waters (Taviani et al., 2009). *In situ* video and image observations of echinoids interacting with deep-sea coral are common (see p. 34 in Reed and Ross, 2005; p. 70 in Freiwald et al., 2009; p. 22 in Munoz et al., 2012) and some figure captions suggest that they are ‘grazing’ on the coral (see Freiwald et al., 2009). However, further reports and discussion about the bioerosion behaviour is absent from the deep-sea literature.

In shallow-water habitats, echinoids have long been known to play a crucial role in tropical coral reef development and stability. The echinoid genera *Diadema*, *Echinometra*, *Echinostrephus* and *Eucidaris* have been described as the major bioeroders in shallow-water habitats (Bak, 1994; Glynn, 1997). Their role effectively modulates the balance between reef accretion and destruction, hence playing a crucial function in tropical coral reef stability (Bromley, 1978; Glynn et al., 1979; Bak, 1994). Yet in deep-sea habitats this

position of echinoids as ecosystem engineers has largely been overlooked. Tooth scratches by regular echinoids, *Gnathichnus pentax*, have been documented on *Lophelia* material from the Pleistocene (*e.g.*, Bromley, 2005), but no other accounts of contemporary echinoid bioerosion have been reported in the deep-sea literature.

Here, we report 44 gut content observations of the echinoids *Gracilechinus elegans* (formerly known as *Echinus elegans*), *Gracilechinus alexandri*, *Cidaris cidaris*, and *Araeosoma fenestratum* collected in six canyons in the Bay of Biscay, France, as well as two canyons on the north side of the Porcupine Bank and on the Goban Spur, Ireland. This evidence is complemented by *in situ* video observations suggesting active predation on the living framework of reef building coral, *Lophelia pertusa* and *Madrepora oculata*. The study describes and discusses this previously unreported bioerosion activity by deep-sea echinoids.

2. Materials and methods

2.1 Study area

All echinoid specimens used in this study were collected during three cruises (BOBECO with the ‘*Pourquoi pas?*’; CE10004 and CE11006 with the ‘*Celtic Explorer*’) in the Northeast Atlantic, within French and Irish waters (Fig. 1): eight sites in the Bay of Biscay, in six different canyons (one site within the Croizic, Guilvinec, Crozon, and Morgat Douarnez canyons and two sites in the Lampaul and the Petit Sole canyon during BOBECO); four sites on the Irish continental shelf (two sites on the Goban Spur during CE11006; and two in canyons on the north side of the Porcupine Bank during CE10004). Reef building coral was present at all sites where specimens were collected.

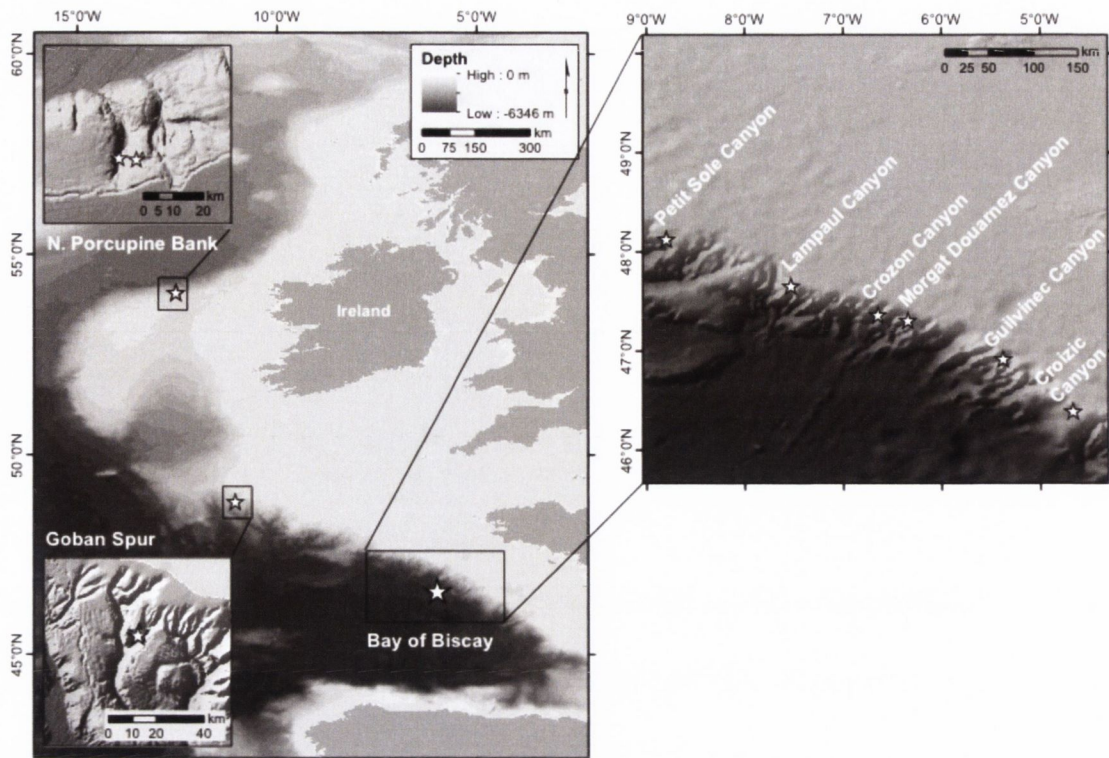


Fig. 1. Location of the study area and sampling stations in canyons on the Irish continental shelf and Bay of Biscay, NE Atlantic Ocean.

2.2 Collection and treatment of samples

Echinoids were collected randomly at preselected random points in a quadrat (during the BOBECO cruise with the ‘*Pourquoi pas?*’) and along transects (during the CE10004 and CE11006 cruises with the ‘*Celtic Explorer*’) spanning coral habitat. Actual collection took place during 12 dives, eight with the remotely operated vehicle (ROV) Victor 6000 (during the BOBECO cruise) and four conducted with ROV Holland I (two each during the Irish cruises, CE10004 and CE11006). Echinoids were collected *in situ* with either the mechanical arm or suction hose of the ROVs. Upon recovery, specimens were dissected on board and gut content analyses were performed immediately following dissection. When needed, corallites found in the gut contents were bleached for one hour with sodium hypochlorite to facilitate observation of the cup and septa for identification of the coral.

3. Results

A total of 78 echinoids belonging to five different species were collected during three cruises. Among this collection, 44 echinoids belonging to four taxa had coral fragments in their gastrointestinal tract (Table 1). Both living and dead coral fragments were found during dissections. A thick layer of mucus accompanied the living coral, but was not present when only dead coral was observed in the guts.

Table 1. Source of samples and summary of echinoids collected during BOBECO, CE10004, and CE11006 cruises. Two categories were formed, one for live coral ('coral') and dead coral ('coral rubble'). The presence of mucus or coral tissue is indicated in brackets ('mucus, tissue').

Cruise ID	Locality	Site ID	Depth (m)	No. of Echinoids	Species	Type of coral observed in gut contents
CE10004	North side of Porcupine Bank (Canyon 2)	E74	1350	2	<i>G. elegans</i>	Coral (mucus, tissue)
				1	<i>C. cidaris</i>	-
	North side of Porcupine Bank (Canyon 2)	E108	1300	6	<i>G. elegans</i>	Coral (mucus, tissue)
				2	<i>G. alexandri</i>	-
CE11006	Goban spur	E12	1380	2	<i>G. alexandri</i>	Coral (mucus)
				1	<i>G. alexandri</i>	-
				1	<i>G. alexandri</i>	Coral
BOBECO	Croizic Canyon, Bay of Biscay	PL468	800-850	3	<i>C. cidaris</i>	Coral (mucus)
				2	<i>C. cidaris</i>	-
				1	<i>A. fenestratum</i>	-
				1	<i>C. cidaris</i>	Coral (mucus, tissue)
	Guilvinec Canyon, Bay of Biscay	PL469	800-900	2	<i>C. cidaris</i>	-
				3	<i>C. cidaris</i>	Coral rubble
				1	<i>A. fenestratum</i>	Coral
				1	<i>G. alexandri</i>	Coral
	Lampaul Canyon, Bay of Biscay	PL470	1500	1	<i>G. elegans</i>	Coral (mucus, tissue)
				1	<i>G. alexandri</i>	-
				1	<i>S. grimaldii</i>	-
				4	<i>C. cidaris</i>	Coral rubble
	Petit Sole Canyon, Bay of Biscay	PL471	700	4	<i>C. cidaris</i>	-
				1	<i>C. cidaris</i>	Coral (mucus), coral rubble
				9	<i>C. cidaris</i>	-
				2	<i>C. cidaris</i>	Coral
	Petit Sole Canyon, Bay of Biscay	PL476	700	2	<i>C. cidaris</i>	Coral rubble
				1	<i>A. fenestratum</i>	Coral
				2	<i>C. cidaris</i>	Coral rubble
				1	<i>A. fenestratum</i>	Coral
	Lampaul Canyon (2), Bay of Biscay	PL478	500-1000	2	<i>C. cidaris</i>	Coral rubble
				1	<i>A. fenestratum</i>	Coral rubble

Crozon Canyon, Bay of Biscay	PL479	1100-1200	1	<i>A. fenestratum</i>	Coral (mucus), coral rubble
			1	<i>A. fenestratum</i>	Coral
			1	<i>A. fenestratum</i>	Coral, coral rubble
			1	<i>A. fenestratum</i>	Coral rubble
			1	<i>A. fenestratum</i>	-
Morgat Douarnez Canyon, Bay of Biscay	PL480	700-900	2	<i>A. fenestratum</i>	Coral
			1	<i>A. fenestratum</i>	Coral
			2	<i>A. fenestratum</i>	-
			3	<i>C. cidaris</i>	Coral
			7	<i>C. cidaris</i>	-

In total, nine specimens of *G. elegans* were collected in the NE Atlantic, one in Lampaul Canyon and eight on the north side of the Porcupine Bank. All contained coral fragments encased in a thick mucus layer within their gastrointestinal tract (Fig. 2; Table 1). The presence of live coral in the guts of these echinoids is further supported by polyp tissue found attached to the coral skeleton (See Table 1; Fig. 2C and D). These contents consisted only of the living skeleton of *L. pertusa* and *M. oculata*.

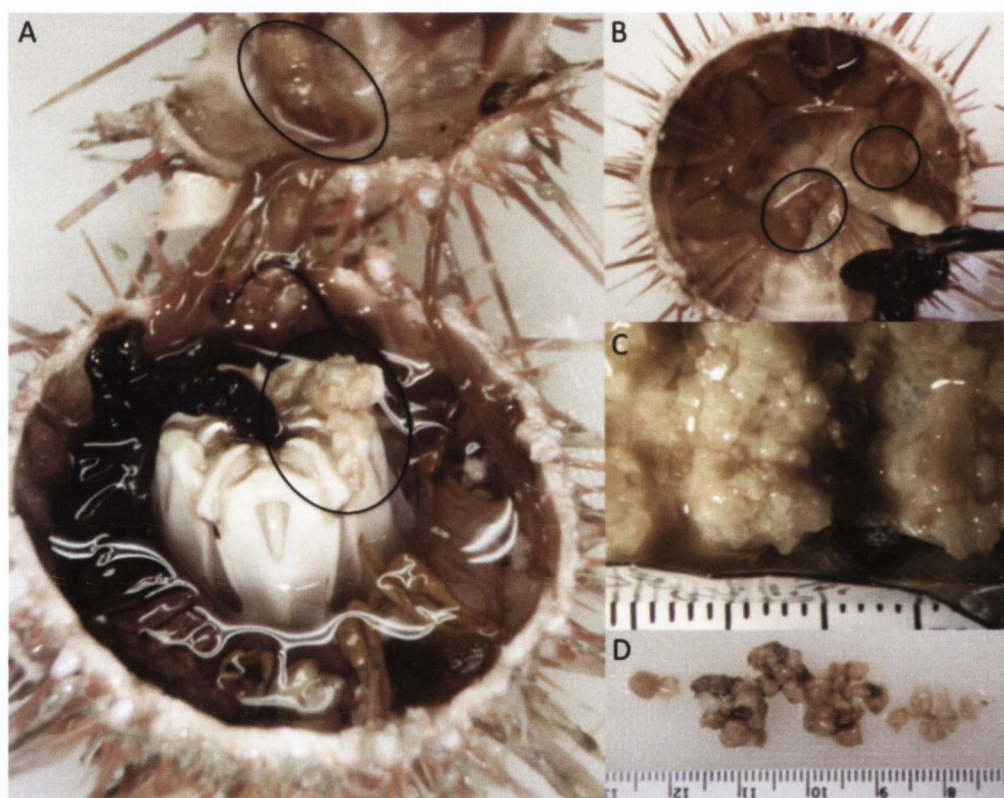


Fig. 2. Coral fragments (circled above) are shown in the gastrointestinal tract of specimens of *Gracilechinus elegans* collected at sites E74 (A) and E108 (B) on the north side of the Porcupine Bank, Ireland. (C) Pooled coral fragments found in the gastrointestinal tract of the five *G. elegans* specimens collected at site E108. (D) Coral fragments obtained from the gut contents of *G. elegans* collected in Lampaul Canyon, France.

Eight specimens of *G. alexandri* were collected at the French and Irish sites (see Table 1). Coral fragments were found in four specimens spanning both locations. While other material, including sediment, appeared to have been ingested by *G. alexandri*, only fragments of the coral framework that were living (*i.e.*, including soft tissue) were present in its gastrointestinal tract.

A total of 46 specimens of *C. cidaris* were collected, but only those from the Bay of Biscay had coral in their gastrointestinal tract. Upon dissection, 21 specimens had coral fragments in their guts; ten of these contained living fragments of *L. pertusa* and *M. oculata*. Similarly, ten of the fourteen *A. fenestratum* specimens collected contained coral fragments in their gastrointestinal tract and in eight of these the fragments included soft tissue (Fig. 3). For both taxa, mucus also accompanied gut contents containing live coral, but it was not present in specimens containing fragments of the dead coral infrastructure.

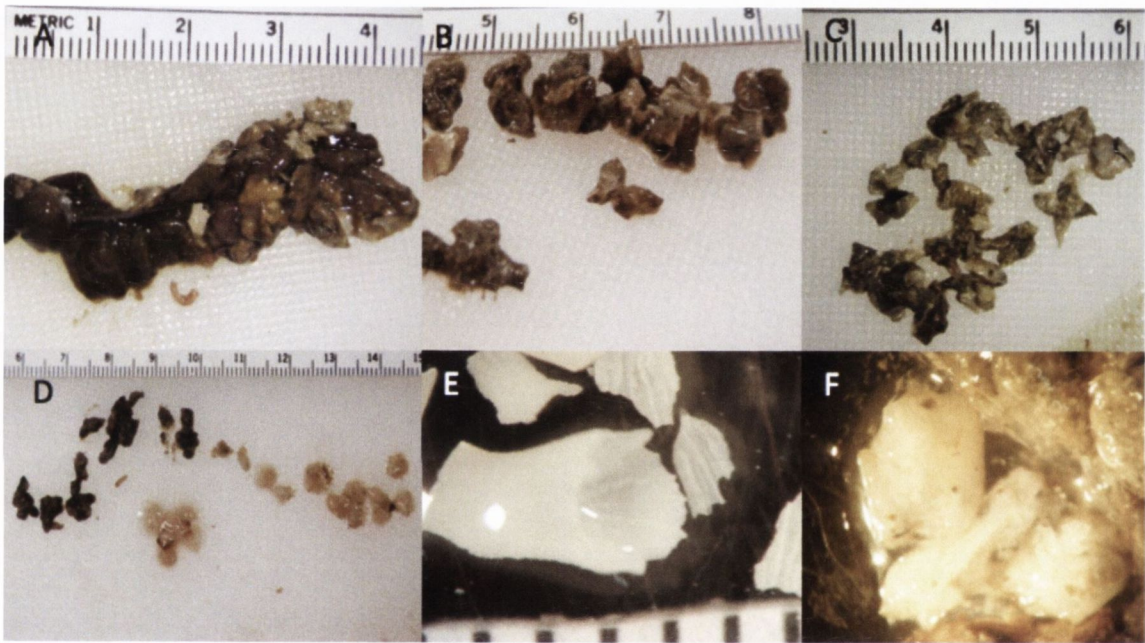


Fig. 3. Gut contents of *Cidaris cidaris* and *Araeosoma fenestratum*. (A) Coral rubble filled gastrointestinal tract of *C. cidaris* from Petit Sole Canyon in site PL471. (B) Coral rubble observed in the guts of *C. cidaris* from Guilvinec Canyon in site PL469 and (C) Crozon Canyon in site PL479. (D) Living coral fragments observed among sediment in guts of *C. cidaris* from Guilvinec Canyon in site PL469. (E) Bleached *Madrepora oculata* cup observed in the guts of *C. cidaris* in Croizic Canyon, site PL468. (F) Living coral fragments observed in *A. fenestratum* from Crozon Canyon, PL479 (8x magnification).

Other items, including sediment, foraminifera, fragments of hydroids, crinoid, carrier crab, and sponge material, were also found in the guts of *G. alexandri*, *C. cidaris*, and *A. fenestratum*. *In situ* video observations revealed specimens of all the above mentioned echinoids either in contact with or in close proximity to *L. pertusa* and *M. oculata* (Fig. 4).

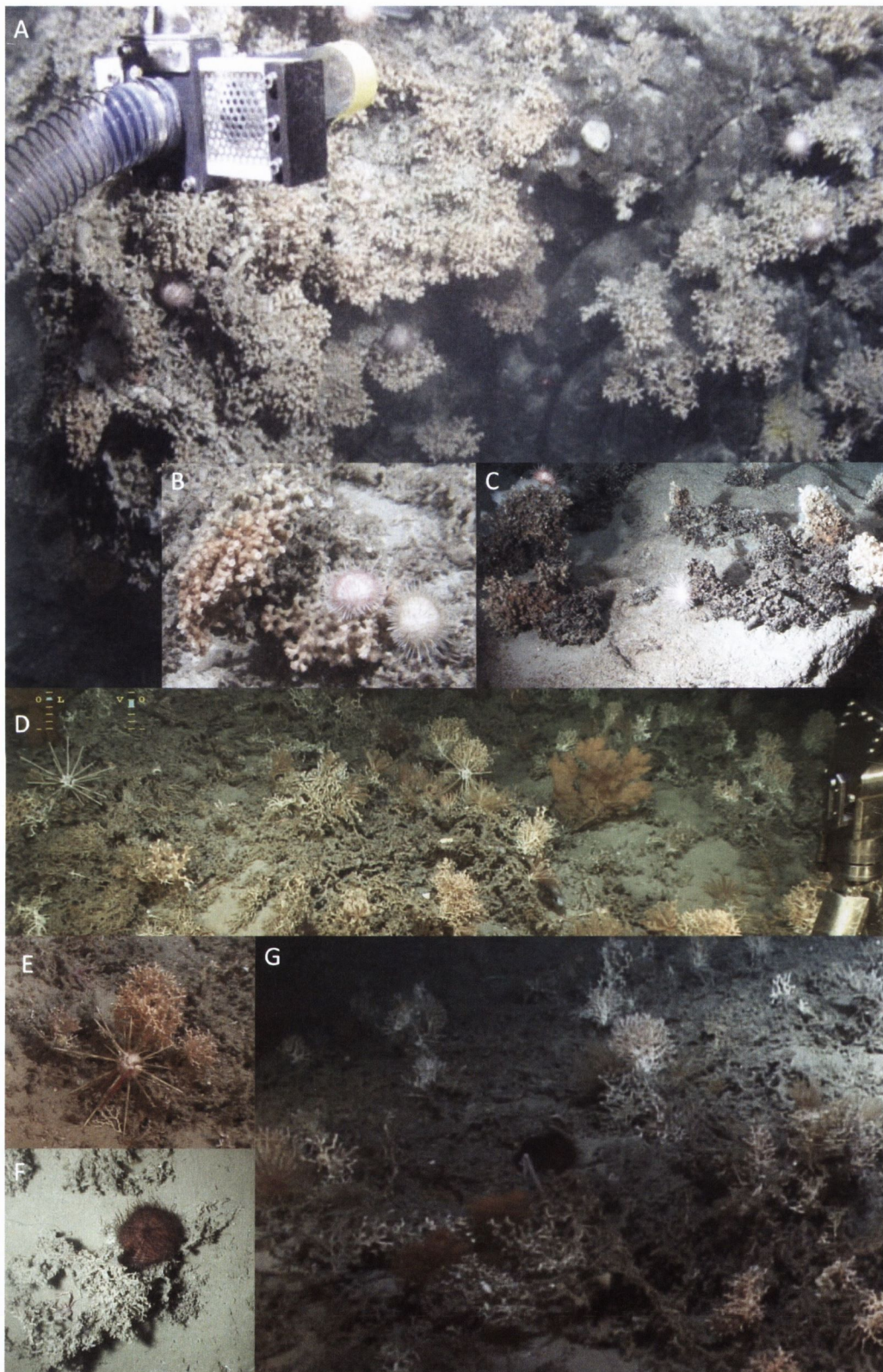


Fig. 4. *In situ* video observations of echinoids interacting with living and fossil coral fragments. (A) Image displaying large density of *Gracilechinus elegans* on *Lophelia pertusa* in canyons on the north side of the

Porcupine Bank, Ireland obtained from the HD camera of ROV Holland I. (B) Two colour morphs of *G. elegans* feeding on *L. pertusa*. (C) *Gracilechinus alexandri* and *G. elegans* on coral in Lampaul Canyon, Bay of Biscay captured with the HD camera of ROV Victor 6000. *Cidaris cidaris* on coral in Guilvinec Canyon (D), and on *Madrepora* in Morgat Douarnes Canyon (E), Bay of Biscay. *Araeosoma fenestratum* on coral rubble in Guilvinec (F) and Croizic (G) canyons, Bay of Biscay. (Photographs A and B courtesy of the Marine Institute from the NUI Galway-led cruise CE10004; Photographs C to G courtesy of Ifremer, BOBECO cruise 2011).

4. Discussion

In combination with gut content analyses, video observations support the hypothesis of bioerosion by the deep-sea echinoids *G. elegans*, *G. alexandri*, *C. cidaris*, and *A. fenestratum*. However, they also suggest that *G. alexandri*, *C. cidaris* and *A. fenestratum* do not exclusively feed on coral since other food remains were found in their gastrointestinal tracts. Also, while genus *Gracilechinus* appears to consume the living part of the coral, specimens of *C. cidaris* and *A. fenestratum* apparently feed on both the living and dead coral framework (Table 1).

Dead coral is associated with a diverse assemblage of attached organisms (Jensen and Fredricksen, 1992; Mortensen and Fossa, 2006), which might serve as an attractive food source for the echinoids. Bioerosion of the dead coral may take place indirectly as a result of this feeding behaviour. In the case of live corals, the production of mucus is believed to deter biofouling (Wild et al., 2004; 2008). However, the mucus itself could provide a nutritious food source for echinoids. *Lophelia* and *Madrepora* produce large quantities of nitrogen-rich mucus, especially when stressed (Wild et al., 2004; 2008). This material is rich in proteins, such as glycoproteins, and therefore might be particularly attractive to grazers. Echinoid bioerosion in shallow-water reefs is generally thought to be a secondary effect of grazing by highly adapted species on communities of symbiotic algae such as diatoms and cyanobacteria (Bak, 1994; Glynn, 1997). In the case of reefs in the deep sea, where photosynthetic algae are absent, bioerosion may be a consequence of grazing on fauna attached to dead corals, mucus associated with live polyps, or the polyps themselves. It also requires that the bioeroding animal possesses a powerful jaw mechanism, such as the Aristotle's lantern of echinoids.

4.1 Evidence in the literature

4.1.1 Ecotypes of *Lophelia*

Our results suggest that, while it is clear that megafaunal taxa, such as echinoids, are important components of the benthic foodweb, their role as a potential structuring force for deep-sea coral reefs may have been underestimated. Indeed, endolithic bioerosion is thought to be a major cause of anomalous morphological traits found in several *Lophelia* populations, by triggering defensive mechanisms resulting in the development of coenosteum-thickened (calcareous skeleton of coral) ecotypes of *Lophelia* (Beuck et al., 2007). However, the efficiency of enhanced aragonite deposition leading to the discontinuous expansion of *Lophelia* polyps and irregular tectura secretion as a response to endolithic bioerosion is questioned by Freiwald and Wilson (1998), who suggest that this strategy might be more effective against encrusting organisms rather than against boring infestations. This apparent discrepancy further supports our contention that grazing megafauna may be a previously overlooked structuring force for deep-sea coral reefs.

4.1.2 Biogeographical patterns

The relationship between *Lophelia-Madrepora* reefs and echinoids presented in this study is further strengthened by the geographical range and depth overlap between the coral and echinoid taxa. In fact, global habitat suitability models predict the largest cold-water scleractinian occurrences in the North Atlantic where the observed bioeroding echinoids reside (Davies et al., 2008; Davies and Guinotte, 2011). For example, *G. alexandri* inhabits an area extending southward from Iceland to the Bay of Biscay and the Azores (Mortensen, 1927). Similarly, *G. elegans* is found throughout the NE Atlantic from north to southern Norway and southern Iceland to the Azores (Mortensen, 1927; Moyse and Tyler, 1990; Southward and Campbell, 2006). Also, *C. cidaris* and *A. fenestratum* are common species in the North Atlantic, spanning much of this region (Mortensen, 1927; Moyse and Tyler, 1990; Southward and Campbell, 2006; Kroh, 2011; Kroh and Hansson, 2011). *C. cidaris* is distributed along the Norwegian margin and as far south as the Mediterranean (Mortensen, 1927; Southward and Campbell, 2006; Kroh and Hansson, 2011). *A. fenestratum* is

commonly found in large numbers on the American side of the Atlantic and from southern Danish waters to Portugal (Mortensen, 1927; Moyse and Tyler, 1990; Kroh, 2011).

These echinoids span a wide range of depths that overlap with those inhabited by cold-water corals. The ranges for particular species are as follows: *G. alexandri* 800-3120 m; *G. elegans* 50-2000 m; *C. cidaris* deeper than 130 m; *A. fenestratum* 145-900 m (Mortensen, 1927; Moyse and Tyler, 1990; Southward and Campbell, 2006). These span the entire depth range of cold-water corals, which are largely restricted between 50-1000 m at high latitudes and up to 4000 m (below the warm water masses) at lower latitudes (Roberts et al., 2006).

Despite similarities in their biogeographic patterns, video observations suggest that the echinoids do not feed exclusively in cold-water coral reefs. Density estimates are available for some deep-sea echinoids (see Grassle, 1975), but habitat associations are currently unavailable. We have observed specimens of *G. elegans*, *G. alexandri*, *C. cidaris*, and *A. fenestratum* in video records from areas with and without corals. However, when in the vicinity of coral habitat, echinoids are generally observed on the live and dead coral infrastructure rather than on the sediment and rubble areas surrounding the reef. In fact, *A. fenestratum* was most often seen on the dead coral, *G. elegans* and *G. alexandri* are mostly observed on live coral, while *C. cidaris* is found on both dead and live parts of the reef. These observations suggest that, where they co-occur with *Lophelia-Madrepora* reefs, these echinoids exploit the corals as a food source, and in the process cause bioerosion of the reefs.

5. Conclusions

This study has identified a potentially major gap in knowledge about *Lophelia-Madrepora* reefs and their associated bioeroding community. Bioerosion by *G. elegans*, *G. alexandri*, *C. cidaris* and *A. fenestratum*, reflects a previously unreported behavior by deep-sea echinoids, which might have important consequences for the stability of deep-sea reef systems. Possible echinoid bioerosion impacts on *Lophelia-Madrepora* reefs warrant further investigation in order to better understand the relationship between deep-sea corals and echinoids.

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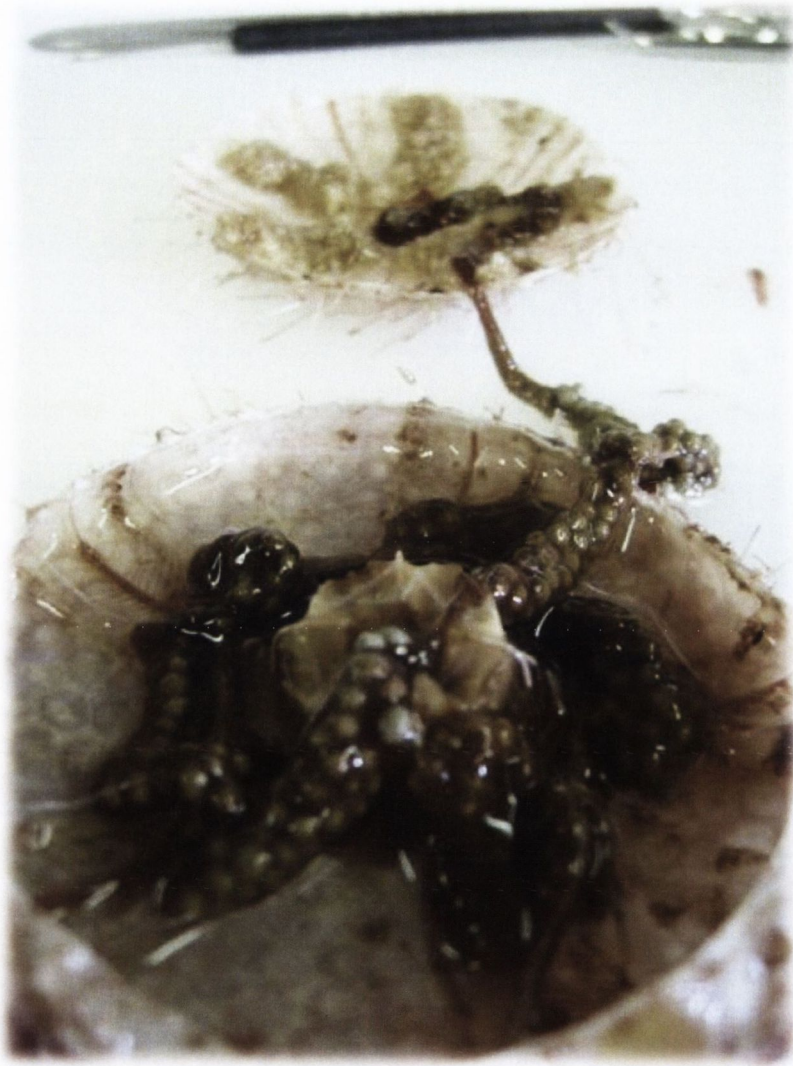
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Sediment filled guts of Phormosoma placenta

Nutrition for growth and reproduction in coexisting deep-sea echinoids: Perspectives from a stable isotope analysis

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Abstract

The role of nutrition in echinoid growth and reproduction as well as the mechanisms utilized to cope with food limitations in the deep sea remains under studied. We investigate echinoid feeding strategies within deep-sea submarine canyons in the NE Atlantic using a stable-isotope approach. Ten echinoid species were collected with a remotely operated vehicle. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable isotope analyses (SIA) were conducted on echinoid tissues in order to investigate food sources assimilated with respect to nutrient partitioning between coexisting taxa, and seasonal dietary changes in food supply. Gut contents analysis was conducted in conjunction with SIA.

Echinoid taxa spanned three benthic trophic levels. This large trophic range might suggest an expansion of the trophic niches of echinoid taxa possibly to reduce interspecific competition for limited food resources. Evidence of nutrient partitioning among coexisting taxa was also found in the carbon data. Significant interspecific differences were found in the $\delta^{13}\text{C}$ signatures of the somatic and reproductive tissues suggesting that different sources of carbon are assimilated into all tissues after the deposition of phytodetritus has taken place on the deep sea floor. However, this pattern differed for the data obtained before the deposition of phytodetritus; similar sources of carbon were assimilated into somatic tissues of different taxa, while some of these different taxa utilized significantly different sources of carbon to manufacture their reproductive tissues.

While specific food sources could not be resolved from the carbon data of the present study, enriched $\delta^{15}\text{N}$ values suggest that echinoids incorporate foods with distinctly higher $\delta^{15}\text{N}$ values than that of POM and sediment, which could result from opportunistic feeding as well as bioerosion of the live coral framework and consequent grazing of fauna attached to the dead coral infrastructure.

Seasonally deposited phytodetritus was incorporated into the reproductive tissues of the seasonal breeder, *G. alexandri*, but not those of continuous breeders, Cidaroida and Echinothurioida. The material however was also found to support somatic tissue growth in cidaroids. These results suggest that seasonal breeders might utilize surface-derived phytodetritus to manufacture reproductive tissues, while continuous breeders might only utilize it for somatic tissue growth or not at all. Results for seasonal dietary shifts were compromised by poor spatial repeatability and thus require further investigation to understand better the role of phytodetritus in fuelling the growth and reproduction of deep-sea echinoids.

