Behaviour and patterns of habitat utilisation by deep-sea fish: analysis of observations recorded by the submersible Nautilus in "98" in the Bay of Biscay, NE Atlantic

By

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Abstract

Analysis of video recordings performed by the submersible “Nautile” in the Bay of Biscay, NE Atlantic indicated that demersal fish species are associated to different types of deep-sea habitats. Four different dive transects were analysed with respect to environmental characteristics. A total of 19 fish groups were ordinated by means of canonical correspondence analysis, and the investigation was performed at the individual fish level. Microhabitat fauna was dominated by a diversity of suspension feeders indicating different gradients of bottom hydrology, particularly vertical and horizontal current flow. Physical, geological and biological factors revealed different strategies of habitat selection in fish. The most represented species, the orange roughy (*Hoplostethus atlanticus*) showed a clear association with complex bottoms, including coral reefs. Others, such as *Coryphaenoides rupestris* and *Synaphobranchus kaupi*, showed higher flexibility of adjustment to changing environments. These traits can be utilised in the study of the environmental impact of deep-sea fishing. Based on the same dives, the locomotory behaviour of 13 fish species was studied with basis on a qualitative analysis of selected individuals. The main swimming modes used in shallow waters were also detected in the demersal environment. Clear differences in locomotory behaviour were found among fish species, reflecting both convergence and diversity of strategies of utilization of the demersal niche space.

Key words: Submersible observations, deep-sea fisheries, deep-sea microhabitats, biodiversity, habitat use, Locomotory modes.

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I would like to dedicate this work to my family, who kindly incentive me during my studies.

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1. Introduction

1.1. Deep-sea fisheries

Many coastal fisheries are in a state of depletion and require urgent attention and remedial action (Charles, 2001). Further, there are few areas within the shallow continental shelves left to be explored (Haedrich *et al*., 2001). The deep-sea is the largest habitat on earth and deep-demersal fish comprise about 6.4% of the total number of fish species known (Merrett & Haedrich, 1997). New fisheries targeting deep-water species have been established as a result of the over-exploited state of the traditional stocks (Gordon, 2001; Haedrich *et al*., 2001; Piñeiro *et al*., 2001). In the late 1970's the slope-dwelling fish orange roughy, *Hoplostethus atlanticus*, were found off New Zealand and considered a valuable resource. A specific deep-water fishery was developed and a "gold rush" started; by the 1980's the total production of this fishery exceeded 60000 tonnes (Merret & Haedrich, 1997; Clark *et al*., 2001) and this gave rise to similar initiatives elsewhere. Thus, several European countries carried out fishery surveys to explore the potential of deep-water fish. In his comprehensive review Gordon (2001) concluded that we are still lacking a great deal of research on deep-water fish and fisheries. Owing to the state of affairs the ICES Study group on the Biology and Assessment of Deep-sea Fisheries Resources, strongly advised a precautionary approach to the management of deep-water populations in the Northeast Atlantic (Anon., 1999).

Deep-water species are considered to be very sensitive to exploitation due essentially to, slow growth rate, high longevity and low fecundity (Clark *et al*., 1994; Smith *et al*., 1995; Lorance & Dupouy, 2001; Magnússon, 2001; Morales-Nin, 2001). Deep-water fisheries are generally started after an initial discovery of large concentrations of fish. High yields are achieved in the first few years, but then drop off abruptly (Haedrich *et al*., 2001). Some of these fisheries are not "new". For example, the Norwegian long-line fishery for ling *Molva molva* (Gordon, 2001b), and the Spanish deepwater long-line fisheries for forkbeard *Phycis blennoides* and common mora *Mora moro* have been long established (Piñeiro *et al*., 2001). The black scabbard fish *Aphanopus carbo* is the target of the oldest (documented) deep-sea fishery in the world, which takes place off the island of Madeira (Merret & Haedrich, 1997; Haedrich *et al*., 2001). For centuries this fishery, which only supplied the local markets, seemed to be sustainable. However, since the onset of export the fishery expanded and the landings have decreased considerably (Merrett & Haedrich, 1997).

