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ABSTRACT

The abundance and behaviour of fish on and around coral reefs at Twin Mounds and Giant Mounds, carbonate mounds located on the continental shelf off Ireland (600–1100 m), were studied using two Remotely Operated Vehicle (ROV) dives. We recorded 30 fish taxa on the dives, together with three species of Scleractinia (*Lophelia pertusa*, *Madrepora oculata* and *Desmophyllum cristagalli*) and a diverse range of other corals (Antipatharia, Alcyonacea, and Stylasteridae). Stands of live coral provided the only habitat in which *Guttigadus latifrons* was observed whereas *Neocyttus helgae* was found predominantly on structural habitats provided by dead coral. Significantly more fish were found on structurally complex coral rubble habitats than on flatter areas where coral rubble was clogged with sand. The most common species recorded was *Lepidion eques* (2136 individuals), which always occurred a few cm above bottom and was significantly more active on the reefs than on sedimentary habitats. *Synaphobranchus kaupii* (1157 indiv.), *N. helgae* (198 indiv.) and *Micromesistius poutassou* (116 indiv.) were also common; *S. kaupii* did not exhibit habitat-related differences in behaviour, whilst *N. helgae* was more active over the reefs and other structured habitats whereas *M. poutassou* was more active with decreasing habitat complexity. Trawl damage and abandoned fishing gear was observed at both sites. We conclude that Irish coral reefs provide complex habitats that are home to a diverse assemblage of fish utilising the range of niches occurring both above and within the reef structure.

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1. Introduction

Some cold-water corals live in such dense aggregations that they provide structurally complex habitats which support a diverse assemblage of associated invertebrate life (Le Danois, 1948; Burdon-Jones and Tambs-Lyche, 1960; Buhl-Mortensen and Mortensen, 2004; Metaxas and Davis, 2005; Mortensen et al., 2008) and fish (Auster, 2005; Costello et al., 2005; Reed et al., 2006; Ross and Quattrini, 2007; Roberts et al., 2008; Harter et al., 2009). Cold-water coral reefs have been classified as 'Essential Fish Habitat' (EFH) in the western Pacific (Witherell and Coon, 2000). While it is debatable whether cold-water corals are 'essential' to fish, as the fish recorded to date may survive well in other habitats, it is clear that corals provide an important source of three dimensional structure in the predominantly sedimentary habitats of deeper waters (Auster, 2005, Roberts et al., 2008; Harter et al., 2009). A comparison of visual surveys at eight locations from Ireland to Norway led Costello et al. (2005) to conclude that reefs formed by *Lophelia pertusa* attract elevated concentrations of fish in the NE Atlantic. These authors tentatively related the elevated abundance of fish to the occurrence of reefs in waters rich in

zooplankton (benefiting zooplanktivorous fish) at sites with increased availability of benthic invertebrates (benefiting invertivores). This combination of elevated zooplankton and benthic invertebrates provides appropriate habitat for at least some of the fish recorded (rockfish, *Sebastes* spp.). Faunal abundance and diversity on coral sites is consistently higher compared to near-by non-coral sites (Mortensen et al., 2008; Roberts et al., 2008; D'Onghia et al., 2010; Du Preez and Tunnicliffe, 2011), suggesting corals may function as refuge; for some species, the provided structure is a significant factor (Du Preez and Tunnicliffe, 2011). Husebø et al. (2002) conclude that in Norway the *L. pertusa* reefs were used by the tusk *Brosme brosme* for feeding and for physical shelter by the ocean perch *Sebastes marinus*, and Mediterranean *L. pertusa* and *Madrepora sp.* reefs were nurseries e.g. for *Helicolenus dactylopterus* (rockfish), *Merluccius merluccius* (European hake), *Micromesistius poutassou* (blue whiting), or *Phycis blennoides,* of which some are commercially exploited species (D'Onghia et al., 2010).

Throughout the world, cold-water coral habitats are highly vulnerable to the impacts caused by current fishing practices. These impacts are long-lasting and visible even after many years of closure to fisheries (Althaus et al., 2009). Bottom-trawling in particular can quickly damage coral structures that take thousands of years to develop, so an understanding of the ecological role of cold-water coral reefs is important for the sustainable

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management of fisheries (Hall-Spencer et al., 2002; Koslow, 2007). In the NE Atlantic, complaints from long-line fishermen led to a ban on trawling within selected coral-rich provinces off Norway (Fosså and Alvsvåg, 2003). In 2003, an area called the 'Darwin Mounds' off NW Scotland became the first cold-water coral protected area in the European Union (Commission Regulations EC 1475/2003 and 263/2004, Davies et al., 2007) and was followed in 2007 by further bans on trawling by the EU and the North East Atlantic Fisheries Commission on coral-rich areas around Hatton and Rockall Banks west of Scotland (NEAFC Recommendation IX-2007). Currently there is no protection of coral-rich provinces within the Irish Exclusive Economic Zone but the present study contributes to a rapidly increasing body of evidence concerning the importance of coral rich areas off Ireland (De Mol et al., 2002; Hall-Spencer et al., 2002; Freiwald and Roberts, 2005; Roberts et al., 2008; Dorschel et al., 2009).

