Effects of cold-water corals on fish diversity and density (European continental margin: Arctic, NE Atlantic and Mediterranean Sea): Data from three baited lander systems

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ABSTRACT

Autonomous photographic landers are a low-impact survey method for the assessment of mobile fauna in situations where methods such as trawling are not feasible or ethical. Three institutions collaborated through the CoralFISH project, each using differing lander systems, to assess the effects of cold-water corals on fish diversity and density. The Biogenic Reef Ichthyofauna Lander (BRIL, Oceanlab), Autonomous Lander for Biological Experiments (ALBEX, NIOZ) and the Marine Environment MOnitoring system (MEMO, CoNISMa) were deployed in four CoralFISH European study regions covering the Arctic, NE Atlantic and Mediterranean, namely Northern Norway (275–310 m depth), Belgica Mound Province (686–1025 m depth), the Bay of Biscay (623–936 m depth), and Santa Maria di Leuca (547–670 m depth). A total of 33 deployments were carried out in the different regions. Both the time of first arrival (T_{arr}) and the maximum observed number of fish (MaxN) were standardised between the different lander systems and compared between coral and reference stations as indicators of local fish density. Fish reached significantly higher MaxN at the coral stations than at the reference stations. Fish were also found to have significantly lower T_{arr} in the coral areas in data obtained from the BRIL and MEMO landers. All data indicated that fish abundance is higher within the coral areas. Fish species diversity was higher within the coral areas of Atlantic Ocean while in Northern Norway and Santa Maria di Leuca coral areas, diversity was similar at coral and reference stations but a single dominant species (*Brosme brosme* and *Conger conger* respectively) showed much higher density within the coral areas. Indicating that, while cold-water coral reefs have a positive effect on fish diversity and/or abundance, this effect varies across Europe's reefs.

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1. Introduction

Cold-water corals (CWC) are one of the major contributors to deep-sea habitat complexity (Roberts, 2006; Ross and Quattrini, 2007). Reef forming species, such as the most common *Lophelia pertusa* (Biber et al., 2014), are capable of forming cold-water coral reefs at the kilometres scale (Costello et al., 2005). Cold-water coral reefs are found in all the world's oceans and the Mediterranean Sea (Mortensen et al., 1995; Ramirez-Llodra et al., 2010), forming on hard substrates where environmental conditions are favourable (see Freiwald and Roberts (2005), Section IV).

Cold-water coral reefs engineer habitat (Buhl-Mortensen et al., 2010) by developing what may be a small and low profile hard surface into a complex habitat (Morris et al., 2012); modifying current regime, providing further hard substrate and a three dimensionally complex structure that offers shelter to mobile organisms (Roberts and Ormond, 1987). The reefs are often the only available three dimensional structures in the area (Costello et al., 2005; D'Onghia et al., 2011; Tissot et al., 2006). Within the shallow water tropical coral reefs a positive correlation between substratum structural complexity and fish species richness or diversity has been repeatedly established (Gratwicke and Speight, 2005; Luckhurst and Luckhurst, 1978; Risk, 1972; Roberts and Ormond, 1987). The factors identified as affecting fish abundance have been inconsistent between studies (Roberts and Ormond, 1987).

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Anecdotal evidence that fish aggregate around structures has been known to fishermen since the 1700s when artificial reefs were first used as aggregation devices (Gratwicke and Speight, 2005), as has increased local biodiversity around corals, both shallow and deep (Fosså et al., 2002; Gratwicke and Speight, 2005; Husebø et al., 2002; Koslow et al., 2000; Krieger and Wing, 2002; Reed et al., 2005). It is consistently reported that fish aggregate at cold-water reefs (Auster et al., 2005; Roberts and Hirshfield, 2004). Previous studies have highlighted that CWC habitats are probably important areas for commercial fish species (Costello et al., 2005; D'Onghia et al., 2010; Durán Muñoz et al., 2011; Roberts and Hirshfield, 2004; Stone, 2006). Reduction in catch has also been noted when a reef is damaged (Fosså et al., 2002). However the functional role of the corals in fish diversity and abundance is still not fully understood (Auster, 2005; Auster et al., 2005; D'Onghia et al., 2011; Krieger and Wing, 2002; Ross and Quattrini, 2007; Tissot et al., 2006) and quantitative studies are scarce (Biber et al., 2014). The potential benefits for fish provided by cold-water coral reefs are: greater food supply, an ambush site, spawning site and nursery ground (Costello et al., 2005; D'Onghia et al., 2010; Foley et al., 2010; Husebø et al., 2002; Roberts, 2002; Roberts and Hirshfield, 2004).

The CoralFISH project is a European Union (EU) Seventh Framework Program that aims to quantify and scientifically validate the anecdotal observation and conflicting evidence that cold-water corals are important to fish in different geographic areas. The project studied six key European marine eco-regions: (i) Region 1: Northern Norway – eastern Norwegian Sea; (ii) Region 2: Iceland; (iii) Region 3: Porcupine Seabight/Rockall Trough; (iv) Region 4: Bay of Biscay; (v) Region 5: The Azores; and (vi) Region 6: Mediterranean – Ionian Sea. One of its tasks was to assess the interaction between corals, fish and fisheries in order to develop monitoring and predictive modelling tools for ecosystem based management in the deep waters of Europe and beyond (Grehan, 2012).

Trawling is common method for sampling mobile marine fauna (e.g. Merrett and Haedrich, 1991). But trawling is not appropriate to study cold-water coral habitats due the (i) difficulty to use trawls on rough seabed and (ii) the potential adverse impacts on corals. An alternative non-intrusive method that has seen increasing utilisation, and is the focus of this paper, is the assessment of fish diversity and abundance using baited cameras. Because of the deep water environment in this study, baited cameras were mounted on autonomous landers. This method is extremely cost and time efficient, allowing the system to be left unsupervised to perform a pre-programmed task (Bagley et al., 2004, 2007; Cappo et al. 2004; King et al., 2007; Jamieson and Bagley, 2005), causes minimal damage to the habitat and organisms it observes (Cappo et al. 2004; King et al., 2007; Stobart et al., 2007; Harvey et al., 2012; Santana-Garcon et al., 2014) and is potentially more representative than other baited methods (Harvey et al. 2012).

Fishes are mobile and are unlikely to pass their whole lifespan within a single coral mound, likely moving between mounds and adjacent areas during their normal activity patterns. To investigate the utilisation of the CWC habitat relative to the surrounding seabed by fish species we performed paired deployments of baited camera landers on coral mounds and off the mounds in the immediate surrounding area in four different CWC regions in the Arctic, NE Atlantic and Mediterranean Sea.

Table 1
Summary of main characteristics of autonomous lander deployments. Region refers to the CoralFISH study regions – Region 1 – Northern Norway, Region 3 – Belgica Mound Province, Region 4 – Bay of Biscay, Region 6 – Santa Maria di Leuca. Dep is the deployment number. The date is given in the format dd/mm/yyyy. C: coral habitat; R: reference area. Time is the time (GMT) that the lander arrived at the seabed. Period recorded is given in minutes at the seabed.