Keywords: Somatic tissues, muscle, test, reproductive tissue, gonad, bioerosion, crinoid predation, France, Ireland, gut content analysis.

1. Introduction

Echinoderms thrive in the deep sea as a diverse and abundant taxon that is the dominant deposit-feeding component of the megafauna (Booolootian et al., 1959; Tyler et al., 1982; Billett et al., 1988; Gooday and Turley, 1990; Jumars et al., 1990; Gage and Tyler, 1992; Young et al., 1993; Thurston et al., 1994; Ambrose et al., 2001; Samadi et al., 2007 Iken et al., 2001; Hudson et al., 2003; Wigham et al., 2003; Hudson et al., 2004). It is clear that deep-sea echinoderms have adapted to restricted food conditions, but our understanding of these adaptations and their nutrition is limited. Holothurians, for example, partition nutrients within the sediment to minimize competitive interactions between species (Billett et al., 1988; Miller et al., 2000; Wigham et al., 2003; FitzGeorge-Balfour et al., 2010), but this same feeding selectivity has not been established for other classes of the echinoderms. As well, holothurians, echinoids, and ophiuroids exploit ephemeral sources of surface-derived phytodetritus seasonally deposited to the deep sea floor, but its contribution to the total spectrum of nutrients assimilated is unknown because evidence linking it to seasonal growth and reproduction remains circumstantial (Tyler et al., 1982; Tyler and Gage, 1984b; Billet et al., 1988; Tyler, 1988; Gooday and Turley, 1990; Tyler et al., 1993; Campos-Creasey et al., 1994; Tyler et al., 1995).

In the NE Atlantic, the deposition of phytodetritus occurs in strong seasonal pulses coupled to surface ocean productivity (Billett et al., 1983; Gooday and Turley, 1990; Jumars et al., 1990; Thurston et al., 1994; Duineveld et al., 2004). This photosynthetically produced organic material (POM) enters deep-sea habitats as small planktonic remains through passive sinking (Gooday and Turley, 1990; Gage and Tyler, 1992). As fresh material it is thought to be organically rich, but as it is remineralized and degraded it loses its nutritive quality (Smith et al., 1996; Iken et al., 2001). As such, it is thought to be rapidly consumed for reproductive growth, especially to fuel the energetically expensive vitellogenesis taking place during summer months (Tyler et al., 1982; Tyler and Gage, 1984b; Gage et al., 1986; Tyler, 1988). However, some seasonally reproducing deep-sea echinoids, such as *Gracilechinus elegans* and *G. alexandri*, have been shown to consume the protein-rich mucus associated with live coral polyps, and/or the polyps themselves as well as the sessile invertebrate fauna attached to dead coral infrastructure (Stevenson and Rocha, 2013). Under these circumstances, consumption of phytodetritus to fuel vitellogenesis is puzzling since it is likely to be relatively poor in organic nitrogen in comparison to other materials, such as the mucus associated with live coral polyps and the fauna attached to dead coral infrastructure. This leads to questions regarding the effects of this seasonally pulsed phytodetrital material: how does it coordinate the timing of reproductive events in seasonally breeding deep-sea echinoids? Does it contribute energy towards their somatic growth and reproduction? Continuous reproduction still remains the predominant form of reproduction in the deep sea (Tyler, 1988). Does phytodetritus also fuel growth and reproduction in echinoids that employ a continuous mode of reproduction?

Traditional approaches used to study these aspects of feeding ecology consist of gut content analyses (Jumars and Self, 1986; Tyler et al., 1993; Campos-Creasey et al., 1994; Tyler et al., 1994; Stevenson and Rocha, 2013). Gut content analyses can serve as a preliminary tool to determine parts of an organism's diet, giving a snapshot of the food ingested over a short period of time thereby providing some clues towards the diet of the specimen observed. However, it does not provide information on the food source assimilated and therefore utilized as a source of energy to manufacture tissues in an organism.

Carbon and nitrogen stable isotope analyses (SIA) of tissues provide a useful alternative for investigating both long- and short-term diets of organisms (Peterson and Fry,

1987; Iken et al., 2001). Using these isotopes, ecological processes and activities can be traced and reconstructed (West et al., 2006). $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures have provided valuable information on energy flow, nutrients consumed, and trophic relationships in estuaries, marine, and terrestrial systems (Koike et al., 1987; Peterson and Fry, 1987; Gage and Tyler, 1992; Ambrose and Norr, 1993; O'Reilly et al., 2002; Tayasu et al., 2002; Yatsuya and Nakahara, 2004; Michener and Lajtha, 2007). These allow for the measurement of carbon and nitrogen assimilated by the organism and thus outline nutritionally important materials ingested (Melville and Connolly, 2003). In marine benthic food webs trophic enrichment steps were established at 3-3.8‰ and 1‰ shift for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively (Hobson and Welch, 1992; Sherwood and Rose, 2005). Shifts in $\delta^{15}\text{N}$ signatures are particularly useful in trophic positioning and $\delta^{13}\text{C}$ signatures are most useful in identifying the food source in an organism's diet (Suchanek et al., 1985; Mincks et al., 2008; van Oevelen et al., 2009).

SIA can also provide a time-integrated measure of feeding history (Vander Zanden and Rasmussen, 2001; Tomas et al., 2006). Isotopic shifts can be seen in migratory birds, animals that undergo metamorphosis, and others changing diets due to shifts in food sources (Phillips and Eldridge, 2006). Due to varying turnover rates, isotopic enrichment differs between tissue types; looking at the isotopic composition of multiple tissues simultaneously can provide a more complete dietary history of the animal under investigation (Tieszen et al., 1983; Iken et al., 2001; Phillips and Eldridge, 2006). Blood plasma, liver, and gonads, for example, are known to have high turnover rates, so these tissues tend to reflect a more recent diet consumed during the shorter period of tissue formation (Tieszen et al., 1983; Iken et al., 2001; Phillips and Eldridge, 2006). 'Long-lived' tissues, such as muscle and bone, tend to have a lower turnover rate and thus provide an integrative measure of the food assimilated over a longer time span (Tieszen et al., 1983; Iken et al., 2001; Phillips and Eldridge, 2006; Tomas et al., 2006).

This study aims to investigate the feeding mechanisms of deep-sea echinoids via stable isotope analyses; we specifically (i) compare the history of food sources assimilated by coexisting echinoid taxa to see if nutrient partitioning is taking place resulting in the reduction or avoidance of interspecific competition for limited food sources, and (ii) examine how seasonal dietary shifts linked to the deposition of surface productivity might affect tissue formation in seasonal and continuous breeders. From this we test the null

hypothesis that deep-sea echinoids feed at similar trophic levels ($\delta^{15}\text{N}$ signatures compared across similar tissues), on similar food sources ($\delta^{13}\text{C}$ signatures compared across similar tissues), and their tissue formation is not affected by seasonal dietary shifts linked to the seasonal deposition of surface productivity (achieved by comparing $\delta^{13}\text{C}$ signatures of tissues in spring and late summer; before and after deposition, respectively).

2. Materials

2.1 Study area

Samples were collected in three geographic locations within the NE Atlantic ocean: six sites (E37, E52, E74, E85, E96 and E108) in two adjacent canyons on the north side of the Porcupine Bank, on the Irish continental margin; five sites (E4, E12, E14, E19, E64) in the Whittard Canyon on the Goban Spur, southern margin of the Irish continental shelf; and seven neighbouring canyons (Saint Nazaire, Croizic, Guilvinec, Lampaul, Petite Sole, Crozon, Morgat Douarnez canyons) in the Bay of Biscay, France (Figure 1).



Fig. 1. Location of the study area and sampling stations in canyons on the Irish continental shelf and Bay of Biscay, France, NE Atlantic Ocean.

The Porcupine Bank is located to the west of Ireland; it is bounded to the east by the shallow Irish continental shelf and to the west by the deep Rockall Trough. In relation to global ocean circulation patterns, surface productivity is coupled to the warm water influx and northeasterly flowing Gulf Stream into the NE Atlantic (Scoffin, 1988). On the southern Irish continental margin, the Whittard Canyon System stretches for almost 300 km with feeder branches carved in the Irish, UK, and French continental slopes. Regular seasonal deposition of aggregated POM is known to reach the seafloor on the Porcupine Abyssal Plain (PAP) in May/June (Billet et al., 1983; Lampitt, 1985; Rice et al., 1994).

The Bay of Biscay is a sedimentary basin that lies on the western coast of France and extends from Brest south to the Spanish border and west to Cape Ortegal. Submarine canyons here are subject to semi-diurnal tidal cycles and heavy currents determined by canyon topography, but a clear seasonal input of material is observed at the end of winter (Khripounoff et al., 2014). Sampling took place in the spring (April/May) and late summer (September) such that samples were available before and after the seasonal downward flux of surface productivity in June - August (Tyler, 1988; Lampitt et al., 2001).

2.2 Sampling procedure

All echinoid specimens used in this study were collected during four sampling campaigns CE10004, CE11006, CE12006 with RV Celtic Explorer (CE), which took place at the end of April, over three consecutive years (2010-2012); and BOBECO with *NO Pourquoi pas?* in September, 2011 (Table 1). The echinoids were collected randomly in preselected quadrats (during BOBECO cruise) and transects (during the CE cruises) spanning coral habitat. Collection took place with the mechanical arm of ROV Holland I (CE cruises) and Victor 6000 (BOBECO). All specimens were dissected on board the RV immediately upon recovery of the ROV.

Table 1. Summary of echinoids collected. *N* - number of individuals measured for $\delta^{13}\text{C}$ (‰) and $\delta^{15}\text{N}$ (‰).

Location (cruise number)	Date	Site	Species	<i>N</i>			
North of Porcupine Bank, Ireland (CE10004)*	May 23 rd – Jun 3 rd , 2010	Canyon 1	<i>Echinus affinis</i>	1			
			<i>Phormosoma placenta</i>	3			
			<i>Tromikosoma uranus</i>	1			
		Canyon 2	<i>Cidaris cidaris</i>	1			
			<i>E. affinis</i>	26			
			<i>Gracilechinus elegans</i>	8			
			<i>Gracilechinus alexandri</i>	2			
			Goban Spur, Ireland**	Apr 22 nd – May 10 th , 2011	West Whittard Canyon (CE11006)	<i>G. elegans</i>	1
						<i>G. alexandri</i>	6
<i>Hygrosoma petersii</i>	5						
<i>Sperosoma grimaldii</i>	7						
Apr 12-29 th , 2012	West Whittard Canyon (CE12006)	<i>Histocidaris purpurata</i>		2			
Bay of Biscay, France (BOBECO)***	Sep 9 th – Oct 11 th , 2011	Saint-Nazaire (PL467)		<i>G. alexandri</i>	1		
		Croizic (PL468)		<i>C. cidaris</i>	5		
				<i>Araeosoma fenestratum</i>	1		
		Guilvinec (PL469)	<i>C. cidaris</i>	6			
			<i>A. fenestratum</i>	1			
		Lampaul (PL470, PL478)	<i>G. alexandri</i>	2			
			<i>G. elegans</i>	1			
		Petite Sole (PL471, PL476)	<i>S. grimaldii</i>	1			
			<i>C. cidaris</i>	2			
			<i>A. fenestratum</i>	3			
			<i>C. cidaris</i>	22			
		Crozon (PL479)	<i>A. fenestratum</i>	1			
			<i>C. cidaris</i>	1			
		Morgat-Douarnez (PL480)	<i>A. fenestratum</i>	4			
			<i>C. cidaris</i>	10			
			<i>A. fenestratum</i>	3			
		Total:				127	

*Only test and gonad tissues were collected

**Only muscle and gonads were collected

***All three tissues were collected

Ten echinoid species (*Gracilechinus elegans*, *Gracilechinus alexandri*, *Echinus affinis*, *Cidaris cidaris*, *Histocidaris purpurata*, *Tromikosoma uranus*, *Phormosoma placenta*, *Sperosoma grimaldii*, *Hygrosoma petersii*, and *Araeosoma fenestratum*) ranging in test diameter size between 3-15 cm were collected for the study. The type and number of

specimens collected varied at each site (Table 1). Specimens were brought to the surface within 7 hrs of capture. Species were dissected onboard the vessel immediately upon recovery. Prior to dissection, individuals were photographed and the test diameter and height (where applicable) with and without spines were measured for identification. All specimens were identified to the lowest possible taxonomic level; Smith (2005) and Smith and Kroh (2011) were primarily used for species identifications, but were supported by Southward and Campbell (2006) and the Encyclopedia of Life.

Muscle (from Aristotle's lantern), test, and gonads were carefully dissected from each specimen. These tissues were mostly selected on the basis that they are the most abundant tissues available in the echinoid, but also provide a time-integrated measure of food source and trophic positioning. Gonads were collected from specimens during all cruises (CE10004, CE11006, CE12006, BOBECO); test was not collected during CE11006; and muscle was collected from each individual, except for samples obtained in the canyons north of the Porcupine Bank (CE10004; Table 1). These were preserved in a -80°C freezer (for the CE cruises) or oven dried at 60°C for 48 hrs (for BOBECO cruise) for later stable isotope analyses (SIA). After tissues were collected, gut contents were visually inspected, and photographed. A Leica WILD M 10 microscope was utilized to facilitate the identification of visible contents, such as coral, hydroids, sponge, and worms.

Sediment and live coral fragments from *Lophelia pertusa* and *Madrepora oculata* were collected in sites adjacent to those where echinoids were collected. Sediment samples were collected using a Duncan and Associates box corer (for CE10004 and CE11006), Reineck box corer (for CE12006) and a benthic chamber (for BOBECO). Sediment samples were stored at -20°C for future isotope analyses. Coral samples were collected with the mechanical arm of the ROV and stored at -80°C (for CE11006) or oven dried at 60°C for 48 hrs (for BOBECO). Note that while sediment samples were collected for the French sites, they yielded insufficient organic material for SIA so isotope signatures are unavailable for the French sites.

Particulate organic material (POM) was only collected from the Irish sites during CE11006 and CE12006 cruises. POM was obtained as follows: 2-4 L were filtered from the water above the boxcore (for CE11006 and CE12006) and 10 L from CTD (Conductivity, Temperature, and Depth instrument; for CE12006) bottles were filtered through a pre-

combusted 47 mm GF/F filter and stored at -80°C for future SIA. CTD water was collected both from the surface and 10 m above the seafloor.

2.3 Stable isotope analyses

Tissues, sediment, POM, and coral were dried at 60°C for 48hrs and then ground to a homogeneous fine powder using a mortar and pestle. Gonads did not undergo further preparation. Test (the interambulacral region), muscle, sediment, and coral samples were acidified to remove inorganic carbon. They were acidified by adding 1M HCl drop-by-drop until gas evolution ceased. Samples were observed under a dissecting microscope to make sure that carbon dioxide had been fully evolved. These acidified samples were re-dried at 70°C, ground again, and stored in a desiccator until analysed.

Stable-isotope analyses for CE10004 were performed at Durham University using a Costech Elemental Analyzer (ECS 4010) coupled to a ThermoFinnigan Delta V Advantage. Due to cost limitations and low quantity of test and gonad samples available, a single replicate was run for each sample. Abundances of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were expressed in per mil (‰) relative to the Vienna-Pee Dee Belemnite and atmospheric nitrogen standards, respectively. These were reported in delta (δ) notation according to the following equation:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = ([R_{\text{sample}}/R_{\text{standard}}] - 1) \times 10^3$$

where $R = {}^{13}\text{C}:{}^{12}\text{C}$ or ${}^{15}\text{N}:{}^{14}\text{N}$. Data accuracy was monitored through routine analyses of in-house standards, which are stringently calibrated against international standards (e.g., USGS 40, USGS 24, IAEA 600, IAEA N1, IAEA N2). Analytical uncertainty for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ measurements were $\pm 0.1\text{‰}$ for replicate analyses of the international standards and typically $<0.2\text{‰}$ for replicate sample analyses.

Stable isotope analyses of samples from CE11006, CE12006 and BOBECO cruises were performed with Thermo Deltaplus CF-IRMS in the Geochemistry Laboratory at Trinity College Dublin in summer 2012 and fall 2013. The mass spectrometer was coupled to the CE Instruments 1112 Flash Elemental Analyser by a Conflo III Interface, and was operated using ISODAT software. All carbon isotope ratios were measured relative to the universal standard Pee Dee Belemnite (PDB), and the working standard L-Alanine ($\delta^{13}\text{C} =$

–27.00 ‰) was used to calibrate the data to the PDB scale. All data are reported using the delta (δ) notation where $\delta = 1000 * ((R_{\text{sample}} - R_{\text{standard}})/R_{\text{standard}})$ and $R = {}^{13}\text{C}/{}^{12}\text{C}$.

2.4 Statistical analyses

All statistical analyses were performed in R version 3.0.0 (R Core Team, 2013) for Mac OS X. Assumptions of homogeneity of variance were tested with Bartlett test ($\alpha = 0.05$) and normality was verified through visual inspection of residuals plots. Data that violated test assumptions were dealt with as outlined below.

2.4.1 Interspecific differences in food resources

To investigate interspecific differences as well as compare echinoid isotopic signatures to those of possible food sources, such as POM, corals, and sediment, a generalized linear mixed effect model (GLMM) with a Gaussian distribution was conducted using package ‘MASS’ and ‘nlme’ (Venables and Ripley, 2002). Upon detection of significance in the GLMM, a Tukey posthoc test ($\alpha = 0.05$) with package ‘multcomp’ (Pinheiro et al., 2014). Fixed factors were species and food sources; and sampling station was assigned as a random factor.

No amount of transformation could resolve the heterodasticity of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures in some tissues, so a simultaneous inference procedure for multiple comparisons of means was used to overcome violations to model assumptions. This procedure allows for multiple comparisons in the presence of unequal group variances in an unbalanced design and does not make assumptions regarding the distribution or variance homogeneity (Herberich et al., 2010). Packages “multcomp” (Pinheiro et al., 2014) and “sandwich” (Zeileis, 2006) were utilized to perform this test. The following underwent inference testing: $\delta^{15}\text{N}$ for test in Irish and French sites, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ in muscle for Ireland, $\delta^{15}\text{N}$ for gonad tissue in both regions, and $\delta^{13}\text{C}$ for gonads in Irish sites (Table 2).

Table 2. Summary of specific statistical tests performed on the stable isotope data for Irish and French sites. GLMM – Generalized linear mixed effect model.

GLMM	Inference
$\delta^{13}\text{C}$ test (Ireland)	$\delta^{15}\text{N}$ test (Ireland)
$\delta^{13}\text{C}$ test (France)	$\delta^{15}\text{N}$ test (France)
$\delta^{13}\text{C}$, $\delta^{15}\text{N}$ muscle (France)	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$ muscle (Ireland)
$\delta^{13}\text{C}$ gonad (Ireland)	$\delta^{15}\text{N}$ gonad (Ireland)
	$\delta^{13}\text{C}$, $\delta^{15}\text{N}$ gonad (France)

2.4.2 Seasonal dietary shift

Sufficient numbers of individuals of *G. alexandri* were obtained from both regions to compare across temporal scales (Irish cruises in the spring vs. French cruises in late summer), but this was not possible for the other species collected in this study since there were insufficient samples available across both seasons. Species whose isotopic signatures did not differ significantly were pooled into a higher taxonomic level and subsequently compared to determine if seasonal dietary shifts were present. In Ireland, the echinothurids *S. grimaldii*, and *H. petersii* (*P. placenta* was excluded due to highly enriched ^{13}C tissue relative to the two other taxa) were grouped into order Echinothurioida and then compared to the echinothurid *A. fenestratum* in France. For the Cidaroida, *H. purpurata* (in Ireland) was compared with *C. cidaris* (in France). A Welch two sample t-test was performed, but where assumptions of normality and homogeneity of variance were violated a non-parametric alternative (Wilcoxon rank sum test) was used instead.

3. Results

3.1 Gut content analyses

Overall, sediment and coral -both live and dead fragments- were the most common and abundant materials found in the gastrointestinal tract of echinoids collected in Ireland and France, but gut contents also contained a wide array of other invertebrate material, such as bivalves, Foramnifera, bryozoans, hydroids, crustacean exoskeleton, crinoid, and sponge material (Table 3).

Table 3. Gut content of all specimens collected in Ireland and France. NA – Not applicable; guts absent due to damage upon ascent.

Species name	Cruise ID	Specimen ID	Gut content
<i>A. fenestratum</i>	BOBECO	PL468-CCAA8-U6	Sediment, crustacean exoskeleton (hard to tell)
		PL469-CCB2-U6	Sediment, coral (dead), bivalve, bryozoan
		PL476-CCC1-U9	Sediment (small amount), majority crustacean exoskeleton (including claw), coral (live and dead)
		PL478-CCA5-U5	Majority sediment, some coral (live with mucus)
		PL478-CCA6-U4	Coral only (live and dead), 2 bivalves
		PL478-GBT3-U3	Majority sediment, some coral (dead)
		PL479-CCB4-U1	Sediment, coral (mucus, live and dead), barnacle plate (tergum or scutum?), 2x gastropod, crinoid, sponge (<i>Poecillastra?</i>), bryozoans, hydroids, polychaete, grit
		PL479-CCA8-U2	Some sediment, coral (dead), sponge (<i>Poecillastra?</i>), hydroid, mostly filled with crinoid material
		PL479-CCA6-U4	Sediment, coral (mucus, 4x polyp tissue, living and dead), sponge, hydroid, some crinoid, Foraminifera
		PL479-behindCC-U5	Majority sediment, coral (live with polyp tissue, and dead), crinoid, rope like material (?)
		PL480-CCB4-U1	Mostly sediment, coral (live)
		PL480-Unk-U2	Sediment, some crinoid pieces
		PL480-Unk-U3	Mostly sediment, some crinoid pieces
<i>C. cidaris</i>	CE10004 BOBECO	E74-U3	Sediment
		PL468-CCA5-U1	Coral (live with mucus, and dead)
		PL468-CCBB1-U2	Coral (live with mucus, and dead), sponge, grit, Foraminifera
		PL468-CCC1-U3	Sediment only; guts mostly empty
		PL468-CCAA4-U4	Sediment
		PL468-CCAA8-U5	Sediment, coral (live with mucus)
		PL469-PBT1-U1	Sediment, coral (live with mucus and polyp tissue; and dead), hydroid, Foraminifera
		PL469-CCA1-U2	Sediment, sponge, echinoid spine, Foraminifera, calcareous tubes of polychaete
		PL469-CCB6-U3	Sediment
		PL469-CCA7-U4	Sediment, majority coral (dead)
		PL469-CCA3-U5	Majority coral (dead), echinoid spine, flatworm
		PL469-CCC1-U7	Majority coral (dead)
		PL471-CCA1-U1	Sediment, coral (dead); guts mostly empty
		PL471-CCB1-U2	Sediment
		PL471-CCA6-U3	One piece of hydroid, and one piece of sponge; guts mostly empty except for these two pieces
		PL471-CCA3-U4	Majority coral (dead)
		PL471-CCA5-U5	Majority sediment, coral (dead), bryozoan
		PL471-CCB7-U6	Sediment; guts mostly empty
		PL471-CCA8-U7	Mostly sediment, some coral (dead), calcareous tube of polychaete, bryozoan, grit
		PL471-GBT-U8	Sediment, coral (dead)
		PL476-CCB4-U1	Sediment, majority coral (mucus, polyp tissue, live and dead)
		PL476-CCA4-U2	Sediment
		PL476-CCA5-U3	Sediment
		PL476-CCB5-U4	Empty
		PL476-CCA6-U5	Sediment, hydroid; guts mostly empty
		PL476-CCC4-U6	Coral (live with mucus)

		PL476-CCC7-U7	Coral (dead), hydroid, 8 flatworms (still alive!)
		PL476-CCC2-U8	Majority coral (dead), sponge
		PL476-CCB1-U10	Sediment, coral (dead, one small piece), hydroid
		PL476-CCB2-U11	Sediment
		PL476-CCB7-U12	Empty
		PL476-CCB3-U13	Sediment, coral (dead, sponge spicules on coral)
		PL476-CCB4-U14	Sediment
		PL476-CCC5-U15	Sediment, hydroid
		PL478-CCA8-U1	Coral (dead), majority sponge (<i>Poecillastra?</i>)
		PL478-GBT1-U2	Majority sediment, coral (dead), crustacean exoskeleton, sponge
		PL479-CCB2-U3	NA
		PL480-CCB8-U4	Sediment, coral (live with mucus and polyp tissue), hydroid; guts mostly empty
		PL480-CCA6-U5	Majority sediment, grit, some tubes (amphipod tubes?)
		PL480-CCA8-U6	Sediment
		PL480-CCB1-U7	Sediment, coral (live with mucus and polyp tissue); gut mostly empty
		PL480-CCA4-U8	Sediment, hydroid
		PL480-CCA6-U9	Majority sediment, hydroid
		PL480-CCB6-U10	Sediment, hydroid
		PL480-CCB6-U11	Sediment
		PL480-CCB6-U12	Sediment
		PL480-GBT2-U13	Sediment, majority coral (live)
<i>E. affinis</i>	CE10004	E37-U1	NA
		E85-U1	Sediment, Foraminifera
		E85-U2	Sediment
		E85-U3	Sediment
		E85-U4	Sediment
		E85-U5	Empty
		E85-U6	Empty
		E85-U7	Sediment, grit
		E85-U8	Sediment; guts very empty
		E85-U9	NA
		E96-U1	Sediment
		E96-U2	Sediment
		E96-U3	Sediment
		E96-U4	Sediment
		E96-U5	Sediment
		E96-U6	Sediment
		E96-U7	Sediment
		E96-U8	Sediment
		E96-U9	Sediment
		E96-U10	Sediment
		E96-U11	Sediment
		E96-U12	Sediment
		E96-U12	Sediment
		E96-U13	Sediment
		E96-U14	Sediment
		E96-U15	Sediment
		E96-U16	Sediment
<i>G. alexandri</i>	CE10004	E108-U2	Sediment
		E108-U6	Sediment
	CE11006	E4-U2	Sediment, coral

		E12-U3	Sediment, coral (live with mucus); guts mostly empty
		E12-U4	Majority sediment, coral (live with mucus)
		E12-U5	Sediment
		E14-U1	NA
		E14-U2	Sediment, coral (dead)
	BOBECO	PL467-CCA3-U1	Clay, grit
		PL470-CCB5-U1	Sediment, coral (live and dead); guts mostly empty
		PL470-CCB7-U3	Sediment; guts mostly empty
<i>G. elegans</i>	CE10004	E74-U1	Coral (live with mucus and polyp tissue)
		E74-U2	Coral (live with mucus and polyp tissue); guts mostly empty
		E108-U1	Coral (live with mucus and polyp tissue)
		E108-U3	Coral (live with mucus and polyp tissue)
		E108-U4	Coral (live with mucus and polyp tissue)
		E108-U5	Coral (live with mucus and polyp tissue)
		E108-U7	Coral (live with mucus and polyp tissue)
		E108-U8	Sediment, coral (live with mucus and polyp tissue)
	CE11006	E4-U1	Sediment
	BOBECO	PL470-CCB4-U2	Coral (live with mucus and polyp tissue)
<i>H. petersii</i>	CE11006	E19-U1	Clay
		E19-U2	Clay
		E19-U3	Sediment
		E19-U6	Sediment
		E19-U7	NA
<i>H. purpurata</i>	CE12006	E64-U1	Sediment, hydroid
		E64-U2	Sediment, hydroid
<i>P. placenta</i>	CE10004	E52-U2	Sediment
		E52-U3	Sediment
		E52-U4	Sediment
<i>S. grimaldii</i>	CE11006	E19-U4	Sediment
		E19-U5	Sediment
		E19-U8	NA
		E19-U9	Sediment
		E19-U10	Sediment; guts mostly empty
		E19-U11	Sediment
		E19-U12	Sediment
	BOBECO	PL470-CCB3-U4	Sediment
<i>T. uranus</i>	CE10004	E52-U1	Sediment

Sediment, crustacean, crinoid, and coral material were the most recurrent and abundant materials found in *A. fenestratum* (Fig. 2). Of the 13 *A. fenestratum* specimens dissected, the gut contents of seven were primarily composed of sediment, one contained a crustacean exoskeleton, one contained coral, one crinoid, and three with a combination of sediment, coral, and crinoid material. Live and dead coral material was found in similar proportions throughout the dissection of *A. fenestratum*. Six of the 13 *A. fenestratum* specimens collected were found to have recently ingested crinoid skeletal material; some specimens contained up to 90% of this material in their guts (Fig. 2C). To investigate this content further, the material was further macerated in sodium hypochlorite to determine

which skeletal structures were present. The material was found to belong to comatulid crinoids, most likely *Koehlermetra porrecta* as it is the dominant crinoid observed in sites sampled. The skeletal material consisted of brachials, cirri, which included several articulated ossicles, and at least one broken centrodorsal. Other echinothurids collected and dissected, such as *H. petersii*, *P. placenta*, *T. uranus*, and *S. grimaldii* contained clay or coarser sediment only, with no traces of crinoid material in their guts (Table 3). Upon dissection of *S. grimaldii*, one specimen was found infested with a newly discovered endoparasitic copepod; this new species and new relationship was subsequently described in Anton et al. (2013).

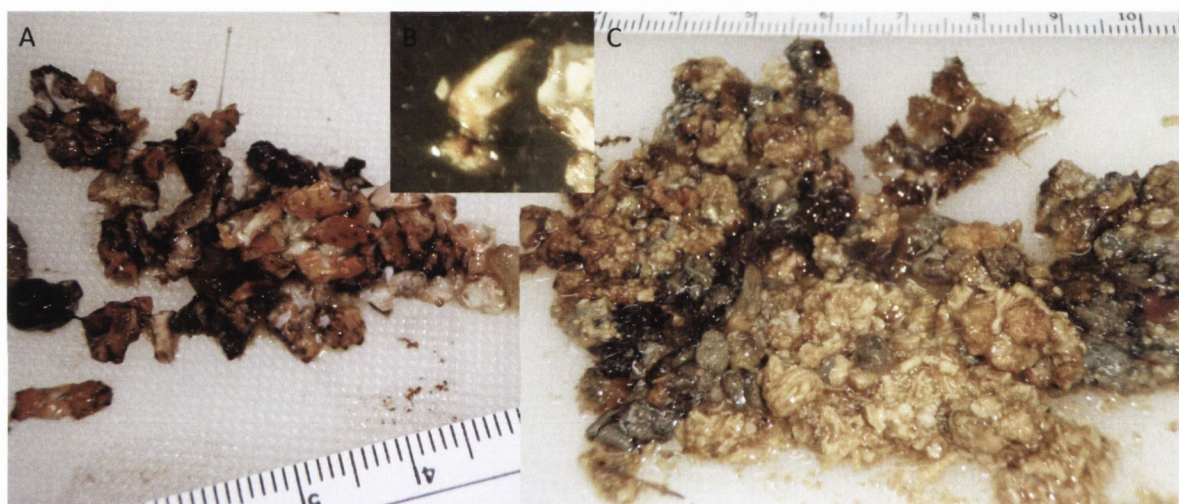


Fig. 2. Gut contents of *A. fenestratum* primarily composed of crustacean (A, B) and crinoid (C) skeleton.

The gastrointestinal tract of *E. affinis* was filled with sediment, except one specimen that had one intact Foraminifera (Table 3). The guts of *G. alexandri* specimens were mostly found full of sediment and in a few cases contained live and dead coral fragments, but coral fragments never formed a large proportion of the gut contents.

All but two *G. elegans* specimens dissected, from both Ireland and France, contained only coral fragments (Table 3). All fragments were from recently ingested living *Lophelia-Madrepora* coral only, some still contained polyp material and mucus.

C. cidaris contained the most diverse gut contents of all echinoid taxa collected (Table 3). As in the case of *A. fenestratum*, *C. cidaris* gut contents were primarily composed of sediment and coral fragments. Of those cidaroids with coral-filled guts, 17% of specimens contained live and dead coral fragments; 23% had live coral fragments; and

the remaining 60% of specimens had recently ingested dead coral fragments only. Undigested bivalve shells, Foraminifera, live flatworms, echinoid spines, hydroids, crustacean exoskeleton, polychaete and amphipod tubes, and sponge material were found among the sediment and coral fragments.

H. purpurata was the only other cidaroid found during this study; its diet differed conspicuously from that of *C. cidaris*. *H. purpurata* gut contents were found full of sediment with traces of hydroid material.

3.2 Nutrient partitioning between coexisting taxa

3.2.1 Trophic positioning and food sources in Irish sites

POM and sediment were taken to be the trophic base of the ecosystem. Highly significant differences were found between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of potential food sources (POM, sediment, and the coral *L. pertusa*) and those of the test and muscle tissues for all taxa (Fig. 3; Table 3). Since ^{13}C is only weakly enriched across trophic levels, $\delta^{13}\text{C}$ signatures are less useful in analysing food webs so we focused on $\delta^{15}\text{N}$ values to determine trophic positioning of echinoids. Muscle tissue was 7.04 - 11.61 ‰, test 5.13 – 11.44 ‰, and gonad 4.70 – 8.32 ‰ enriched in ^{15}N relative to the trophic baseline, POM and sediment.