Extensive trawling surveys have provided a detailed overview of the benthic fish assemblages of the NE Atlantic (e.g. Haedrich and Merrett, 1988; Merrett et al., 1991; Gordon and Bergstad, 1992; Merrett, 1992; Gordon et al., 1996; Bergstad et al., 1999) with studies focussed mainly on commercially important families such as the gadoids and macrourids (e.g. Mauchline and Gordon, 1984; Kelly et al., 1997; Coggan et al., 1999). Baiting experiments have provided information about population densities, swimming speeds and activity levels of some deepwater fish (Armstrong et al., 1992; Collins et al., 1999), and in recent years behavioural observations of benthic deepwater fish communities have been made using submersibles and ROVs (Johnson et al., 2003; Widder et al., 2005; Lorance and Trenkel, 2006; Ross and Quattrini, 2007). For example, the behavioural ecology of seven benthic fish found in the North Eastern Atlantic was described (Lorance et al., 2002; Uiblein et al., 2002, 2003) along with consideration of how fish species associate with specific habitat types and how habitat type influences fish behaviour (Uiblein et al., 2003).

Here, we present an analysis of ROV footage to compare the benthic fish communities on and around coral reefs on the Porcupine Bank in the NE Atlantic. Descriptions of the study area and some preliminary expedition results have been published within Myers and Hall-Spencer (2004) and Wheeler et al. (2005). We assess the association of fish species with different substrate types and note and compare evidence of fishing activity around the reefs. As little is known about the deep-sea fish we were able to observe, we describe in detail the behaviour of the three most abundant species across a range of habitat types.

2. Methods

We studied fish associations on and around coral reefs on Twin Mounds and Giant Mounds which are carbonate mounds situated 9 km apart on Porcupine Bank in the NE Atlantic (Fig. 1, Table 1). Geological and physical features of Twin Mounds and Giant Mounds were recently described by Dorschel et al. (2009). Video was collected during Expedition ARK-XIX/3a in June 2003 using ROV 'Victor 6000' (operated by IFREMER) aboard the RV 'Polarstern' (operated by the Alfred Wegener Institute).

Observations were made throughout each dive using only the main colour camera, pointing at a 30° angle downwards-forward. A four point parallel laser system (distance between two opposite points=23 cm) was available to assess object size, although this was only accurate when the target was perpendicular to the laser beams. Although most of each dive was spent filming a 2.5 m wide strip of seabed with the ROV on average 2.65 m (all data collected was observed < 5 m) above bottom, the data do not represent a true transect. As there was some variation in altitude and each site was passed over only once, no true replication of observations was possible. Consequently, our data are more qualitative than quantitative. However, acknowledging the problems associated with observing
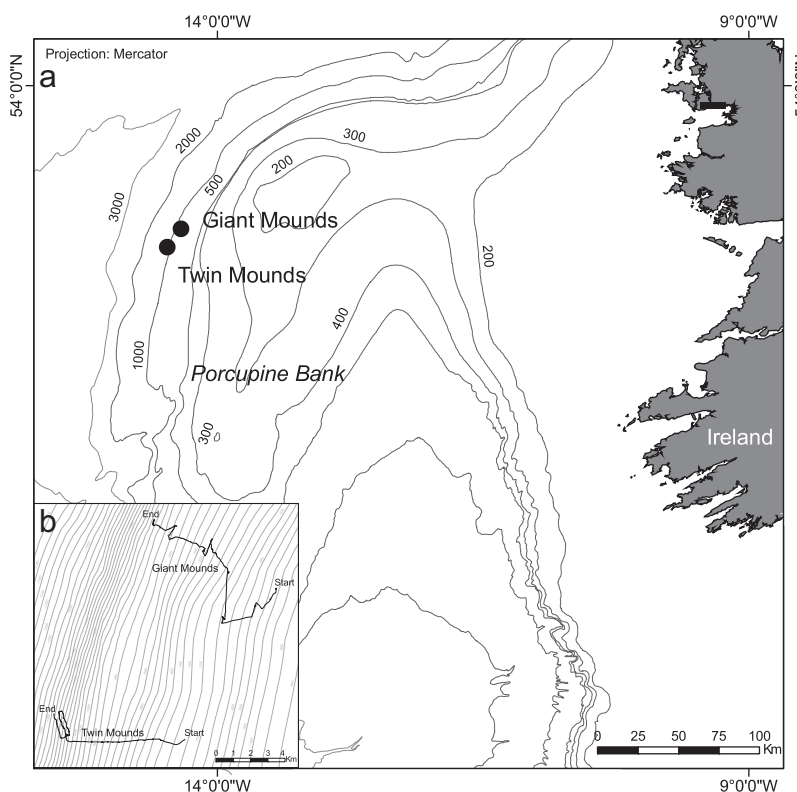

Fig. 1. (a) Study sites at Twin Mounds and Giant Mounds at Porcupine Bank, Northeast Atlantic. (b) Dive tracks at Twin Mounds (13 km) and Giant Mounds (14 km).