| Region	Dep	Cruise RV	Date	Deployment/Site	C/R	Depth (m)	Time	Lander	Latitude	Longitude	Period recorded (min)
1	1	CoralFISH G O Sars	10/03/2010	K1/2-1	R	275	23:49	BRIL	66 57.70′N	11 25.10′E	904
	2		11/03/2010	HL5-1	C	310	3:04		66 57.79′N	11 06.75′E	577
	3		11/03/2010	HL5-2	C	304	21:34		66 57.79′N	11 06.76′E	879
	4		09/03/2010	K1/2-2	R	282	15:00	ALBEX	66 57.13′N	11 26.59′E	495
	5		11/03/2010	HL5-3	C	304	11:58		66 58.08′N	11 6.24′E	1772
3	6	CoralFISH Pelagia	17/10/2009	Galway summit	C	884	16:12	BRIL	51 27.09′N	11 45.15′W	1342
	7		18/10/2009	Galway base	C	970	19:34		51 27.09′N	11 46.05′W	1680
	8		21/10/2009	Thérèse summit	C	878	16:14		51 25.67′N	11 46.35′W	1193
	9		22/10/2009	Thérèse base	C	1024	20:11		51 25.71′N	11 47.02′W	1175
	10		25/10/2009	Poseidon summit	R	685	17:43		51 27.36′N	11 41.67′W	921
	11		17/10/2009	Galway base	C	965	16:39	ALBEX	51 27.11′N	11 45.87′W	1121
	12		18/10/2009	Galway summit	C	786	20:05		51 27.11′N	11 45.19′W	877
	13		20/10/2009	Thérèse summit	C	916	20:15		51 25.66′N	11 46.32′W	936
	14		21/10/2009	Thérèse base	C	1024	20:35		51 25.68′N	11 47.00′W	935
	15		22/10/2009	Poseidon summit	R	680	9:23		51 27.40′N	11 41.99′W	2013
4	16	BoBEco Pourquoi Pas?	25/09/2011	Sorlingues canyon	C	936	7:17	BRIL	48 7.20′N	8 48.70′W	1368
	17		26/09/2011	Sorlingues canyon	R	763	17:22		48 8.48′N	8 48.02′W	1117
	18		06/10/2011	Lampaul canyon	R	623	18:05		47 36.03′N	7 33.31′W	1323
6	19	MAGIC/CoralFISH Universitatis	11/04/2010	1 – MS04	R	670	12:35	BRIL	39 36.00′N	18 29.53′E	515
	20		12/04/2010	2 – MS04	C	654	13:32		39 36.74′N	18 30.55′E	2091
	21		14/04/2010	3 – MS04	R	667	13:53		39 36.02′N	18 29.56′E	504
	22		15/04/2010	4 – MS04	C	651	9:29		39 36.73′N	18 30.55′E	420
	23		16/04/2010	5 – MS04	C	642	6:29		39 36.73′N	18 30.54′E	391
	24		12/04/2010	6 – MS04	R	670	14:15	ALBEX	39 36.02′N	18 29.57′E	286
	25		14/04/2010	7 – MS04	C	660	14:30		39 36.71′N	18 30.58′E	220
	26		15/04/2010	8 – MS04	R	667	10:00		39 36.01′N	18 29.55′E	253
	27	CoralFISH Universitatis	16/06/2010	1 – MS08	C	547	15:43	MEMO	39 33.69′N	18°12.73′E	849
	28		17/06/2010	2 – MS04	C	622	14:18		39 36.91′N	18 30.30′E	324
	29		17/06/2010	3 – MS04	R	620	20:54		39 36.83′N	18 28.87′E	937
	30	OBAMA Universitatis	05/11/2010	1 – MS04	C	648	11:20		39 36.75′N	18 30.50′E	1097
	31		06/11/2010	2 – MS04	C	610	8:12		39 37.14′N	18 30.12′E	278
	32		06/11/2010	3 – MS08	R	624	16:10		39 34.66′N	18 15.71′E	782
	33		07/11/2010	4 – MS08	R	615	7:28		39 35.28′N	18 08.47′E	168
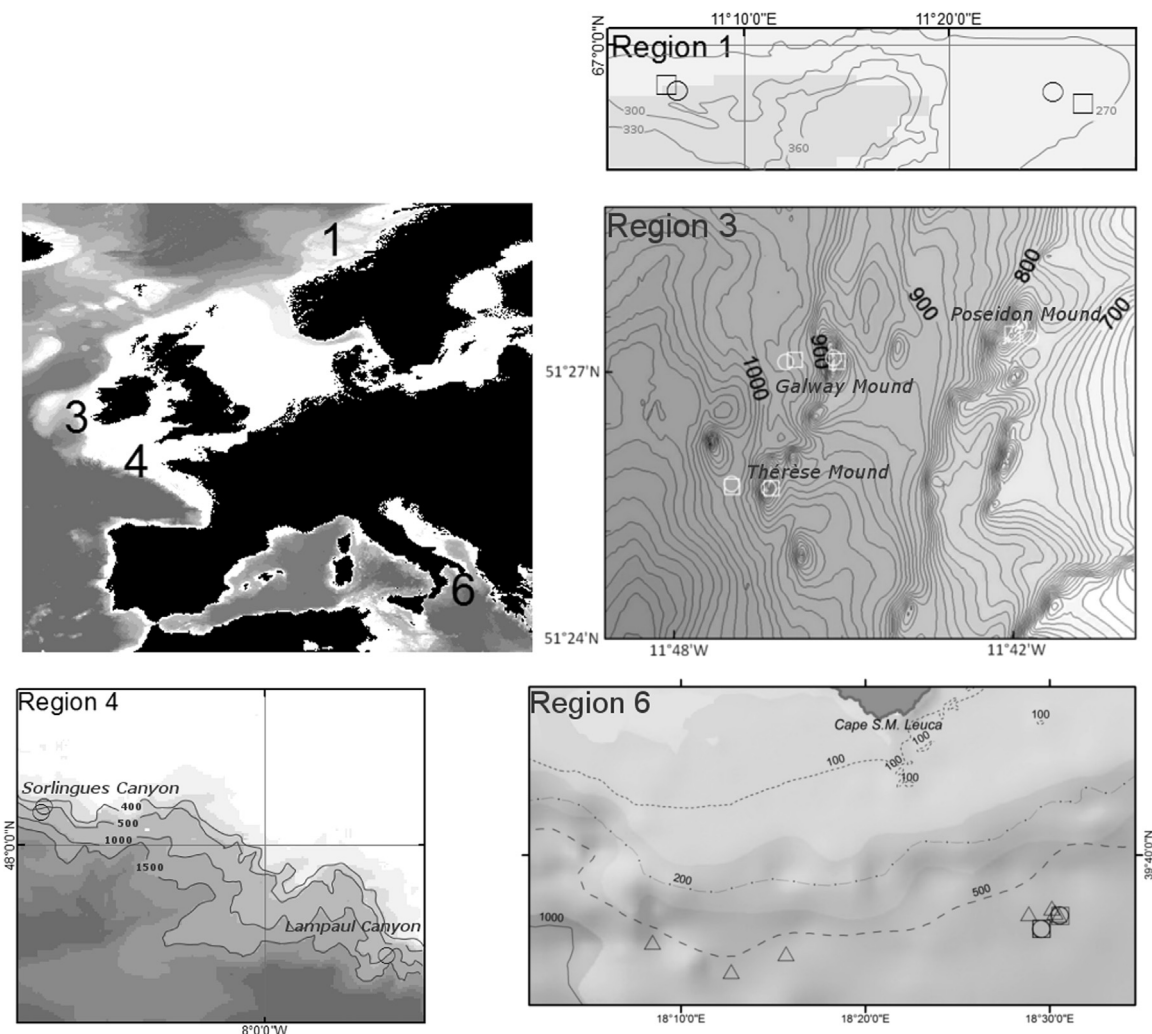
Fig. 1. The location of lander deployments within this study. Numbers on the map of Europe relate to the zoomed insets of the study regions. The map of Regions 1 is adapted from Kutti et al. (2013) Deployments by the BRIL lander are represented by circles, ALBEX by squares and MEMO by triangular markers. Region 1 – Northern Norway, Region 3 – Belgica Mound Province, Region 4 – Bay of Biscay, Region 6 – Santa Maria di Leuca.

2. Materials and methods

2.1. Study areas

Within 4 of the 6 study regions of the CoralFish project, landers were deployed on a coral location and at a nearby non-coral reference station, the precise configuration depending on the nature of the seabed and the coral province. Thirty three lander deployments were carried out during the project, summarised in Table 1 and the geographical location is shown in Fig. 1.

In the CoralFISH Region 1 (Northern Norway), the study was conducted in the Træna coral reef field (Fig. 1), located on the northern slope of the inner part of the Trænadjupet Trough, approximately 45 km north of the Arctic Circle in the eastern Norwegian Sea. It was selected following extensive survey by The Institute of Marine Research (IMR) (Kutti et al., 2013). For the purpose of the lander study a high density coral area was selected at 300 m depth (HL5 in Kutti et al. (2013)) as the coral habitat and, 13 km to the east, a sedimentary sea-bed at 275 m depth (an area between K1 and K2 in Kutti et al. (2013)) as a reference area. The reefs are clearly visible on the sonar images casting a shadow revealing a three dimensional structure. This allowed precise lander placement without impacting the reef. The lander coral site location was not directly on a coral mound but was surrounded on three sides by reefs < 100 m away.

In the CoralFISH Region 3, (The Belgica Mound Province – BMP; Fig. 1) the study was carried out about 100 km from the south west coast of Ireland on the edge of the continental shelf and on the eastern side of the Rockall Trough. The seabed structure of the BMP is described in detail in Biber et al. (2014). The province contains three main mounds; the Galway and Thérèse mound summits (at ∼880 m depth) with total coral cover and the shallower Poseidon mound (at ∼690 m depth) with no coral (Biber et al., 2014). The coral cover on the Galway and Thérèse mound summits included living polyps of both *L. pertusa* and *Madrepora oculata* whereas the bases of the mounds might be considered a transition zone (Costello et al., 2005) featuring both living coral and coral debris. The coral deployments were on the summit and base of Galway and Thérèse mounds and the reference deployments were on the summit of the Poseidon mound. The initial experimental design classified the bases of Galway and Thérèse mounds as reference deployments; however the lander systems recorded high coral cover and the deployments were reclassified, resulting in an imbalanced experimental design in this region.

In the CoralFISH Region 4 (Bay of Biscay: Fig. 1), three deployments were carried out, one coral location in the Sorlingues canyon and two reference deployments, one in the Sorlingues canyon and one in the Lampaul canyon. The seabed structure in the Region is described by De Chambure et al. (2013). For analysis
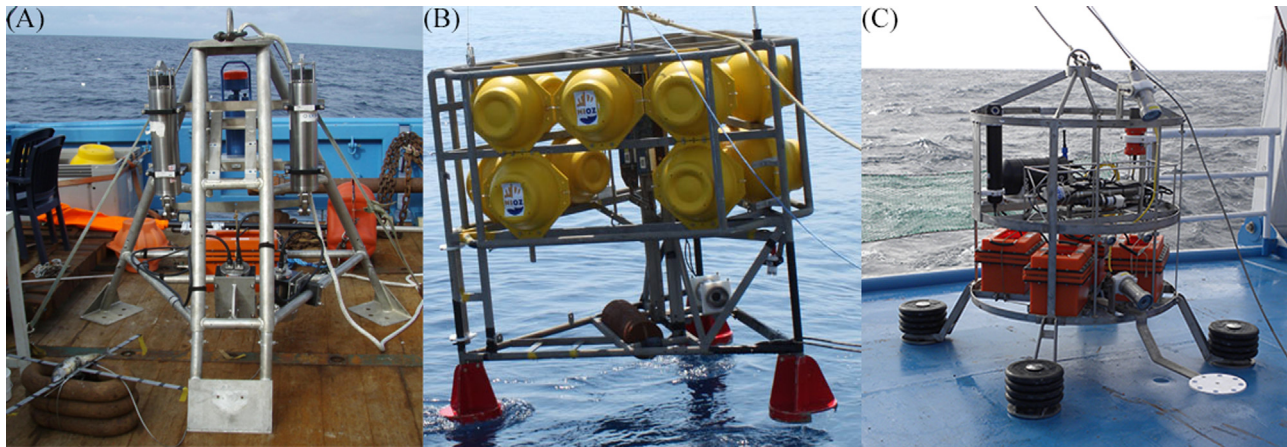
Fig. 2. The lander systems employed. a) BRIL, b) ALBEX and c) MEMO.

purposes these deployments are pooled with the BMP data where appropriate and referred to as NE Atlantic.