Similarly, *L. pertusa* was significantly enriched in ^{15}N and ^{13}C relative to POM (for $\delta^{15}\text{N}$ signatures only) and sediment; and was 2.29 ‰ enriched in ^{15}N relative to this trophic base (Table 3). Echinoid ^{15}N tissue enrichment relative to *L. pertusa* ranged from 4.74 - 9.31 ‰ for the muscle, 2.83 - 9.14 ‰ for test, and 2.41 - 6.03 ‰ for the gonad tissue.

To help decipher potential food sources, $\delta^{13}\text{C}$ signature comparisons were made between echinoids and *L. pertusa*. Echinoids were highly significantly enriched in ^{13}C , except for the gonad material, which was depleted in ^{13}C (Table 3). ^{13}C differences between echinoid taxa and *L. pertusa* ranged between 5.20 - 5.93 ‰ for the muscle, 3.94 – 5.16 ‰ for the test tissue, and a depletion of 1.41 ‰ to enrichment by 2.22 ‰ for the gonad tissue.

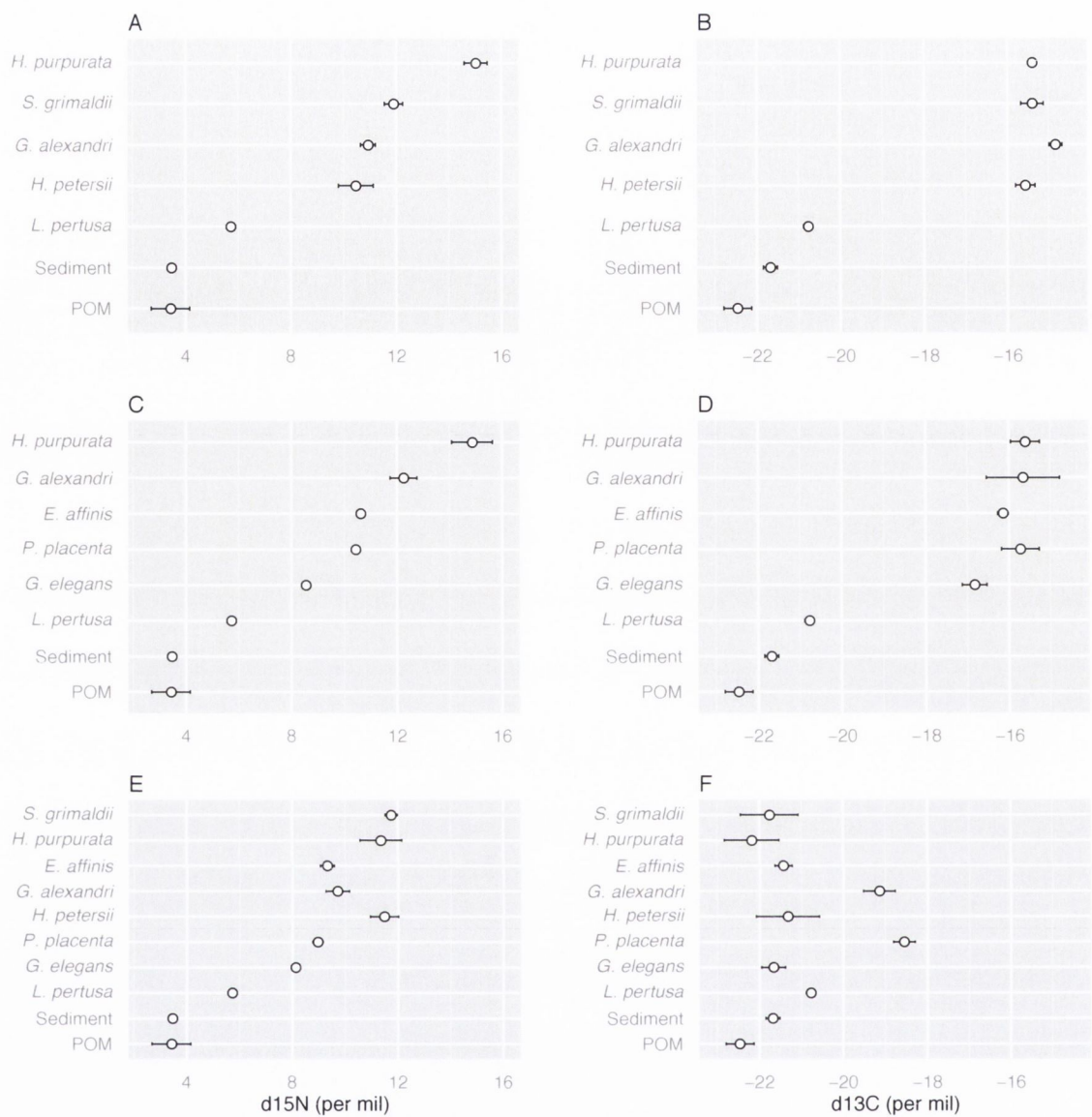


Fig. 3. Stable isotope signatures (mean $\pm$ SE) for $\delta^{15}\text{N}$ of (A) muscle, (C) test, and (E) gonad tissues; and $\delta^{13}\text{C}$ of (B) muscle, (D) test, (F) gonad tissues of echinoids, sediment, coral, and POM from the Irish sites. Note that the order of species on the Y-axis was held constant to facilitate interpretation.

Table 3. Summary of Tukey posthoc test for $\delta^{13}\text{C}$ signatures between species ($P < 0.05$) in Irish sites. NA – Not applicable, for those taxa whose tissues were not collected or insufficient material was available for analyses.

$\delta^{15}N$ signatures:																	
	Potential food sources			Muscle				Test				Gonad					
	POM	Sediment	<i>L. pertusa</i>	<i>G. alexandri</i>	<i>H. purpurata</i>	<i>H. petersii</i>	<i>S. grimaldii</i>	<i>G. alexandri</i>	<i>H. purpurata</i>	<i>E. affinis</i>	<i>P. placenta</i>	<i>G. alexandri</i>	<i>H. purpurata</i>	<i>E. affinis</i>	<i>P. placenta</i>	<i>H. petersii</i>	<i>S. grimaldii</i>
POM	-	1	0.08														
Sediment		-	< 0.001														
<i>L. pertusa</i>			-														
<i>G. alexandri</i>	< 0.001	< 0.001	< 0.001	-	<0.001	1	0.4	-	0.4	0.3	0.2	-	0.9	1	0.9	0.3	<0.01
<i>H. purpurata</i>	< 0.001	< 0.001	< 0.001		-	<0.001	<0.001		-	<0.01	<0.01		-	0.7	0.4	1	1
<i>E. affinis</i>	< 0.001	< 0.001	< 0.001	NA	NA	NA	NA			-	0.9			-	1	<0.01	<0.01
<i>P. placenta</i>	< 0.001	< 0.001	< 0.001	NA	NA	NA	NA				-				-	<0.01	<0.01
<i>H. petersii</i>	< 0.001	< 0.001	< 0.001			-	0.6	NA	NA	NA	NA					-	1
<i>S. grimaldii</i>	< 0.001	< 0.001	< 0.001				-	NA	NA	NA	NA						-
<i>G. elegans</i>	< 0.01	< 0.01	< 0.01	NA	NA	NA	NA	<0.01	<0.01	<0.01	<0.01	0.04	0.1	<0.01	0.03	<0.01	<0.01

$\delta^{13}C$ signatures:																	
	POM	Sediment	<i>L. pertusa</i>														
POM	-	0.4	0.001														
Sediment		-	< 0.01														
<i>L. pertusa</i>			-														
<i>G. alexandri</i>	< 0.001	< 0.001	< 0.001	-	0.4	0.2	0.6	-	1	0.9	0.9	-	<0.01	<0.01	1	<0.01	<0.01

<i>H. purpurata</i>	< 0.001	< 0.001	< 0.001		-	1	1		-	0.9	1		-	1	<0.01	1	1
<i>E. affinis</i>	< 0.001	< 0.001	< 0.001	NA	NA	NA	NA			-	0.9			-	<0.01	1	1
<i>P. placenta</i>	< 0.001	< 0.001	< 0.001	NA	NA	NA	NA				-				-	<0.01	<0.01
<i>H. petersii</i>	< 0.001	< 0.001	< 0.001			-	1	NA	NA	NA	NA					-	1
<i>S. grimaldii</i>	< 0.001	< 0.001	< 0.001				-	NA	NA	NA	NA						-
<i>G. elegans</i>	< 0.001	< 0.001	< 0.001	NA	NA	NA	NA	0.5	0.5	0.8	0.5	<0.01	1	1	<0.01	1	1

3.2.2 Interspecific comparisons in Irish sites

$\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures were comparable between the muscle and test, but these were relatively enriched in heavier isotope compared to that of the gonad tissue. As well, there was very little variation in the muscle and test $\delta^{13}\text{C}$ signatures (approximately 1 ‰), while that of the gonads spanned 3.5 ‰.

$\delta^{15}\text{N}$ signatures of the test and muscle tissues of *Histocidaris purpurata* were significantly enriched in ^{15}N relative to the test and muscle tissues of *G. elegans* (test only), *G. alexandri* (muscle only), *Hygrosoma petersii*, and *S. grimaldii* (Table 3). As well, $\delta^{15}\text{N}$ signatures of the test of *P. placenta*, *G. alexandri*, and *E. affinis* were significantly enriched in ^{15}N relative to that of *G. elegans*.

$\delta^{15}\text{N}$ isotopic signatures of the gonad tissue of *G. alexandri*, *E. affinis*, *P. placenta*, *H. petersii* and *S. grimaldii* were significantly enriched in ^{15}N relative to that of *G. elegans* (Table 3). *S. grimaldii* and *H. petersii* gonad tissue was significantly enriched in ^{15}N relative to that of *G. alexandri* (relative to *S. grimaldii* only), *E. affinis*, and *P. placenta* (Fig. 3).

No significant differences were detected between the $\delta^{13}\text{C}$ isotopic signatures of the test and muscle tissues of species sampled in the Irish sites (Fig. 3; Table 3). However, these similarities do not extend to the gonad tissue. The gonads of *G. alexandri* and *P. placenta* were significantly enriched in ^{13}C relative to that of *G. elegans*, *H. purpurata*, *E. affinis*, *H. petersii*, and *S. grimaldii*.

Statistical comparisons between *T. uranus* and other echinoids could not be performed due to insufficient samples ($N = 1$).

3.2.3 Trophic positioning and food sources in French sites

Isotopic analyses for the French sediment samples failed due to insufficient organic material in the samples so that isotopic signature comparisons between echinoid tissues and the trophic base of the ecosystem were not possible. Instead, comparisons were made with the coral *M. oculata*. Highly significant differences were found between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of potential food sources (*L. pertusa* and *M. oculata*) and those of the test and muscle tissues for all taxa (Fig. 4; Table 4). In terms of $\delta^{15}\text{N}$ signature comparisons for trophic positioning: muscle tissue was 3.57 – 5.68 ‰, test 2.68 – 5.46 ‰, and gonad tissue

was 1.91 – 2.23 ‰ enriched in ^{15}N relative to *M. oculata*. $\delta^{13}\text{C}$ signature comparisons were used to help decipher potential food sources: muscle tissue was 4.89 – 6.79 ‰, test 4.62 – 5.76 ‰, and gonad tissue was 0.53 - 2.59 ‰ enriched in ^{13}C relative to that of *M. oculata*.

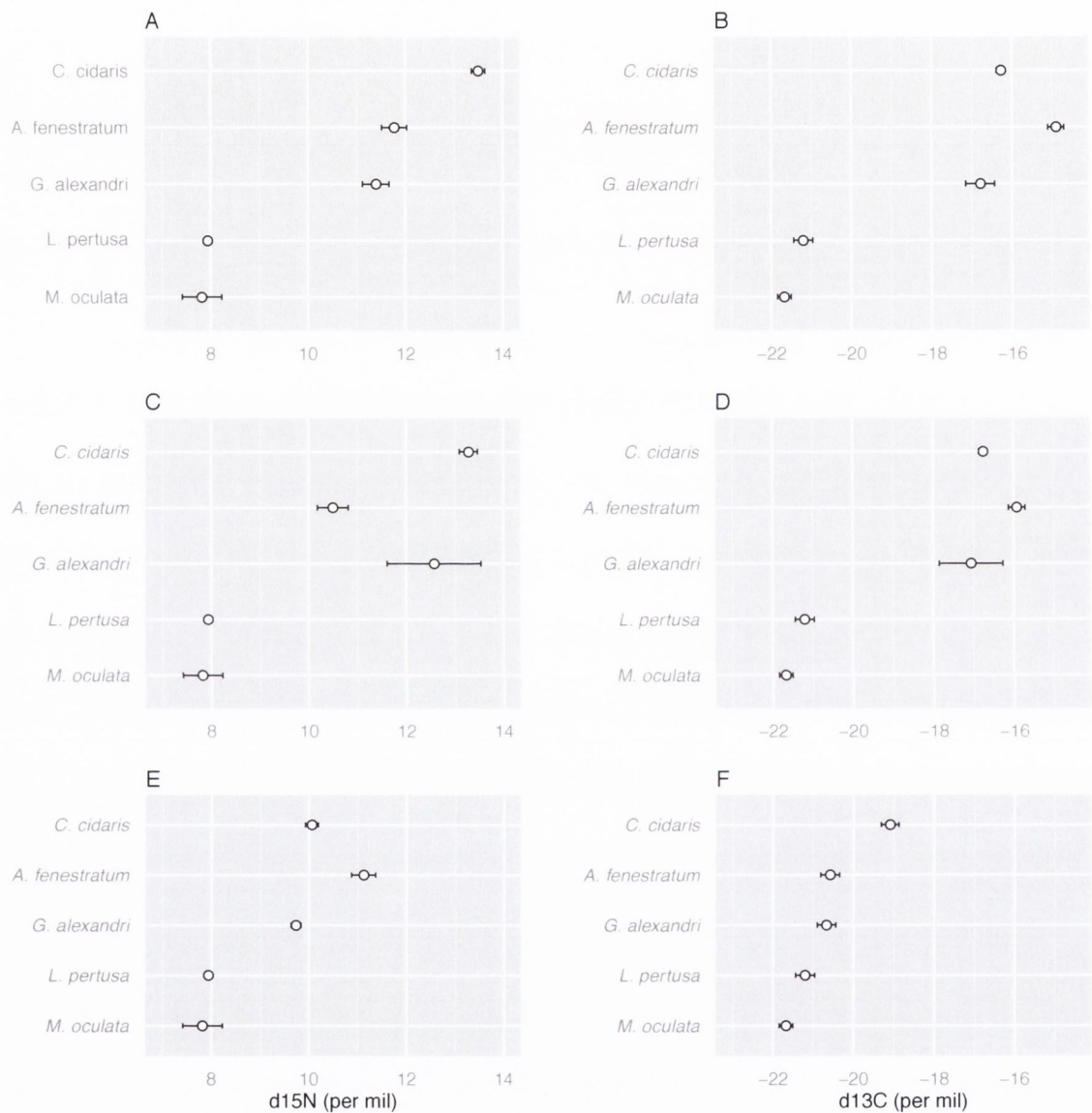


Fig. 4. Stable isotope signatures (mean $\pm$ SE) for $\delta^{15}\text{N}$ of (A) muscle, (C) test, and (E) gonad tissues; and $\delta^{13}\text{C}$ of (B) muscle, (D) test, (F) gonad tissues of echinoids and *L. pertusa* and *M. oculata* coral in French sites.

Table 4. Summary of Tukey posthoc test for $\delta^{13}\text{C}$ signatures between species ($P < 0.05$) in French sites.

$\delta^{15}\text{N}$ signatures:											
	Potential food sources		Muscle			Test			Gonad		
	<i>L. pertusa</i>	<i>M. oculata</i>	<i>C. cidaris</i>	<i>A. fenestratum</i>	<i>G. alexandri</i>	<i>C. cidaris</i>	<i>A. fenestratum</i>	<i>G. alexandri</i>	<i>C. cidaris</i>	<i>A. fenestratum</i>	<i>G. alexandri</i>
<i>L. pertusa</i>	-	1									
<i>M. oculata</i>		-									
<i>C. cidaris</i>	< 0.001	< 0.001	-	< 0.001	0.01	-	< 0.001	1	-	< 0.01	< 0.001
<i>A. fenestratum</i>	< 0.001	< 0.001		-	1		-	0.4		-	0.4
<i>G. alexandri</i>	0.001	0.01			-			-			-

$\delta^{13}\text{C}$ signatures:											
<i>L. pertusa</i>	-	0.8									
<i>M. oculata</i>		-									
<i>C. cidaris</i>	< 0.001	< 0.001	-	< 0.001	0.7	-	0.001	0.9	-	< 0.001	< 0.001
<i>A. fenestratum</i>	< 0.001	< 0.001		-	0.01		-	0.09		-	1
<i>G. alexandri</i>	< 0.001	< 0.001			-			-			-

Similarly, *L. pertusa* was significantly enriched in ^{15}N and ^{13}C relative to those of POM (for $\delta^{15}\text{N}$ signatures only) and sediment; and was 2.29 ‰ enriched in ^{15}N relative to the trophic base (Table 4). *L. pertusa* was enriched in ^{15}N relative to *M. oculata*, but this difference was not statistically significant.

3.2.4 Interspecific comparisons in French sites

As in the Irish sites, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures were comparable between the muscle and test, but these were relatively enriched in heavier isotope compared to that of the gonad tissue. However, there was very little variation in the $\delta^{13}\text{C}$ signatures of the three tissues (approximately 1-2 ‰).

Significant interspecific differences were found in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of the test, muscle, and gonad tissues (Fig. 4; Table 4). More specifically, *C. cidaris* $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were highly significantly different from those of *A. fenestratum* in all tissues. However patterns of enrichment were not significant between tissues: in the muscle and test tissues *C. cidaris* was enriched in ^{15}N and depleted in ^{13}C compared to that of *A. fenestratum*, but the opposite was true for the gonad tissue. $\delta^{15}\text{N}$ signatures of *C. cidaris*

muscle and gonad differed significantly from that of *G. alexandri*; in both cases *C. cidaris* was enriched in ^{15}N relative to that of *G. alexandri*. As well, *C. cidaris* was significantly enriched in ^{13}C relative to *G. alexandri*, but only in the gonad tissue. Isotopic signatures of *A. fenestratum* and *G. alexandri* did not differ statistically in any tissue except for $\delta^{13}\text{C}$ signatures of the muscle tissue where *A. fenestratum* was found to be significantly enriched in ^{13}C relative to that of *G. alexandri*.

Statistical comparisons between *S. grimaldii* and other echinoids could not be performed since only one individual was obtained.

3.3 Seasonal dietary shift

Significant differences in $\delta^{13}\text{C}$ signatures were detected between tissues sampled in spring (Ireland) vs. those in late summer (France; Fig. 5; Table 5). Significant differences were observed in the muscle tissue of the Cidaroida and Echinothurioida. Cidaroida muscle tissues of specimens collected in Ireland were significantly more enriched in ^{13}C compared to those in France. The opposite was true for the Echinothurioida; specimens collected in France were significantly more enriched in ^{13}C than those collected in Irish sites. Significant differences were also present in the gonad tissues of *G. alexandri*. Here, specimens in Irish sites were significantly enriched in ^{13}C relative to those collected in French sites. No significant differences were observed in the $\delta^{13}\text{C}$ signatures of the test material.

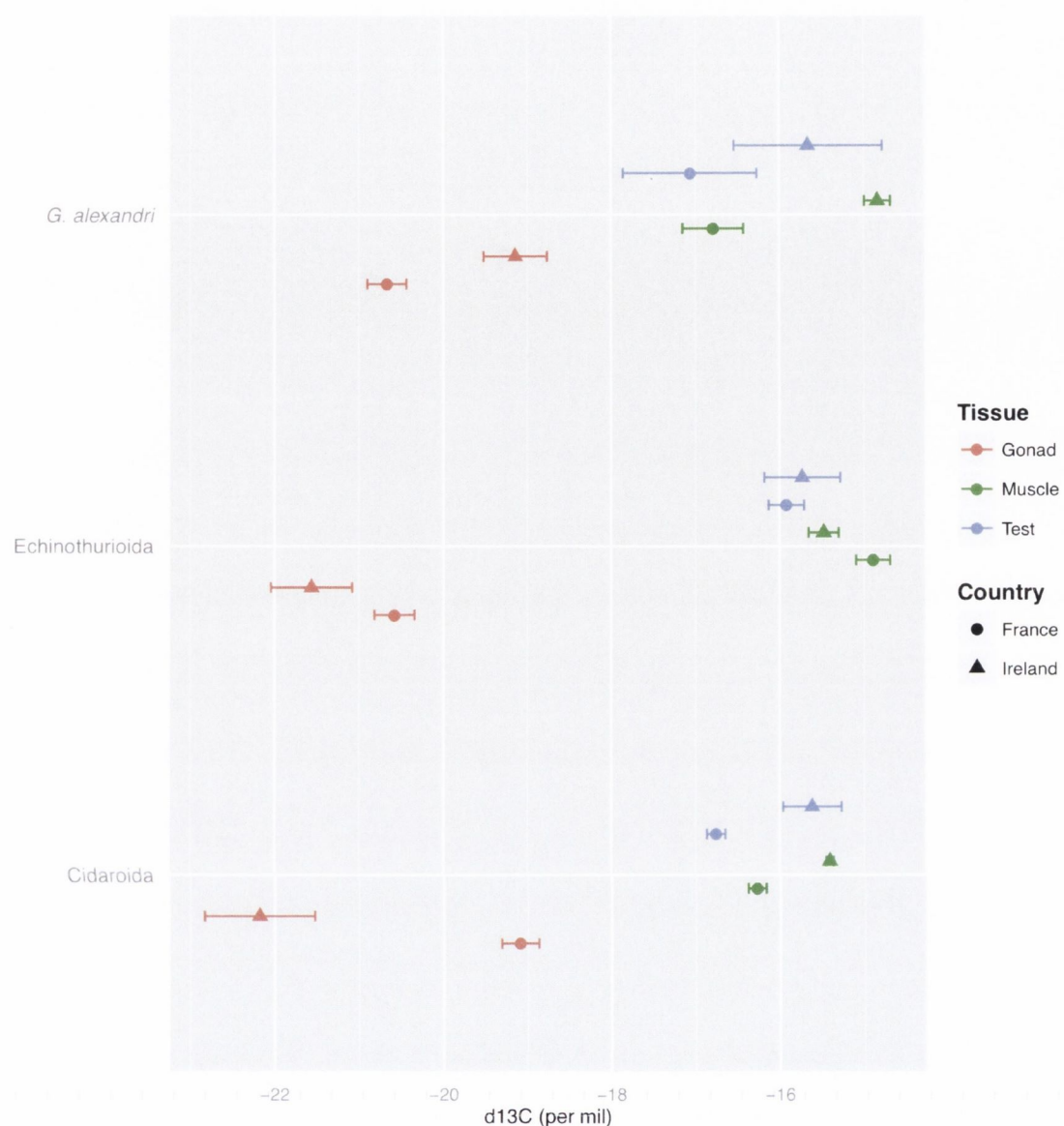


Fig. 5. Comparison of $\delta^{13}\text{C}$ signatures of (A) muscle, (B) test, and (C) gonad tissues (mean $\pm$ SE) between Irish and French sites for three echinoid taxa. Irish sites depict the period of food consumption prior to the deposition of phytodetritus to the deep sea floor; and French sites represent the period of post-phytodetrital deposition.

Table 5. Comparison of $\delta^{13}\text{C}$ signatures between Irish and French sites for three echinoid taxa. Results of the T-test are provided ($P < 0.05$). Where assumptions were violated a non-parametric test (Wilcoxon rank sum test) was performed. W - Wilcoxon rank sum test statistic; t - Welch two sample t-test statistic. NA – Not applicable.

Echinoid taxa	Muscle			Test			Gonad		
	t	W	P-value	t	W	P-value	t	W	P-value
Echinothurioida	2.182	-	0.04	-0.378	-	0.7	1.834	-	0.09
Cidaroida	-	14	< 0.01	-3.144	-	0.2	4.477	-	0.1
<i>G. alexandri</i>	-4.957	-	0.08	-1.182	-	0.3	-3.437	-	< 0.01

4. Discussion

4.1 Gut contents

The gut contents of *E. affinis* and all echinothurids (except *A. fenestratum*) were sediment filled, which is the usual type of material found in the guts of deposit feeders. But those of *A. fenestratum*, *C. cidaris*, *G. elegans*, and *G. alexandri* unexpectedly held a wide range of materials. Recurrent large amounts of various invertebrates, such as coral (live and dead fragments), crustacean, and crinoid skeletal material were found in the guts of specimens collected.

Four taxa were found with coral filled guts. This observation was previously reported in Stevenson and Rocha (2013), so it will not be discussed in detail here. However, an interesting comparison worth highlighting is the different preferences for live and/or dead coral. *A. fenestratum* and *G. alexandri* showed evidence of recent ingestion of similar quantities of live and dead coral, but *G. elegans* fed only on live coral, and *C. cidaris* primarily fed on dead coral. This might help explain why *C. cidaris* had such a varied invertebrate rich diet compared to all other echinoids. From these results, it is safe to assume that the associated organisms attached to the dead coral framework are likely to be the target food source for *C. cidaris*, while *G. elegans* probably feeds on the polyp and mucus of the live coral framework. These materials are thought to provide nutritious organic nitrogen-rich alternatives to particles in the sediment (Stevenson and Rocha, 2013).

Aside from coral material described above, was the crinoid skeletal material found in *A. fenestratum*. The presence of articulated cirral ossicles suggests that fresh rather than scavenged crinoid material was consumed since ligaments connecting ossicles decay within days to a few weeks (Baumiller, 2003). It is unclear at this point whether the large amount

of crinoid skeletal material was consumed by active predation on crinoids by *A. fenestratum* or simply via accidental bycatch while feeding on the coral infrastructure (e.g. see the large numbers of crinoid colonising the CWC reef in Fig. 6). However, the presence of at least one centrodorsal in the gut contents of *A. fenestratum* might suggest that cirri and brachial arms were not autotomized and subsequently ingested, but rather consumed as part of a full crinoid individual. *In situ* video stills obtained in sites where specimens were collected further complement this crinoid-echinothurid interaction (Fig. 6). As well, recent work on shallow water echinoids in Palau reveal evidence of echinoid traces on junior crinoids and confirm palatability of crinoid material for echinoids as they willingly consume this material (personal communication with Prof. Tomasz Baumiller). While *in situ* video observations and traces of echinoid predation on crinoids in Palau support this hypothesis of active predation, it still remains a dubious hypothesis given that crinoids are highly mobile echinoderms that can quickly move away from an approaching echinoid. Despite this unresolved relationship, the finding still represents an important contribution towards echinothurid feeding ecology since research on the diet of this taxon is limited due to their abyssal distribution and primitive soft bodied exterior, which make it very difficult to capture and examine the gut contents of dredged material (Emson and Young, 1998).



Fig. 6. *In situ* observation of *A. fenestratum* interacting with crinoids in a crinoid colonized dead cold-water coral reef in the Bay of Biscay (A, B). Close-up still image of crinoid specimens colonizing a reef (C). (Image courtesy of Ifremer, BOBECO cruise 2011)

The other echinothurids encountered in the study did not contain invertebrate material in their gastrointestinal tract; these were filled with sediment only. It is noteworthy that these taxa were collected outside coral reef habitats, on vast plains of sediment in Ireland, while *A. fenestratum* specimens were collected in coral habitats in France. As facultative omnivores, echinoid utilise food sources which are largely determined by the material available at the time and place of the observed feeding echinoid (Birkeland, 1989). So the lack of invertebrate content in the guts of *H. petersii*, *P. placenta*, *T. uranus*, and *S. grimaldii* is probably linked to the habitat the specimens were occupying at the time of capture and is unlikely to reflect the full range of their diet. It is unknown, however, if these species associate with coral habitats.

4.2 Trophic positioning and food sources assimilated by coexisting echinoids

Overall, a comparison of the trophic positioning and food sources assimilated by echinoid taxa produced important insights about nutrient partitioning among coexisting deep-sea echinoids.

4.2.1 Patterns observed in Irish sites

For most echinoids, $\delta^{15}\text{N}$ signatures were not consistent with the marine benthic food web trophic enrichment step of 3-3.8 ‰. In fact, $\delta^{15}\text{N}$ signatures in Irish sites were highly enriched in ^{15}N compared to POM and sediment. $\delta^{15}\text{N}$ signatures of muscle and test tissues were comparable to those of other surface deposit feeding echinoderms, such as Holothuroidea, Asteroidea, and Ophiuroidea, found on Porcupine Abyssal Plain (PAP), in the NE Atlantic (Iken et al., 2001). Highly enriched $\delta^{15}\text{N}$ values suggest that echinoids do not feed solely on POM and materials found in the sediment and may incorporate foods with distinctly higher $\delta^{15}\text{N}$ values than that of the trophic base. These results are consistent with previous observations of deep-sea echinoids engaging in opportunistic feeding on various types of materials including holothurian faeces and fish carcasses (Jumars et al., 1990; Iken et al., 2001).

The taxa examined in this study spanned a $\delta^{15}\text{N}$ range of 11.6 ‰, corresponding to three benthic trophic levels. This suggests that sympatric echinoid taxa feed at different trophic levels. This large trophic difference between taxa is consistent with previous trophic measurements conducted on deep-sea echinoderms. As in our study, the Holothuroidea in Iken et al. (2001) spanned three trophic levels; and Vanderklift et al. (2006) found similar differences in the trophic positioning of sympatric echinoid species in subtidal rocky reefs of south-western Australia. Occupying different trophic positions might suggest an expansion of echinoid trophic niches, which might help reduce interspecific competition and allow for species coexistence under limited food resources.

G. elegans and *H. purpurata* were the only two taxa found to assimilate significantly different sources of nitrogen into their test and muscle tissues relative to the other echinoids in the study. Tissues of *H. purpurata* and *S. grimaldii* were consistently most enriched in ^{15}N relative to other echinoids suggesting that these two taxa feed at a higher trophic level. And *G. elegans* was consistently found feeding at the lowest trophic

level. The 3 ‰ enrichment in $\delta^{15}\text{N}$ values for *G. elegans* relative to *L. pertusa* is consistent with the observed coral gut contents which suggests that the coral material might make up an important source of energy for somatic tissue formation in this species. A slightly smaller enrichment in the gonads (2.4 ‰) suggests that coral material might partly be invested in reproductive material as well.

Results obtained for $\delta^{15}\text{N}$ of the gonads were not as straightforward to interpret as those of the muscle and test tissues. This is likely to be an artefact of the high lipid content of such material. Since the gonad samples were not defatted prior to SIA, this tissue is not a good food chain marker, but might still be useful for distinguishing food sources in the echinoid diet, using carbon isotopic signatures (Iken et al, 2001). However, sexes were not separated and the development state of gonads were not examined, this might account for the large span in the carbon isotopic signatures of the gonads.

Unlike the nitrogen isotope results discussed above, clear feeding habits were not as obvious in the carbon data. Selective feeding has been described in echinoderms, such as holothurians (Billett et al., 1988; Miller et al., 2000; Wigham et al., 2003; FitzGeorge-Balfour et al., 2010), but evidence for this was only apparent in the gonad tissue not the somatic tissues of echinoids analyzed during the present study. The lack of significant differences between Irish taxa test and muscle $\delta^{13}\text{C}$ values suggest that these taxa assimilate similar sources of carbon during the formation of somatic tissues. Differences found in the gonad tissue of *G. alexandri* and *P. placenta* relative to those of *G. elegans*, *Histocidaris purpurata*, *E. affinis*, *Hygrosoma petersii*, and *S. grimaldii* suggest that the two species incorporate different sources of carbon into their gonads than that of the other taxa. What is more, the gonads of *G. elegans*, *H. purpurata*, *E. affinis*, *H. petersii*, and *S. grimaldii* were within 1 ‰ of POM suggesting that these species might primarily utilize carbon material from fresh POM to manufacture their reproductive tissue. For *H. purpurata*, *E. affinis*, *H. petersii*, and *S. grimaldii* this is consistent with their sediment-filled gut contents, but conflict with the coral rich gut contents of *G. elegans*. The ^{13}C enriched gonads of *G. alexandri* and *P. placenta* suggests that these taxa incorporate sources of carbon that originate from food with distinctly higher $\delta^{13}\text{C}$ values than that of POM and material in the sediment. In summary, the lack of significant differences observed in the $\delta^{13}\text{C}$ values of somatic tissues suggests that echinoids assimilate similar sources of carbon for somatic tissue growth, while apparent significant differences in gonad $\delta^{13}\text{C}$ signatures suggest that

some echinoids might utilize different sources of carbon to manufacture their reproductive tissues.