Table 1

Details of the study sites Twin Mounds and Giant Mounds on the Porcupine Bank, Northeast Atlantic, during the ARKTIS XIX/3 survey (additional information can be found in the cruise report under http://epic.awi.de/Publications/BerPolarforsch2004488.pdf and in Dorschel et al., 2009).

	Twin Mounds	Giant Mounds
Depth (m)	750–1120	650–1060
Date and time of survey	12.06.2003 16:03:44 to 13.06.2003 09:43:04	14.06.2003 08:05:28 to 15.06.2003 03:14:28
Start coordinates	53°05′25″N 14°48′05″W	53°10′16″N 14°43′37″W
End coordinates	53°06′13″N 14°55′19″W	53°11′33″N 14°47′06″W
Dive track length (km)	13	14
Studied footage time (h)	16.5	17.0
Velocity range (knots)	0.0–1.3	0.0–1.3

Table 2

Behavioural categories used to classify observed fish behaviour during each dive.

Behaviour	Description
'stationary'	Fish sitting on the seabed or showing no locomotion movements.
'station holding'	Fish swimming sufficiently against the current to hold position over the substrate.
'associated'	Fish observed in or associated with 3D structures.
'active forward'	Fish swimming actively forward (displacement).
'disturbed'	Abrupt changes in direction, accelerating swimming speed, sudden increased fin beating or apparent disorientation.

deep sea fish communities by ROV (Adams et al., 1995; Trenkel et al., 2004a, 2004b), it was possible to reliably estimate fish abundance and to make some quantitative measurements of fish behaviour. Due to the patchiness and high spatial and area heterogeneity of substrates, the most reliable and robust method was to calculate average fish abundance over an entire substrate (see below).

Footage was only considered less than 5 m from the sea bed and at ROV speeds below 1.3 knots. Footage was excluded if the ROV was stationary for a period of time. From footage suitable for data collection, a still image was taken every minute and the substrate type below the ROV was noted. The substrate type was divided into four categories (coral, sand, bedrock and three-dimensional (3D) structured, which consisted of patchy or dense dropstones and rocky outcrops). The coral habitat was further divided into the following sub-categories; (1) live coral, (2) coral rubble, (3) mixed living and dead coral and (4) sand-clogged coral, based on the expedition cruise report (Klages et al., 2004) which is similar to other published studies (Dorschel et al., 2007; Dorschel et al. 2009). This allowed the total time of footage over a particular substrate type to be calculated for each dive, using a total of 2029 still images. The footage was then analyzed again; this time, each fish encountered was recorded and for each fish observed the fish species, body position in relation to sea bed, behaviour (Table 2), substrate type and depth, and any evidence of fishing were noted. Combining the data on time spent over each substrate and fish occurrences, we adopted the 'fish counts per minute' method of Costello et al. (2005) to compare fish abundance between habitats, i.e. the total number of fish observed in each habitat was divided by the minutes spent filming in each habitat.

Evidence of fishing at the sites was noted in each of the 2029 still images and frequency of trawling damage occurring at each site and on each substrate type calculated from these.

To compare abundance of fish on each substrate type (as fish per minute counts), a Fisher's exact test for count data in contingency was used to test the difference between the observed and the exact probability (expected) of abundance (Fisher, 1922). Within a site, we tested whether the observed abundance of fish across substrates differed significantly from that expected if they were equally distributed across all substrates. The behavioural patterns of five fish species were considered in detail. For each species, firstly, within one habitat, the frequency a specific behaviour was observed for was compared to see if some behaviours

Table 3

Percentage of total time each substrate category was filmed during each dive.

Substrate	Twin Mounds (%)	Giant Mounds (%)
Coral	48.4	50.3
-live coral	5.9	15.5
-dead coral	36.5	6.9
-mixed dead and living coral	1.7	14.6
-sand-clogged coral	4.3	13.2
Bedrock	1.0	9.5
Sand	35.9	30.0
3D structured	14.6	10.2

were performed more frequently than would be expected by chance. Secondly, across different habitats, the performance of each specific behaviour was compared to understand if that behaviour was performed equally in each habitat. Fisher's exact test was also applied to test whether trawling damage was independent of substrate type, assuming equal probabilities of trawling damage on all substrates. All statistical analysis was carried out using the software package R (Crawley, 2007).