In the CoralFISH Region 6 (Santa Maria di Leuca -SML cold-water coral province; Fig. 1), the study was conducted along the Apulian margin, off Cape Santa Maria di Leuca (Italy) in the Northern Ionian Sea (Central Mediterranean; D'Onghia et al., 2012). The seabed structure is described by Savini and Corselli (2010) and in more detail by Savini et al. (2014). It consists of a broad north-eastern sector characterised by mass-transport deposition, with a very complex hummocky seafloor consisting of widespread mound-like reliefs, a central ridge where drift sedimentation was recognised by documenting the action of contour currents from the north-east and a western sector with prominent fault-scarps. Living colonies of *M. oculata* and *L. pertusa* were collected between 425 and 1100 m in depth (Tursi et al., 2004; Mastrototaro et al., 2010). The deployments in the coral area were located in two different areas of the SML coral province: on a coral mound in the north-eastern sector (MS04 site, Atlantis Mound), and in the fault-related scarps in the western sector (MS08 site; Vertino et al., 2010). The non-coral reference areas were on the soft bottoms of both the inter-mounds of MS04 and MS08 sites and in a westernmost muddy area (Fig. 1).

2.2. Baited lander systems

Three different lander systems were used in this study (Fig. 2). All were placed on the seabed where a piece of mackerel as bait attracted scavenging animals within view of a camera.

The Biogenic Reef Ichthyofauna Lander (BRIL; Fig. 2a) is a baited, free-fall, photographic lander based on the ROBIO II design described by Jamieson and Bagley (2005). It was developed and operated by the University of Aberdeen, Oceanlab, specifically for the CoralFISH project. To minimise any damage to reef environments the lander frame (an aluminium roughly equilateral pyramid with ~180 cm sides) did not contact the seabed but was suspended 2 m above the sea floor on a wire strop. The only contact with the sea floor was the ballast clump. The camera looked down at the ballast, reference cross and bait, which are jettisoned at the end of the deployment, and captures 2×1.5 m of the seabed. The camera was a 6000 m depth rated Kongsberg digital stills camera (OE14-208, Kongsberg, Norway) based on the Canon Power Shot G5 encased in titanium alloy housing. Photographs were taken at 60 s intervals. Images were 2592×1944 pixels in jpeg format with minimal compression and were stored on an internal 4 gigabyte compact flash card. Illumination was provided by a visible white light flashgun (OE11-242 Kongsberg, Norway) slaved directly to the main camera. As there is a known distance between the camera and the bait, the camera settings are

optimised to this distance, removing the need for more than one flash per image. The camera and the flash system were both powered by a Bennex Deep Sea Power & Light battery (USA). The BRIL ballast was released by two acoustically activated releases (IXSEA, Oceano 2500, France) connected in parallel to a release yoke. Only one IXSEA Oceano unit is required to fire for the ballast to release. Buoyancy was provided by eight VITROVEX 17 in. diameter glass sphere (Nautilus, Germany) floats on a mooring line attached to the apex of the lander. The mooring terminated in a flag and 20 m of polypropylene floating rope to allow grappling and recovery.

The Autonomous Lander for Biological Experiments (ALBEX; Fig. 2b) was constructed and operated by the Royal Netherlands Institute for Sea Research (NIOZ). It is the largest of the three landers. Its buoyancy of 12 VITROVEX 17 in. diameter glass spheres (Benthos, USA) in protective shells, is mounted directly to the lander frame. The triangular lander is 2.25 m tall with the bottom 0.4 m above the sea floor supported on three legs spaced 2.5 m apart. During the 2009 deployments the baited camera system comprised two digital video heads (Sony FCB-EX20DP) in custom made housings (NIOZ) and 2 white halogen lights (Seapoint 20 W), with all four connected to a programmable control unit and battery pack in a custom made titanium housing (NIOZ). Camera 1 pointed at the bait at 1.25 m distance while camera 2 pointed at the background. The program of the video system was limited by the maximum recording time of 90 min. Not knowing when the first scavenger would arrive, the program consisted of continuous coverage of the first 40 min after bait exposure, followed by 1 min duration sequences at increasing intervals from 5 min initially to 3 min later in the deployment with the recording duration reducing to 30 s by the end. The video images had an effective pixel resolution of approximately 830×530. During the SML deployments of the ALBEX the camera system consisted of a High–Definition (HD) video camera (Sony™ HDR-SR12E) built into a titanium housing and 2 custom made infra-red (IR) high output LED light sources. Power for camera and lights is supplied by an external source which in this case consisted of a glass sphere (Benthos, USA) containing series of Lithium batteries (total 300 Ah). The camera is fully programmable and can record up to 10 h of video. Infra-red light was used because fish cannot see light of these frequencies, and so are not influenced by this light source. The first hour was recorded continuously, followed by 1 min duration sequences at increasing intervals from 2 min initially to 20 min later in the deployment with the recording duration reducing to 30 s by the end. The videos were shot with a resolution of 1440×1080 pixels and 60 interlaced fields per second. The camera had a horizontal position, about 40 cm above the bottom

directed at the bait at 1.25 m distance. The maximum dimensions of the visible frame were about 1.5×1 m^2, caused by the quick absorption of the infra-red light. The changes to this lander system occurred between cruises at different regions and therefore the influence of changes in illumination and sampling resolution cannot be explored within this study.

The Marine Environment MOnitoring system (MEMO; Fig. 2c) was constructed and operated by the National Interuniversity Consortium for Marine Sciences (CoNISMa), Italy. MEMO consists of a stainless steel metallic frame (ø 2.15 m – h 1.65 m); 2 digital cameras (Sony ICX414) with 2 LED lights (12 V, 700 mA), multiple environmental sensors, 4 Deep-Sea batteries; an acoustic modem; ICT infrastructure (hardware) capable of managing the entire system (Capezzuto et al., 2012; D'Onghia et al., 2014). The system lands directly on the seabed where its dual cameras record in both a horizontal and oblique (45°) view, capturing about 0.80×0.95 m^2 and 1.6×1.1 m^2 of the seabed respectively. The distance from each camera to the bait is 75 and 130 cm respectively. Both cameras record 1920×1080 pixels images at four frames a second and they are later converted to bitmap 1024×756 pixel images. It is not a free-fall system but rather is lowered to the seabed by winch, a surface buoy remains connected for recovery. It stands on three legs spaced 1.33 m apart with the base of the frame 0.32 m above the sea floor. While the data are recorded internally as with the other systems it is possible to communicate with MEMO via an acoustic modem (LinkQuest UWM2000) making this the only system that allows real-time viewing of the data. The system is managed and the data are recorded by a control unit (AGEOTEC ICT). While interval recording is possible the system recorded continuously during the collection of the data described here. The MEMO lander can operate up to a depth of 1200 m for 48 consecutive hours.

2.3. Data analysis

Analysis was conducted after each cruise. All fish were identified to the lowest possible taxonomic level. Fishbase (Froese and Pauly, 2013) along with standard taxonomic texts (Whitehead et al., 1984) were used for species identification. Once confirmed, example images were added to a database of lander reference images. The presence/absence of species in relation to study region, habitat type and lander type was arranged in taxonomic order. Those that were distinct from other observed species but could not be placed within a taxonomic order due to the image lacking the diagnostic characteristics were grouped as unidentifiable.

Each of the CoralFISH partners (Oceanlab, NIOZ and CoNISMa – LRU of Bari) analysed their own data to the same template. For each minute after bait touchdown (t) the numbers of each fish species (N_t) were counted. The time of first arrival (T_{arr}) of each species and maximum number of each species (MaxN) were recorded as indices of local fish density (Farnsworth et al., 2007; Martinez et al., 2011; Priede and Merrett, 1996).

For most statistical analysis, data from the BMP and Bay of Biscay (CoralFISH Regions 3 and 4) were combined to give three main groups; Arctic (CoralFISH Region 1 Northern Norway), NE Atlantic (Regions 3 and 4 Belgica Mound Province and Bay of Biscay) and the Mediterranean Sea (Region 6 Santa Maria di Leuca). Species accumulation curves were produced for the coral and non-coral reference stations in each of these three study regions. They were calculated in the R package "BiodiversityR" (Kindt and Coe, 2005) through 100 permutations using the "exact" method; attempting to find the expected (mean) species richness in pooled deployments. Error bars were added denoting $\pm$ one standard deviation. The same package was used to produce the Shannon index and expected total species richness in the coral and reference sites of each region according to First order jackknife

estimate of extrapolated richness. The first order jackknife was selected as it gives better estimated species richness when sample sizes are low (Smith and Belle, 1984).

