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Echinoid associations with coral habitats differ with taxon in the deep sea and the influence of other echinoids, depth, and fishing history on their distribution

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ABSTRACT

Patterns of habitat use by animals and knowledge of the environmental factors affecting these spatial patterns are important for understanding the structure and dynamics of ecological communities. Both aspects are poorly known for deep-sea habitats. The present study investigates echinoid distributions within cold water coral (CWC) habitats on continental margins off France, Australia, and New Zealand. It further examines the influence of habitat-related variables that might help explain the observed distribution of echinoid taxa.

Six echinoid taxa were examined from video and photographic transects to reveal taxon-specific distribution patterns and habitat-related influences. The Echinoidea were found in all habitats studied, but tended to aggregate in architecturally complex habitats associated with living cold-water corals. However, a taxon-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 were associated with these habitats, and some had a random association with the habitats examined, while others displayed non-random associations.

Echinoid distribution was correlated with several variables; the presence of other echinoids, depth, and fishing history were the most influential factors.

This study indicates that image data can be a useful tool to detect trends in echinoid habitat associations. It also suggests that refinement of the methods, in particular with studies conducted at a more precise taxon and habitat scale, would facilitate better quantitative analyses of habitat associations and paint a more realistic picture of a population's ecology. Most deep-sea ecological studies to date have been conducted at a relatively coarse taxonomic and habitat resolution, and lack sufficient resolution to provide useful information for the conservation of vulnerable deep-sea habitats.

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). Understanding habitat use 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. Bromley, 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 (although not facultative inhabitants of reefs) have a range of effects on the distribution of coral, as well as the abundance, species composition, and the diversity of associated species (Sammarco, 1982). *Echinometra viridis* A. Agassiz, 1863, for example, grazes locally and creates small algae-free patches on reefs, 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* Philippi, 1845 appears

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to affect coral settlement, while *E. viridis* does not. *Echinothrix diadema* and *E. calamaris* consume coral among their diet of sponges and algae (Schultz, 2005; Miskelly, 2002). 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* (Blainville, 1825), *Diadema setosum* (Leske, 1778), *Diadema savignyi* (Audouin, 1809), *Echinothrix diadema* (Linnaeus, 1758) and *Echinothrix calamaris* (Pallas, 1774), each associate with different parts of the reef (Coppard and Campbell, 2005). 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 cold water coral (CWC) habitats.

Coral habitats in the deep sea are often observed in the form of dense matrix-forming corals and their broken skeletal remains. These habitats provide structure for various organisms, increasing local benthic diversity (Henry and Roberts, 2007). The coral infrastructure may offer refuge from predators where complex habitats provide more shelter from predators than those habitats that are less complex (Etnoyer and Morgan, 2005). In this respect, deep-sea echinoids have been found to primarily seek refuge from predators in the coral infrastructure rather than arrange themselves in defensive aggregates (Stevenson et al., 2014). CWCs typically form architecturally complex habitats that are thought to intercept organic matter in the water column 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 all serve as a food source for deep-sea echinoids (Stevenson and Rocha, 2013; Stevenson and Mitchell, 2016). 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 CWC 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) competition: the presence of other echinoids leading to a species-specific hierarchy on nutritiously valuable substrates in the deep sea (Stevenson and Mitchell, 2016); (2) predation: predator presence influencing habitat choice (Stevenson et al., 2014); (3) water depth: bathymetric stratification is 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 (e.g. slope vs. seamounts): features possess a different mosaic 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 to fishing impacts or are early colonisers (see Althaus et al., 2009, Clark and Rowden, 2009).

The aims of this study were to:

(i) Document the distribution of echinoids in CWC habitats;
(ii) Determine whether echinoids are associated with specific CWC 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 areas

Patterns of habitat associations by deep-water echinoids were investigated in three geographic regions: waters off France in the NE Atlantic, and waters off Australia and New Zealand in the SW Pacific. These study areas 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 study areas facilitated the comparison of patterns across a broad geographic range. The data for the Australian and New Zealand study areas permitted comparisons of patterns of habitat association in nearby regions with similar habitat type. The French study area had fewer available habitat typologies than Australia and New Zealand, so comparison of distribution patterns in the French study area to those of the SW Pacific allowed for an additional investigation of shifts in distribution in the presence of a smaller range of habitat types.

In the French study area, 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, NE Atlantic (Fig. 1A). The Bay of Biscay lies on the western coast of France and extends from the coast of Brest south to the Spanish border and west to Cape Ortegal. Canyons sampled in this study ranged in depth between 524 and 1324 m. A total area of 7.03 ha was sampled in this study area. Fishing data were unavailable.

In the Australian study area, data were compiled from photographic surveys south of Tasmania, SW Pacific (Fig. 1B). A total area of 1.63 ha (ha) was surveyed across 17 seamounts and 3 slope areas 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 area 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 study area, data were obtained from the 'Graveyard seamount complex' which is located on the northern flank of the Chatham Rise, SW Pacific (Fig. 1C). This complex consists of 20 seamounts spanning summit height depths of 750–1250 m (Mackay et al., 2005) and elevations of 100–300 m (Clark et al., 2010b). A total area of 2.84 ha was surveyed in this study area. The study focused on six of these seamounts, four trawled (Diabolical, Morgue, Zombie, Graveyard) and two unfished (Ghoul, Gothic). The region has been heavily trawled since the 1990s, but three seamounts were closed to trawling in 2001 (Clark and Rowden, 2009). Note that Morgue's SW ridge has never been trawled due to its steep walls. Further site details can be found in Clark et al. (2010b).

2.2. Extracting data from photographic transects; continuous video and photographic surveys

In the French study area, 15 continuous video transects (consisting of a total of 25 h of video recording) were captured with the vertically