4.2.2 Patterns observed in French sites

There was no material available for the POM/sediment trophic baseline in the French system so it was not possible to determine the trophic positioning of echinoids in France relative to this baseline. However, $\delta^{15}\text{N}$ signatures for muscle, test, and gonad material of *A. fenestratum* and for the muscle and test tissues of *G. alexandri* were compatible with a diet primarily composed of coral material, which was consistent with the materials found in their guts. The enrichment step of these tissues was within the expected 3-3.8 ‰ range from that of *L. pertusa* and *M. oculata*. On the other hand, *C. cidaris* muscle and test tissues were greatly enriched in ^{15}N compared to the corals, *G. alexandri*, and *A. fenestratum*. These results suggest that coral material might be an important source of organic nitrogen for somatic tissue growth in *A. fenestratum* and *G. alexandri*, but not for *C. cidaris*. Gut contents filled with dead coral fragments teeming with associated invertebrates is likely to place *C. cidaris* in a higher trophic position (Jensen and Frederiksen, 1992).

Trends observed for $\delta^{13}\text{C}$ values of gonad tissue in French sites were consistent with those observed in the Irish sites; sympatric echinoid species were found to incorporate different sources of carbon into their reproductive tissues. Here, *C. cidaris* was found to incorporate different sources of carbon into its gonad tissue than *A. fenestratum* and *G. alexandri*. Significant differences were also found in the $\delta^{13}\text{C}$ values of the muscle and test tissues of *A. fenestratum* relative to those of *C. cidaris*; and *A. fenestratum* vs. *G. alexandri* in the muscle tissue. This suggests that selective feeding and hence assimilation of different sources of carbon for somatic tissue growth might be taking place. Furthermore, all tissue $\delta^{13}\text{C}$ values of *C. cidaris* and *A. fenestratum* differed significantly suggesting that these taxa assimilate different sources of carbon from their food to manufacture both their somatic and reproductive tissues.

4.2.3 Limitations for food source determination and scope for future work

Deciphering specific food sources of echinoids via SIA can be a daunting task as the feeding ecology of echinoids is complex. Food sources vary with season (Lawrence, 1975; Carpenter, 1981), microhabitat (Atkinson et al., 1973), habitat (Lewis, 1964; Randall et al., 1964), age and size of the specimen (Lawrence, 1975). Echinoid diets are also composed of the secondarily consumed substratum on which the intended animal and plant material is attached to (Birkeland, 1989). Specific lipid biomarkers, such as fatty acids and sterols (Kiriakoulakis et al., 2005), carotenoid and chlorophyll pigments (Hudson et al., 2003), and compound specific isotope analyses (Lichtfouse, 2000) might provide a better alternative than SIA for studying deep-sea echinoid nutrition and its role in growth and reproduction.

4.3 Seasonal dietary changes

This part of the study was compromised by the poor spatial repeatability of the samples collected for temporal comparisons. Ideally, echinoids should have been sampled repeatedly in time from the same location to gain insight on seasonal dietary shifts. But gale force winds during two research cruises planned along the Irish continental margin paralyzed all sampling activities and consequently had to be rescheduled. In the hopes of obtaining sufficient samples to make seasonal comparisons, echinoids collected after the deposition of phytodetritus were obtained during the BOBECO cruise, in French rather than Irish canyons. As such, results should be interpreted with caution since it is possible that dietary differences observed between taxa in Irish and French sites are a consequence of location rather than seasonal dietary change.

The taxa utilized to study seasonal dietary shifts in this study were not ideal. The comparison within the Echinothurioida and Cidaroida collected before and after the deposition of phytodetritus is not likely to be representative of a seasonal dietary shift since the comparison was made between taxa that have very different diets. As reflected in the gut content analyses, the guts of *A. fenestratum* contained very different contents from those of the other echinothurids with which they were compared. Similarly, for the cidaroids, *C. cidaris* was compared to *H. purpurata*, which possessed very different gut contents. Due to their crinoid and coral rich diets, *A. fenestratum* and *C. cidaris* would automatically be more enriched in ^{13}C than the other sediment consuming echinothurids

thereby masking any possible shifts in diet over time. *E. affinis*, for example, is a small species unlikely to be able to exploit other food sources than detritus and thus would have been a better candidate to examine whether seasonal dietary changes can be detected via SIA. Unfortunately, no specimens of *E. affinis* were found in France; it is very difficult to obtain replicates of similar species of echinoids over time.

Notwithstanding these problems, significant trends in the carbon isotope data were observed over time; the depletion of ^{13}C in *G. alexandri* gonads and Cidaroida muscles over time is consistent with the consumption of surface derived phytodetritus deposited in early summer. The negative shift in carbon isotopic signatures of these tissues might reflect the larger contribution of phytodetrital material incorporated into tissues when temporarily changing from a diet rich in invertebrate material described above, to that of phytodetritus. The incorporation of phytodetrital material in the reproductive tissue of *G. alexandri*, the somatic tissue of the Cidaroida, and lack thereof for the echinothurids is consistent with the seasonal reproductive strategy employed by some members of the genus *Gracilechinus* (Tyler and Gage, 1984b; Gage et al., 1986) and continuous reproduction observed in echinothurids and cidaroids (Tyler and Gage, 1984a). Seasonal breeders, such as *G. alexandri*, might utilize surface-derived phytodetritus to manufacture reproductive tissues, while continuous breeders, such as echinothurids and cidaroids, might utilize it for growth or not at all. The absence of a seasonal shift in the tissues of echinothurids may suggest that phytodetritus is not assimilated and thus not stored into its tissues for further use. Aside from the gonad and body wall, the food canal is also known to function as a nutrient-storage organ in echinoids (Fuji, 1961; Lawrence et al., 1966; Mercier and Hamel, 2009). The cells lining the epithelium of the food canal are a useful storage organ for some species of echinoids and since this tissue was not analyzed in the present study it is therefore possible that echinothurids do utilize phytodetritus, but store it in the cells of their food canal rather than the gonad and body wall. For the shift observed in *G. alexandri* gonads, perhaps it is this assimilation into reproductive tissues of seasonal breeders that triggers their reproductive events.

Results from Campos-Creasey et al. (1994) partly agree with those of the present study. The short-lived radionuclide ^{210}Po varies seasonally in response to the vertical flux of organic matter (Bacon et al., 1985). Campos-Creasey et al. (1994) found an increase in ^{210}Po in the gut, gonad, and test material after the deposition of phytodetritus thereby

showing ingestion as well as incorporation of the phytodetrital material into gonad and test materials. In the present study, incorporation of phytodetrital material was observed only in the gonad material of the seasonal breeder, *G. alexandri*, not its somatic tissues. This lack of consistency between tissues might undermine the viability of the results; alternatively, rates of metabolic activity in different tissues and the energetics of echinoid tissue formation might serve as a plausible explanation for the change in $\delta^{13}\text{C}$ composition in some tissues but not others. This has been demonstrated by Tieszen et al. (1983) who fed gerbils a corn diet for a fixed period of time before changing their diet to wheat. The half-life for carbon ranges from 6.4 days for more metabolically active tissues such as fat and liver, to 47.5 days for less active tissues such as hair and skeleton (Tieszen et al., 1983). As such, upon completion of the study only the more metabolically active tissues, such as liver, showed complete turnover of the carbon from a corn diet to that of a wheat diet. Dietary shifts were not reflected in all tissues, especially those that were less metabolically active, such as hair (Tieszen et al., 1983). As well, echinoids channel energy to different organs based on their diet; when fed an algal diet, small echinoids are known to direct their energy to somatic growth, such as test and lantern growth, while large echinoids use this energy for reproductive investments and increasing gut biomass (Otero-Villanueva et al., 2004). Perhaps the inconsistency between tissues might be due to differences in metabolic activity and/or energetics of tissue formation.

5. Conclusions

Important insights were made on the nutrition of deep-sea echinoids; specific patterns of foods consumed and assimilated were drawn from gut content and stable isotope analyses. Echinoids spanned three benthic trophic levels suggesting an expansion of the trophic niches of echinoid species possibly to reduce interspecific competition for limited food resources. Nutrient partitioning was also observed in the carbon data. These results suggest that food sources are assimilated differently before and after the deposition of phytodetritus. Before its deposition, echinoids incorporate similar sources of carbon for somatic growth, but utilize different sources of carbon to manufacture their reproductive tissues. However, after the deposition of phytodetritus has taken place, interspecific differences are observed for all tissues.

While specific food sources were not distinguished in the present study, highly enriched $\delta^{15}\text{N}$ values in all tissues suggest that echinoids incorporate foods with distinctly higher $\delta^{15}\text{N}$ values than that of POM and sediment, which could result from opportunistic feeding as well as bioerosion of the coral framework and consequent grazing of fauna attached to the dead coral infrastructure.

The investigation of the role of surface-derived phytodetritus in echinoid tissue formation suggests that seasonal breeders, such as *G. alexandri*, might utilize this material to manufacture reproductive tissues, while continuous breeders, such as echinothurids and cidaroids, might utilize it for somatic tissue growth or not at all. Results were compromised by the lack of consistency between tissues and poor spatial repeatability and thus require further investigation to clarify the function of surface-derived phytodetritus in echinoid nutrition.

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Lepidion feeding on Cidaris cidaris

Predation has no competition:

Factors influencing space and resource use by echinoids in deep-sea coral habitats, as evidenced by continuous video transects

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Abstract

Predation and competition are highly influential factors determining space use in foraging animals, and ultimately contribute to the spatial heterogeneity observed within habitats. Deep-sea echinoids do not use deep-sea coral habitats uniformly; here we investigate the influence of competition and predation on space and resource use via continuous video transect observations - a tool that has not previously been employed for this purpose. This study therefore also evaluates video analyses as a potential tool to help decipher behavioural mechanisms by the deep sea megabenthic community.

Substrate choice (substrate immediately below the echinoid), positioning on the coral, and echinoid aggregate size, were observed within continuous video transects. Simultaneously, the presence/absence of possible predators (e.g. fish and decapods) as well as competitors (both inter- and intraspecific) were recorded. These observations were compiled from fifteen video transects spanning five submarine canyons in the Bay of Biscay, France.

Two dominant coexisting echinoid taxa, echinothurids and *Cidaris cidaris* (Echinodermata: Echinoidea), were observed in the study. Highly significant patterns were detected among echinoids near fish and decapod predators. A shift to the base of the coral infrastructure was correlated to the presence of fish, and fewer individuals were observed in the open areas of the reef and a greater number were found in the mid and top sections of the coral when in the presence of decapods. Aggregates formed irrespective of the presence

of predators. Aggregations are likely to form for feeding and/or breeding rather than for defensive purposes; and migration along the coral infrastructure may be a predator-driven behaviour as echinoids seek refuge from predators.

For echinothurids, no significant trends were detected in the inter- and intraspecific competition data. For *C. cidaris*, significant shifts in substrate use were correlated to the presence of interspecific competitors (echinothurids), whereby an increase in dead coral substrate usage was observed. Despite this finding, further investigation is required in order to clarify the role of competition in deep-sea echinoid space and resource use.

Resource partitioning among coexisting species is often attributed to competitive interactions, but observations suggest that predation risk might play a stronger -or more detectable- role in structuring echinoid space and resource use in deepsea coral habitats. As well, the study successfully detected patterns in the video data thereby confirming that video observations could be useful for similar ecological studies on other deep dwelling megabenthos.

Keywords: Echinoid, *Cidaris cidaris*, Echinothuriidae, predation, competition, refuge, space use, deep-sea, video transects, Bay of Biscay, NE Atlantic.

1. Introduction

A principal objective in ecology is to study the factors driving spatial distribution and abundance patterns of populations, ultimately leading to the understanding of the observed community structure (Paine, 1974). Such factors are clear for neritic habitats where spatial differences in patterns of abundance, distribution, and behaviour have been attributed to food availability, competition, and predation (Paine, 1974; Menge and Sutherland, 1976; Sammarco, 1980; Sih et al., 1985; McClanahan, 1988; Birkeland, 1989; Rochette and Himmelman, 1996; Privitera et al., 2008; Orrock et al., 2013). In deep-sea ecology, the topic of predation and competition has received a large amount of theoretical and conceptual consideration as we strive to determine the relative importance of predation and competition in structuring deep-sea communities. These factors form the basis of two major -and conflicting- theories explaining processes structuring the deep-sea faunal community and thus permitting for high species diversity. The first argues the importance of biological

disturbances, such as nonselective predation, in maintaining high benthic diversity (Dayton and Hessler, 1972), whereas the second attributes it to specific competitive interactions restrained by niche diversification (Sanders, 1968; Slobodkin and Sanders, 1969; Grassle and Sanders, 1973). While analytical work has been conducted to test these hypotheses (E.g., Rex, 1976; Micheli et al., 2002; McClain, 2005; Gallucci et al., 2008a, 2008b; McClain and Barry, 2010), such studies still remain rare. As such, much debate remains regarding the role of predation and competition in structuring deep-sea communities and thus maintaining high species diversity.

Imagery from deep-sea video transects are conventionally used to map habitats and quantitatively investigate megafaunal assemblages in these environments (Smith et al., 1993; Priede and Merrett, 1998; Lampitt et al., 2001; Solan et al., 2003; Jones et al., 2007; Howell et al., 2010). They permit continuous observation of a wide area, which can then be used to gather information about species diversity, community assemblage, and spatial distributions (Solan et al., 2003; Jones et al., 2007; Althaus et al., 2009; Williams et al., 2010). While video transects have proven to be a powerful tool to study these aspects of deep-sea megafaunal ecology, no study has yet exploited it to investigate the relative importance of biological interactions, such as predator-prey and competitive interactions.

Ecological studies are technically challenging and/or costly to execute in deep-sea environments. Nevertheless, video data has recently become plentiful and readily available, making them an ideal resource to address questions about predator-prey and competitive interactions. Given a large enough sample size, one would expect to be able to tease out the underlying patterns within a community. Prior knowledge of such interactions between species in a community is required in order to make informed management decisions that will protect vulnerable ecosystems such as deep-sea coral habitats. These corals are incredibly important both from an ecological and economic point of view and while extensive anthropogenic damage has been observed on cold-water coral (CWC) reefs, there still exists insufficient protection for these fragile ecosystems (Koslow, 2007).

Furthermore, despite the dominant role of echinoids in neritic habitats very little is known about their behaviour in deep-sea environments. Deep-sea echinoids are not ecologically distinct from their warm-water counterparts; they are broad generalist feeders that have been observed to utilize space differently depending on the quality of the food resource available (Booolootian et al., 1959; Emson and Young, 1998; Hollertz, 2002;

Stevenson and Rocha, 2013). Shallow-water echinoids show significant partitioning of food and space to avoid both predators and competitors (McClanahan, 1988). As such, predation risk and competitive interactions may also help shape patterns of resource use by deep-sea echinoids.

Consequently, the study primarily aims to explore the relative importance of predation and competition as organizing factors for the two dominant coexisting echinoid taxa, echinothurids and *Cidaris cidaris* (Echinodermata: Echinoidea), found in coral habitats, using continuous video transects. It specifically investigates behavioural responses, such as space and resource use, which are defined as substrate preference and positioning on the coral infrastructure (*i.e.*, dead and live coral reef).

1.1 Predation of echinoids

Predation pressures have a strong influence on the population structure, distribution, abundance, and behavioural adaptations of shallow-water echinoids (Carpenter, 1984, Scheibling and Hamm, 1991; Vadas and Elner, 2003). Predators of tropical coral and shallow-water temperate reef echinoids primarily consist of reef-fish species and decapods (Muntz et al., 1965; Birkeland, 1989; Scheibling, 1996; Barnes and Crook, 2001). Here, aggregative and flight responses have been proposed as prominent and effective mechanisms to reduce predation risk from such predators (see Scheibling, 1996; and Vadas and Elner, 2003). Due to the sheer number of individuals in an aggregate it reduces the risk of predation of any one individual (Bernstein et al., 1983). For predators, such as crabs, an aggregate is much harder to handle than one individual (Bernstein et al., 1983).

Analytical work conducted on deep-sea communities has revealed significant positive correlations between gastropod predator diversity and overall infaunal diversity (Rex, 1976). Also, experimental work has shown that predation possesses a strong effect on the organization of infaunal assemblages (Thistle et al., 2008; Gallucci et al., 2008a, 2008b) and hydrothermal communities (Micheli et al., 2002), but the effect of predators on the behaviour of deep-sea megabenthos largely remains unknown. It is likely, however, that behavioural adaptations coincide with those observed in their shallow-water counterparts.

1.2 Inter- and intraspecific competition

Competitive interactions have been deemed a crucial player in explaining deep-sea diversity patterns (Sanders, 1968; Slobodkin and Sanders, 1969; Grassle and Sanders, 1973). For example, a minimum distance found in the morphospace of deep-sea gastropod species suggests that these gastropod communities might be structured by competition (McClain, 2005). And megabenthic disturbance by mobile deposit feeders and scavengers near submarine canyon cliff faces reinforces the importance of habitat modifiers in the deep sea (McClain and Barry, 2010). Studies directly testing this hypothesis in the deep sea are lacking, but this paradox has been thoroughly tested in shallow water echinoids. Under food-limited conditions, inter- and intraspecific competition is frequently observed and niche partitioning is common among shallow-water echinoids (Sammarco, 1980; McClanahan, 1988; McClanahan and Muthiga, 1988; Shulman, 1990; McClanahan, 1992; Privitera et al., 2008). For example, the sympatrically occurring taxa, *Echinometra mathaei*, *Diadema savignyi*, and *Diadema setosum*, are spatially specialized to avoid competition with each other (McClanahan and Muthiga, 1988). They utilize different sized burrows and crevices when avoiding predators. In experimental trials, *Echinometra lucunter* and *Echinometra viridis* commonly engage in agonistic interactions between conspecifics and congeners, where encounters result in pushing, biting, and subsequent conquest of a location (Shulman, 1990).

Like *Echinometra* and *Diadema*, the two deep-sea echinoid taxa under observation in the present study, echinothurids and *C. cidaris*, co-occur in *Lophelia-Madrepora* reefs and surrounding habitats (Stevenson and Rocha, 2013). Where they co-occur within *Lophelia-Madrepora* reefs, these echinoids preferentially feed on the coral infrastructure (*i.e.*, dead and living reef) because it represents a potentially important and nutritious food source for echinoids (Stevenson and Rocha, 2013). While echinothurids and *C. cidaris* share these similarities in space and food resource use, it is unclear whether competition is taking place, but given that they depend on a similar food source within the same habitat then we assume that there is some degree of competition taking place for the coral resource as both food and refuge space.

The study, investigates the effects of predation (*i.e.*, fish and decapods) and competition (*i.e.*, inter- and intraspecific) on behavioural responses for space and resource

use by *C. cidaris* and individuals belonging to the family Echinothuriidae. It specifically tests the null hypothesis that predation and competition have no effect on echinoid aggregation patterns and space use, such as positioning on the coral infrastructure (*i.e.*, live and dead reef structure) and substrate use. In view of the evidence presented, (i) a greater number of echinoids observed sheltering below the coral infrastructure when in the vicinity of fish and decapod predators, (ii) aggregations form when in the presence of a predator, and (iii) fewer members of the weaker echinoid taxa are expected on the coral infrastructure when in the presence of the dominant competitor.

2. Materials and methods

2.1 Study area

A series of fifteen continuous video transects were collected with a vertical high definition camera of the remotely operated vehicle (ROV) Victor 6000 during the BOBECO research cruise 2011 onboard ‘*NO Pourquoi pas?*’ in the Bay of Biscay, France. Fifteen video transects (comprising 25 hrs of video recording) were obtained from five neighboring canyons: three transects in Croisic, five in Guilvinec, three in Petit Sole, two in Crozon, and two in Morgat-Douarnenez canyons (Fig. 1). The bathymetric dataset was obtained from Bourillet et al. (2003) for Fig. 1A, D; Bourillet and Loubrieu (1995) and Bourillet et al. (2012) for Fig. 1B, E, F; and Bourillet (2012) for Fig. 1C. The bathymetric dataset was obtained from Bourillet et al. (2003) for Fig. 1A, D; and Bourillet et al. (2012) for Fig. 1B, C, E, F.

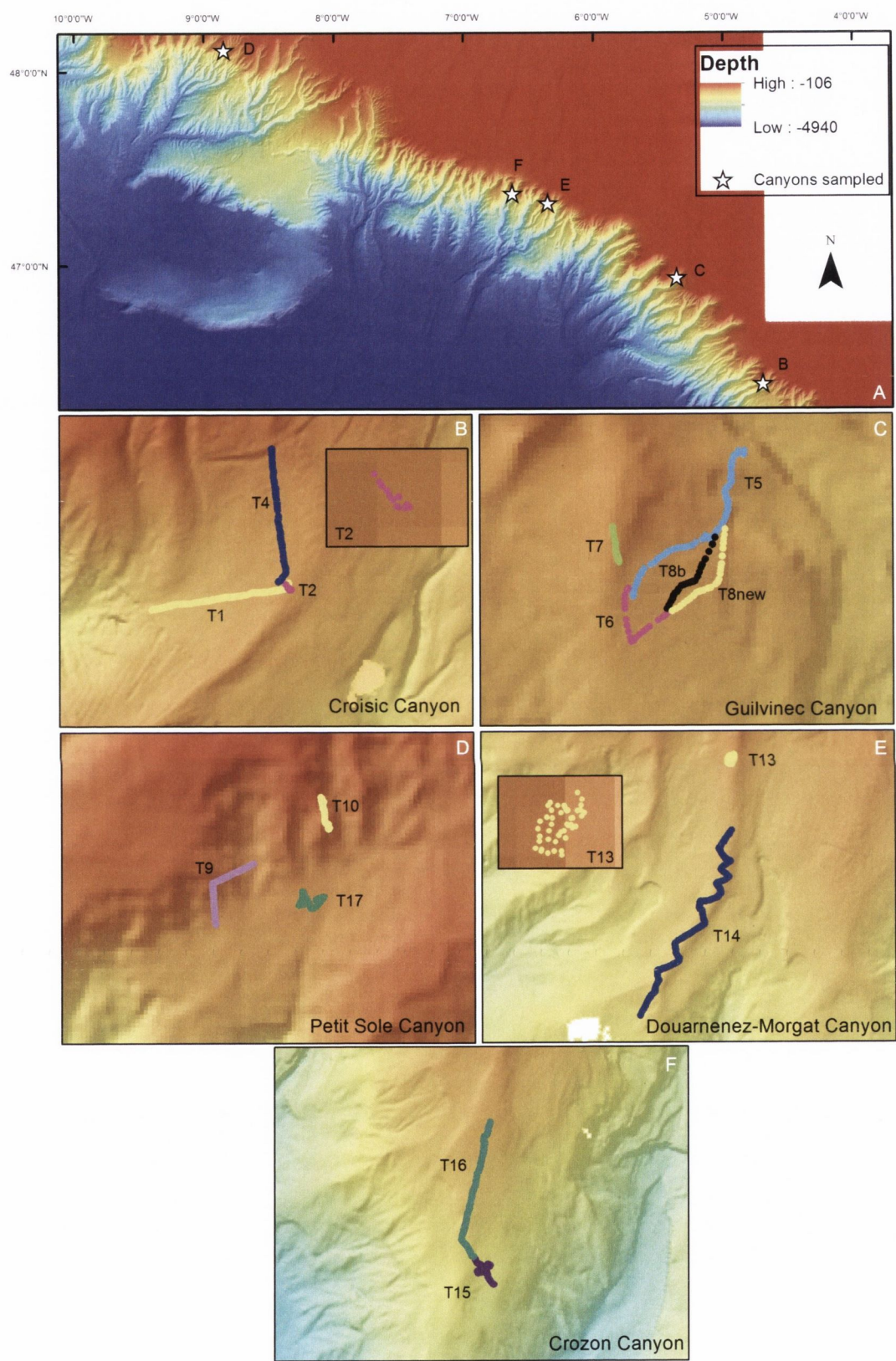


Fig. 1. Location of the study area and video transects (T) in canyons in the Bay of Biscay, France (A). Transects T1, T2, T4 in Croisic canyon (B); T5, T6, T7, T8b, 'T8new' in Guilvinec Canyon (C); T9, T10, and

T17 in Petit Sole Canyon (D); T13 and T14 in Douarnenez-Morgat Canyon (E); T15 and T16 in Crozon Canyon (F).

2.2 Video survey

Continuous video transects were obtained within adjacent canyons. Transects were nearby but never overlapping (Fig. 1). While we attempted to maintain constant ROV cruising speed (0.5 kt) and altitude (2 m from the bottom), the ROV did reach a maximum altitude of 5 m due to strong currents encountered in some parts of the transects. Consequently, the transects vary in width from 2 m to a maximum of 12 m. Photographs where the bottom floor was obscured (from high altitude or frames that were out of focus) were excluded from the analyses.

2.3 Image analyses

To determine the influence of predation and competition on deep-sea echinoid resource use, we compared echinoid microspatial preferences in the presence and absence of (i) interspecific competitors, (ii) fish, and (iii) decapod predators.

To study echinoid response patterns to predators, we collected data on echinoid positioning on coral substrate (*i.e.*, at the base/top of dead/living coral). For coral positioning, ‘top’ and ‘bottom’ refer to the extreme top and bottom portions of the coral, respectively. Intermediate heights are located between the top and bottom sections. ‘Open’ refers to the positioning of echinoids in exposed areas of coral containing habitats, so on sediment, rubble, remains, but still within the coral-containing habitat. The presence and absence of surrounding predators (fish and decapods) was noted for each video frame containing an echinoid. Predators of deep-sea echinoids are not well documented, however, *Chimaera fulva* and *Chimaera lignaria* are known to feed on deep-sea echinoids (Walker et al., 2008) and several fish taxa, such as *Molva molva*, *Alopecephalus bairdii*, *Epigonus telescopus*, *Helicolenus dactylopterus*, *Chimaeras* spp, and the spiny eels are known to supplement their diet with echinoderms (Howell et al., 2009). Decapods as well as octopi have also been observed predating on deep-sea echinoids (Stevenson personal observations). As such, the presence of *Chimaeras* spp, *Molva molva*, *Mora moro*, *Lepidion* spp, *Trachyscorpia* spp and sharks; as well as decapods *Bathynectes* spp, *Chaceon affinis*,

and other unidentified crabs were noted along each transect. Note that octopi have also been observed feeding on echinoids (Stevenson personal observations), but they were excluded from this study due to the low frequency of octopi observations.

Aggregation patterns were also recorded whereby the number of conspecifics within each aggregate were counted. An ‘aggregate’ was defined as a loose cluster of echinoids in the vicinity of each other, whereby in most cases spines were interlocked. With the help of physical objects in the image and the video time stamp we were able to gauge the proximity of echinoids within a transect.

To determine microhabitat preferences associated with competitive interactions, the substrate immediately below each echinoid was recorded along with the presence or absence of inter- and intraspecific competitors in proximity (or within the image) of the observed echinoid. Five substrates were identified: sediment, rubble, remains (coral debris), dead reef, and live coral.

Community composition varies with depth and seafloor characteristics (Williams et al., 2010) and habitat type is a good indicator of zonation for these parameters, so analyses within habitat type were compared. Thus for each echinoid encountered we recorded the habitat type utilized. Nine categories were used in our study. Habitats characterized by coral infrastructure consisted of ‘isolated colony on hard substrate’, ‘isolated colony on soft substrate’, ‘loosely-packed framework of *Lophelia* and/or *Madrepora*’, ‘colonized cold-water coral (CWC) reef’, ‘dead reef’, and ‘living CWC reef’; and habitats devoid or with fine, broken and low lying coral material were ‘CWC rubble’, ‘CWC remains’, and ‘sediment’. These nine categories were formulated from the CoralFish Northeast Atlantic and Mediterranean Cold-Water Coral Habitats Catalogue (Guillaumont et al., 2012).

2.4 Statistical analyses

All statistical analyses were performed in R version 2.15.1 (R Core Team, 2012) with packages ‘nnet’ and ‘MASS’ (Venables and Ripley, 2002).

A multinomial generalized linear model (GLM) was used to test the significance of echinoid positioning on coral in the presence/absence of predators (*i.e.*, fish, decapods and their interaction); the response matrix consisted of four columns (*i.e.*, four positions: ‘top’, ‘bottom’, ‘intermediate’, and ‘open’). ‘Top of coral’ and ‘bottom of coral’ which refer to

the extreme top and bottom portions of the coral, respectively; and 'intermediate' heights located between these top and bottom sections; 'Sea floor' which identifies echinoids positioned in exposed areas of coral containing habitat (*i.e.*, on sediment, rubble, remains, but still within the coral containing habitat). Models were compared with an analysis of deviance (*i.e.*, 'anova' function, test = 'Chisq').

Note that the presence of inter- and intraspecific competitors was initially added to the model to verify whether these might affect coral positioning, but they were removed from the final predator-prey model because they showed no significant correlation with coral positioning ($p = 0.2$ and 0.3 , respectively).

Similar to the predation model, a multinomial GLM was used to test the significance of substrate use in the presence/absence of a competitor (*i.e.* inter- and intraspecific). The response matrix consisted of five substrates (*i.e.*, sediment, rubble, remains, dead reef, live coral). Statistical comparisons were only conducted for loosely packed and dead CWC reef habitats. Similar comparisons could not be made for habitats of isolated colonies of Scleractinia on hard and soft substrate due to insufficient numbers ($N = 1$) of *C. cidaris* and echinothurids encountered together.

3. Results

3.1 Predation effects on echinoid behaviour

A total of 2,405 *C. cidaris* and 781 echinothurids were observed along the video transects. A significant change in space use (coral positioning in this case) by *C. cidaris* within coral containing habitats (isolated colonies of scleractinia on soft and hard substrate, dead CWC reef, loosely packed reef, colonized reef, living CWC reef) was correlated to the presence of fish ($p < 0.001$) and decapods ($p = 0.003$). More specifically, when in the vicinity of fish, *C. cidaris* were four times less likely to be found at the top of the coral infrastructure; and proportionally, there were twice as many individuals observed at the base of the coral (Fig. 2). In the presence of decapods, there were four times fewer *C. cidaris* observed in the open areas of the reef and the odds of finding *C. cidaris* on the coral infrastructure in the presence of a decapod were twice that in their absence (Fig. 2). There were very few observations made with both predators ($N = 3$) present, but during these encounters *C. cidaris* were only found on the coral infrastructure and never in the open areas of the reef

(Fig. 2). Fish and decapod effects were significant in each other's presence but their interaction effect was not (Table 1).

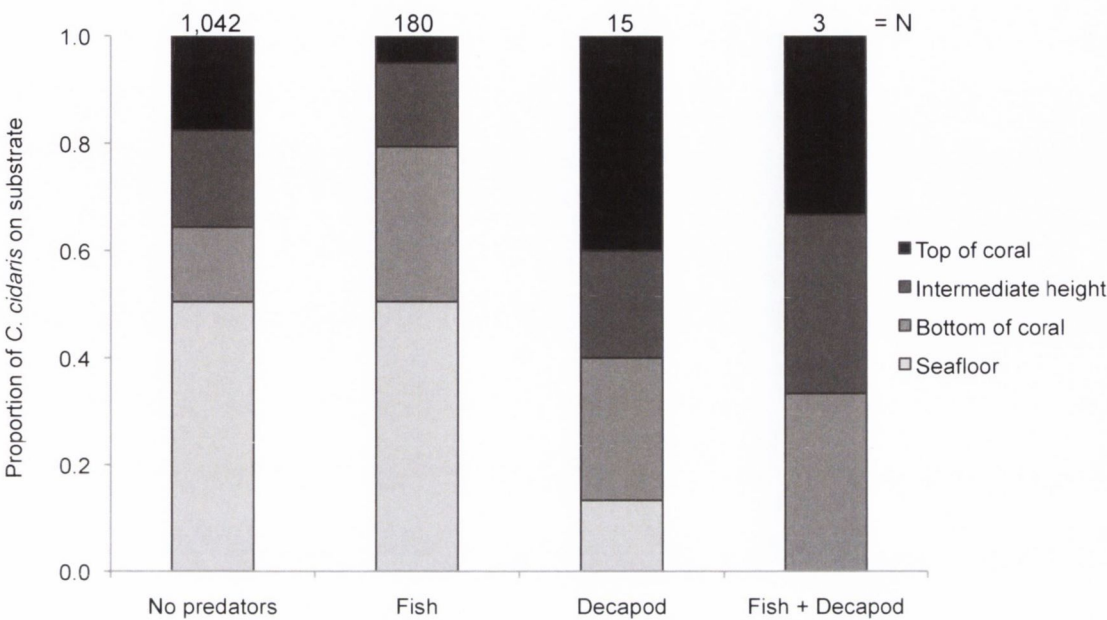


Fig. 2. Coral positioning by *Cidaris cidaris* in coral containing habitats when in the presence and absence of fish and decapod predators. Both the live and dead coral infrastructures were considered for coral positioning (top, intermediate, bottom heights). N is the total number of individuals observed in that group.