The time of first fish arrival (T_{arr}) and the maximum number of fish in a single still/ video frame (MaxN) were recorded for each species in a deployment, as was a T_{arr} and MaxN value for each deployment including fish of any species. The data were found to be greatly affected by the different lander systems, often to a highly significant degree. The sampling was also unbalanced, both between landers and habitat type. All figures present unstandardised data however statistical testing of the T_{arr} and MaxN of each deployment was only possible following standardisation. Standardisation was achieved by dividing all values by the average for the reference deployments of that lander; giving the reference stations an average value of one and scaling the coral stations relative to that. Standardisation against the reference stations rather than the whole dataset was chosen due to the high variation in the coral deployments. The imbalanced structure of the data caused these outlying values to distort the data in an unrepresentative way. ANOVA was performed in Minitab 16. All further analysis not stipulated, including plots, was conducted in R (R Development Core Team, 2005).

3. Results

Table 2 shows the occurrence of fish species in the four regions. Northern Norway (Region1) had the lowest species richness with a total of five species observed, four on the reference site and three at the coral site. *Phycis blennoides* (Fig. 3b) and *Molva molva* were unique to the reference areas while *Pollachius virens* was unique to the coral area. *Brosme brosme* (Fig. 3a) was the most numerous species attending the bait (up to seven individuals in an image). Other species were limited to single images of individuals towards the edge of the field of view. With the exception of a single *P. virens*, which was photographed while four *B. brosme* were present, all bait visitation by other fish species occurred when there were one or fewer *B. brosme* within the field of view.

The species accumulation curve (Fig. 4a) for the reference area shows a consistently higher and steeper curve than that of the coral area. This is reflected in the expected total species in each of the areas, where larger fish species diversity is predicted at the reference area (Table 2).

The BMP (Region 3) had the highest species richness with 21 species present, 18 of which were found on the coral sites and 10 on the reference site. The majority of sightings were of five dominant species that were present in both habitat types: *Hexanchus griseus*, *Synaphobranchus kaupii* (Fig. 3e), *Lepidion eques* (Fig. 3f), *Mora moro* (Fig. 3h) and *P. blennoides*. Eleven species were unique to the coral areas while three were unique to the reference area. The small rockling-like fishes: cf *Gaidropsarus argentatus* (Fig. 3c) and cf *Benthocometes robustus* (Fig. 3d), were only seen in coral areas emerging from the coral lattice itself. The estimate of total species (Table 2) in the coral and reference areas predict approximately twice the fish species diversity in the coral areas.

Deployments in the Bay of Biscay (Region 4) were dominated by the same actinopterygian species as the BMP: *S. kaupii*, *L. eques*, *M. moro* and *P. blennoides*. The shark, *H. griseus* was not observed. Ten fish species were observed in the coral area including four distinct but unidentifiable small fish species. A predatory sebastid *Trachyscorpia cristulata echinata* (Fig. 3g) was observed frequently but only in the coral area while *Molva dypterygia* and *Conger conger* were seen consistently only in the reference areas.

The estimated total species present (Table 2) in the coral and reference areas predict approximately equal species diversity in

Table 2
List of the species observed by the 3 landers in the coral and reference stations in each region, with indication of depth range of occurrence during the study. Region 1 – Northern Norway, Region 3 – Belgica Mound Province, Region 4 – Bay of Biscay, Region 6 – Santa Maria di Leuca. B: BRIL, A: ALBEX and M: MEMO. Number of species, unique species, Shannon index and first-order jackknife estimate of total species per habitat and region are also reported.

	Species	Depth	Region 1		Region 3		Region 4		Region 6	
			Coral	Reference	Coral	Reference	Coral	Reference	Coral	Reference
Chondrichthyes										
Carcharhiniformes	*Galeus melastomus*	680–878			B	BA	B	B		
Squaliformes	*Centrophorus granulosus*	642–651							B	
	Centrophorus squamosus	916–970			BA					
	Etmopterus spinax	547							M	
	Dalatias licha	642–670							B	BA
Hexanchiformes	*Hexanchus griseus*	547–1025			BA	B			M	BAM
Osteichthyes										
Anguilliformes	*Synaphobranchus kaupii*	623–970			BA	B	B	B		
	Conger conger	547–686				B		B	BAM	BAM
	Large eel*	878			B					
Elopiformes	Halosaur*	1025			B					
Gadiformes	*Pollachius virens*	310	B							
	cf *Gaidropsarus argentatus*	878–970			B					
	Brosme brosme	275–310	BA	A						
	Molva dypterygia	623						B		
	Molva molva	275–686		B		B				
	cf *Coelorinchus caelorhincus*	878			B					
	Coryphaenoides rupestris	970			B					
	Small Grenadier*	878				B				
	Merluccius merluccius	620–624								M
	Lepidion eques	623–970			BA	BA	B	B		
	Mora moro	667–970			BA	BA	B	B	B	
	Phycis blennoides	275–970		B	BA	BA	B	B	BAM	BM
Lophiiformes	*Lophius piscatorius*	786–884			BA					
Myctophiformes	*Lampanyctus crocodilus*	547–620							M	M
Ophidiiformes	cf *Benthocometes robustus*	878–970			B					
Perciformes	*Lepidopus caudatus*	547							M	
	Polyprion americanus	615–670							M	AM
	Pagellus bogaraveo	547–667							M	A
Scorpaeniformes	*Helicolenus dactylopterus*	547–878			BA	BA			BAM	BAM
	Trachyscorpia cristulata echinata	963						B		
	Sebastes viviparus	304	B	B						
Unidentifiable										
	Small dark fish 1	936						B		
	Small dark fish 2	936						B		
	Small slender fish	936						B		
	Small red fish	936						B		
	Eel like fish	970			B					
	Slender fish	970			B					
	Small pelagic	1025			B					
	Number of species		3	4	18	10	10	7	12	10
	Unique species		1	2	11	3	5	2	4	1
	Shannon index		0.39	1.00	2.23	2.19	2.02	1.77	1.73	1.88
	First-order jackknife		4.33	5.50	25.00	12.50	9.00	9.00	13.38	9.71

* The asterisk (*) indicates species only identified to order level.

the coral and reference stations of the Bay of Biscay. The BMP and Bay of Biscay were pooled during the production of a species accumulation curve (Fig. 4b).

In the SML coral province (Region 6) 13 species were observed, 12 in the coral area and 10 in the reference sites. Four species were found only in the coral areas; two small shark species, *Etmopterus spinax* and *Centrophorus granulosus,* and the teleosts *Lepidopus caudatus* and *M. moro. Merluccius merluccius* was the single species found only in the reference areas. Deployments in SML were dominated by the European conger *C. conger* (Fig. 3i) which was observed in all but one deployment, by all landers and in both habitat types. *Helicolenus dactylopterus* (Fig. 3j) was also observed by all landers in both habitat types while *Pagellus bogaraveo* was identified by MEMO and ALBEX landers in both coral and reference stations respectively.

The estimated total species in the coral and reference areas (Table 2) predict higher species diversity in the coral areas. The species accumulation curves for the coral and reference areas are very similar initially; however the curve for the reference areas appears to begin to reach an asymptote at a lower number of species than the coral curve (Fig. 4c).