3. Results

The amount of time spent over each substrate is shown in Table 3. The live coral framework was dominated by *L. pertusa* and *Madrepora oculata*, (although *Desmophyllum cristagalli* was also seen), but solitary antipatharian and anthozoan corals, as well as anthozoan reefs were also observed. The adjacent coral rubble zones supported a rich assemblage of sessile and vagile invertebrate fauna. Large particle aggregates ('marine snow') and swarms of planktonic copepods were observed for the majority of the dives and were abundant near the seabed. Fish abundance and community composition differed between sites (Table 4) although the two commonest species, the North Atlantic codling *Lepidion eques* and the northern cutthroat eel *Synaphobranchus kaupii*, were recorded in similar abundances at each site. At Twin Mounds the false boarfish *Neocyttus helgae* was the third most common species observed, but this species was not seen at Giant Mounds. Conversely, the *M. poutassou* was the third most abundant species at Giant Mounds, but was not observed at Twin Mounds.

Table 4
The abundance of fish taxa recorded at Twin Mounds (53°06′N 14°55′W, 750–1120 m depth) and Giant Mounds (53°12′N 14°46′W, 650–1060 m depth) on Porcupine Bank, Irish Continental Slope, 13–15 June 2003 by the ROV "Victor 6000". Percentage values are the abundance of a species as a percentage of the total number of fish seen.

Twin Mounds			Giant Mounds		
Fish taxa	Individuals	%	Fish taxa	Individuals	%
Lepidion eques Günther, 1887	1286	45.46	*Lepidion eques* Günther, 1887	850	42.99
Synaphobranchus kaupii Johnson, 1862	652	23.05	*Synaphobranchus kaupii* Johnson, ,1862	504	25.49
Neocyttus helgae Holt and Byrne, 1908	198	7.00	*Micromesistius poutassou* Risso, 1827	116	5.87
Unidentified Macrouridae	120	4.24	Unidentified Macrouridae	42	2.12
Guttigadus latifrons Holt and Byrne, 1908	53	1.87	*Helicolenus dactylopterus* Delaroche, 1809	35	1.77
Molva dypterygia Pennant, 1784	26	0.92	*Mora moro* Risso, 1810	22	1.11
Molva sp.	24	0.85	*Phycis blennoides* Brünnich, 1768	21	1.06
Mora moro Risso, 1810	22	0.78	*Coryphaenoides rupestris* Gunnerus, 1765	18	0.91
Chimaera monstrosa Linnaeus, 1758	20	0.71	*Notacanthus bonapartei* Risso, 1840	16	0.81
Notacanthus bonapartei Risso, 1840	16	0.57	*Deania calcea* Lowe, 1839	12	0.61
Coryphaenoides rupestris Gunnerus, 1765	15	0.53	*Nezumia aequalis* Günther, 1878	12	0.61
Nezumia aequalis Günther, 1878	12	0.42	*Chimaera monstrosa* Linnaeus, 1758	10	0.51
Scyliorhinidae	12	0.42	*Lophius* sp.	7	0.35
Lophius sp.	11	0.39	*Arctozenus risso* Bonaparte, 1840	7	0.35
Rajidae	9	0.32	*Hoplostethus atlanticus* Collett, 1889	5	0.25
Unidentified Moridae	9	0.32	*Molva dypterygia* Pennant, 1784	5	0.25
Hoplostethus atlanticus Collett, 1889	8	0.28	*Molva* sp.	5	0.25
Molva molva Linnaeus, 1758	7	0.25	*Centrophorus* sp.	1	0.05
Phycis blennoides Brünnich 1768	7	0.25	cf. *Gaidropsarus* sp.	1	0.05
Unidentified Gadiform (possibly *Merluccius merluccius* Linnaeus, 1758)	6	0.21	*Molva molva* Linnaeus, 1758	1	0.05
Helicolenus dactylopterus Delaroche 1809	5	0.18	Rajidae	1	0.05
Deania calcea Lowe, 1839	4	0.14	*Trachyscorpia cristulata* Goode and Bean, 1896	1	0.05
Trachyscorpia cristulata Goode and Bean, 1896	4	0.14			
Arctozenus risso Bonaparte, 1840	2	0.07			
Centrophorus sp.	1	0.04			
Squalidae	1	0.04			
unidentified	299	10.81	unidentified	285	14.42
Total	2829		Total	1977	

At both sites, more fish were found in 3-D structured habitats than in coral habitats (Fig. 2A), although only at Giant Mounds was the association of fish with specific habitats significantly different from random (Fisher's exact test, $p=0.011$). The abundance of fish was, as a trend, associated with specific coral habitats (although not significantly, Fisher's exact test, $p=0.09$) at Giant Mounds, with the highest levels of fish found on rubble habitats, fewer on live coral thickets and fewer still in areas of decreasing habitat complexity; although a similar pattern was seen at Twin Mounds (Fig. 2B), the association was not significant (Fisher's exact test, $p=0.12$).