Table 1. Effect of fish and decapod predators on space use by *C. cidaris* in coral-containing habitats. Results from the multinomial GLM are displayed in the table. The model tested the effect of fish, decapods, their effect in each other's presence (Models: Fish, Fish and Decapod; Decapod, Fish and Decapod), and their interaction, on *C. cidaris* coral positioning. Significant interactions are highlighted.

	Model	Residual Df	Residual Deviance	Df	LR statistic	Pr(Chi)
	1	2427	3065.7			
	Fish	2424	3028.5	3	37.19	<0.001
	1	2427	3065.7			
	Decapod	2424	3051.7	3	14.04	0.003
	Fish	2424	3028.5			
	Fish and decapod	2421	3014.4	3	14.12	0.003
	Decapod	2424	3051.7			
	Fish and decapod	2421	3014.4	3	37.26	<0.001
	Fish and decapod	2421	3014.4			
	Fish, decapod, and their interaction	2418	3012.5	3	1.94	0.6

A significant change in coral positioning by echinothurids was correlated to the presence of fish in coral habitats ($p < 0.001$; Fig. 3). In the presence of fish, there was a

small decrease in echinothurids occupying the exposed areas of the coral habitat, but echinothurid positioning on the coral infrastructure showed a clear shift from the top to bottom sections of the coral. More specifically, there was a two-fold decrease in echinothurids observed at the top of the coral; none were observed at the intermediate sections, and a four-fold increase in echinothurids observed at the base of the coral when in the presence of fish (Fig. 3). In the presence of decapods, a similar trend to that of *C. cidaris* was observed, whereby the proportion of echinothurids encountered in exposed areas ('open') decreased, while the proportion in the top and intermediate sections of the coral infrastructure increased. However, this should be interpreted with caution as few observations were made in the presence of decapods ($N = 4$), and these did not show statistical significance ($p = 0.2$).

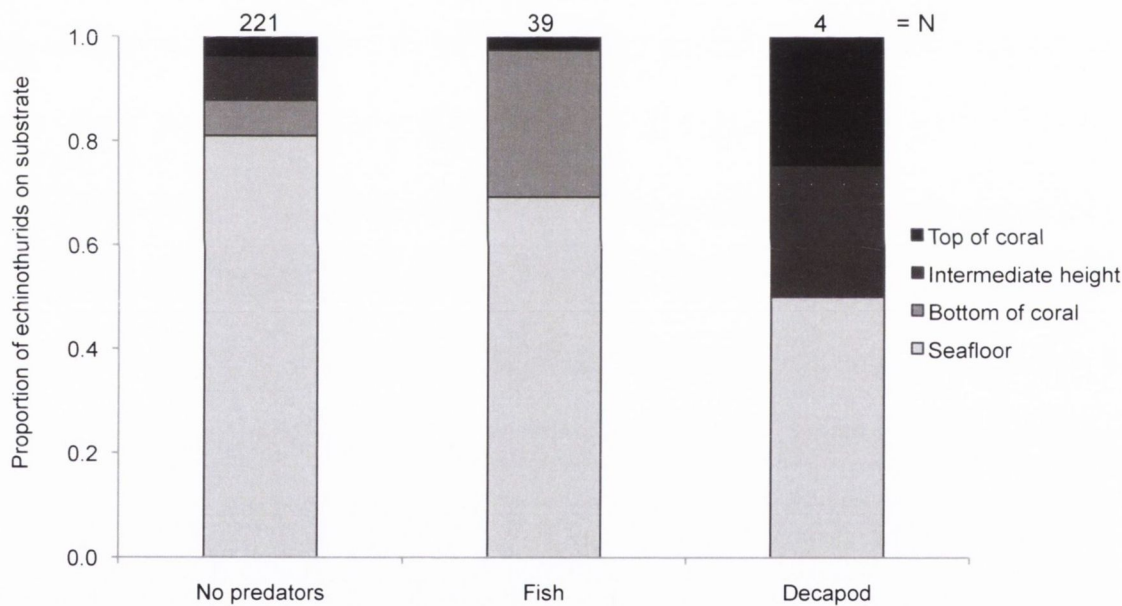


Fig. 3. Coral positioning of echinothurids in coral containing habitats when in the presence or absence of fish and decapod predators. Both the live and dead coral infrastructures were considered for coral positioning (top, intermediate, bottom heights). N - total number of individuals observed in that group.

3.2 Taxa-specific aggregation patterns in the presence/absence of predators

C. cidaris were most frequently encountered in solitude or in pairs (Fig. 4). Large aggregates (>7 members) -with a maximum of 10 individuals- were rarely observed.

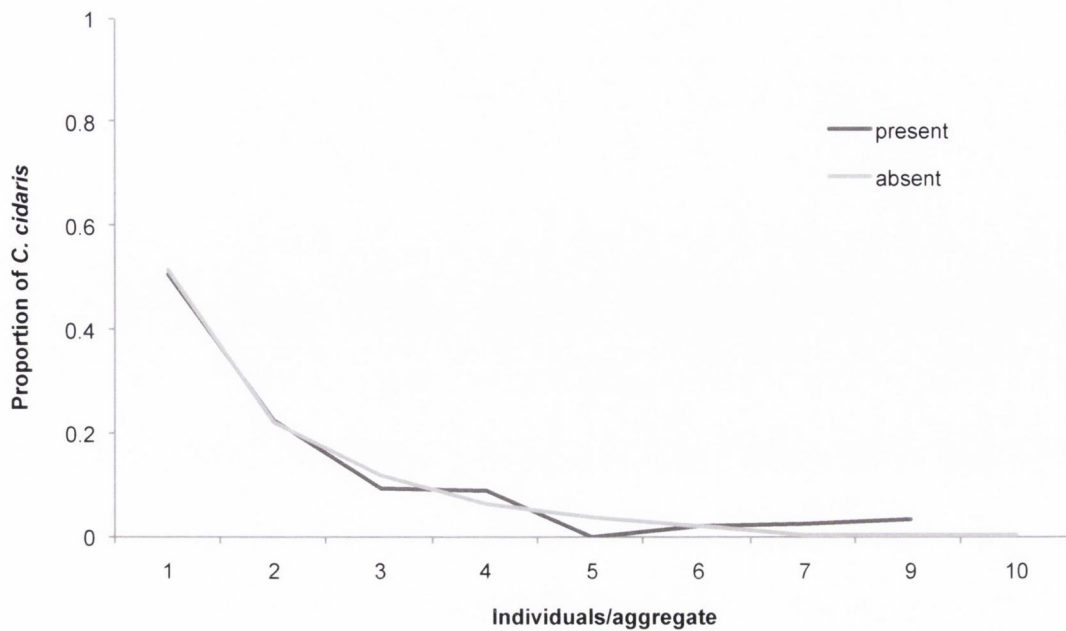


Fig. 4. *Cidaris cidaris* aggregative behaviour in the presence and absence of fish and decapod predators. The proportion of *C. cidaris* aggregates were pooled from all transects. Mean number of individuals per aggregate in the presence 2.22 and absence 2.07 of predators.

Echinothurids were mostly found in solitude and aggregates with >3 members were occasionally observed, but groups with >6 individuals were never encountered (Fig. 5). For both taxa, these patterns were not altered by the presence of fish (Fig. 4, 5). In fact, the average aggregate size in the presence of fish only increased slightly from that in their absence (*C. cidaris*: 2.22 vs. 2.07 individuals/aggregate; echinothurids: 1.39 vs. 1.13 individuals/aggregate).

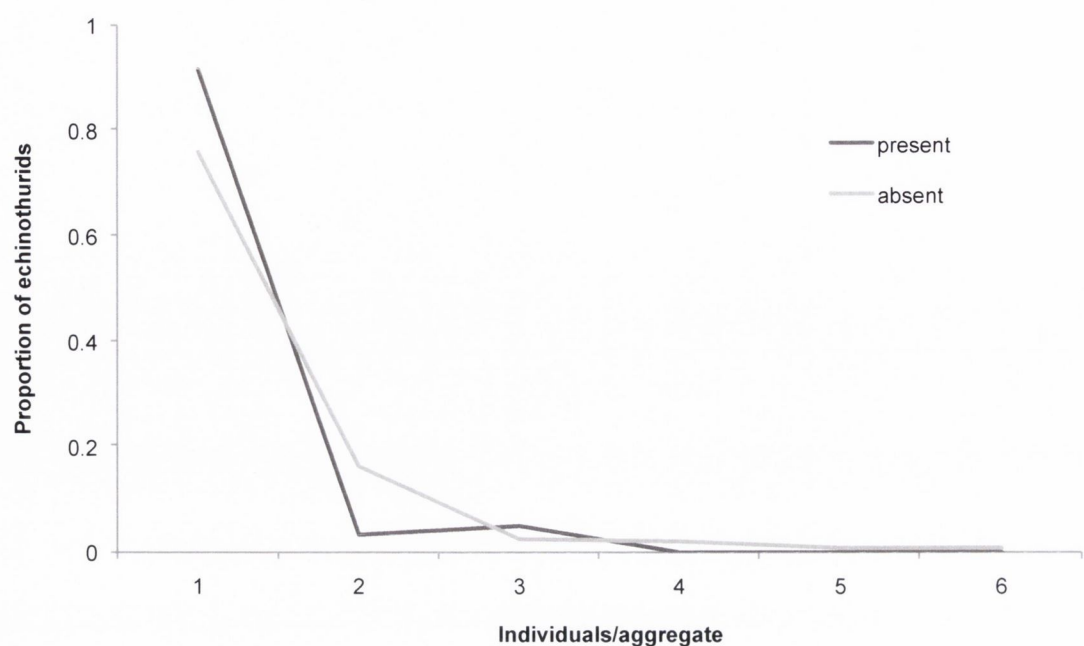


Fig. 5. Echinothurid aggregative behaviour in the presence and absence of fish and decapod predators. Proportion of aggregates of echinothurids were observed along all transects. Mean number of individuals per aggregate in the presence 1.39 and absence 1.13 of a predator.

3.3 Competition

3.3.1 Substrate utilization by echinothurids in the presence of *Cidaris cidaris*

No significant patterns were detected for echinothurid substrate utilization in the presence of *C. cidaris* competitors (Fig. 6; Table 2).

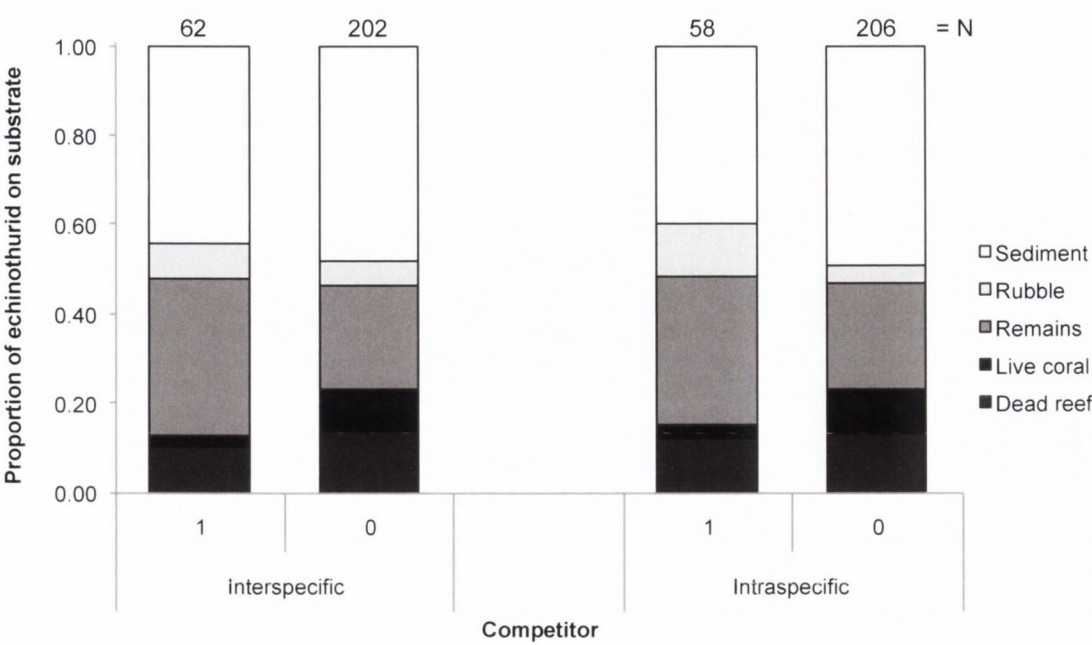


Fig. 6. Coral infrastructure usage by echinothurids in the presence (1) and absence (0) of intra- and interspecific (*Cidaris cidaris*) competitors. Proportions represent numbers of echinothurids on each substrates. Only habitats found containing live coral and dead reef infrastructure were included in the figure.

Table 2. Effect of inter- and intraspecific competition on echinothurid substrate use within coral containing habitats. Results from the multinomial GLM are displayed in the table. The model tested the effect of inter- and intraspecific competition, and their effect in each other’s presence (Models: inter, inter and intra; intra, intra and inter), and their interaction, on echinothurid substrate choice. Inter = interspecific competition (*i.e.* presence of *Cidaris cidaris*); Intra = intraspecific competition (*i.e.* presence of other echinothurids). Significant interactions are highlighted.

	Model	Residual Df	Residual Deviance	Df	LR statistics	Pr(Chi)
	1	908	689.4			
	Intra	904	675.8	4	9.60	0.05
	1	908	689.3			
	Inter	904	681.7	4	7.62	0.1
	Intra	904	679.8			
	Intra and inter	900	673.8	4	5.93	0.2
	Inter	904	681.7			
	Intra and inter	900	673.8	4	7.91	0.1
	Intra and inter	900	673.8			
	Intra, inter, and their interaction	896	668.9	4	4.98	0.3

3.3.2 Substrate utilization by *Cidaris cidaris* in the presence of echinothurids

A significant shift in substrate use by *C. cidaris* was correlated to the presence of interspecific (echinothurids), but not intraspecific competitors (Fig. 7; Table 3). *C. cidaris* showed a two-fold increase in dead coral infrastructure usage when in the presence of echinothurids; no change of remains substrate usage; a slight decrease in live coral and sediment substrate utilization; and no *C. cidaris* were observed on rubble.

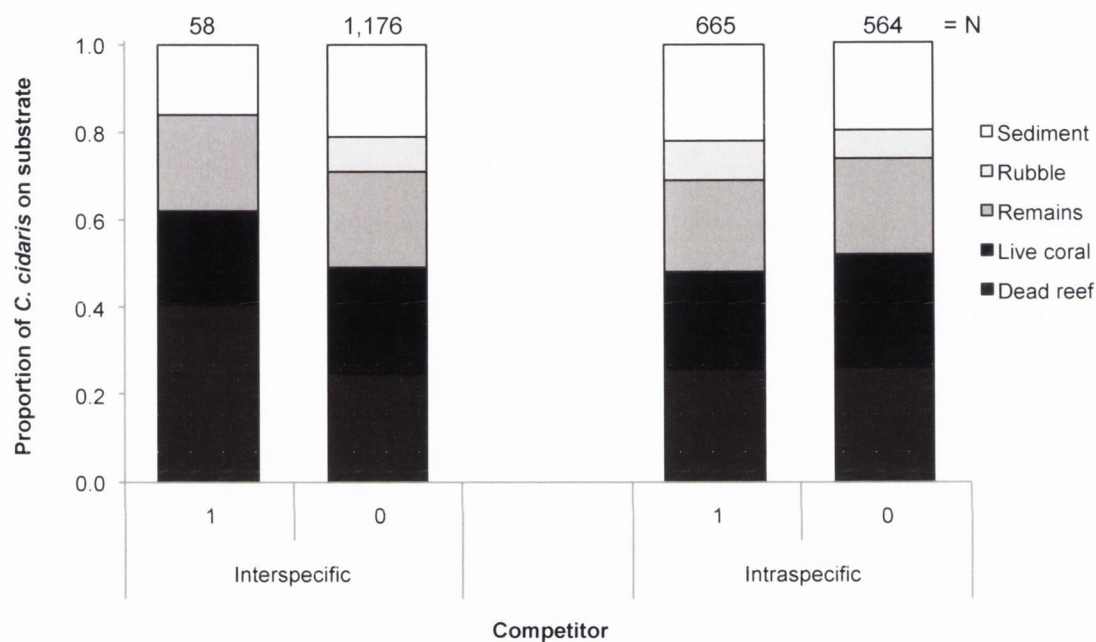


Fig. 7. Coral infrastructure usage by *Cidaris cidaris* in the presence (1) and absence (0) of intra- and interspecific (echinothurid) competitors. Proportions represent numbers of *C. cidaris* on each substrate. Only habitats found containing live coral were included in the figure.

Table 3. Effect of inter- and intraspecific competition on *C. cidaris* substrate use within coral containing habitats. Results from the multinomial GLM (analyzed in the R package) are displayed in the table. The model tested the effect of inter- and intraspecific competition, and their effect in each other's presence (Models: inter, inter and intra; intra, intra and inter), and their interaction, on *Cidaris cidaris* substrate choice. Inter = interspecific competition (*i.e.* presence of echinothurids); Intra = intraspecific competition (*i.e.* presence of other *C. cidaris*). Significant interactions are highlighted.

	Model	Residual Df	Residual Deviance	Df	LR statistics	Pr(Chi)
	1	3236	3835.1			
	Intra	3232	3827.4	4	7.67	0.1
	1	3236	3835.1			
	Inter	3232	3822.4	4	12.70	0.01
	Intra	3232	3827.4			
	Intra and inter	3228	3815.5	4	11.97	0.02
	Inter	3232	3822.4			
	Intra and inter	3228	3815.5	4	6.95	0.1
	Intra and inter	3228	3815.5			
	Intra, inter, and their interaction	3224	3805.3	4	10.14	0.04

4. Discussion

4.1 Behavioural responses to predators

In this study, *C. cidaris* and echinothurids were found at all levels on the coral substrate (extreme top and bottom as well as intermediate heights) when in the absence of fish predators, but when in the presence of fish, a clear shift from the top and intermediate to the bottom sections of the coral was observed. This suggests that echinoids might avoid these parts of the coral infrastructure when under predation threat by fish and might predominantly seek shelter at the base of the coral structure. The behavioural response observed in the presence of echinivorous decapods differed slightly to that in the presence of fish. Here, echinoids from both taxa were most often encountered on the coral infrastructure and infrequently observed in the exposed areas of the reef, suggesting that echinoids might escape decapod predation by migrating up the coral infrastructure -away from the ground- to remain out of reach from decapods.

The correlation between predators and positioning on the coral infrastructure is unlikely to be a response to currents or food availability since food availability on the coral infrastructure (*i.e.*, associated organisms on the dead infrastructure or mucus lining the surface of live coral) is unlikely to differ in significant amounts along the height of the

coral. As well, the significant change in echinoid positioning on the coral infrastructure in the presence of a predator suggests that this is most likely an artifact of predator avoidance rather than a foraging behaviour. Ebling et al. (1966), Dance (1987), Kitching (1987), and Barnes and Crook (2001) found similar predator-driven migratory patterns to the tops of boulders in populations of the shallow-water echinoid *Paracentrotus lividus*. Cowen (1983), Harrold and Reed (1985) and Mann (1985) found predator avoidance to be the dominant behaviour whereby echinoids remained in hiding when food was abundant and competition was minimal.

Most studies argue that predation tends to elicit a flight response, as described above, in shallow-water echinoids, but others postulate that defensive aggregates are also a feasible behavioural shift resulting from predation threat (see Scheibling, 1996; and Vadas and Elner, 2003). Experimental studies have found predators to be a major contributor to conspecific aggregation in the presence of a predator (see Pearse and Arch, 1969; Bernstein et al., 1981, 1983; Scheibling and Hamm, 1991), but such defensive aggregates were not observed in our study. When comparing aggregation patterns in video frames containing predators to those without, it was found that aggregates formed irrespective of the presence of predators. When aggregates were observed, these did not appear to be associated with the presence of predators; large aggregates of echinoids formed most often when there were no predators in the vicinity and solitary individuals were often encountered in the presence of predators. In fact, large aggregates were rarely observed in our study; numbers never exceeded 10 individuals per aggregate, suggesting that aggregation is rarely observed in deep-sea echinoids. Also, there was no difference between the aggregation patterns detected in habitats where spatial refuge was available over those that were absent (e.g. aggregates were as frequent in dead, colonized, and living CWC reefs vs. sediment, rubble and remains habitats).

Vadas et al. (1986) found a similar response, where conspecific aggregations were unaltered by the presence of predators. They argue that aggregates are an artifact of feeding rather than a defense against predators. Similarly, Scheibling and Hamm (1991) showed that populations of *Strongylocentrotus droebachiensis* (both juvenile and adult size classes) formed exposed feeding aggregates irrespective of the presence or absence of predators; and aggregations of *Lytechinus variegatus* only form around food or food with predators (Vadas and Elner, 2003). However, the aforementioned studies conflict with those of

Bernstein et al. (1981, 1983) who found that large echinoids tend to aggregate when in the presence of predators such as crabs. Pearse and Arch (1969) also argue that *Diadema setosum* forms aggregates for protection against predators as their spines provide a structural defense against predators. Feeding (Booolootian et al., 1959) and seasonal breeding (Young et al., 1992) aggregates have also been documented among deep-sea echinoids, but -in agreement with the present study- there is no mention of defensive aggregates in the deep sea. Echinoids such as *C. cidaris*, which possess a similar spine morphology to *Diadema*, may also aggregate for protection, but the dispersed and sparse echinoid densities observed in the study render common defense ineffective in the submarine canyons of the Bay of Biscay. By expanding the study over a broader geographic scale we may be able to compare denser populations such as those found in the southwest Pacific, and thus better understand factors influencing aggregation patterns in deep environments.

Experimental work conducted in the deep sea supports the notion that predators have a strong structuring role on the benthic invertebrate fauna (Rex, 1976; Micheli et al., 2002; Gallucci et al., 2008a, 2008b; Thistle et al., 2008). Rex (1976) argues that predators are a key factor in biological accommodation in the deep sea and that this contribution is largely depth dependent. Likewise, Micheli et al. (2002) suggest that large epibenthic predators influence hydrothermal vent communities by regulating the activities of small mobile grazers and thus influence the structure of these communities through chains of species interactions. It is by this same logic that the predators (fish and decapods) in the present study might influence the organization of echinoids in deep-sea coral reef habitats and subsequently affect the chain of interactions between echinoids and their competitors or prey. While this might not directly explain the high species diversity observed in deep-sea benthos, it does indirectly provide support for Dayton and Hessler's (1972) hypothesis, which highlights the importance of predation in structuring communities and hence promote high species diversity in the deep sea.

Overall, sheltering from predators has been shown to be an effective avoidance tactic for echinoids in shallow-water systems (Ebling et al., 1966; Carpenter, 1984; Vadas et al., 1986; Dance, 1987; Kitching, 1987; Scheibling and Hamm, 1991; Barnes and Crook, 2001; Hagen et al., 2002). The absence of an obvious trend in aggregation numbers, and the strong correlation between predator and substrate positioning in the present study suggests

that deep-sea echinoids in the submarine canyons of the Bay of Biscay may also respond to predators by becoming more cryptic (*i.e.*, in this case, sheltering at the base of the coral substrate) rather than aggregating for protection.

4.2 Behavioural responses to inter- and intraspecific competition

Experimental work directly testing the hypothesis of competitive interactions as a structuring force for deep-sea communities are largely lacking, but several studies have attributed observed deep-sea diversity patterns to such interactions (Sanders, 1968; Slobodkin and Sanders, 1969; Grassle and Sanders, 1973; McClain, 2005; McClain and Barry, 2010). McClain (2005) explains that the minimum distance found in the morphospace of deep-sea gastropod species suggests that these gastropod communities might be structured by competition. And megabenthic disturbance by mobile deposit feeders and scavengers near submarine canyon cliff faces reinforces the importance of habitat modifiers in the deep sea (McClain and Barry, 2010). The findings of the present study only partly agree with those of the aforementioned studies on competitive interactions in the deep sea. While no significant trends in intra- and interspecific competition were detected for echinothurids, significant patterns did emerge for *C. cidaris* interactions with their interspecific competitors. A shift towards dead reef substrate usage was correlated with the presence of echinothurids suggesting that there might be a correlation between *C. cidaris* substrate choice and interspecific competition. However, we were perplexed by the lack of a corresponding shift by echinothurids. Live and dead coral infrastructure is thought to be a nutritionally valuable resource for deep-sea echinoids (Stevenson and Rocha, 2012) that might drive competitive interactions. If *C. cidaris* were to show competitive dominance for this resource over echinothurids, then we would have expected to see a response by echinothurids when in reality there seemed to be no correlation between echinothurids and their interspecific competitors (*C. cidaris* in this case).

The observed correlation might be better explained by teasing out the patterns within specific habitats. Where nutritious resources were available, such as living CWC reef, loosely packed, and dead reefs, there was a change in substrate usage by echinothurids in the presence of a competitor (*i.e.*, *C. cidaris*). Fewer echinothurids were observed on the

coral infrastructure (dead and live combined) in the presence of *C. cidaris*. McClanahan (1988) observed competitive hierarchy between three coexisting species of shallow-water echinoids that shared similar diets and a broad within-habitat distribution, but these species differed in their microspatial preferences. Such patterns were also observed by Privitera et al. (2008) who found coexistence via food resource partitioning by *Paracentrotus lividus* and *Arbacia lixula* in the infralittoral zones of the Mediterranean and NE Atlantic. In our study, similar patterns of hierarchal structuring as well as coexistence due to microhabitat and diet diversification among deep-sea echinoids were obscured by anomalous patterns and insignificant correlations. Further investigation is required in order to clarify the role of competition in deep-sea coral habitats.

Alternately, the lack of significance might be attributed to factors such as small population size. According to Menge and Sutherland (1976) competition tends to regulate community structure only once it approaches or has reached its carrying capacity, only then do the species in that community actually compete. It is possible that competition might not be an influential factor for echinoid space and resource use in the submarine canyons of the Bay of Biscay.

4.3 Limitations of the study and directions for future research

It is pertinent to consider the dispersion effect that an ROV might have on benthopelagic fish. Nearby fish might be attracted or repelled by the lights of the camera and thus possibly interfere with the outcomes of the study. Few studies have investigated this issue, however, Cailliet et al (1999) compared different methods for observing deep-sea fish. Trawls, camera sleds, and submersibles were compared for benthic habitats. Here, submersibles detected similar fish taxa and density as trawls and sleds. It is also worthwhile noting that deep-sea fish do present behavioural responses to the noise and light produced by ROVs (Lorance and Trenkel, 2006; Uiblein, 2011). Lorance and Trenkel (2006) observed the behavioural changes of several fish including Chimaeridae and *Trachyscorpia* spp -two taxa important to the present study- and showed a change from their natural stationary or a slow moving position to nervous control movements and lateral avoidance. Some fish sat and waited (one species), others remained active and continued to engage in bottom hunting (three taxa), while others displayed little activity in their bottom habitat (three

taxa). While fish reactions to anthropogenic cues clearly alter their natural behaviour, the fish reportedly remain within the field of view, which is a key factor required in the present study. However, it is clear that the feasibility of ecological studies similar to the present study are highly dependent on prior understanding of animal behaviour. It is possible that certain taxa flee from the site before entering the field of view and may become an issue when conducting behavioural studies (Uiblein, 2011).

Often predation mediates coexistence of echinoid taxa via predation on the competitive dominant (McClanahan, 1988). The interplay between predation and competition has yet to be investigated. For example, McClanahan (1988) found coexistence possible between the top echinoid competitor *Echinometra mathaei* and its subordinate *Diadema savignyi* and *Diadema setosum*. *E. mathaei* was consistently ranked as the top competitor for crevice space, however high predation rates were found for *E. mathaei* while low rates were found on the coexisting *Diadema* spp. Given that predation played a significant role over competition in our study, perhaps predation might play a similar role in mediating the coexistence between *C. cidaris* and echinothurids. Laboratory based experimental work will help refine our understanding of behavioural responses resulting from these interactions.

5. Conclusions

While our study was purely observational, trends drawn from a large sample size (3,188 echinoids) suggest that space and resource use may be predominantly predator-driven and thus supports Dayton and Hessler's (1972) predation hypothesis for the remarkably high species diversity in the deep sea. The behavioural shift depicted in our study suggests that crypsis might be the dominant defensive function for deep-sea echinoids. We argue that the taxa in the submarine canyons studied may predominantly utilize flight responses, rather than an aggregative behaviour, to reduce predation risk. Thus aggregations are likely to form for feeding or breeding rather than for defensive purposes. Interspecific competition may influence species-specific hierarchy on nutritiously valuable substrates in the deep-sea, but the lack of statistical significance in these trends warrants further investigation in order to clarify the role of competition in deep-sea coral habitats. From this it is clear that understanding factors affecting space use and interactions by deep-sea megabenthos may

help us tease out the underlying mechanisms regulating deep-sea community structure and thus contribute to important concepts such as the paradox of high deep-sea diversity. Most importantly, the study has shown that video data may serve a useful role in discerning the relative importance of these interactions in deep-sea environments, which are necessary for gaining a better understanding of the ecological processes taking place in vulnerable deep-sea habitats, such as coral reefs.

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Caenopedina porphyrogigas and *Dermechinuds horridus* in a coral habitat

Echinoid taxa-specific distribution and abundance in deep-sea coral habitats

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Abstract

Patterns of animal habitat use and knowledge of the environmental features affecting these spatial patterns are important for understanding the structure and dynamics of ecological communities. Both aspects remain underdeveloped for deep-sea habitats. The present study investigates echinoid taxa-specific distributions within deep-sea coral habitats on the French, Australian, and New Zealand continental margins. It further examines habitat-related variables that might influence echinoid species distributions.

A total of six echinoid taxa were examined from photographic and video transects. Taxa-specific distribution patterns and habitat-related influences were revealed in the study. As a group, the Echinoidea were found to utilize all habitats available to them, but tended to aggregate in architecturally complex habitats, such as living, loosely-packed, and colonized cold-water coral reefs. However, a taxa-specific investigation found that such associations were largely an artefact of the dominant taxa observed in a specific region. Despite the food and shelter resources offered to echinoids by matrix-forming coral habitats, not all taxa preferred these habitats. Some taxa revealed a random association with habitats, while others displayed non-random associations. Two distinct habitat associations were detected in the study: *Dermechinus horridus* and *Caenopedina porphyrogigas* had a much greater preference for living types of habitats, while *Gracilechinus multidentatus*, *Caenopedina otagoensis*, *Cidaris cidaris*, Echinothuriidae, and Cidaroidae were more

widespread over different types of habitats suggesting a more generalist association for available habitats.

The echinoid population structure was significantly affected by habitat-related variables; of these variables, interspecific competition, depth, and fishing history were the most influential factors in determining the distribution patterns of echinoids. All taxa in France and Australia were significantly more likely to be found in the absence of an interspecific competitor, but those in NZ were unaffected by competitors. The effect of fishing history varied by species, *Caenopedina* species were indifferent, *D. horridus* and *G. multidentatus* associated with untrawled sites, while echinothurids associated with trawled sites. Echinoid distribution was restricted by depth limitations, a pattern often observed among deep sea taxa.

Patterns held regionally (Australia vs. NZ), but differed at a broader geographic scale (SW Pacific regions vs. France) suggesting that video and image data can be used as a powerful tool to successfully and consistently detect trends in echinoid preferences. Refinement of the methods would facilitate better quantitative analyses of habitat associations with studies conducted at a more precise taxon and habitat scales. Most deep-sea ecological studies to date have been conducted at a wider resolution (e.g., taxon class Echinoidea, and habitat categories ‘seamount’, ‘continental slope’), which lack sufficient spatial resolution to resolve sufficient ecological understanding and subsequent conservation planning of vulnerable deep-sea habitats.