A difference was apparent in the times of first fish arrival between the lander systems (Fig. 5). Both BRIL and MEMO showed faster first fish arrival in the coral areas relative to the reference areas however ALBEX showed an inverse pattern in all regions. The fastest first arrival times were recorded by BRIL. The difference between the lander systems was most apparent at the coral deployments. ALBEX and MEMO recorded significantly longer T_{arr} values than the BRIL in the coral deployments (Kruskal–Wallis $H_1 = 3.83$, $P = 0.050$) but there was no significant difference in reference deployments (Kruskal–Wallis $H_1 = 0.907$, $P = 0.3425$). The
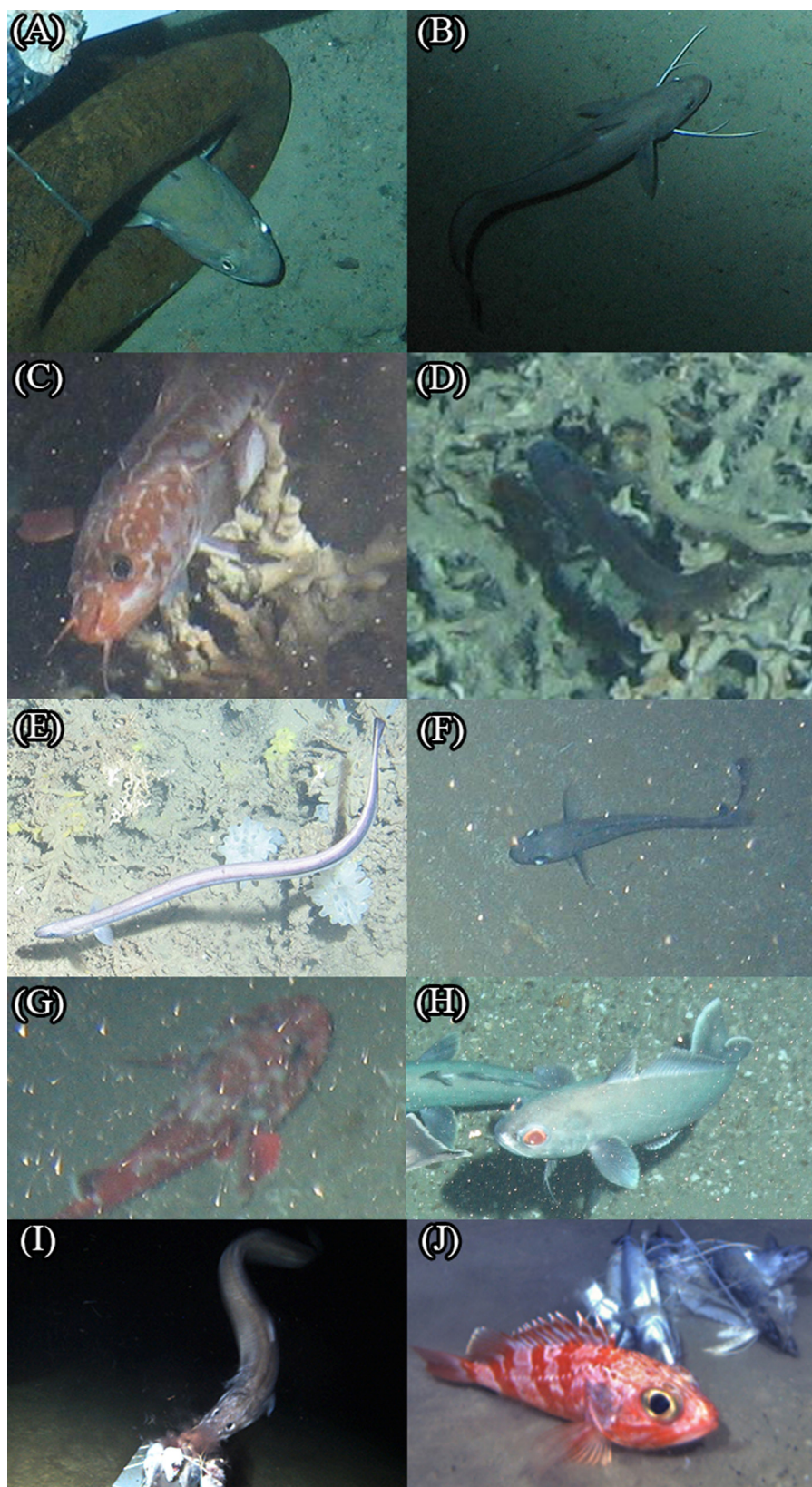
Fig. 3. Digital frames recorded by landers. a) *Brosme brosme* navigating the ballast links (Region 1 – Northern Norway, BRIL), b) *Phycis blennoides* (Region 1 – Northern Norway, BRIL), c) cf *Gaidropsarus argentatus* within the coral structure (Region 3 – Belgica Mounds Province, BRIL), d) cf *Benthocometes robustus* on the coral reef (Region 3 – Belgica Mounds Province, BRIL), e) *Synaphobranchus kaupii* (Region 3 – Belgica Mounds Province, BRIL), f) *Lepidion eques* (Region 3 – Belgica Mounds Province, BRIL), g) *Trachyscorpia cristulata echinata* (Region 4 – Bay of Biscay, BRIL), h) *Mora moro* (Region 4 – Bay of Biscay, BRIL), i) *Conger conger* striking at the bait (Region 6 – Santa Maria di Leuca, MEMO), j) *Helicolenus dactylopterus* on the seabed next to the lander frame (Region 6 – Santa Maria di Leuca, MEMO).
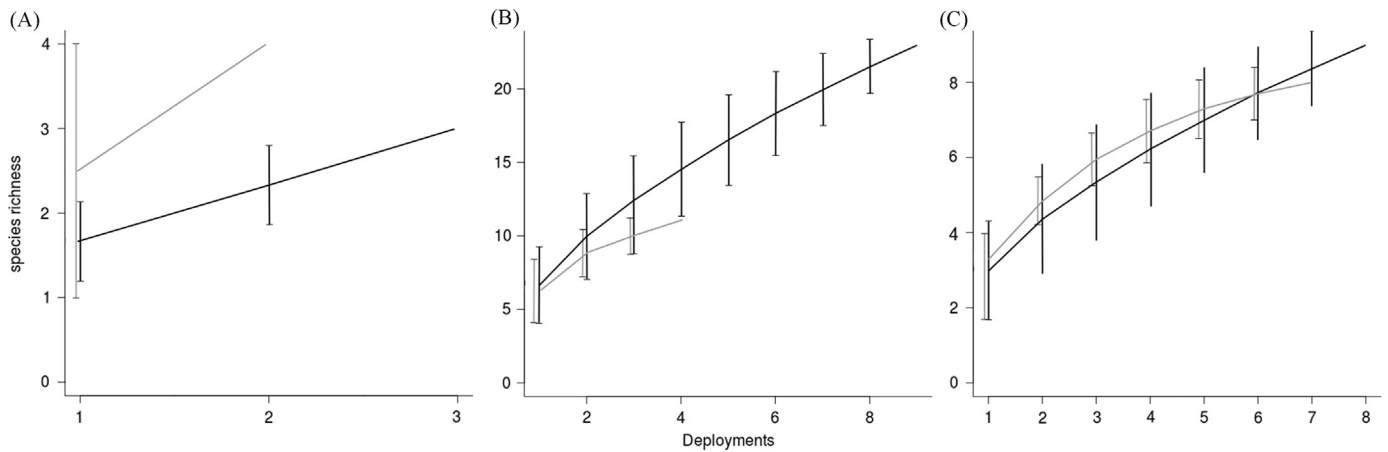
Fig. 4. Species accumulation curves for a) the Northern Norway (Region 1), b) NE Atlantic (Regions 3 and 4 pooled) and c) Santa Maria di Leuca (Region 6). The graphs illustrate the average pooled species richness for increasing pooled deployments for both coral (black) and references (grey) deployments. The error bars denote one ± standard deviation and are offset for clarity.

difference was most apparent in the ALBEX which was found to also give significantly longer T_{arr} values in the coral areas than the other two landers combined (Kruskal–Wallis $H_1=4.48$, $P=0.034$) while no significant difference was found in the reference stations (Kruskal–Wallis $H_1=0.144$, $P=0.704$).

To overcome the differences between the lander systems the data were standardised. A General Linear Model, excluding the ALBEX data, indicated that coral has a significant effect on the arrival time of the first fish ($F_1=6.52$, $P=0.021$) with a pre-standardisation mean T_{arr} on coral of 20.5 min and 135.4 min at reference sites. Since the population density is proportional to $1/T_{arr}^2$ (Priede et al., 1990) this implies a fish density 43.8 times higher on the coral than at adjacent reference sites. A significant difference was not detected between the BRIL and MEMO lander systems ($F_1=1.69$, $P=0.212$), or the study regions ($F_3=1.74$, $P=0.2$), indicating that the difference in T_{arr} between coral and reference stations is similar in all regions.

The maximum number of fish in a single photograph/video frame was found to be higher in the coral areas consistently for all landers and regions with the exception of a single deployment by MEMO (visible as an outlier in Fig. 6) and the BRIL deployments in SML where MaxN was equal on and off coral.

Following standardisation between the different landers GLM was significant for the influence of the coral ($F_1=5.85$, $P=0.023$) and region ($F_3=4.74$, $P=0.009$). The lander system used did not have a significant effect on the data once standardised ($F_2=1.73$, $P=0.196$).

Patterns are present in the MaxN and T_{arr} of individual species (Fig. 7). Of those species that are found in both coral and reference deployments most had equal or higher MaxN and lower T_{arr} values in the coral areas. The exceptions are *P. blennoides*, *L. eques* and *S. kaupii* which showed a larger MaxN and smaller T_{arr} in the reference areas, indicating a greater population density away from cold-water coral reefs.

4. Discussion

Baited landers are particularly suited to studies in fragile habitats, minimising harm to the habitat and providing data on fish diversity and abundance without removing animals. Different fish species respond to bait differently; however and many will not respond at all and thus be missing from the assessment. Previous studies in the NE Atlantic vary in their estimates, with species attracted to baited landers accounting for between one and two thirds of those caught via trawl, but landers are able to account for

large mobile species which elude trawling (Cousins et al., 2013; Priede et al., 1994; Priede and Merrett, 1996). All sampling methods have some inherent sampling bias (Bergstad, 2013), and indeed a significant difference was found between very similar systems within this study. Projects that use multiple sampling methods such as CoralFISH increase confidence in our data reflecting actual trends.