The behaviour of the most common fish found on and around the reefs differed between species and some species showed clear differences in behaviour between different habitats (Fig. 3). Bedrock habitats comprised less than 1% of footage at Twin Mounds and, therefore, were excluded from behavioural analyses at both sites. Sixty to eighty percent of observed *S. kaupii*, a scavenging eel, were performing active behaviour regardless of habitat (Fig. 3A). *Lepidion eques* was always recorded within a few centimetres above bottom and displayed a larger variety of behaviours. There was a tendency for *L. eques* to be found associated with structures that were emergent from the seabed, such as boulders, drop stones and solitary corals. *L. eques* were more stationary and less active on sandy substrata at both sites (Fisher's exact test, $p=<0.001$ at both sites; Fig. 3B) with more individuals associated with a 3-D structure (Fisher's exact test, $p=0.006$ for Giant Mounds, $p=0.008$ at Twin Mounds). *Neocyttus helgae*, a laterally flattened fish, was most active above coral 3-D structured habitats (Fisher's exact test, $p=0.007$) whereas *M. poutassou*, a fusiform fish, appeared to be more active above sandy substrata than coral (Fig. 3C), although this was not statistically significant (Fisher's exact test, $p=0.71$).

Interestingly, two species of fish were particularly associated with coral habitats. *N. helgae* presence was tied to coral habitat (Fisher's exact test, $p<0.001$) and it was found most frequently above dead coral rubble (Fisher's exact test, $p=0.06$) whereas *Guttigadus latifrons* was mainly found amongst dense living coral thickets (Fisher's exact test, $p=0.006$), and was not observed on non-coral habitat. The behaviour of *G. latifrons* differed between dead and living coral habitat (Fig. 4). In particular, *G. latifrons* spent more time active and within living coral (Fisher's exact test, $p=0.08$) whereas when it was sighted in association with dead coral it tended to be more stationary and less hidden. On one occasion on Giant Mounds, a fish strongly resembling *Gaidopsarus sp.* was found among living pink *L. pertusa*. However, we cannot be certain about the identification of this individual.

At Giant Mounds the reefs appeared not to be heavily impacted by trawling, although one monofilament net was seen, filled with fresh coral rubble and broken live coral fragments. No trawl tracks could be seen in the proximity of the net, suggesting that this was a lost gill-net. At Twin Mounds there was widespread evidence of the impacts of fishing where recently broken coral, lost gear and trawl tracks seen during 14% of the recording time (as opposed to 4% at Giant Mounds). The occurrence of fishing evidence at Twin Mounds was linked to substrate type (Fisher's exact test, $p=0.0008$), positively correlated with patchy live coral (boulders on sand, overgrown with coral such as drop stones) and a negatively correlated with sandy coral rubble and dead coral.

4. Discussion

Dense aggregations of scleractinian corals were discovered in deep waters off SW Ireland during dredging surveys aboard HMS Porcupine (Duncan, 1873) but the invertebrate diversity of these habitats did not begin to be fully appreciated until the more detailed dredge and grab studies of Le Danois (1948). Traditionally, scientific fish trawls were avoided on these grounds, due to
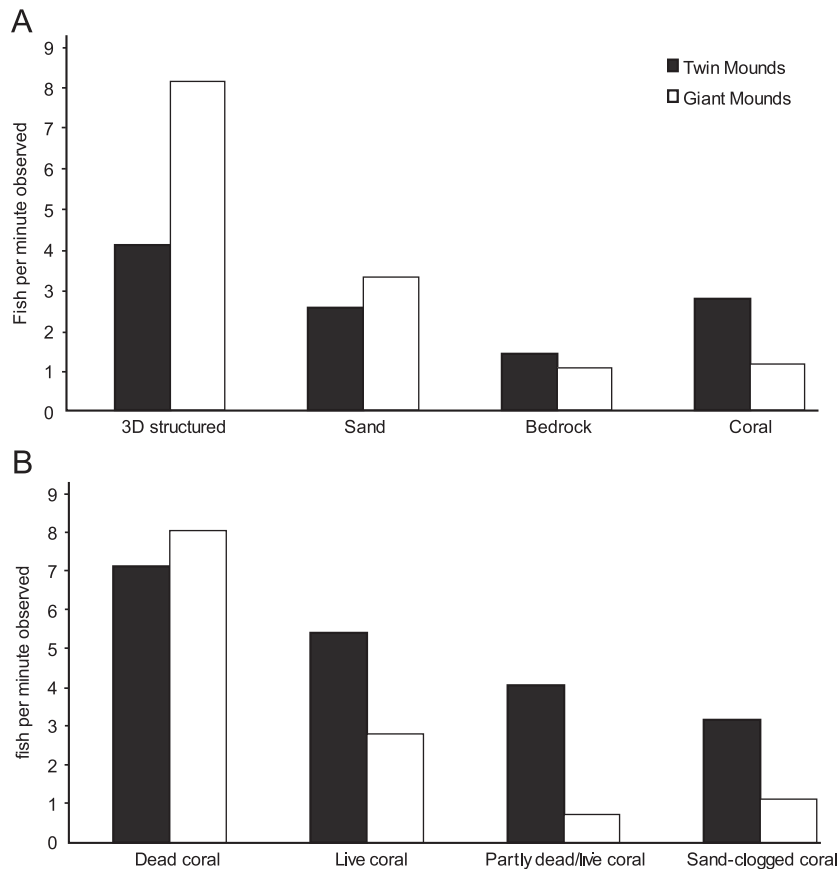
Fig. 2. (A) Fish abundance, expressed in fish seen per minute, in each habitat type and (B) coral sub-habitats at Twin Mounds (black bars) and Giant Mounds (white bars).