Keywords: habitat associations, deep sea, sea urchin, NE Atlantic, SW Pacific, zero-inflation, habitat characteristics, fishing intensity, interspecific competitors, predator activity

1. Introduction

Understanding patterns of habitat use is an important aspect of animal ecology as it is the necessary first step towards understanding the ecological interactions between species and their predators, prey, competitors, and environment that shape these distributions (Heithaus et al., 2006). This is particularly important for ecologically important taxa like echinoids, which play a pivotal role in nutrient recycling and system engineering of shallow-water habitats (e.g., Bromely, 1978; Glynn et al., 1979; Sammarco, 1980; Koike et al., 1987; Jumars et al., 1990; Scheibling and Hamm, 1991; Bak, 1994; Glynn, 1997; Sauchyn and Scheibling, 2009). In tropical shallow-water coral reef habitats echinoid species have a range of effects on coral distribution, abundance, species composition, and the diversity of associated species (Sammarco, 1982). *Echinometra viridis*, for example, grazes locally and creates small algae-free patches, while *Diadema* spp. are more efficient grazers and clear algae from larger areas of the reef, even at low population densities (<16 inds m^{-2}) (Sammarco, 1982). *Diadema antillarum* appears to affect coral settlement, while *E. viridis* does not. In these shallow coral habitats, species-specific impacts are dependent on habitat preferences whereby species have evolved and adapted ways of exploiting different parts of the reef to allow for coexistence with competitors (Coppard and Campbell, 2005). For example, *Echinometra mathaei*, *Diadema setosum*, *Diadema savignyi*, *Echinothrix diadema* and *Echinothrix calmaris*, each associate with different parts of the reef (Coppard and Campbell, 2005). *E. mathaei* is highly competitive and can be found in all zones of the reef, but *Diadema* and *Echinothrix* spp. tend to remain within boulder zones. While important species-specific reef interactions and habitat associations have been described for shallow-water systems, relatively few studies have examined interactions and associations in deep-sea coral habitats.

Coral habitats in the deep sea are often formed by dense amounts of matrix-forming corals and their broken skeletal remains. These provide structure for various organisms, increasing local benthic diversity (Henry and Roberts, 2007). The coral infrastructure may provide shelter from predators; complex habitats provide more refuge from predators than those habitats that are less complex (Etnoyer and Morgan, 2005). In tropical coral reefs, fish species richness has been shown to be closely associated with topographic complexity and substrate rugosity (indicators of habitat complexity) (Risk, 1972, Connell and Jones,

1991). This may also apply to echinoids in the deep sea, which have been shown to primarily seek refuge from predators in the coral infrastructure rather than form defensive aggregates (Chapter 4). Deep-sea corals typically form architecturally complex habitats that are thought to intercept organic matter that would otherwise not settle on the sea floor (Gage and Tyler, 1992; Freiwald et al., 2004; van Oevelen et al., 2009). This accumulation of detrital material and associated organisms on the dead coral infrastructure, as well as the protein rich mucus layer on living coral, may both serve as a food source for deep-sea echinoids (Stevenson and Rocha, 2013). Thus, in the deep sea, echinoid selection for complex habitats may be linked to predator avoidance tactics and availability of food.

Understanding the environmental features driving species-specific distributions is important for the proper development of wildlife management and conservation plans (Calenge, 2007; Dumas et al., 2007). The distribution and abundance of echinoids in shallow-water coral reefs have been attributed to a combination of biotic and abiotic factors, such as predation, behavioural processes, wave activity, water depth, substratum composition, and food availability (Lawrence, 1975; McClanahan, 1988; Dotan, 1990; Coppard and Campbell, 2005; Dumas et al., 2007). Very little is known about the environmental factors that influence echinoid distribution in deep-water coral habitats.

In addition to the physical habitat properties of the coral itself, at least six habitat-related predictor variables have been identified that might play a role in shaping echinoid distributions: (1) the presence of other echinoids leading to a species-specific hierarchy on nutritiously valuable substrates in the deep sea (Chapter 4); (2) predator presence influencing habitat choice (Chapter 4); (3) water depth: bathymetric stratification is a commonly observed in deep-sea communities often linked to factors correlated with depth such as temperature, oxygen concentration, food availability and pressure (Clark et al., 2010a); (4) geomorphology (slope vs seamounts): features possess a different mosaics of habitats which may lead to differences in species associations and distributions (Cartes et al., 2009; Bo et al., 2011); (5) proximity of features (e.g. seamounts): proximity may lead to connectivity for species colonisation between nearby features (Miller et al., 2010); and (6) fishing history: removal of substrate and/or habitat forming organisms by fishing activities may alter the community composition, certain taxa might be more resistant fishing impacts or are early colonisers (see Althaus et al., 2009).

Broad geomorphological habitat categories (O'Hara, 2007) and coarse taxonomic resolution (Araujo et al., 2005) have been deemed as the wrong scale for conservation planning. Geomorphological habitat categories such as 'seamounts' and 'continental slope' are too broad to locate meaningful conservation areas (O'Hara, 2007). Similarly, utilizing coarse taxonomic resolution can provide false positives that mask local patterns of environmental variation (Araujo et al., 2005). Finer habitat categories and taxonomic resolution could help locate important environmental features for conservation planning.

The aims of our study were to

- (i) Document the distribution of echinoids in deep-sea coral habitats.
- (ii) Determine whether echinoids are associated with specific deep-sea coral habitats.
- (iii) Explore relationships between echinoid distribution and six habitat-related predictor variables.
- (iv) Determine if the patterns of distribution differ with taxonomic resolution.

2. Materials and methods

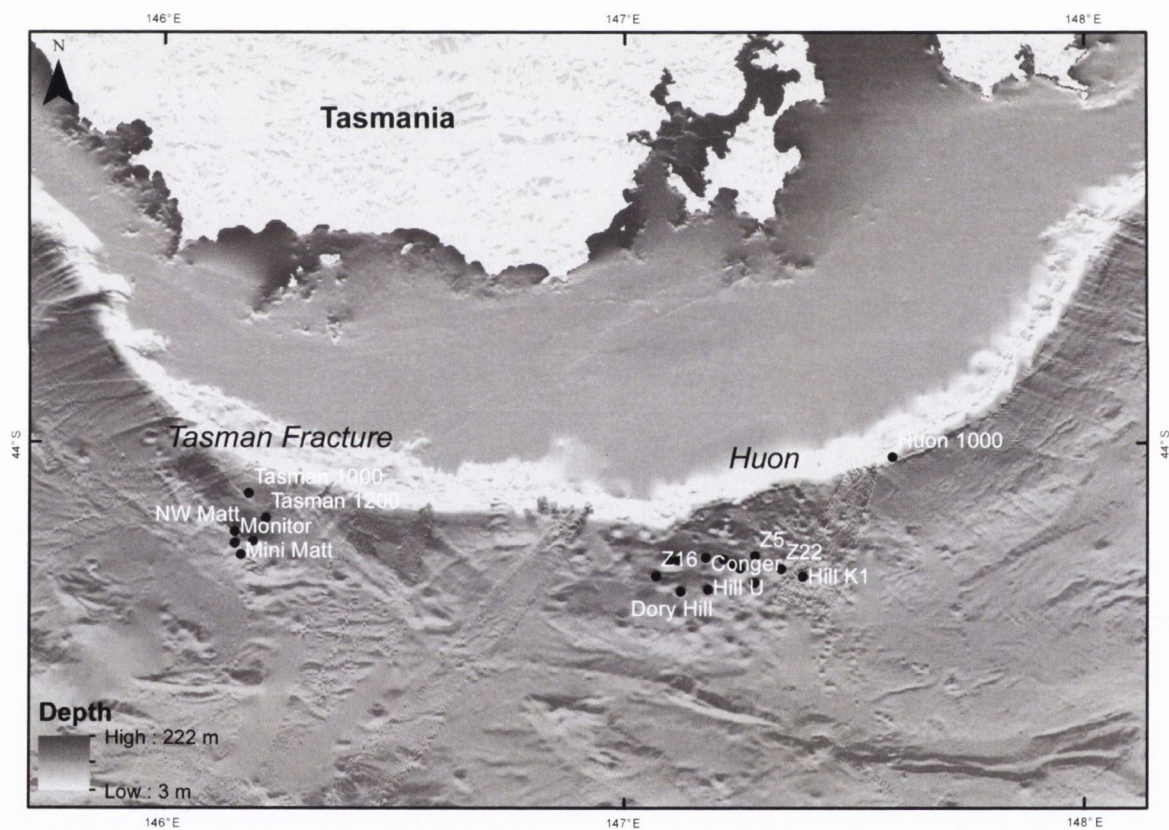
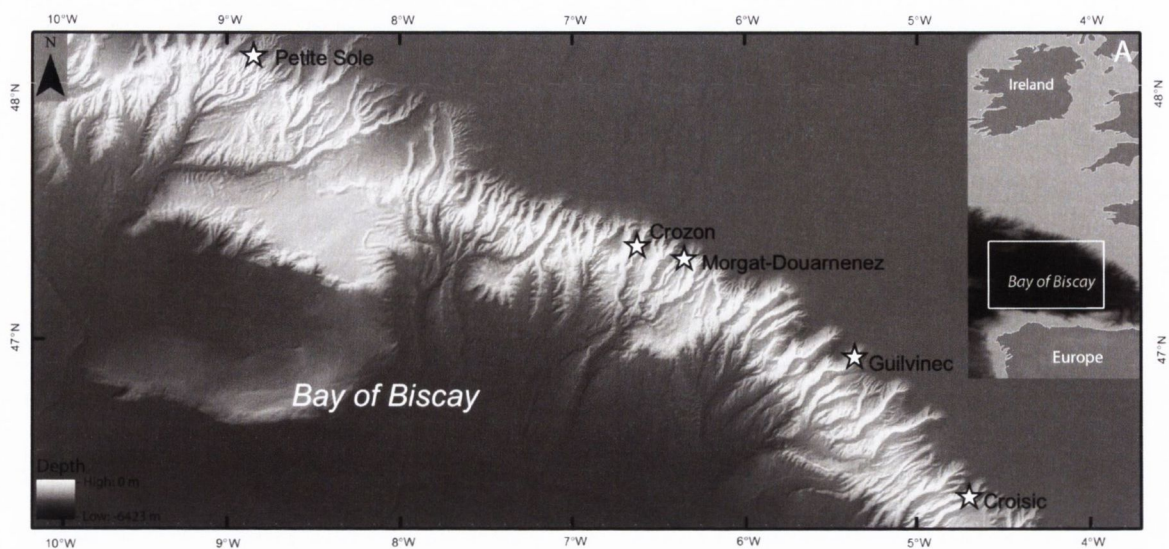
2.1 Study area

Patterns of habitat associations by deep-water echinoids were investigated in three geographic regions: waters off France, in the NE Atlantic, and New Zealand and Australia, in the SW Pacific. These regions were chosen on the basis of high quality video and still image data taken at deep-sea habitats, including coral habitat, which were readily available from surveys conducted by *L'Institut Française de Recherche pour l'Exploration de la Mer* (Ifremer), the National Institute of Water and Atmospheric Research (NIWA), and the Commonwealth Scientific and Industrial Research Organisation (CSIRO). Analyses of data from these regions facilitated the comparison of patterns across a broad geographic scale. The data for the New Zealand and Australian regions permitted comparisons of patterns of habitat association in nearby regions with similar habitat type. The French region had fewer available habitat typologies, so comparison of patterns found in the French region to those of the SW Pacific allowed us to investigate whether shifts in habitat association may take place when a different array of habitat types is available.

In the NE Atlantic, data were collected from continuous video transects in five neighbouring canyons (Croisic, Guilvinec, Petite Sole, Crozon, and Morgat-Douarnenez canyons) in the Bay of Biscay, France (Fig. 1A). The Bay of Biscay lies on the western coast of France and extends from Brest south to the Spanish border and west to Cape Ortegal. Canyons sampled in this study ranged in depth between 524 to 1324 m. A total area of 7.03 ha was sampled in this region. Fishing data were unavailable.

In the Australian region, data were compiled from photographic surveys south of Tasmania, Australia (Fig. 1B). A total area of 1.63 ha was surveyed across 17 seamounts and 3 slope areas was surveyed on the continental margin, south of Tasmania. Two areas were studied: the ‘Tasman Fracture’ and the ‘Huon’ areas, both of which are composed of a steep continental slope and two fields of adjacent seamounts. The seamounts are cone-shaped mounds with summit depth of 700-1400 m, and elevation from the surrounding seafloor of 200-300 m (Dunstan et al., 2012). Deep-sea fisheries in the Tasmanian region started in the early 1990s, certain seamounts were subsequently closed to fishing in 2001 while others still remain fished (Williams et al., 2010). Further details about site fishing histories are outlined in Table 1.

In the New Zealand region, data were obtained from the ‘Graveyard seamount complex’ which is located on the northern flank of the Chatham Rise (Fig. 1C). This complex consists of 20 seamounts spanning summit height depths of 750 to 1250 m (Mackay et al., 2005) and elevations of 100 to 300 m (Clark et al., 2010b). A total area of 2.84 ha was surveyed in this region. The study focused on six of these seamounts, four fished (Diabolical, Morgue, Zombie, Graveyard) and two unfished (Ghoul, Gothic). The region has been heavily fished since the 1990s, but some seamounts were closed to fishing in 2001 (Clarke and Rowden, 2009). The seamounts were fished to varying degrees which are specified in Table 1. Note that Morgue’s SW ridge has never been fished due to its steep walls. Further site details for the Graveyard complex seamounts can be found in Clark et al. (2010b).



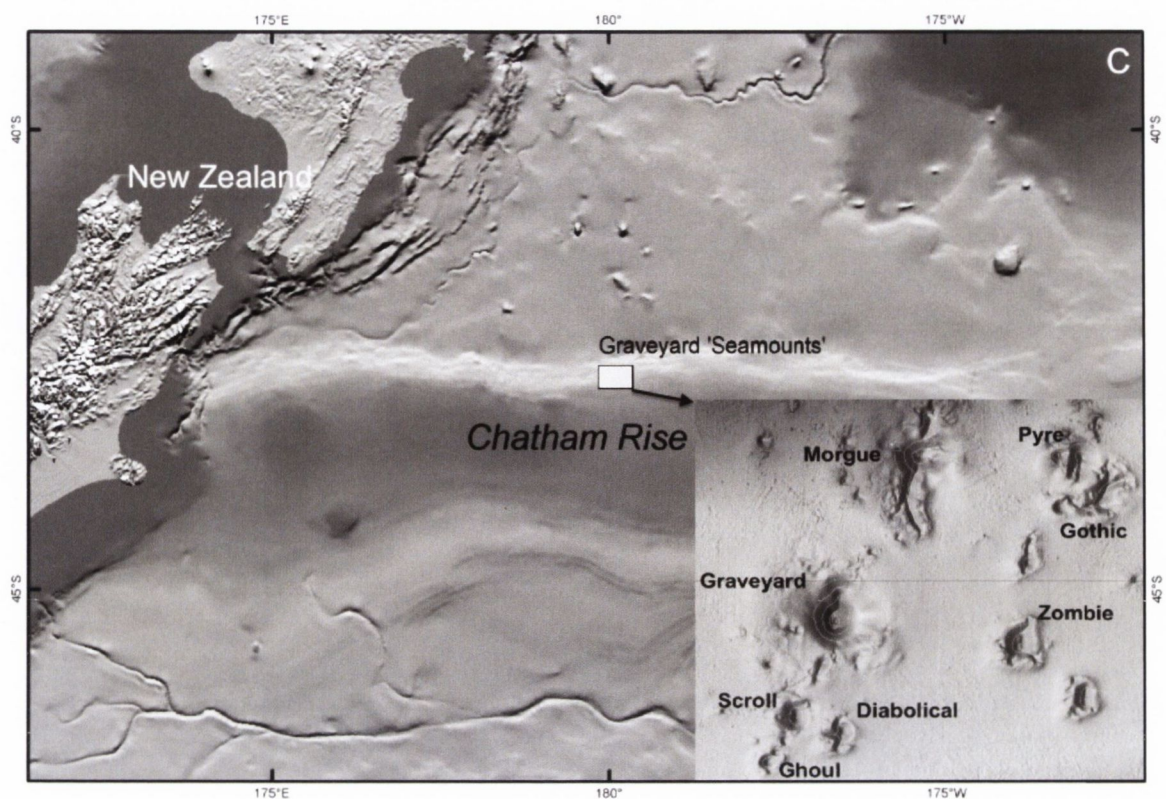


Fig. 1. Location of the study areas and sampling sites in the NE Atlantic and SW Pacific. (A) Five canyons in the Bay of Biscay, off France; (B) 21 seamounts and three slope sites of the ‘Tasman Fracture’ and ‘Huon’ areas, south of Tasmania, Australia; and (C) eight seamounts on the Chatham Rise, east of New Zealand.

Table 1. Details for French, Australian, and New Zealand sites. For Australian and New Zealand sites, trawling has ceased in the area unless otherwise indicated. TF – Tasman Fracture.

Geographi c region	Area	Site	No. transects	Seabed area analyzed (ha)	Depth range (m)	Distance to nearest seamount (km)	Fishing history
France	Bay of Biscay	Croisic canyon	3	0.888	694-1048	-	-
		Guilvinec canyon	5	1.032	778-941	-	-
		Petite Sole canyon	3	1.715	524-981	-	-
		Crozon canyon	2	1.028	108-1394	-	-
		Douarnenez-Morgat canyon	2	2.146	697-1195	-	-
Australia	Huon	Huon 1000 slope	3	0.1189	618-1116	19.07	Never trawled
		Hill U seamount	3	0.1245	1099-1314	2.64	Never trawled
		Dory Hill seamount	1	0.0661	1091-1469	3.63	Never trawled
		Sister 2 (north) seamount	2	0.0924	902-1350	1.46	Trawled
		Hill K1 seamount	3	0.0506	1248-1817	4.23	Never trawled

		Z22 seamount	1	0.0475	1236-1490	4.23	Never trawled
		Little Sister (Z56) seamount	1	0.0675	1107-1277	2.22	Never trawled
		Conger seamount	1	0.0101	1047-1278	3.12	Trawled
		Z16 seamount	1	0.0208	1057-1404	2.16	Never trawled
		Hill B1 seamount	1	0.0329	1139-1405	4.23	Never trawled
		Sister 1 (south) seamount	1	0.0899	864-1280	1.46	Trawled
		Z5	1	0.0526	1176-1250	4.00	Never trawled
	Adjacent to Huon	Pedra seamount	1	0.0101	720-1343	1.35	Trawled (still active)
		Mongrel seamount	2	0.1539	833-1194	1.35	Trawled (still active)
	TF	Monitor seamount	1	0.0173	1104-1390	2.88	Trawled
		NW Matt seamount	1	0.0280	1098-1257	2.88	Trawled
		Mini Matt seamount	1	0.0570	1178-1442	3.02	Never trawled
		Main Matt seamount	3	0.2662	690-1188	3.09	Trawled
		TF 1200 slope	2	0.0430	1079-1288	6.09	Never trawled
		TF 1000 slope	1	2,544	964-1290	6.6	Never trawled
New Zealand	Chatham Rise	Morgue seamount	10	0.5708	910-1269	6.92	Trawled (heavily)
		Morgue SW ridge	1	0.0825	927-1144	6.92	Never trawled
		Graveyard seamount	9	0.7250	766-1128	4.15	Trawled (heavily)
		Diabolical seamount	8	0.2766	898-1079	1.22	Trawled (intermediate)
		Ghoul seamount	4	0.2090	924-1077	1.22	Never trawled
		Zombie seamount	8	0.4734	896-1121	6.80	Trawled (intermediate)
		Gothic seamount	10	0.4935	760-1190	6.80	Never trawled

2.2 Photographic and video surveys

For the transects conducted in the NE Atlantic, 15 continuous video transects (consisting of 25 hrs of video recording) were captured with the vertical high definition camera of the remotely operated vehicle (ROV) Victor 6000 (Ifremer, survey BOBECO) onboard ‘*NO Pourquoi pas?*’. Transects were nearby but never overlapping. While we attempted to maintain constant ROV cruising speed (0.5 kt) and altitude (2 m from the bottom), the ROV did reach a maximum altitude of 5 m due to strong currents encountered in some parts of the transects. Consequently, transects vary in width from 2 m to a maxi2.2 Extracting data from photographic transects; continuous video and still image surveys

For transects conducted in the French region, 15 continuous video transects (consisting of 25 hrs of video recording) were captured with the vertical high definition camera of a remotely operated vehicle (ROV) (Ifremer, survey BOBECO *NO 'Pourquoi pas'*). Transects were close to one another but never overlapping, and conducted by the ROV at a height of 2-5 m above the seafloor. Transects varied in width from 2 m to a maximum of 12 m. Further details can be found in Khripounoff et al. (2014).

In the Australian region, 30 photographic transects were conducted using a towed camera system (CSIRO, survey SS200611, RV *Southern Surveyor*). Photographic transects were run as in the New Zealand region, from summit to base of the seamount. Images were taken at 10 s intervals, a total of 3,640 images were analysed. Images were individually geo-referenced which allowed for the determination of depth estimates and the calculation of distance to the nearest seamount feature (Table 1). Further details can be found in Williams et al. (2010).

In the New Zealand region a total of 50 photographic transects were obtained with a towed camera system (NIWA, survey TAN0905, RV *Tangaroa*). All images were captured using a vertical still camera every 15 s, a total of 6,620 images were analysed. Photographic transects were run from summit to base of the seamount. The camera sled was maintained at a target altitude of 2-4 m above the seabed. Depth and position of sites were obtained from towed camera navigation files. Further site details can be found in Clark et al. (2010b).

2.3 Image analyses

2.3.1 Habitat type

Frame grabs were captured at 1 min intervals for the entire length of the video transect. This subsample of the transect was used to determine the proportion of each habitat within that particular transect by scoring the habitat type in each image. The proportion of each habitat type represented in the transect (PH) was then estimated from these data.

For the SW Pacific region, the amount of habitat encountered was determined by scoring the habitat type in all images analyzed and calculating its total area.

Habitat types (the dominant biotic or abiotic substrate characterizing an area of the site under observation) were determined for each image. There were 17 habitat types in

three coarse groups: five categories of non-living habitats (rocky or sediment substrates), three categories based on by dead coral frameworks and eight categories based on living coral frameworks (Table 2). These categories were formulated from the CoralFish Northeast Atlantic and Mediterranean Cold-Water Coral Habitats Catalogue (Guillaumont et al., 2012); descriptions and details for each habitat may be found here. The living coral framework categories include three categories of cold water coral (CWC reefs); the distinction between these is noteworthy. ‘Living CWC reefs’ primarily possess reef-building stony coral, such as *Lophelia pertusa* and *Madrepora oculata* (in French region) and *Madrepora oculata*, *Solenosmilia variabilis* and *Enallopsammia robusta* (in New Zealand and Australian regions) while ‘mixed CWCs’ include gorgonians and stylasterids, and are not dominated by reef-building stony coral. A ‘colonized CWC reef’ primarily consists of reef-building stony coral colonized by corals such as gorgonians and antipatharians, that are growing on the dead/live stony coral reef.

Table 2. Habitat types, catagorized by coarser groups, that were used in the study. CWC – Cold-water coral.

Coarse groups	Specific categories
Non-living habitats:	Bedrock Boulders Gravel Sediment Sand overlay
Dead coral framework:	Dead CWC reef framework CWC rubble CWC remains
Living coral framework:	Living CWC reef Mixed CWCs Colonised CWC reef Loosely-packed framework Isolated colonies of Scleractinia on hard substrate Isolated colonies of Scleractinia on soft substrate Stylasterids (on hard substarte) Gorgonians on hard substarte Gorgonians on soft substrate

2.3.2 Echinoid taxonomic resolution

Analyses were undertaken at two taxonomic resolution; first as class Echinoidea and second at a lower taxonomic level. Species level identification was attempted for all observations, however the families Echinothuriidae in all regions and the Cidaroidae (subclass) in the New Zealand region, whereby they could not be resolved to species level from image data. *Cidaris cidaris* and Echinothuriidae were observed in the French region. *Dermechinus horridus*, *Caenopedina otagoensis*, *C. poryphyrogigas*, *Gracilechinus multidentatus*, *Poriocidaris purpurata* and Echinothuriidae were observed in the Australian region. *Caenopedina porphyrogigas*, Echinothuriidae and Cidaroidae in the New Zealand region.

2.3.3 Calculation of echinoid abundance and distribution

For the French region, a frame grab was taken for every echinoid encountered along the video transect. The density of echinoid species X (ED) in each habitat type (ES) was calculated using equation (1), where the total area of each transect (ha; TA) was calculated from ArcGIS area matrices generated by Adelie software (©Ifremer). And PH represents the proportion of that habitat type found in the transect. The total area observed at each site is provided in Table 1.

$$ED = ES / (PH \cdot TA) \quad (1)$$

For the New Zealand and Australian regions, echinoid species were identified and counted in each image and densities in photographic transects were calculated as follows. Image area and habitat type were assigned to both the echinoid occupied and unoccupied images. From this, echinoid counts were divided by the total seabed area observed for each transect (consisting of both occupied and unoccupied images). The seabed area for the images taken in the New Zealand region were calculated using parallel laser pointers (20 cm apart) and measured with ImageJ. Where the laser dots were absent or obscured in the image, area was estimated based on the sizes of the organisms in the image. For the Australian images, seabed area of a defined area within the oblique field of view was

calculated using stereo photogrammetric methods (Althaus et al., 2009). The total areas surveyed for the sites in both regions in the SW Pacific are provided in Table 1.

2.3.4 Predators

The presence of predators encountered in each image was noted. Predators of deep-sea echinoids are not well documented, but fishes such as *Chimaera fulva* and *Chimaera lignaria* are known to feed on deep-sea echinoids (Walker et al., 2008); *Molva molva*, *Alopecephalus bairdii*, *Epigonus telescopus*, *Helicolenus dactylopterus*, and some members of the Notacanthidae are known to include echinoderms in their diet (Howell et al., 2009). Rays and other sharks may also supplement their diet with echinoids. Decapods as well as octopi have also been observed predating on deep-sea echinoids (Stevenson personal observations). In this study, the presence of *Chimaeras* spp., *Molva molva*, *Mora moro*, *Lepidion* spp, *Trachyscorpia* spp., sharks, rays, and octopi, as well as decapods *Bathynectes* spp, *Chaceon affinis*, and other unidentified crabs were noted as potential predators along each transect.

2.4 Statistical analyses

All statistical analyses were performed in R version 3.0.0 (R Core Team, 2013). For all tests, significance was determined at $P < 0.05$.

2.4.1 Habitat associations

A Chi-squared goodness-of-fit test was used to assess whether echinoids followed an expected distribution pattern within available habitats, hence identifying whether a preference exists for certain habitats. If echinoids have a random association with habitat typologies then their observed numbers should be proportional to the relative amount of habitat observed. As such, expected numbers of echinoids were obtained from the habitat survey and observed frequencies were obtained from the number of echinoids surveyed. For example, the expected probability (P_{Exp}) of observing a species in a certain habitat is the ratio of the amount (in m^2) of that habitat observed over the sum of the area of all habitats present (equation 2). The expected count of each taxon was obtained by multiplying the expected probability for the taxon by the total number of observations made

for the particular taxon (*i.e.*, all habitats combined). Note that the scaling refers to the number of individuals rather than number of species/diversity.

$$P_{\text{Exp}}(\text{Taxon X}) = \frac{\text{Total area of habitat A}}{\sum \text{all habitats}} \quad (2)$$

Since transect areas were of unequal size, all transects were standardized to 1000 m² (for the New Zealand and Australian regions) and 0.5 ha (for the French region) to make counts comparable across transects. The average observed counts were calculated for each habitat type and species.

Chi-squared goodness of fit tests were subsequently used to explore the association between echinoids and specific habitats. Transects where no echinoids of that particular taxon were observed were not considered in this part of the analysis. Where observed counts for echinoids were less than five, Yates continuity correction was applied to prevent overestimation of statistical significance for the small sample size (Yates, 1934).

2.4.2 Habitat-related variables influencing echinoid distribution

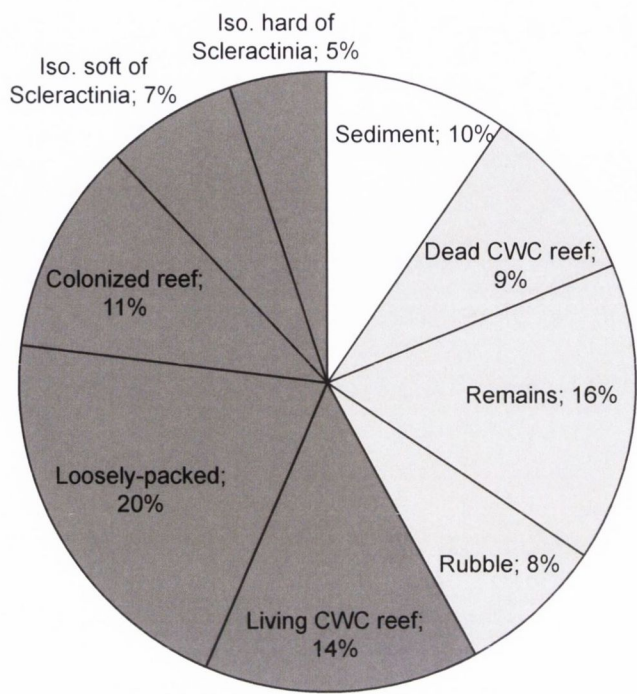
In the introduction we identified 6 general factors that may influence the habitat use and distribution of echinoids; one of these, the presence of predators can be further divided based on the predator type (fish, octopi, decapod) (see Table 3). Here we used these 8 factors as predictors of spatial distribution in a binomial general linear mixed model (GLMM); they were set as fixed factors. Data from canyons in the French region were omitted from this analysis due to insufficient information about the habitat-related variables. To account for spatial autocorrelation, transects within the same seamounts were included in the model as a random factor. Since presence/absence of echinoids were used as a response variable, the image area was set as an exposure variable to offset the varying area of each image. The GLMM was performed with package ‘MASS’ (Venables and Ripley, 2002) and ‘nlme’ (Pinheiro et al., 2014).

3. Results

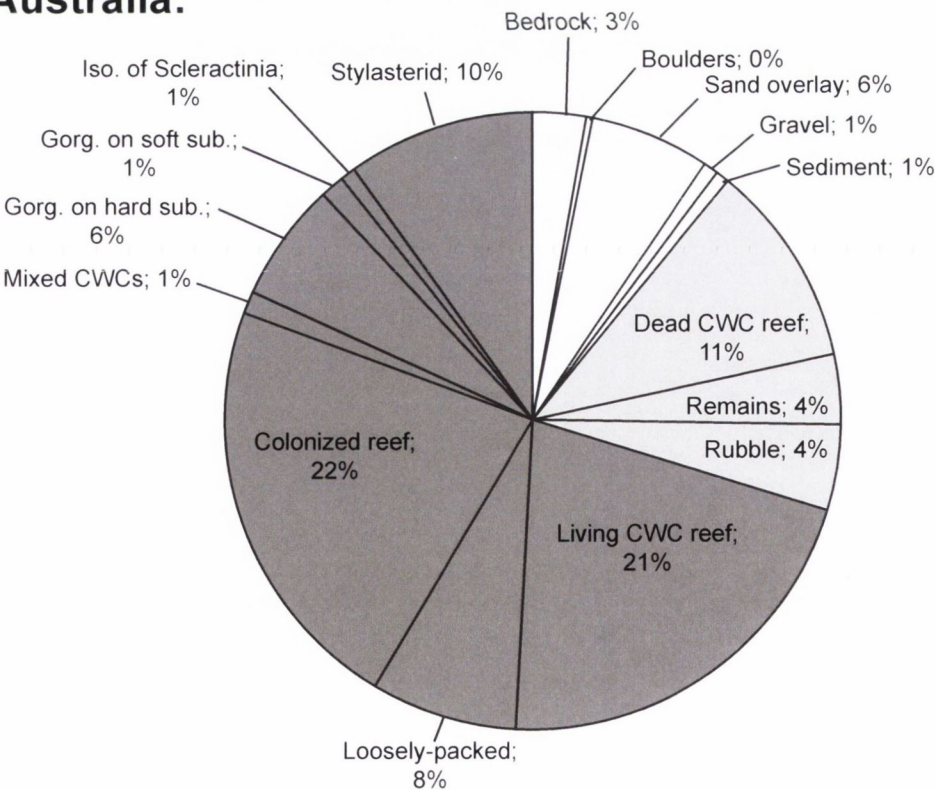
3.1 *Habitat associations for class Echinoidea*

A total of 3,187 echinoids were observed in the French, 1,955 in the Australian, and 143 in the New Zealand region. As a single taxonomic group, echinoids were found to use all habitats available to them (Fig. 2). In all regions, they were most often observed in images containing living coral framework, consisting of 57%, 70%, and 43% of observations in the French, Australian, and New Zealand regions, respectively. In the French region, living and loosely-packed CWC reefs, and their remains had the highest occupancy (14-20%) out of nine habitats observed. Echinoids were relatively equally distributed among the rest of habitats found at French sites. On Australian seamounts, living and colonized CWC reefs had the highest occupancy (21-22%) out of the 16 habitats under observation. These two habitats alone accounted for more than 40% of habitats occupied by echinoids in the study; echinoids were rarely observed ($\leq 4\%$) in the remaining habitats (Fig. 2). In the New Zealand region, living and dead CWC reefs had the highest occupancy (19-24%), followed by the bedrock habitat (16%). Echinoids were equally and rarely ($\leq 7\%$) spread over the rest of habitats (Fig. 2).