Some studies have suggested that biological diversity in European cold-water coral reefs is as much as three times that of the surrounding soft sediment (Henry and Roberts, 2007; Mortensen et al., 1995; Ramirez-Llodra et al., 2010). Studies in the south eastern United States reported fish diversity in coral habitat to be about double (Ross and Quattrini, 2007). The sample size required to reach a species accumulation curve asymptote with baited lander data is often problematic (Malcolm et al., 2007). In our case the number of deployments is also unbalanced in favour of coral deployments, due mainly to the reclassification of deployments in the BMP. In the cold-temperate regions (the BMP and Bay of Biscay) both the number of species observed and the shape of the species accumulation curve suggested a greater number of fish species in the coral deployments relative to their reference deployments. Appearing to confirm cold-water coral areas as a diversity hot-spots (Henry and Roberts, 2007; Ramirez-Llodra et al., 2010; Ross and Quattrini, 2007). This higher diversity was not seen in the Northern Norway and SML deployments, where approximately equal species diversity was observed, as was found by Mortensen et al. (1995) in the Northern Norway. In the Northern Norway deployments more species were both observed and statistically predicted in the reference areas. In the hot-temperate SML a very similar number of fish species was observed both at the coral and reference areas however these were not the same species. The benthopelagic fauna distributed in the CWC habitat is not taxonomically different from the overall regional fauna but the preferential distribution of some benthopelagic species within the coral megahabitats previously detected in the SML coral province by different methods was confirmed (D'Onghia et al., 2010, 2011, 2012; Maiorano et al., 2013).

A general reduction in reef biodiversity from South to North has been reported (Ramirez-Llodra et al., 2010) potentially explaining the difference seen between the NE Atlantic and the Northern Norway deployments. The Mediterranean deployments at SML deviate from this trend but are unusual in their high deep-water temperature, salinity and limiting colonisation through the strait of Gibraltar, resulting in reduced diversity compared with the Atlantic equivalents (Bouchet and Taviani, 1992; Moranta et al., 1998; Zibrowius, 2003). Although the Mediterranean deep-water
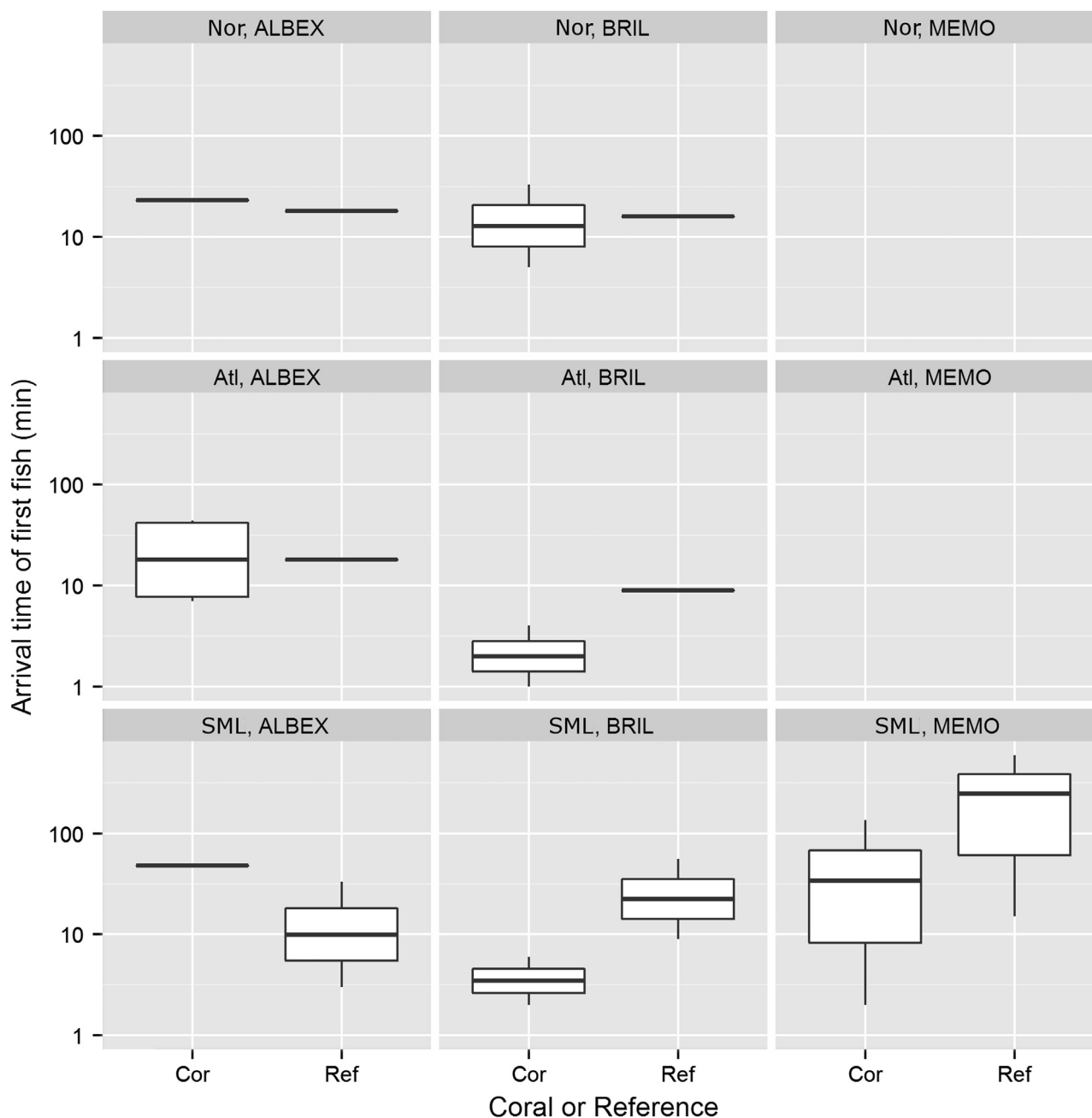
Fig. 5. Boxplots of the time of the first fish arrival (T_{arr}). The plots are arranged as a matrix with columns for each lander system and rows for each region; Nor (Northern Norway – Region 1), Atl (NE Atlantic – Regions 3 and 4) and SML (Santa Maria di Leuca – Region 6). The x-axis denotes the habitat type: Cor (coral) and Ref (reference). T_{arr} (y-axis) is presented on a log scale. The MEMO lander was only deployed in Region 6 but is included in the other regions to make the matrix more legible.

coral systems are generally considered less diverse than the Atlantic ones (Zibrowius, 2003), data recently collected by different gears could suggest a different situation, especially considering the lower number of studies carried out so far in Mediterranean deep-water corals habitats (Danovaro et al., 2010). Accordingly, relative to the Mediterranean Sea as a whole, the SML cold-water coral province is considered a diversity hotspot (D'Onghia et al., 2010, 2011; Mastrototaro et al., 2010).

A difference in T_{arr} was not detected between regions; however MaxN was found to vary significantly with region. Comparisons between the regions studied must be tentative however. While the same habitat types are assessed there are differences between the study areas that are known to have an effect on fish diversity; such as depth (this study spans a depth range of 275 m in Northern Norway to 1024 m in the BMP), time of year and topography (from

predominantly flat areas in Northern Norway and SML to seamounts and canyons in the BMP and Bay of Biscay; Bergstad, 2013). The focus of this study is to compare the fish communities on and off CWC reefs at the different depths, latitudes and topographies which they occur. The differences in the time of year the data was collected may have affected our conclusions comparing different regions.

The time of first arrival (T_{arr}) data has a wide variation both intrinsically (Farnsworth et al., 2007) and due to the landers recording at differing time resolutions. The ALBEX lander possessed a trend inverse to that found by the other two systems; consistently recording longer arrival times in coral areas. The ALBEX lander is the largest of the lander systems and brings with it a substantial and complex structure to the seabed. Arrival times have been found to be effected by such structures as fish homing
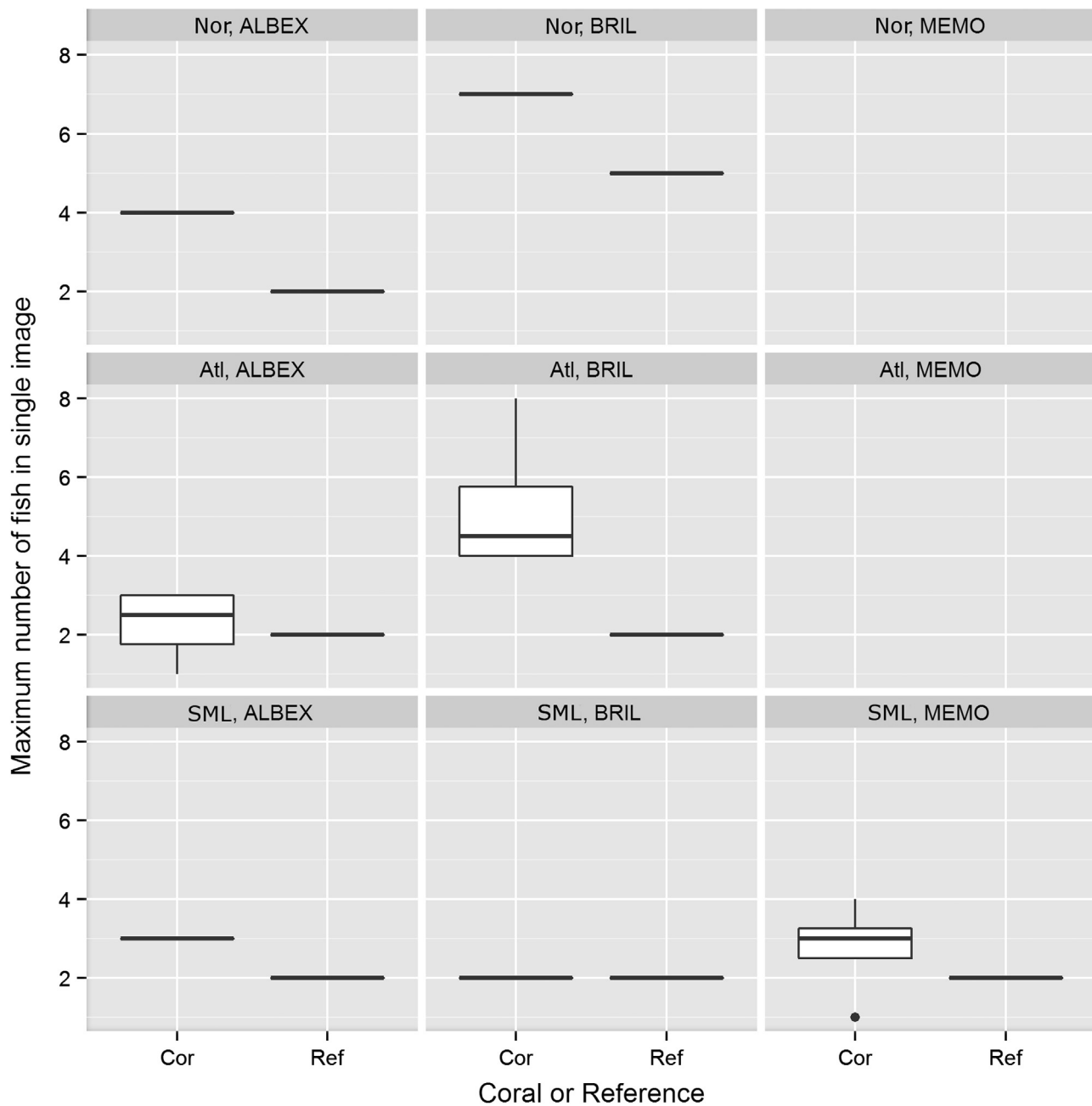
Fig. 6. Boxplots of the maximum number of fish observed in a single photo/video frame (MaxN). For arrangement of plots and explanation of terms see Fig. 5.