the dangers of losing the gear, but the advent of robust rockhopper trawls in the late 1980s allowed large-scale commercial fishing operations to expand into the coral-rich provinces off Ireland targeting demersal species such as roundnose grenadier, *Coryphaenoides rupestris*, orange roughy, *Hoplostethus atlanticus*, leafscale gulper shark, *Centrophorus squamosus* and the Portuguese dogfish, *Centroscymnus coelolepis*, with a range of large fish species caught as by-catch (Hall-Spencer et al., 2002). Although an analysis of commercial trawls can tell us which fish species occur around Irish coral reefs, detailed insights into the interactions of demersal fish on these deep-water reefs had to wait until the direct observations of Costello et al. (2005). Their observations of the Irish coral reefs recorded 13 fish taxa (6 identified to species, 1 to genus, 3 to family and 3 unknown), based on ca 3 h of video from a drop-down camera and ca 4 h worth of still-photographs taken every 12 s from a camera suspended below the ship. In the present study we analysed 33.5 h of high quality ROV video, observing 30 taxa (18 identified to species, 5 to genus, 7 to family). We found *S. kaupii* and *L. eques* to be the most common during the course of our surveys; Costello et al. (2005) also found that *S. kaupii* and fish from the Moridae family were common over the reefs.

A remarkable difference between the areas surveyed was the site-dependent presence/absence of *M. poutassou* and *N. helgae*. *Micromesistius poutassou* is a migrant species in Rockall Trough and feeds mainly on zooplankton, but also on other pelagic crustaceans and cephalopods (Mauchline and Gordon, 1984). Cold-water corals feed mainly on zooplankton and organic matter (Mortensen, 2001; Freiwald, 2002; Davies et al., 2009), and thus grow in places of sufficient plankton and organic matter input (Thiem et al., 2006; Kiriakoulakis et al., 2007); it is not surprising therefore to find this fish species above coral reef sites. The observed absence of *M. poutassou* at Twin Mounds could be due to fishing, but other

factors could also be responsible such as abundance of food. The presence of *N. helgae* may also be associated with the rich zooplanktonic input of coral sites (Auster 2005) but why this fish was not observed at Giant Mounds is unknown. Information gathered from other ROV cruises indicates that the high abundance of *N. helgae* seen at Twin Mounds is rather exceptional (P. Lorance, Ifremer Nantes, France, pers. comm. 2006).