France:



Australia:



New Zealand

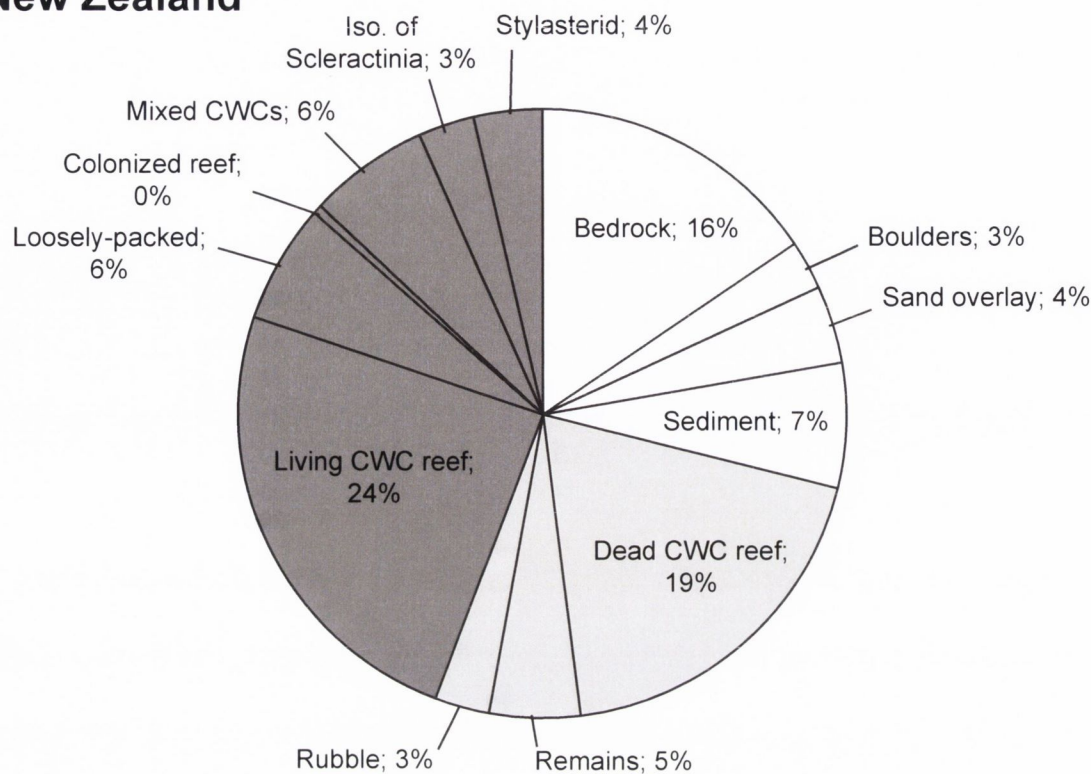


Fig. 2. Distribution of Echinoidea among living, dead and non-living habitats in the Bay of Biscay off France; the ‘Tasman Fracture’ and ‘Huon’ CMRs south of Tasmania, Australia; and ‘Graveyard seamount complex’ east of New Zealand. Shades of grey identify three broad habitat categories: ‘living coral infrastructure’ (dark grey), ‘dead coral infrastructure’ (light grey), and ‘non-living habitats’ (white).

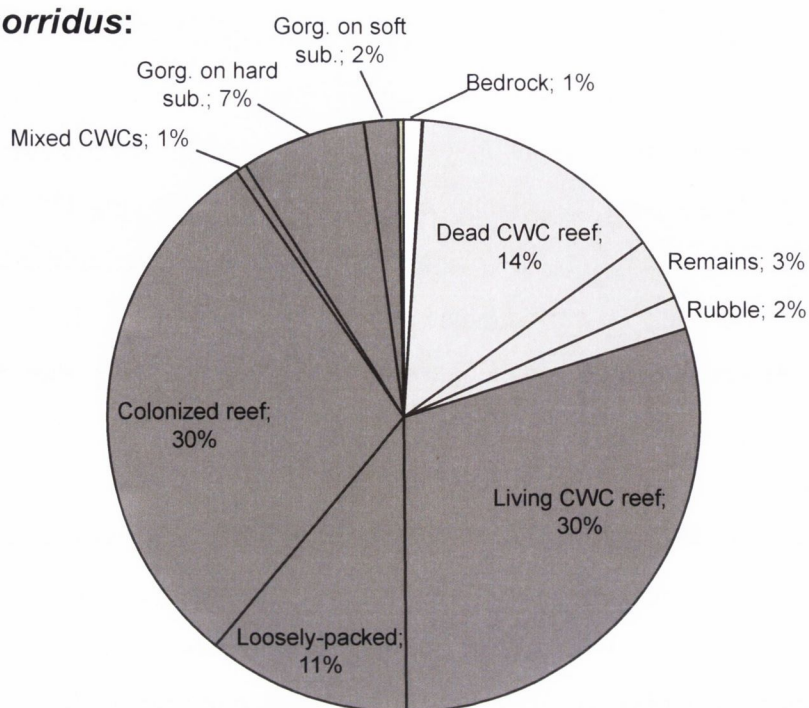
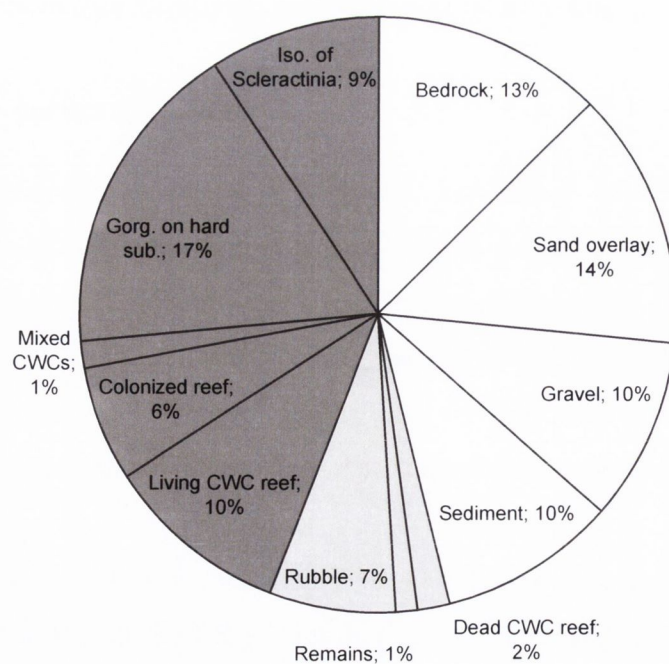
3.2 Taxa-specific habitat associations

French sites were dominated by *C. cidaris*, consisting of 75% of total echinoid observations, and 25% echinothurids. In Australia, *D. horridus* was the dominant taxon in this study -contributing to 66% of total observations- followed by *C. otagoensis* (12%), *C. porphyrogigas* (9%), echinothurids (7%), *G. multidentatus* (5%), and *P. purpurata* (<1%). In NZ, Echinothurids and *C. porphyrogigas* were the dominant taxa, consisting of 42 and 48% of observations, respectively, and the Cidaroidae formed the remaining 10% of observed taxa.

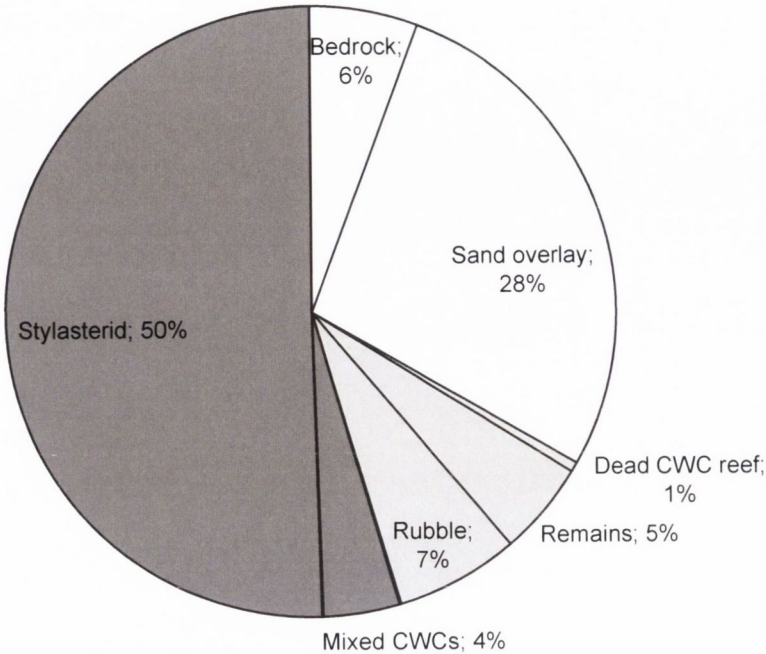
Quantitative comparisons were only possible for the data available on echinothurids and *C. cidaris* observed in the French region; and *D. horridus* observed in the Australian region. In the overall test, *C. cidaris* had a random association with respect to habitats available ($df = 8$, $\chi^2 = 11.272$, $P = 0.2$), while *D. horridus* and echinothurids exhibited a

significant non-random association with available habitats (*D. horridus*: $df = 4$, $\chi^2 = 10.986$, $P = 0.03$; echinothurid: $df = 5$, $\chi^2 = 12.584$, $P = 0.03$).

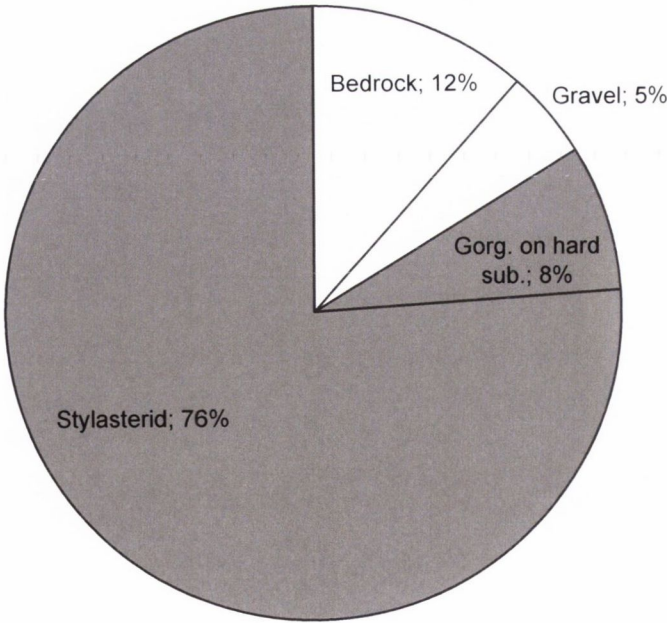
The investigation of species-specific habitat associations revealed a very different usage of habitats compared to patterns of class Echinoidea; some taxa were found in certain habitats but were absent from others. *D. horridus* was mostly found in living habitats (81% of observations), with a strong association with colonized and living CWC reefs (both claiming 30% of observations; Fig. 3). Quantitative analyses revealed a highly significant positive association between *D. horridus* and living CWC reefs ($df = 1$, $\chi^2 = 6.724$, $P < 0.01$), but no significant associations were detected with colonized CWC reefs (Table 2). In other words the proportion of *D. horridus* found in these habitats was similar to the proportion of habitat observed. This species was also found in loosely-packed CWC reef and gorgonian (on hard substrate) habitats, but rarely in gorgonian (on soft substrate) and mixed CWC habitats. In dead habitats, 14% of observations were made in dead CWC reefs. *D. horridus* was rarely found in rubble, remains and bedrock habitats. A significant negative association was observed between this species and rubble, but no significant associations were observed with any of the other habitats.

Australian taxa:***D. horridus*:*****G. multidentatus*:**

***C. otagoensis*:**

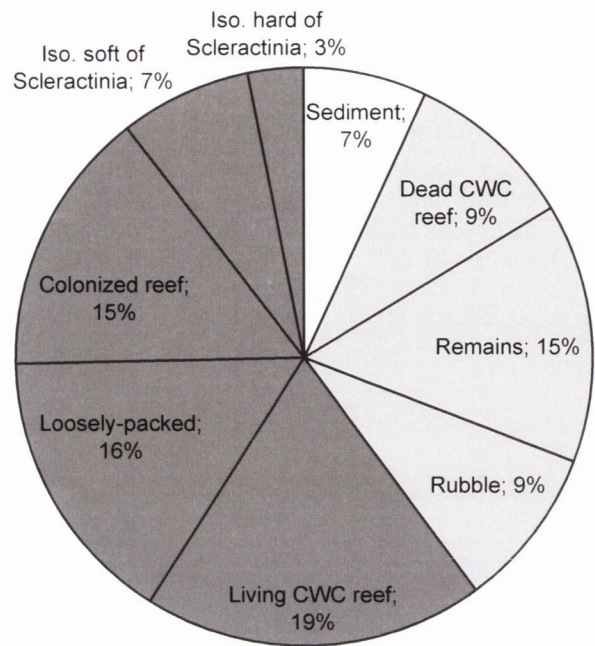


***P. purpurata*:**



French taxa:

C. cidaris:



New Zealand taxa:

Cidaroidae:

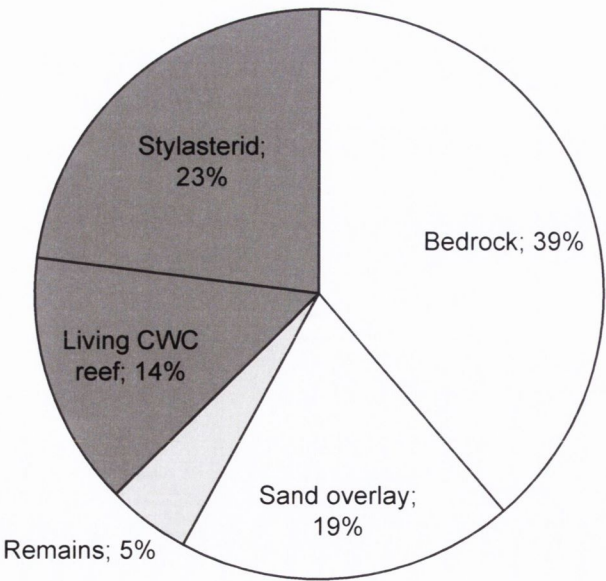


Fig. 3. Taxa-specific proportion of echinoids observed in habitats in the Bay of Biscay off France; the ‘Tasman Fracture’ and ‘Huon’ commonwealth marine reserves (CMR) south of Tasmania, Australia; and the ‘Graveyard seamount complex’ east of New Zealand. Shades of grey identify three broad habitat categories: ‘living coral infrastructure’ (dark grey), ‘dead coral infrastructure’ (light grey), and ‘non-living habitats’ (white).

Gracilechinus multidentatus was encountered in all three broad habitat types observed; it was as often observed in living and non-living habitats (Fig. 3). Within the living habitats *G. multidentatus* was mostly observed in gorgonians (on hard substrate) habitats (17%). It was also found in slightly lower numbers in colonized and living CWC reefs (7 and 10%, respectively). In non-living habitats it was found in relatively similar numbers among bedrock, sand overlay, gravel, and sediment habitats (10-14%). A small number of encounters were recorded in the dead coral habitats.

C. otagoensis was most frequently observed in living habitats, but this was mainly due to the high frequency of observations (50%) in stylasterid habitats (Fig. 3). It was also frequently observed in sand overlay habitats and to a lesser extent in bedrock, mixed CWC reefs, rubble, and remains habitats.

Cidaroidae were rarely observed in the New Zealand region, but when encountered, these echinoids were primarily found in non-living habitats, such as bedrock and sand overlay, and in living coral infrastructure, stylasterid and living CWC reef habitats (Fig. 3). Cidaroids in NZ were rarely encountered in dead coral infrastructure habitat (<5% of total observations).

Similar to cidaroids patterns on New Zealand seamounts, *P. purpurata* in the Australian region were most often associated with stylasterid and bedrock habitats. This species, along with echinothurids, cidaroids, and *C. otagoensis*, were the only taxa observed among stylasterids (Fig. 3). *P. purpurata* was rarely found in other habitats as its presence in gravel and gorgonian (on hard substrate) habitats comprised < 1% of total observations.

Table 2. Habitat-related variables influencing echinoid distribution. Results from chi-squared tests are displayed in the table (Df =1; P < 0.05). Cells left blank refer to habitats devoid of the particular species. NS = Not Significant, NA = Not Applicable. Grey shaded cells indicate habitats that were not observed in the region specified. Only those taxa and regions provided had sufficient numbers to conduct chi-squared tests.

Habitat	<u>Australia</u>			<u>France</u>					
	<i>D. horridus</i>			<i>C. cidaris</i>			Echinothuriidae		
	χ^2	P-value	Association	χ^2	P-value	Association	χ^2	P-value	Association
Non-living habitats:									
Bedrock	2.394	0.1	NS						
Boulders	NA	NA	NA						
Sand overlay	NA	NA	NA						
Gravel	NA	NA	NA						
Sediment	NA	NA	NA	3.920	0.05	NS	0.974	0.3	NS
Dead framework:									
Dead CWC reef	0.0397	0.8	NS	2.373	0.1	NS	0.000	1	NS
Remains	3.082	0.08	NS	0.136	0.7	NS	3.106	0.08	NS
Rubble	4.229	0.04	-	1.429	0.2	NS	0.373	0.5	NS
Living framework:									
Living CWC reef	6.724	0.01	+	0.0142	0.9	NS	3.365	0.07	NS
Loosely-packed framework	2.386	0.1	NS	2.788	0.1	NS	0.509	0.5	NS
Colonized CWC reef	0.0594	0.8	NS	2.064	0.2	NS	NA	NA	NS
Mixed CWCs	0.000	1	NS						
Gorgonians on hard substrate	0.000	1	NS						
Gorgonians on soft substrate	0.269	0.6	NS						
Isolated colonies of Scleractinia (hard)	NA	NA	NA	0.000	1	NS	1.047	0.3	NS
Isolated colonies of Scleractinia (soft)				0.225	0.6	NS	0.176	0.7	NS
Stylasterid	NA	NA	NA						

Caenopedina porphyrogigas were encountered in the Australian and New Zealand regions, and general patterns of habitat association were similar in both regions. *C. poryphyrogigas* were almost exclusively observed in images containing living and dead coral infrastructure; and observations in non-living habitats were rare (<1% total in the Australian and <5% in the New Zealand region; Fig. 4). In the Australian region, the species were evenly distributed between living and dead coral infrastructure while there was an indication of an association with living coral infrastructure (consisting of 62% of observations) in the New Zealand region. Distribution within living coral habitats differed slightly. The species was mostly found in colonized (32% of observations) and living CWC reef habitats (37%) in the Australian and New Zealand regions, respectively. The species was infrequently encountered in gorgonian (on hard substrate), living, and loosely-packed CWC reefs (3-8%) in the Australian region. The species was encountered as frequently in mixed CWCs as in loosely packed CWC reef habitats (10% each); and infrequently encountered among isolated colonies of Scleractinia. For dead habitats, the species was most often observed in association with CWC reef and rubble habitats.

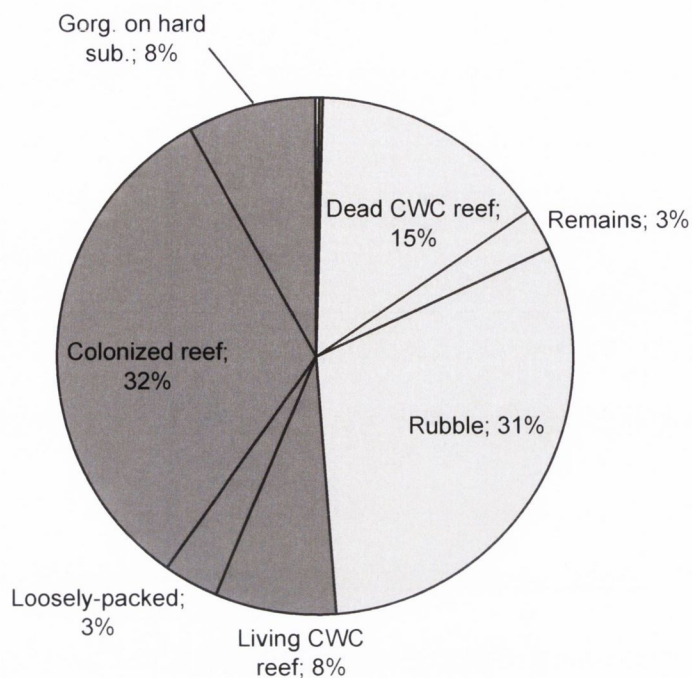
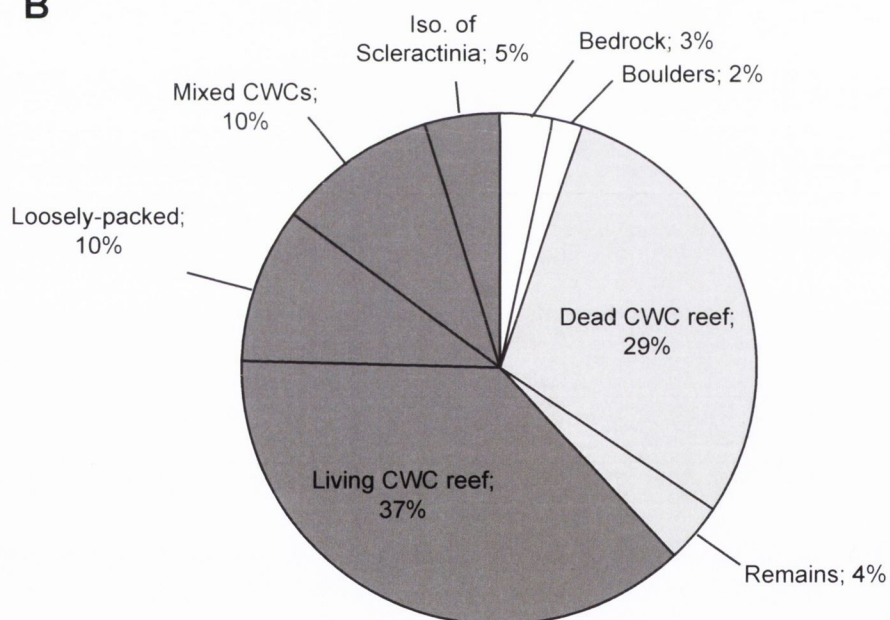
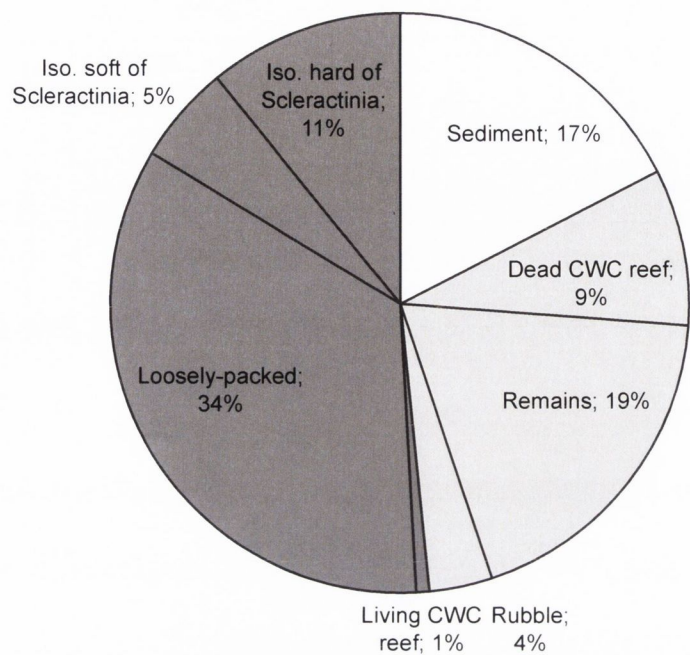
A**B**

Fig. 4. *C. porphyrogigas* observed in habitats in the ‘Tasman Fracture’ and ‘Huon’ commonwealth marine reserves (CMR), south of Tasmania, Australia (A), and in the ‘Graveyard complex seamounts’, NZ (B). Densities were averaged over all transects where the species and habitat were observed. Shades of grey identify three broad habitat categories: ‘living infrastructure’ (dark grey), ‘dead infrastructure’ (light grey), and ‘non-living habitats’ (white).

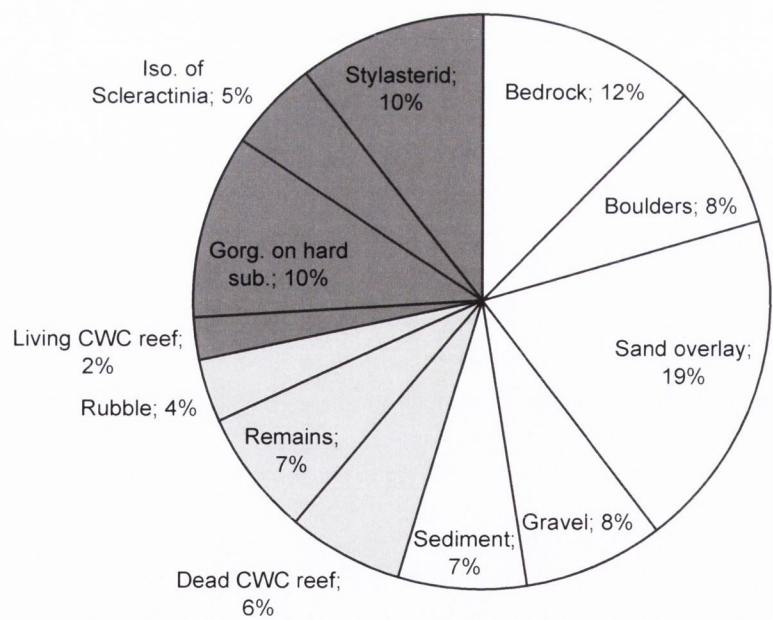
Habitats available to *C. cidaris* and echinothurids in NE Atlantic differed slightly from those available in the SW Pacific. In France, there were few non-living types of habitats observed; only sediment habitat types were encountered in this broad habitat category. *C. cidaris* were most often observed on living CWC reefs; favouring living, loosely-packed, and colonized CWC reefs (15-19% of observations), but were also observed among isolated colonies (Fig. 5). *C. cidaris* were found in dead and non-living habitats, they were found in sediment as often as isolated colonies and had a fairly even distribution between coral remains, rubble and dead CWC reef (9-15%). However, Chi-squared tests did not reveal significant associations with any of these habitats (Table 4).

In the SW Pacific, echinothurids were most frequently encountered in non-living habitats, making up about 54% and 75% of observations at Australian and New Zealand sites, respectively (Fig. 5). Of these habitats, echinoids were most often with sand overlay and bedrock habitats (12-19%) in the Australian region, and similarly, sediment and bedrock (30-33%) in the New Zealand region. In the living coral habitats, echinothurids were only observed among gorgonians (on hard substrate), stylasterid, isolated colonies of Scleractinia, and rarely (2%) in living and colonized CWC reef habitats. In the SW Pacific region, the taxon was found in relatively small numbers ($\leq 7\%$) in all three dead coral habitat types (rubble, remains, and dead CWC reef). Meanwhile, echinothurids in the French region were most often observed in living coral habitats (Fig. 5); this was mostly owing to their strong association with loosely-packed CWC reefs (34%) and isolated colonies of Scleractinia (16% combined). Echinothurids were also found in high density in sediment and coral remains habitats (17 and 19% of observations, respectively), and were found, to a lesser extent, among rubble (4%), dead (9%) and living CWC reefs (1%). Chi-squared tests did not reveal significant associations with the habitats available to echinothurids (Table 2).

A



B



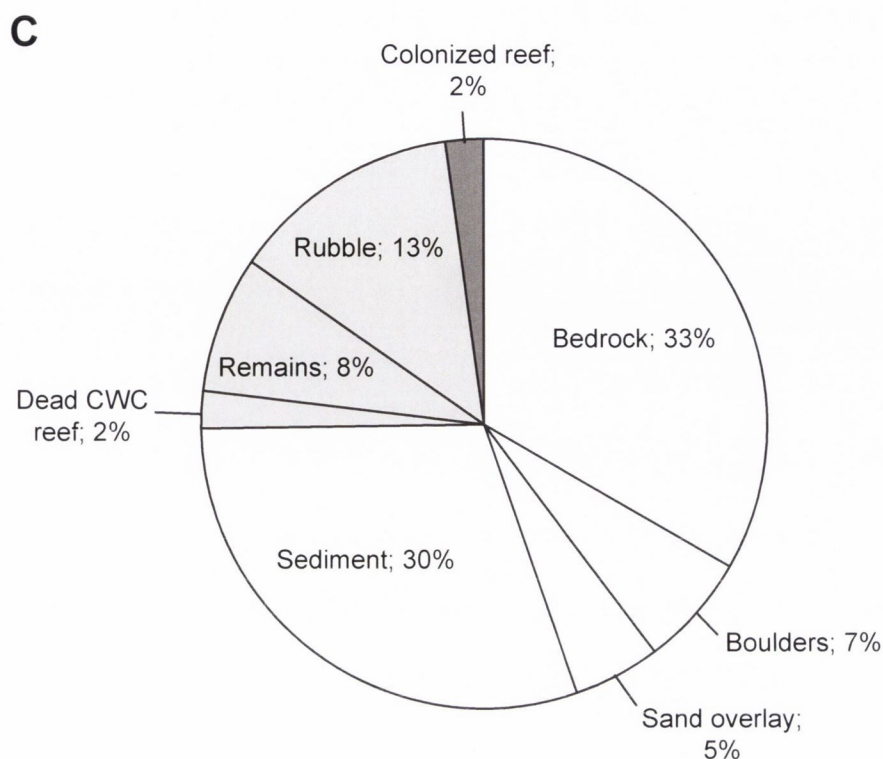


Fig. 5. Echinothurids observed in habitats in the Bay of Biscay, off France (A), ‘Tasman Fracture’ and ‘Huon’ commonwealth marine reserves (CMR), south of Tasmania, Australia (B), and in the ‘Graveyard complex seamounts’, east of New Zealand (C). Shades of grey identify three broad habitat categories: ‘living coral infrastructure’ (dark grey), ‘dead coral infrastructure’ (light grey), and ‘non-living habitats’ (white).

3.3 Habitat-related variables influencing echinoid distribution

The presence of echinoid species in the Australian region was dependent on interspecific competitors. Echinoids were significantly more likely to be found in the absence of an interspecific competitor (Table 3). However, the presence of an interspecific competitor did not affect the distribution of echinoids in the New Zealand region.

Depth also had a significant effect on some echinoid distribution patterns (Table 3). The presence of *D. horridus*, *G. multidentatus*, *C. otagoensis*, *C. porphyrogigas* (in the New Zealand region), and Echinothuriidae (in the New Zealand region) was influenced by depth. These taxa were found in a specific depth range, 700-1800 m (max depth of 1500 m for *G. multidentatus*), and their numbers peaked at 1200 m. In the New Zealand region, the Echinothuriidae were found between 870-1150 m and 950-1150 m for *C. porphyrogigas*.

Fishing history significantly affected the distribution of all taxa except *C. otagoensis*, *C. porphyrogigas* (in the Australian region), and the Cidaroidae (in the New Zealand region), which showed no difference in occurrence between trawled and unfished sites (Table 3). *D. horridus*, *G. multidentatus*, and *C. porphyrogigas* (in the New Zealand) were significantly more often observed at unfished sites, while echinothurids in both the Australian and New Zealand regions were significantly more often observed at trawled sites (Table 3).

Additionally, the probability of observing an echinothurid was significantly greater when there were no predators (Table 3).

Geomorphology affected only the distribution of one taxon, *D. horridus*, which was significantly more likely to be found in seamount than slope areas (Table 3).

Table 3. Habitat-related variables influencing echinoid distribution in the ‘Tasman Fracture Zone’ and ‘Huon’ area, south of Tasmania, Australia (AUS); and the ‘Graveyard complex seamounts’, east of New Zealand. Results from the binomial generalized linear mixed effects model (GLMM) are displayed (P < 0.05). NA – Not applicable.