on the bait investigate the lander structure itself (Jamieson et al., 2006). Both of the landers that settled directly on the seabed (ALBEX and MEMO) had significantly higher T_{arr} values than the BRIL in the coral deployments. This may suggest that fish that are attracted to bait within a coral environment are more likely to be distracted or deterred by the lander structure and exhibit an elevated T_{arr}. Feeding strategies of the same species responding to bait may differ in the different habitat types. Those from the coral areas have been foraging in complex environments while those in the reference areas have been intercepting carrion on the open seabed.

The influence of cold-water corals on the local fish abundance appears to vary both with location and specific fish species (Biber et al., 2014). T_{arr} and MaxN of most species appear to indicate increased density in coral areas with the exceptions of *Phycis blenniodes*, *L. eques* and *S. kaupii*. In the BMP greater densities of *S. kaupii* were also found outside of the coral areas by Biber et al.

(2014); however they found a conflicting result for *L. eques*; a greater density in coral areas. Using a baited lander Heger et al. (2007) reported that on the Galway mound *S. kaupii* and *M. moro* were the dominant fish scavengers, although *L. eques* was observed. Studies that did not attract fish with bait (Costello et al., 2005; Söffker et al., 2011; Biber et al., 2014) reported *L. eques* as the most abundant fish in the area, suggesting it is only weakly attracted to the bait or was not attracted at all and was only observed due to the high local densities. *L. eques* has been noted to avoid ROV lights (Söffker et al., 2011), so may avoid the lander illumination. They did not linger for consecutive photographs but it is not possible to say if this is due to them passing through the shot by chance or avoidance.

Previous studies in Northern Norway have found the number of megafauna species in the coral area to be three times higher than that of the surrounding area (Husebø et al., 2002; Mortensen et al., 1995). Husebø et al. (2002) found significantly more fish (all
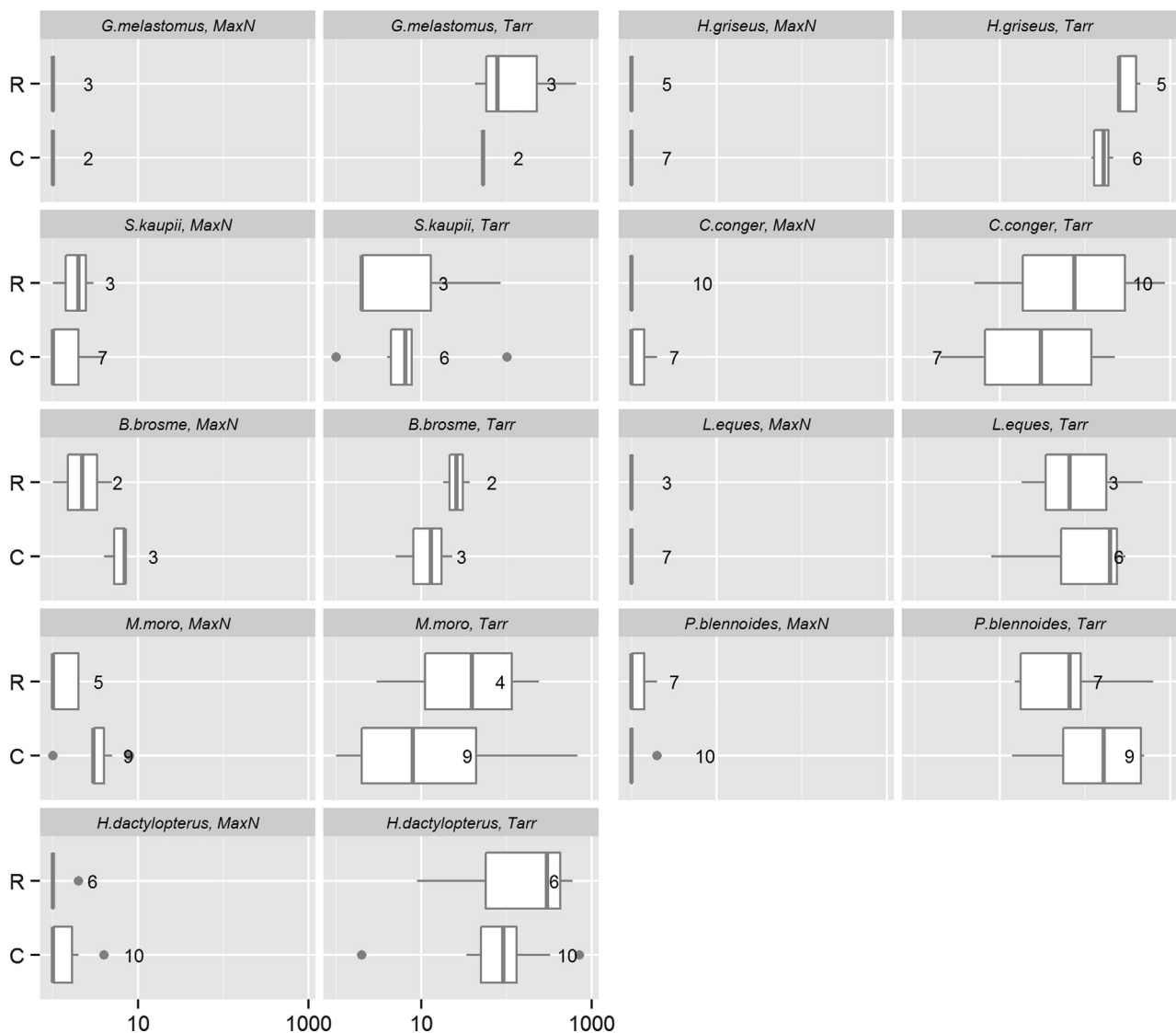
Fig. 7. Boxplots of the MaxN and T_{arr} of species found in both the coral (C) and reference (R) stations. The data is presented on a log scale. The sample size (n) is printed next to each group. Only those species are shown where the sample size is equal or larger than 2 for coral as well as reference area.

species) in the coral areas, specifically 1.6 times more *B. brosme* when sampling with gill nets and long-line. Further south at the Hatton Bank, Biber et al. (2014) recorded *B. brosme* exclusively at coral locations during a video-transect study. In Norway, long-line catches of *Sebastes spp.* have been reported as six times higher in coral areas and *M. molva* and *B. brosme* reported as two to three times higher in coral areas (Fosså et al., 2002; Roberts and Hirshfield, 2004). The major density indicators (T_{arr} and MaxN) consistently suggest higher numbers of *B. brosme* in the coral area but observations of other species were scarce. The long-line fishery uses both squid and mackerel bait with evidence suggesting that squid is a more effective bait for these species, particularly *M. molva* (Løkkeborg and Bjordal, 1992), which was seen only once in the lander data using a mackerel bait. In the current study ling species (*M. molva* in Northern Norway and the BMP and *M. dypterygia* in the case of the Bay of Biscay) were consistently only seen in the reference areas.

B. brosme are large fish that were seen to actively feed on the bait in groups of up to seven individuals. Activity of *B. brosme* at the bait may discourage bait visitation by other species. While generally feeding on decapod crustaceans (Husebø et al., 2002; Mortensen et al., 1995), *B. brosme* is known to feed on smaller fish

(Husebø et al., 2002; Mortensen et al., 1995) and was photographed preying on a *Lepidion sp.* in the Arc mounds during a CoralFISH cruise (Grehan, 2012). The presence of *B. brosme* at the bait may make observations of other species unreliable, particularly in larger numbers as was seen in the coral deployments. Competition at the bait within and between species is often observed and should be considered when assessing baited lander data (Farnsworth et al., 2007; Kaiser and Hiddink, 2007; Malcolm et al., 2007).