Previous research concerning the use of cold-water corals by fish has tended to view the coral structures as one habitat type (Witherell and Coon, 2000; Krieger and Wing, 2002; Auster 2005; Auster et al., 2005; Morgan et al., 2005). As with Costello et al. (2005, but also Ross and Quattrini, 2007; Roberts et al., 2008; Harter et al., 2009; Du Preez and Tunnicliffe, 2011) we divided the reefs into sub-habitats and found that living and dead coral structures supported different fish communities at both study sites, with more fish living in the coral rubble zone than in the areas of live coral. This may relate to food availability since the benthic invertebrate fauna appeared to be more diverse and abundant within rubble zones than in live coral areas (see also Roberts et al., 2008). It is well documented that deep sea coral structures support a high diversity of fish (Costello et al., 2005; Koenig et al., 2005; Reed et al., 2006; Parrish 2006), but it appears this may be due to the three-dimensional structure of the coral rather than the biotic properties of the reef (Harter et al., 2009). The association of particular fish species to deep sea corals has been shown in the western Atlantic off the coast of the U.S. (Ross and Quattrini, 2007), but data for the eastern Atlantic has not yet yielded such conclusive evidence. In our dive footage, one species (*G. latifrons*) was particularly associated with live coral and may, therefore, depend on the presence of cold-water coral reefs for shelter or food. The natural history of *G. latifrons* has, to our knowledge, not yet been studied. This species has small pectoral
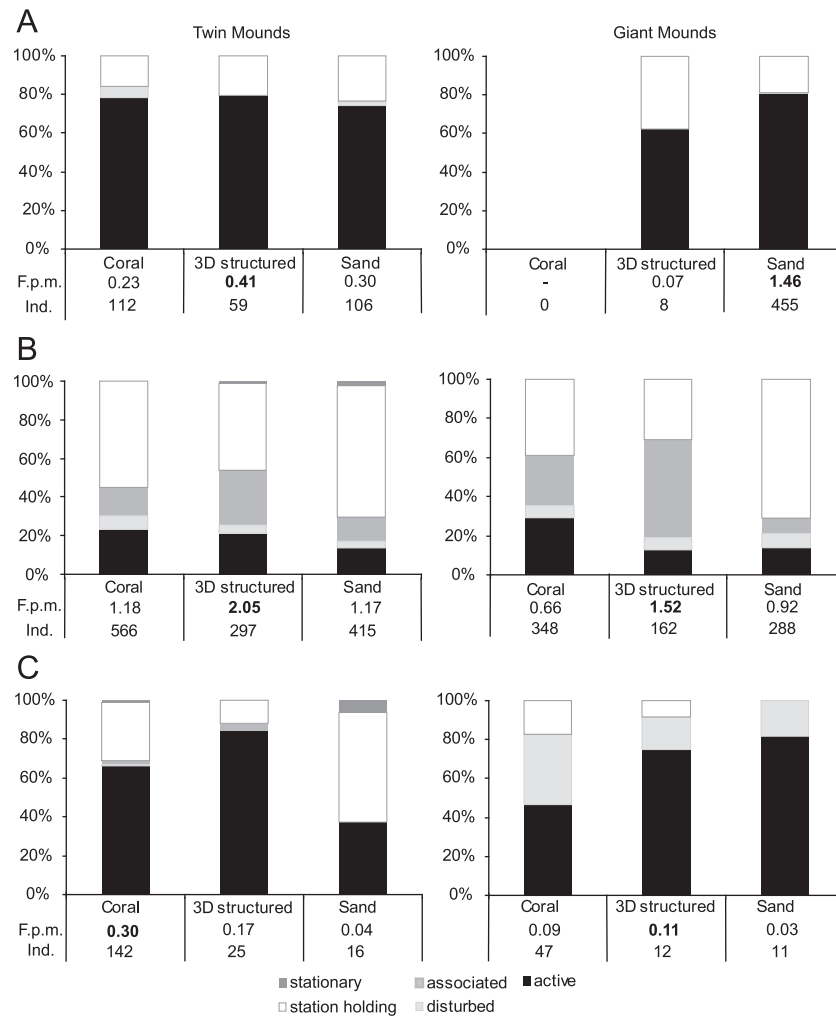
Fig. 3. Percentage of individual fish seen displaying specific behaviours (no action, stationary, hidden/associated, disturbed, active) when observed in different habitat types. (A) *Synaphobranchus kaupii*, (B) *Lepidion eques*, (Ci) *Neocyttus helgae* and (Cii) *Micromesistius poutassou*. Numbers below the bars indicate the total number of individuals observed (Ind.). Fish per minute (f. p. m.) are the total number of fish counted in each habitat divided by the total minutes filmed in each habitat. Highest f. p. m. counts are highlighted in bold font.
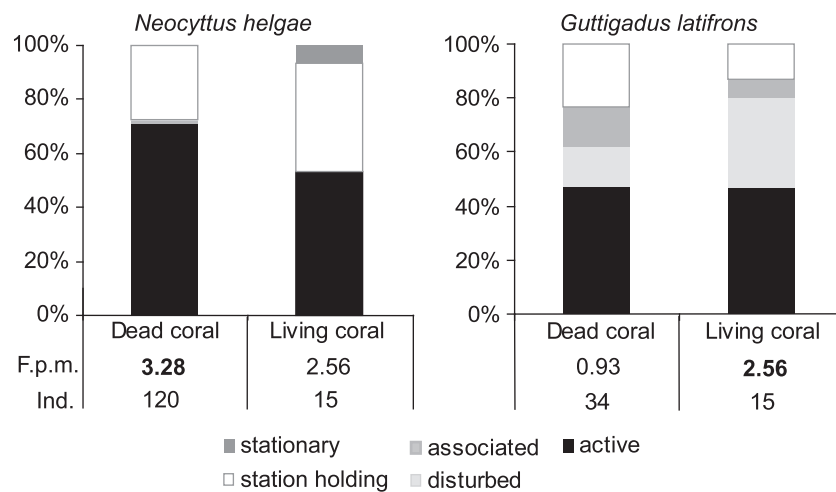

Fig. 4. Percentage of *Neocyttus helgae* and *Guttigadus latifrons* individuals seen displaying specific behaviours (no action, stationary, hidden/associated, disturbed, active) when observed over dead and living coral. Numbers below the bars indicate the total number of individuals observed (Ind.). Fish per minute (f. p. m.) are the total number of fish counted in each habitat divided by the total minutes filmed in each habitat.

fins and a small isocercal caudal fin. Forward movement was elicited through anguilliform undulations. *Guttigadus latifrons* has a wide mouth gape typical of the Gadidae.