	<i>C.</i> <i>otagoensis</i> (AUS)	<i>G.</i> <i>multidentatus</i> (AUS)	<i>D.</i> <i>horridus</i> (AUS)	<i>C. porphyrogigas</i>		Echinothuriidae		Cidaroidae (NZ)
				AUS	NZ	AUS	NZ	
Fishing history	0.4	0.03	< 0.001	0.1	< 0.001	0.04	0.003	0.6
Fish predator	0.7	0.6	0.1	0.6	1	0.02	1	1
Decapod predator	0.1	0.2	0.08	0.3	1	0.1	1	1
Octopus predator	1	1	1	1	NA	1	NA	NA
Distance to seamount	0.74	0.7	0.9	0.6	0.06	0.2	0.5	0.6
Depth	< 0.001	< 0.001	< 0.001	0.9	< 0.001	0.09	0.01	0.8
Interspecific competitor	< 0.001	< 0.001	< 0.001	< 0.001	1	< 0.001	1	1
Geomorphology	0.2	0.9	0.02	0.5	NA	0.7	NA	NA

4. Discussion

As a group, the Echinoidea were found to utilize all habitats available to them, and tended to aggregate in architecturally complex habitats, such as living, loosely-packed and

colonized CWC reefs, as well as remains in France. However, our taxa-specific investigation suggested that this association with the infrastructure supplied by deep-water corals was likely an artefact of the high numbers of *C. cidaris* observed at French sites, and *D. horridus* observed at the Australian sites, which almost exclusively favoured habitats with coral framework. As such, distributional patterns determined at different taxonomic scales (e.g. class Echinoidea vs. taxa-specific) could yield erroneous conclusions about the ecology of a taxon and the functioning of the ecosystem to which it belongs. This is especially true for echinoids that have taxa-specific impacts on coral ecosystems (Sammarco, 1982), it is therefore also important to consider the taxonomic scale when conducting deep-sea ecological research.

Two distinct habitat associations were detected in the study: *D. horridus* and *C. porphyrogigas* had a distinct association with living types of habitats, while *G. multidentatus*, *C. otagoensis*, and the echinothurids were more widespread over different types of habitats suggesting a more generalist association for available habitats. Dumas et al (2007) found similar species-specific habitat preferences for the sympatric species *Diadema setosum* and *Echinometra mathaei* in tropical shallow-water coral reefs. *D. setosum* distributions were found to be best explained by sediment type and biotic cover (Dumas et al., 2007); similar to *G. multidentatus* in the present study, *Diadema setosum* avoided zones exhibiting high architectural complexity, such as that produced by branching corals, while *E. mathaei*, sympatric with *D. setosum*, was most often associated with architecturally complex habitats. Further discussion of the taxa-specific distribution of deep-sea echinoids is provided below.

4.1 Taxa-specific habitat associations

4.1.1 *Caenopedina otagoensis*

C. otagoensis was primarily associated with stylasterid (which mostly occur on bedrock in this study) and sand overlay habitats; and was rarely found in more complex habitats. Both stylasterid and sand overlay habitats are relatively simple, lacking complexity, and are rich in hard substrates suggesting a preference for uniform hard bottom type habitats over complex and soft bottom ones. Alternatively the absence of this species from more complex habitats might be attributed to its relatively small size (diameter size of 15-40 mm; Tracey

et al., 2011). It is possible that the species associates with living infrastructure, but it might not have been detected in the study due to its size. Small taxa are harder to detect in photographic surveys especially since they can easily hide within the coral matrix. However, it is important to note its absence from gorgonian, isolated colonies, and loosely-packed frameworks as well. The species would have been more conspicuous in these habitats due to the relatively sparse infrastructure, which is consistent with the idea of a possible aversion for structurally complex habitats.

Previous studies in shallow-water habitats have demonstrated a close physical linkage between echinoids and habitat substrata (McClanahan and Kurtis, 1991; McClanahan and Muthiga, 2001; Dumas et al., 2007). This apparent preference is likely linked to habitat impacts on echinoid feeding and locomotory behaviour, as well as shelter availability. The habitats with which *C. otagoensis* associates provide relatively little shelter from predators, but perhaps it exploits a food source uniquely available in its apparently preferred hard bottom habitats. Hart and Chia (1990) found size-related differences in food requirements in laboratory experiments conducted on *Echinometra mathaei*. Given the tendency for echinoids to optimize their energy intake by preferentially feeding on nutrient-rich foods over lower quality foods (Lyons and Scheibling, 2007), as well as the added benefit of protection by dense coral infrastructure, the absence of *C. otagoensis* from infrastructure-rich living and dead habitats remains an anomaly that warrants further investigation.

4.1.2 *Dermechinus horridus* and *Caenopedina porphyrogigas* and comparisons between nearby regions (Australia vs. New Zealand)

The apparent preference for living and dead CWC reefs by *D. horridus* and *C. poryphyrogigas* is likely linked to their mode of feeding. A pronounced vertical elongation of the corona and modified secondary spines observed in *D. horridus* has led echinoderm scientists to propose a suspension mode of feeding for this species (Fell, 1976; Kroh, 2012). This theory has not yet been tested, but suspension-feeding has already been described in four other echinoid taxa (e.g., *Dendraster*, *Echinostrephus*, *Echinometra* and *Evechinus* in Kroh, 2012). The dense aggregations of *D. horridus* observed in habitats possessing coral infrastructure may therefore be related to the proposed mode of feeding. While coral

infrastructure may not be a direct source of food for *D. horridus*, its elevated feature may facilitate the capture of organic particles and reduce sediment particle obstructions by elevating *D. horridus* into swifter currents. As well, its absence or rare occurrence from non-complex habitats (e.g., sand overlay, sediment, bedrock, etc) is consistent with the proposed mode of feeding.

C. porphyrogigas was not observed in large numbers in the present study, but much like *D. horridus*, large aggregates have been observed in apparent filter feeding posture on the Louisville Seamount Chain, SW Pacific (Clark et al., in press). *Caenopodina porphyrogigas* has a relatively small Aristotle's lantern (the powerful jaw mechanism of echinoids) relative to its corona size (ranging 5-10% in Kroh, 2012), similar to that of *D. horridus* (which ranges between 2-7%) possibly suggesting that this species also engages in suspension-feeding. However, *C. porphyrogigas* lack all other morphological characteristics of a proposed suspension-feeding echinoid, such as dense secondary spine cover. Unlike *D. horridus*, *C. porphyrogigas* were frequently observed on rubble. As such, this species' co-occurrence with coral reef-building type localities might be attributed to the food resources provided by the live and dead coral infrastructure as well as the broken fragments, rather than the corals ability to provide elevation into the water column provided by the coral (as needed by *D. horridus*).

The data for the Australian and New Zealand regions permitted comparisons of patterns for habitat association in nearby localities with similar habitat typologies. For *C. porphyrogigas*, such comparisons revealed similarities in general patterns of habitat association between these nearby regions.

4.1.3 *Gracilechinus multidentatus* and *echinothurids*

No strong habitat associations were detected for *G. multidentatus* and *echinothurids* in Australian sites. Here, both taxa were widespread and evenly distributed across all habitats available to them suggesting generalist habitat utilization.

This generalist approach by *G. multidentatus* was surprising as it possesses a similar test morphology to *D. horridus* and *C. porphyrogigas* (see Tracey et al., 2011 for dimensions), which suggests that a factor other than morphology might be restricting its exploitation of living coral habitats. Under food-limited conditions, inter- and intraspecific

competition are frequently observed among shallow-water echinoids (Sammarco, 1980; McClanahan, 1988; Shulman, 1990; McClanahan, 1992; Privitera et al., 2008). Experimental trials revealed competition between *Echinometra lucunter* and *Echinometra viridis*, which commonly engaged in agonistic interactions between conspecifics and congeners (Shulman, 1990). Encounters result in pushing, biting, and subsequent conquer of a location (Shulman, 1990). Identifying mechanisms underlying this relationship is beyond the context of the present paper, but competitive hierarchy might serve as a possible hypothesis to explain the generalist approach utilized by *G. multidentatus*. This taxon might be restricted to a wider range of habitats where competitively dominant taxa (*D. horridus* and *C. porphyrogigas* in this case) are infrequently observed. But further work is necessary to determine whether competitive interactions exist between *D. horridus*, *C. porphyrogigas*, and *G. multidentatus*.

4.1.4 Echinothurids and congener comparisons at a broad geographic scale

Results for the echinothurids were also less intuitive than those observed for other taxa because habitat associations differed between the Australian and French regions. Habitats available to *C. cidaris* and echinothurids in the NE Atlantic differed slightly from those available in the SW Pacific. In the French region, there were few non-living types of habitats observed, but in the Australian region echinothurids were not strongly associated with these habitat types where they occurred. Echinothurids did not have a strong habitat association in the Australian region but did reveal a strong association with loosely-packed CWC reefs in the French region. This result suggests that habitat preferences might differ given the different habitats available to them.

Similarities were apparent over a broad geographic scale (NE Atlantic vs. SW Pacific). In all regions, echinothurids were consistently found in similar densities across dead CWC reefs, remains and rubble habitats, but rarely or never found in dense living habitats, such as living CWC reefs, dead CWC reefs, colonized CWC reefs, and mixed CWC habitats. Morphology is known to affect the habitat potential of echinoids (Hill and Lawrence 2003; Coppard and Campbell 2005) and can help estimate the mode of living of echinoids (Fell, 1976). It is possible that the flexible test of echinothurids might prevent the exploitation of dense coral habitats as the coral infrastructure can perforate the soft corona

of the echinothurid (A. Stevenson personal observation) hence its restriction to non-living habitats, rubble, remains, and habitats that are sparsely packed, such as isolated colonies, stylasterid habitat types and ideally loosely-packed CWC reefs.

The strong association by echinothurids in the Australian and New Zealand regions with non-living habitats and specifically for bedrock, sand overlay and sediment, suggests that general patterns of habitat associations are consistent between nearby regions, and further confirmed by the regional similarity found for *C. porphyrogigas*. These results suggest that video and image data can be a powerful tool to successfully and consistently detect trends in echinoid habitat associations.

4.2 Habitat-related variables influencing echinoid distribution

Interspecific competition, depth, and fishing history were the most influential factors in determining the distribution patterns of echinoids. Several studies have discussed a prevalent ability to reduce or avoid competitive interactions through specialized feeding strategies in order to sustain an echinoderm community (Billett et al., 1988; Jumars et al., 1990; Iken et al., 2001; Hudson et al., 2003; Wigham et al., 2003; Hudson et al., 2004). Differential habitat exploitation by echinoid taxa might also reduce competitive interactions required to survive in the deep-sea this ecosystems studied.

Contrary to that observed in French and Australian regions, echinoid taxa were unaffected by the presence of interspecific competitors in the New Zealand region. This result is likely linked to the sparse echinoid population found on the Graveyard complex seamounts, suggesting that competitive interactions do take place and influence deep-sea echinoid distributions but only when dense numbers occur. In the absence of a dense population, deep-sea echinoids are not likely to interact competitively with each other.

Echinoid distributions were restricted by depth, a pattern often observed among deep-sea taxa. Howell et al (2002), for example, found similar depth-related distribution patterns by deep-sea asteroids in the NE Atlantic. *C. otagoensis*, *G. multidentatus*, and *D. horridus*, in the present study, were found at a specific depth range (700-1800 m; maximum depth of 1500 m for *G. multidentatus*), but these three taxa had different habitat associations suggesting that while this factor might restrict their distribution, it is unlikely to be a major factor influencing habitat utilization.

The effect of fishing history varied by species. *C. otagoensis*, *C. porphyrogigas* (in the Australian region), and the Cidaroidae (in the New Zealand) were occurred without bias at trawled and untrawled sites; *D. horridus*, *G. multidentatus*, and *C. porphyrogigas* (in the New Zealand region) were more often and significantly associated with unfished sites; while echinothurids in both regions displayed an affinity with trawled sites. Similar taxa segregation between trawled and untrawled sites were described by Althaus et al (2009) and Williams et al (2010) who found a wide difference in megabenthos assemblage between trawled and untrawled sites; there was a higher abundance of sea urchins, crinoids, gorgonians, and chrysogorgid corals in trawled sites. Some taxa are thought to possess ecological traits that may permit for rapid recolonization or might be able to resist the physical damage (caused by benthic trawls) by exploiting natural refugia for protection (Althaus et al., 2009; Williams et al., 2010), which might help explain the variable effect of fishing history observed for different echinoid taxa.

The lack of significant predator influence on the distribution of all echinoids except the echinothurids was not consistent with previous findings that predation risk played a strong role in structuring echinoid space and resource use within habitats containing coral infrastructure (Stevenson et al., submitted). However, Bell and Westoby (1986) found habitat preference, rather than predation, to be the dominating factor explaining macrofauna distributions in seagrass beds. While predation might influence space and resource use within coral containing habitats (e.g., positioning on coral infrastructure), it does not appear to influence distribution patterns across a wider area (e.g., habitat typology).

The lack of consistency in response to fishing history between *C. porphyrogigas* in the Australian and New Zealand regions, for example, might reflect a flaw in the model used to predict trends in habitat-related variables influencing echinoid distribution, and as such while valuable information may be gained from the GLMM, results should be treated with caution.

5. Conclusions

Taxon-specific distribution patterns and habitat-related influences were revealed in the study. Not all taxa showed preference for matrix-forming coral habitats, despite increased food and shelter they offered.

Two distinct habitat associations were found: *D. horridus* and *C. porphyrogigas* had a much greater association with living types of habitats, while *G. multidentatus*, *C. otagoensis*, *C. cidaris*, Echinothuriidae and Cidaroidae were more widespread over different types of habitats suggesting a more generalist association for available habitats. Echinoid population structure was significantly affected by interspecific competition, depth, and fishing history.

Patterns in echinoid habitat association held regionally (Australian vs. New Zealand region), but differed at a broader geographic scale (SW Pacific regions vs. NE Atlantic).

Video and image data can be a powerful tool to detect trends in echinoid habitat associations. Refinement of the methods are required to improve quantitative analyses of habitat associations, but it is clear that such taxon-specific studies, conducted at a more precise taxon and habitat scale, are necessary. Most deep-sea ecological studies to date have been conducted at a wider resolution (e.g., taxon class Echinoidea, and habitat categories ‘seamount’, ‘continental slope’), which may not be the most appropriate scale to be useful for the proper ecological understanding and subsequent spatial management planning for vulnerable deep-sea habitats.

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*Gall-building copepod infestation of *Sperosoma grimaldii**

Summary and conclusions

1. Overview of thesis

The ultimate aim of the thesis was to probe into the ecology of deep-sea echinoids in order to contribute newfound information to this topic, as well as develop novel tools to facilitate ecological work in deep-sea environments. This was achieved using a multifaceted approach, including analyses of gut content and stable isotopes, as well as video and image analyses. Data and samples for these came from fieldwork in Ireland and France, in the NE Atlantic; and seamounts in Australia and New Zealand, in the SW Pacific.

Firstly, gut contents were collected and analyzed from echinoid specimens collected in NE Atlantic canyons on the Goban Spur and north of the Porcupine Bank in Ireland; and in several canyons in the Bay of Biscay, France. Gut content, carbon and nitrogen stable isotope analyses (SIA) were then performed on various echinoid tissues captured from these sites. Secondly, data about taxa-specific inter- and intraspecific interactions were gathered from over 3000 echinoid observations in high definition continuous video transects from the French canyon data. Lastly, habitat associations were determined from image transects in these same French canyons and seamounts in Australia and New Zealand.

Together these three investigations provided insights into the ecology of deep-sea echinoids, which are reviewed, synthesized, and discussed in the following sections. The implications of this work overall are then summarized, with consideration of future research.

2. Reviewing thesis aims and objectives

The thesis specifically aimed to:

(1) Elucidate the feeding mechanisms of deep-sea echinoids to further illustrate processes of resource exploitation by deep dwelling megabenthos under limited food resources by investigating *(i)* potential food sources for echinoids (Chapter 2 & 3), *(ii)* comparing the history of food sources assimilated by coexisting taxa to see if nutrient partitioning is taking place to reduce interspecific competition (Chapter 3), and *(iii)* examining how seasonal dietary shifts linked to the deposition of surface productivity might affect tissue

formation in seasonal and continuous breeders (Chapter 3) via gut content, $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ SIA.

(2) Investigate the effects of predator-prey and competitive (*i.e.*, inter- and intraspecific) interactions on space and resource use by deep-sea echinoids in coral habitats (Chapter 4).

(3) Document the distribution of echinoids in deep-sea coral habitats, determine whether echinoids associate with specific deep-sea coral habitats. Explore relationships between echinoid distribution and six habitat-related predictor variables. As well as determine if the patterns of distribution differ with taxonomic resolution (Chapter 5).

(4) Evaluate video and image analyses as a potential tool to probe into the ecology of deep-sea megabenthos (Chapters 4 & 5).

2.1 Deep-sea echinoid feeding ecology

2.1.1 Potential food sources for echinoids

Gut content analyses helped elucidate specific food sources consumed by echinoids. More specifically, it supports the notion that deep-sea echinoids are broad generalists and carnivores on sluggish or sessile organisms, but it also shows evidence of carnivory on both sessile and highly mobile invertebrates. The gut contents of *E. affinis* and all echinothurids (except *A. fenestratum*) were sediment filled, which is the usual type of material found in the guts of deposit feeders, but those of *A. fenestratum*, *C. cidaris*, *G. elegans*, and *G. alexandri* unexpectedly held a wide range of materials. Recurrent large amounts of various invertebrates, such as coral (live and dead fragments), crustacean, and crinoid skeletal material were found in the guts of specimens collected.

It is unclear at this point whether the large amount of crinoid skeletal material was consumed by active predation on the highly mobile comatulid crinoids or simply via accidental bycatch while feeding on the coral infrastructure. However, the presence of articulated cirral ossicles suggests that fresh rather than scavenged crinoid material was consumed since ligaments connecting ossicles decay within days to a few weeks (Baumiller, 2003). The presence of at least one centrodorsal in the gut contents of *A.*

fenestratum might suggest that cirri and brachial arms were not autotomized and subsequently ingested, but rather consumed as part of a full crinoid individual. The finding represents an important contribution towards echinothurid feeding ecology since research on the diet of this taxon is limited due to their abyssal distribution and primitive soft bodied exterior, which make it very difficult to capture and examine the gut contents of dredged material (Emson and Young, 1998).

Coral material and its organic parts were found in *G. elegans*, *G. alexandri*, *C. cidaris*, and *A. fenestratum*. From the coral contents observed in the guts of these species it is clear that some echinoids utilize the organic matrix of the coral infrastructure as a food source. While SIA added very little to our understanding of specific food sources consumed, it did show evidence suggesting that coral material might be an important source of organic nitrogen for somatic tissue growth in some echinoid taxa. Also, enriched $\delta^{15}\text{N}$ values suggest that echinoids incorporate foods with distinctly higher $\delta^{15}\text{N}$ values than that of POM and sediment, which could result from opportunistic feeding as well as bioerosion of the live coral framework and consequent grazing of fauna attached to the dead coral infrastructure. It is unclear, however, if these echinoids are targeting *Lophelia-Madrepora* polyps, the diverse sessile organisms associated with the dead coral infrastructure, and/or the protein rich mucus covering the live coral framework, which could all potentially serve as an attractive food source in an environment where organic nitrogen can be otherwise very difficult to obtain.

Research conducted on *Lophelia* skeleton bioerosion to date has largely focused on endolithic (boring and encrusting) forms, such as the sponges *Alectona millari* and *Aka labyrinthica*; the foraminifer *Hyrrokin sarcophaga*; the fungus *Dodgella*; and the sabellid worm *Perkinsiana socialis* (Rogers 2004; Beuck and Freiwald, 2005; Bromley, 2005; Wisshak et al., 2005; Beuck et al., 2007). Among known extant epilithic bioeroders, asteroids, such as the Hippasterinae, are accepted as the main predators of deep-sea coral (Krieger and Wing, 2002). These echinoderms are known to erode gorgonians, alcyonaceans, antipatharians and other deep-sea cnidarians (Krieger and Wing, 2002; Mah et al., 2010). Other predators of the alcyonacean *Primnoa* include nudibranchs and snails (Krieger and Wing, 2002). The rare gastropods, “*Coralliophila*” *richardi* and *Babelomurex sentix* (Coralliophilinae), are known bioeroders of *Lophelia* and *Madrepora* in Mediterranean deep-waters (Taviani et al., 2009). *In situ* video and image observations of

echinoids interacting with deep-sea coral are common (see p. 34 in Reed and Ross, 2005; p. 70 in Freiwald et al., 2009; p. 22 in Munoz et al., 2012) and some figure captions suggest that they are ‘grazing’ on the coral (see Freiwald et al., 2009). However, further reports and discussion about the bioerosion behaviour is absent from the deep-sea literature. As such, the previously unreported active predation on the dead and living frameworks of reef building coral, *Lophelia pertusa* and *Madrepora oculata*, that was presented in Chapter 2 has identified a potentially major gap in knowledge about *Lophelia-Madrepora* reefs and their associated bioeroding community.

2.1.2 Nutrient partitioning among coexisting echinoid species

It is clear that deep-sea echinoderms have adapted to restricted food conditions, but our understanding of these adaptations and their nutrition is limited. Holothurians, for example, have been shown to partition nutrients within the sediment to minimize competitive interactions between species (Billett et al., 1988; Miller et al., 2000; Wigham et al., 2003; FitzGeorge-Balfour et al., 2010), but this same feeding selectivity has not previously been established for other classes of the echinoderms until the present study.

Deep-sea echinoid nutritional information gained from conducting gut content analyses is further complemented by SIA, which offers valuable information regarding trophic positioning, and assimilation of nitrogen and carbon from food sources for somatic and reproductive growth. Sympatric echinoid taxa spanned three benthic trophic levels. This large trophic difference between taxa is consistent with previous trophic measurements conducted on deep-sea echinoderms. As in our study, the Holothuroidea in Iken et al. (2001) spanned three trophic levels; and Vanderklift et al. (2006) found similar differences in the trophic positioning of sympatric echinoid species in subtidal rocky reefs of south-western Australia. Occupying different trophic positions might suggest an expansion of echinoid trophic niches, which might help reduce interspecific competition and allow for species coexistence under limited food resources.

Evidence of nutrient partitioning among coexisting echinoid taxa was also found in the carbon data. Significant interspecific differences were found in the $\delta^{13}\text{C}$ signatures of the somatic and reproductive tissues suggesting that different sources of carbon are assimilated into all tissues after the deposition of phytodetritus has taken place on the deep

sea floor. However, this pattern differed for the data obtained before the deposition of phytodetritus; similar sources of carbon were assimilated into somatic tissues of different taxa, while some of these different taxa utilized significantly different sources of carbon to manufacture their reproductive tissues.

2.1.3 *The role of surface-derived phytodetritus in growth and reproduction*

Holothurians, echinoids, and ophiuroids exploit ephemeral sources of surface-derived phytodetritus seasonally deposited to the deep sea floor, but its contribution to the total spectrum of nutrients assimilated is unknown because evidence linking it to seasonal growth and reproduction remains circumstantial (Tyler et al., 1982; Tyler and Gage, 1984b; Billett et al., 1988; Tyler, 1988; Gooday and Turley, 1990; Campos-Creasey et al., 1994; Tyler et al., 1995). Via stable isotope analyses we show evidence of seasonally deposited phytodetritus being incorporated into the reproductive tissues of the seasonal breeder, *G. alexandri*, but not those of continuous breeders, Cidaroida and Echinothurioida. The material however was also found to support somatic tissue growth in cidaroids. These results suggest that seasonal breeders might utilize surface-derived phytodetritus to manufacture reproductive tissues, while continuous breeders might only utilize it for somatic tissue growth or not at all. The absence of a seasonal shift in the tissues of echinothurids may suggest that phytodetritus is not assimilated and thus not stored into its tissues for further use. Aside from the gonad and body wall, the food canal is also known to function as a nutrient-storage organ in echinoids (Fuji, 1961; Lawrence et al., 1966; Mercier and Hamel, 2009). The cells lining the epithelium of the food canal are a useful storage organ for some species of echinoids and since this tissue was not analyzed in the present study it is therefore possible that echinothurids do utilize phytodetritus, but store it in the cells of their food canal rather than the gonad and body wall. For the shift observed in *G. alexandri* gonads, perhaps it is this assimilation into reproductive tissues of seasonal breeders that triggers their reproductive events. However, results for seasonal dietary shifts were compromised by poor spatial repeatability and thus require further investigation to better understand the role of phytodetritus in fuelling the growth and reproduction of deep-sea echinoids.

2.2 Effects of predator-prey and competitive interactions on space and resource use

Knowledge of factors driving spatial distribution and abundance patterns of populations, ultimately leading to the understanding of the observed community structure are clear for neritic habitats where spatial differences in patterns of abundance, distribution, and behaviour have been attributed to food availability, competition, and predation (Paine, 1974; Menge and Sutherland, 1976; Sammarco, 1980; Sih et al., 1985; McClanahan, 1988; Birkeland, 1989; Rochette and Himmelman, 1996; Privitera et al., 2008; Orrock et al., 2013). In the deep-sea, the topic of predation and competition has received a large amount of theoretical and conceptual consideration, but little analytical work has been conducted to determine the relative importance of predation and competition in structuring deep-sea communities. While our study was purely observational, trends drawn from a large sample size suggest that space and resource use may be predominantly predator-driven and thus supports Dayton and Hessler's (1972) predation hypothesis for the remarkably high species diversity in the deep sea.

Through video analyses of echinoid interactions with predators and competitors (inter- and intraspecific) we found that the coral infrastructure not only provides an important food source for deep-sea echinoids, but also protection from predators. Crypsis might be the dominant defensive function for deep-sea echinoids whereby taxa may predominantly utilize flight responses, rather than an aggregative behaviour, to reduce predation risk. Thus aggregations are likely to form for feeding rather than for defensive purposes; and migration along the coral infrastructure may be a predator-driven behaviour as echinoids seek refuge from predators. Interspecific competition may influence species-specific hierarchy on nutritiously valuable substrates in the deep-sea, but the lack of statistical significance in these trends merit further investigation in order to clarify the role of competition in deep-sea coral habitats. Overall, predation risk might play a stronger -or more detectable- role in structuring echinoid space and resource use in deep-sea coral habitats.

2.3 Taxa-specific habitat associations

Understanding patterns of habitat use is an important aspect of animal ecology as it is the necessary first step towards understanding the ecological interactions between species and

their predators, prey, competitors, and environment that shape these distributions (Heithaus et al., 2006). This is particularly important for ecologically important taxa like echinoids, which play a pivotal role in nutrient recycling and system engineering of shallow-water habitats (e.g., Bromely, 1978; Glynn et al., 1979; Sammarco, 1980; Koike et al., 1987; Jumars et al., 1990; Scheibling and Hamm, 1991; Bak, 1994; Glynn, 1997; Sauchyn and Scheibling, 2009). While this work is well represented for echinoids and their shallow water habitats, relatively few studies have examined interactions and associations in deep-sea coral habitats. The present study has revealed echinoid taxa-specific distribution and abundance in deep-sea coral habitats as well as relationships between echinoid distributions and six habitat-related predictor variables.

Despite the added benefit of food and shelter provided by coral habitats, taxa-specific distribution patterns and habitat-related influences suggest that not all taxa prefer these habitats. Some taxa had a random association with various habitats, while others displayed non-random associations. Two distinct habitat associations were detected in the study: *Dermechinus horridus* and *Caenopedina porphyrogigas* had a much greater preference for living types of habitats, while *Gracilechinus multidentatus*, *Caenopedina otagoensis*, *Cidaris cidaris*, Echinothuriidae, and Cidaroidae were more widespread over different types of habitats suggesting a more generalist association for available habitats.

The echinoid population structure was significantly affected by habitat-related variables; of these, interspecific competition, depth, and fishing history were the most influential factors in determining the distribution patterns of echinoids. All taxa were significantly more likely to be found in the absence of an interspecific competitor. The effect of fishing history varied by species, *Caenopedina* species were indifferent, *D. horridus* and *G. multidentatus* associated with untrawled sites, while echinothurids associated with trawled sites. Echinoid distribution was restricted by depth limitations, a pattern often observed among deep-sea taxa.

Given these desirable perks of deep-sea coral habitats to echinoids –as expressed in Chapters 3, 4 & 5- why don't all echinoid species exploit these coral habitats? For morphologically similar species, such as *D. horridus*, *C. porphyrogigas*, and *G. multidentatus*, competitive interactions might drive the distribution of these taxa whereby the dominating taxa might outcompete weaker species. Morphological restrictions could

interfere with the exploitation of more rugose habitats by taxa such as *C. otagoensis* and the echinothurids.

2.4 The use of deep-sea video and image analyses in ecology

Ecological methods developed for shallow-water habitats have historically been arduously and impractically applied to deep-sea systems, resulting in a lack of specific methods to study the ecology of deep dwelling megabenthos in these systems. However, as demonstrated here and in the works Cuvelier et al. (2009) and Marsh et al. (2012), for example, the recent emergence of high definition deep-sea video and images have opened new opportunities for ecological work using such technology (Danovaro et al., 2014). The use of video and image analyses in the present study has allowed for the detection of patterns and revealed significant and insightful details on deep-sea echinoid community interactions and habitat associations.

3. Scope for future research and implications for conservation of deep-sea coral reefs

Bioerosion by several echinoid taxa in this study reflect a previously unreported behaviour by deep-sea echinoids (Chapter 2 & 3), which might have important consequences for the stability of deep-sea coral reef systems. Possible echinoid bioerosion impacts on *Lophelia-Madrepora* reefs warrant further investigation in order to better understand the relationship between deep-sea corals and echinoids.

Results for seasonal dietary shifts were compromised by poor spatial repeatability (Chapter 3) and thus require further investigation to further understand the role of phytodetritus in fuelling the growth and reproduction of deep-sea echinoids. Specific lipid biomarkers, such as fatty acids and sterols, carotenoid and chlorophyll pigments, and compound specific isotope analyses might provide a better alternative than SIA for studying deep-sea echinoid nutrition and its role in their growth and reproduction.

The study conducted on echinoid habitat interactions with predators and competitors (Chapter 4) should be conducted in other regions in order to see if patterns hold at a broader geographic scale; thereby further adding strength and credibility –or the contrary- to the use of video analyses for the study of community interactions as well as continue to expand our knowledge about this topic. Furthermore, interspecific competition

may influence species-specific space and resource use, but the lack of statistical significance in trends observed merit further investigation in order to disambiguate the role of competition in deep-sea coral habitats.

The coral infrastructure, albeit important for nutrition (Chapter 2 & 3) and protection from predators (Chapter 4), is not utilized by all echinoid taxa (Chapter 5). Whilst this could possibly be linked to competitive interactions with other echinoids and/or morphological restrictions, it clearly requires further investigation to determine why certain taxa associate with the coral infrastructure while others do not despite the added benefits offered by such habitats. Also, it is clear that taxon-specific studies -conducted at a more precise taxon and habitat scale- are necessary (but rare) in deep sea research. Most deep-sea ecological studies to date have been conducted at a wider resolution (e.g., taxon class Echinoidea, and habitat categories ‘seamount’, ‘continental slope’), which might be the wrong scale to be useful for the proper ecological understanding and subsequent conservation planning of vulnerable deep-sea habitats.

Video and image data are conventionally used to map habitats and quantitatively investigate megafaunal assemblages in deep-sea environments and have been overlooked as a tool to study other ecological themes, such as those studied in this thesis (Chapter 4 & 5). It is important to refine and continue to build on these methods to promote quick, affordable, and efficient assessments of ecological processes for use in conservation planning.

Most importantly, the work supports the notion that deep-sea coral habitats are an important resource for the megabenthic community. For echinoids, these coral habitats provide an important source of food and shelter from predators, and as such, understanding ecological processes such as this should be a conservation priority to protect vulnerable deep-sea coral systems and their inhabitants.

4. Concluding remarks

Significant contributions were made to our understanding of deep-sea echinoid ecology as a result of the various analyses that comprised the multifaceted approach used in this research project. Gut content analyses enlightened our knowledge of food sources consumed by echinoids, and SIA has offered valuable information regarding trophic positioning, and

assimilation of nitrogen and carbon from food sources for somatic and reproductive growth. Previously, deep-sea echinoids were regarded as broad generalists and carnivores on sluggish or sessile organisms, but the study additionally suggests that echinoids engage in carnivory on both sessile and highly mobile invertebrates. The study revealed new feeding habits in deep-sea echinoids as some exploit highly desirable material such as the coral infrastructure and highly mobile crinoids. Nutrient partitioning might also be taking place whereby echinoid taxa assimilate different sources of nutrients possibly in order to avoid interspecific competition. Finally, predictable and detectable patterns in space as a response to predators, competitors, and habitats available further contribute to our understanding of deep-sea community interactions and habitat associations.

Most importantly, as we remain at the forefront of deep-sea research we still strive to understand the ecology of deep-sea coral reefs, but associated challenges illustrate the immense complexity of this task. The study emphasizes the value of video and image data as a reliable, effective, and relatively inexpensive tool for conducting ecological research in the deep sea, and with its evolution will no doubt continue to elucidate processes taking place in these systems.

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