It has been suggested that *B. brosme* is associated with the coral by diet (Husebø et al., 2002; Mortensen et al., 1995). Husebø et al. (2002) found 10 times more squat lobsters in coral habitat than the surrounding seabed. Squat lobsters were observed in abundance at coral area deployments in the current study, particularly those with visible coral rubble. Fish have been found to feed on a similar diet in and out of the reef but adjust their diet based on what is abundant (Husebø et al., 2002). This would suggest that while the coral habitat is not essential for *B. brosme* it provides a greatly enriched food source, supporting a higher density.

Within this study *B. brosme* were seen easily navigating three dimensional structure of the lander ballast (Fig. 3a). They were regularly observed to use the anchor links which made up the BRIL

ballast as cover or pass through while seeking the bait. This familiarity with navigating complex structures may indicate a lifestyle associated with complex habitats. It is an example of the exploratory behaviour we believe is occurring outside the camera field of view and elevating the T_{arr} of the ALBEX lander data. Deep-sea fish species observed in other studies, adapted to the largely open seabed of the abyssal plane, appeared disorientated and confused by similar lander systems and are reluctant to pass through confined spaces (Jamieson et al., 2006, Pers. Ob.).

Henry and Roberts (2007) found that there is a characteristic "reef fauna" within the BMP. They suggest that CWC reefs function as shallow reefs do; with a specialised and probably obligate ichthyofauna. These reef species are often new discoveries or species that are considered rare as the reef has protected them from discovery (Ross and Quattrini, 2007). Ten new species of invertebrate macrofauna were found by Henry and Roberts (2007) when sampling the Belgica mounds, eight of which were found on the Galway mound. In the present study almost twice as many fish species were observed and estimated in the coral deployments than the reference deployments.

The rockling-like fishes: cf *G. argentatus* and cf *B. robustus*, were only seen in the coral areas of the BMP. They were seen to emerge from the coral lattice itself and potentially represent an example of essential use of the reef as a habitat. In the western Pacific, cold-water coral reefs have been classified as Essential Fish Habitats (EFH) as certain species have been shown to be strongly associated with the coral (Ross and Quattrini, 2007). In the NE Atlantic, Henry et al. (2013) also provide conclusive evidence on the role of coral habitat as spawning grounds for deep-water sharks such as *Galeus melastomus*. Söffker et al. (2011) reported two fish living among the coral in the BMP. One was described as strongly resembling *Gaidropsarus sp.* (rockling) while the second was identified as *Guttigadus latifrons*, a species closely resembling *B. robustus*. These observations suggest at least two species that are strongly coral associated and make direct use of the coral structure in the BMP. More accurate identification of these species is not possible from the images collected during this study but it is hoped that future work will reveal this highly cryptic element of the fish community that appears to be living within the CWC reefs. Ross and Quattrini (2007) during a study off the south-eastern United States, reported that several fish species spent long periods totally within the coral structure and were only detectable when flushed out through the use of rotenone (a broad-spectrum piscicide). In shallow-water tropical reefs a positive correlation between structural complexity and fish species richness is consistently found in small, strongly site-attached species (Roberts and Ormond, 1987), those species that may be overlooked by many survey methods. In tropical reefs, fish enter the coral structure for both crypsis and to hunt animals within the reef (Bshary et al., 2006). The small rockling-like species likely use the coral to avoid predation; they were among the smallest fish observed at the BMP and would have been vulnerable to predation by many of the other species observed such as *M. moro* and *L. eques* (Carrassón and Matallanas, 2002).

In the BMP *M. moro* and *S. kaupii* were the two species most commonly recorded in images. Both species reached their highest MaxN at the base of the Thérèse mound. This deployment marked an outlier within the *S. kaupii* observations which had tended to show a higher MaxN in the reference sites. All deployments in this region fall within these species common depth range; *S. kaupii*: 400–2200 (up to 4800) m, *M. moro*: 450–2500 m (Froese and Pauly, 2013; Whitehead et al., 1984) and were also most abundant in previous studies in the Porcupine Seabight at this depth (Priede et al. 1994). *S. kaupii* is known to be most abundant between 1000 and 1500 m depth (Bailey et al., 2005), potentially explaining its high occurrence at the base of Thérèse mound; the only deployment beyond 1000 m depth. The Thérèse mound base had the

highest fish abundance but was equal lowest in fish diversity; only 6 species were observed.

The BMP was the most complex of the regions studied and had the highest variation under environmental conditions and habitat types. It was also the most imbalanced of the regions in the number of coral and reference deployments, limiting confidence in any conclusions that can be drawn. Most studies (including this one) group coral as a single habitat (Söffker et al., 2011) but distinct habitats exist within the coral classification (Costello et al., 2005).

The SML coral province was heavily dominated by *C. conger*. This species is very common throughout the north Atlantic, including the Mediterranean and Black Sea (Correia et al., 2009). It was observed at the BMP and Bay of Biscay in small numbers; however in SML the species arrived first in most deployments and consumed most of the bait. Infrequent observations of *C. conger* at the BMP and Bay of Biscay were always on reference deployments indicating that a species' coral association may vary with location.

Interpreting bait visitation by *C. conger* is extremely difficult; the eels fed voraciously at the bait but would do so in rapid strikes (Fig. 3i). *C. conger* would remove large sections of bait and move out of view to consume them. This behaviour prevented accumulation of this species in front of the cameras and lead to a MaxN value rarely above one (although a higher MaxN is observed in the coral deployments; Maiorano et al., submitted this issue). When interpreting lander data, there are major differences between species in their tendency to remain in the vicinity of the bait; making comparisons between species difficult (Bailey et al., 2007). Differences in the size and scarring on individuals confirmed that there was a large number of *C. conger* in the area. T_{arr} was quicker in the coral areas indicating increased abundance of *C. conger* in the coral areas (Maiorano et al., submitted this issue). D'Onghia et al. (2010, 2012) also showed significant difference in abundance and sizes of *C. conger* between the coral and non-coral habitats of the SML coral province. High frequency of occurrence and abundance was also observed using the MEMO lander in the Bari Canyon CWC community (D'Onghia et al., 2014). These results would confirm a preferential distribution of *C. conger* in structurally complex habitats like those built by deep-sea corals. Its congener *C. oceanicus* is commonly observed within the CWC reef structure itself in the western Atlantic (Ross and Quattrini, 2007).

Faster arrival and higher peak numbers also indicate a greater abundance of *H. dactylopterus* in the coral habitat than in the reference area. This species was previously found to show coral association in the SML coral province (D'Onghia et al., 2010, 2012; Maiorano et al., 2013) as well as in the Bari Canyon CWC community (D'Onghia et al., 2014). Although this fish uses a wide range of habitats strictly associated with the bottom, it was also frequently observed in coral habitats (Bourcier and Zibrowius, 1973; Foubert et al., 2005; Ross and Quattrini, 2007). Moreover, *H. dactylopterus* showed similar attraction to the structure of the landers suggesting an association with complex structures (Fig. 3j) as was noted in *B. brosme*. Although *P. bogaraveo* has been often observed in the SML coral habitat, its abundance estimation could be largely biased due to the fast swimming of the different individuals (Maiorano et al., 2013). However, the occurrence of this species in the coral habitat detected in the present study confirms observations by longline surveys and towed cameras in the same region (D'Onghia et al., 2010, 2011, 2012) and by MEMO lander in the Bari Canyon CWC community (D'Onghia et al., 2014).

5. Limitations

A low sample number, spread between multiple factors, hindered the amount of analysis that was possible on this dataset and

prevented the exclusion of other factors such as time of year. The sampling method was also selective in the fish species that were detected and variation in behaviour at the bait was seen to influence the results. However data was collected on cryptic and under sampled species and a clear trend in the influence of CWC was detected. This study forms a specific part of the multi-method approach of the CoralFISH project and readers are encouraged to read the other studies within this special edition, particularly the review paper (Fosså et al., submitted this issue).

The present study was very course in its comparison of developed CWC habitat with open and predominantly sedimentary habitats, rather than other complex habitats such as the more common boulder fields (Auster, 2005). There is still some conflicting evidence as to whether reefs have a greater effect than other structures (Ross and Quattrini, 2007). The selected reference areas are representative of the areas surrounding the CWC reefs, which are often the only complex three dimensional structures in the area (Costello et al., 2005; D'Onghia et al., 2011; Tissot et al., 2006) and represent the likely habitat type following the loss of living coral (Althaus et al., 2009).

6. Conclusions

The combined dataset would strongly indicate an elevated density of fish in the coral areas relative to the reference areas in all regions. Differences were found between regions and species. In Atlantic regions of intermediate latitude (BMP and Bay of Biscay) fish diversity and density are higher in coral areas with some species making direct and potentially essential use of the coral. In Northern Norway, fish species diversity is roughly equal between the coral and reference areas but much higher densities are reached in the coral areas; likely through enriched feeding opportunities. In SML, a similar number of fish species were observed both at the coral and reference areas, although some species appear to be linked to the presence of corals, indicating a habitat preference in some deep-sea species.

Acknowledgements

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