The behaviour of five fish species was studied in more detail. At both sites, we found that *S. kaupii* moved actively forward irrespective of substrate type. Similar observations have been

made by Uiblein et al. (2002, 2003), where active forward moving behaviour of *S. kaupii* remained the most observed behaviour in different environments. For the other four species, substrate type influenced fish behaviour. The bentho-pelagic species *M. poutassou*, which is known to migrate from near the seabed up into the water column depending on season and time of day, increased activity over sandy substrates. Over sand these fish were all swimming actively forwards, maybe to optimise prey location; they are known to eat zooplankton, small crustaceans and cephalopods (Cohen et al., 1990).

Lepidion eques were most commonly found in association with three-dimensional structured habitats where they were significantly more active than when seen on sandy habitats. This increased activity could be due to the animals searching for crustaceans and polychaetes, their preferred prey items (Whitehead et al., 1989). On sandy habitats *L. eques* were found within a few centimetres above bottom, generally stationary, which may help to avoid attracting predators in this exposed environment. In a behavioural study conducted in the Bay of Biscay on several deep sea fish species (Uiblein et al., 2003) *L. eques* was similarly observed displaying station holding behaviour in sandy habitats. The authors suggested that the station holding behaviour might be typical for benthic gadoid species in the deep sea, and noted that they observed similar behaviour in *Molva molva* and *Mora moro* during their dives. At Twin and Giant Mounds we saw the same behavioural pattern for *M. moro* as the Uiblein et al. (2003) study, but the most common behaviour observed for *M. molva* and *Molva dypterygia* was slow active forward movements. The other observed gadoid fish, *P. blennoides*, was often seen moving slowly and close to the substrate, with its long barbels touching the ground. Both *L. eques* and *M. moro* belong to the family of Moridae, so while we cannot confirm the previous observations from Uiblein et al. (2003) for all gadoid species seen during the dives, we can verify that station holding was the typical behaviour for the observed morid species.

The activity of *N. helgae* increased with increasing habitat structure; its deep, laterally flattened, round, body shape is well suited for holding position in or near vertical structures, and has been observed previously associated with structured habitats such as boulders and coral reefs (Miller, 2003; Auster, 2005). It feeds on cnidarians and crinoids (Gartner et al., 1997) although Auster et al. (2005) suggest that this species may associate with coral rich areas to profit from abundant zooplankton. In our study *N. helgae* was more frequent in dead coral areas although it did not appear to behave differently on living and dead coral.

When using ROV for visual surveys of deep sea fish abundance and behaviour, the impact of the ROV itself, particularly the light and sound emitted, needs to be considered (Stoner et al., 2008). Several studies have documented the behavioural responses of deep sea fish to ROV presence (Lorance and Trenkel, 2006; Trenkel et al., 2004a, 2004b) and have generally found that active, pelagic fish show the strongest avoidance and disturbance in response to the ROV (Lorance and Trenkel, 2006). Species-specific responses to ROVs are also likely to vary with environmental conditions (Lorance and Trenkel, 2006; Trenkel et al., 2004a). During our analysis we did consider 'disturbed' behaviours in relation to ROV presence and for some species, e.g. *G. latifrons*, the ROV had a clear affect on behaviour. We cannot exclude the fact that our estimates of abundance were also affected by ROV presence. Numbers of *S. kaupii* during the two dives may be overestimates as it has been shown previously that *S. kaupii* is attracted to ROV lights, in contrast to fish from the Moridae family (particularly *L. eques*) which have been observed in higher abundance when ROV lights are dimmed (Trenkel et al., 2004a). Although the use of ROVs is believed to result in reduced bias when used for qualitative assessments of fish communities based on relative abundance in habitats (Stoner

et al., 2008), it is to date one of the most useful tools for observations of deep-water animals in their natural environment.

In conclusion, Irish coral reefs provide complex habitats that are home to a diverse assemblage of fish which utilise the range of niches occurring both above and within the reef structure. So far, no corallivore fish have been identified in the deep sea and it seems that the structure provided by dead or living coral is more important for benthic fish communities that the coral organism itself. However, the association of *G. latifrons* and cf. *Gaidropsarus* sp. with live coral and the important differences in fish abundance between live coral, dead coral, and other seabed habitats show that seabed features are important for fish diversity. Additionally, the present study found higher fish abundances on complex three-dimensional habitats such as drop-stones. The ecological value of these boulders, which provide habitat for both invertebrates (e.g. corals, sponges, crinoids, crustaceans, Davies et al., 2007; Le Guilloux et al., 2010) and fish (this study) may have been previously underestimated due to their isolated and patchy distribution. This isolated distribution in vast stretches of sand makes them particularly vulnerable to destruction through fishing gear, as these densely populated drop-stones can hardly be detected from the surface.

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