1.2. Deep-sea Habitats

Compared to the continental shelves, slopes are usually more complex topographically, and have irregular bathymetry and outcrops. Strong internal waves and hydrological gradients shape these environments and make fishing more risky than in shallow regions (Merrett & Haedrich, 1997). Geological and physical studies of seamounts have suggested the existence of very distinct deep-sea habitats (Genin *et al.*, 1986). Bottom structure and food availability are important factors determining niche space and habitat selection by fish, as well as their association into different communities (Gaertner *et al.*, 1999; Demestre *et al.*, 2000). In addition, temporal and spatial variability might themselves be important characteristics of niche space, even in seemingly constant deep-water environments (Grassle & Grassle, 1992).

Until now there has been little documentation of microhabitat utilization by deep-sea fishes with regard to the relative contributions of the physical, biological and geological components of the habitat. Recent studies of habitat associations have showed the usefulness of a multidimensional approach for fisheries management and community ecology (Gaertner *et al.*, 1999; Demestre *et al.*, 2000; Uiblein *et al.*, 2001; Else *et al.*, 2002). Photographic (*e.g.* Grassle *et al.*, 1975; Cohen & Pawson, 1977) and videotape recordings from submersibles have been successfully used to assess these habitat associations (*e.g.* Felley & Vecchione, 1995; Yoklavich *et al.*, 2000; Else *et al.*, 2002; Lorance *et al.*, 2002; Uiblein *et al.*, 2002; Uiblein *et al in press*). Uiblein *et al* (2001, *in press*) and Lorance *et al* (2002) presented preliminary indicators of species-specific differences in locomotion and habitat selection. Deep-sea fishes responded behaviourally to the diverse environmental conditions. These are important aspects to take into consideration with regard to deep-sea fisheries. The techniques described above have already allowed an *in situ* monitoring of the availability and vulnerability of target species, *e.g.* orange roughy.

1.3. The Bay of Biscay

The Bay of Biscay, NE Atlantic (Fig. 1) is an essential component for maritime Europe owing to the multiplicity of social and economic uses (Elbée & Prouzet, 2001). The main hydrological and biological characteristics of the water masses of the Bay of Biscay were well documented by Boucher (1985). North Atlantic Central Water characterizes depths between 100 and 800 m depth. Mediterranean water extends northward from Gibraltar at depths between 800 and 1500 m. The North East Atlantic Deep water that originates in the Norwegian Sea is found from 1500 to 3000 m. The pelagic communities of the area are estimated to contain about 300 species. An excess of primary production of 0.5% in relation to zooplankton consumption indicates that the more abyssal ecosystems can be supplied through both phytoplankton decay and zooplankton feces. The semi-diurnal tidal currents are strong (Vangrieshem, 1985) and the meio and macro-fauna are diverse (Dinet *et al.*, 1985).

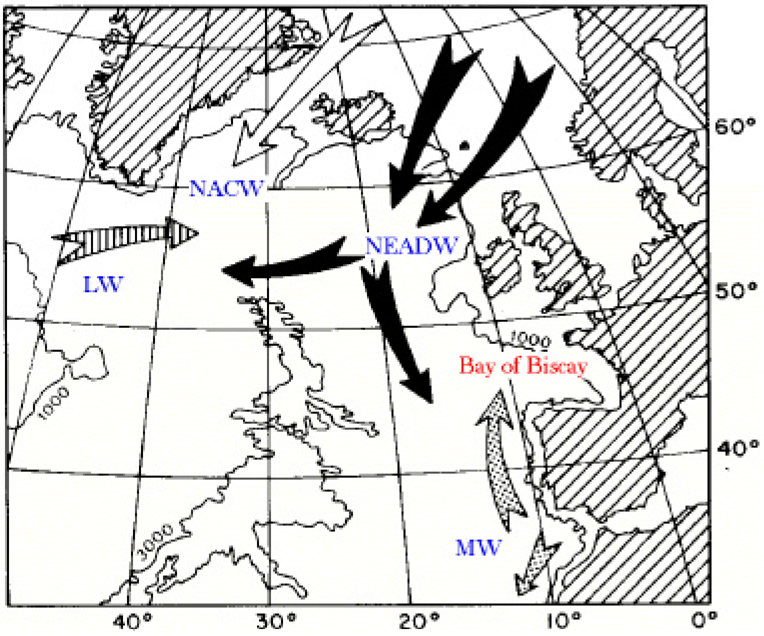


Figure 1. The North East Atlantic showing the main water masses of the Bay of Biscay. NACW, North Atlantic Central Water; LW, Labrador Water; NEADW, North East Atlantic Deep Water; MW, Mediterranean Water (adapted from Boucher, 1985).

1.4. Deep-sea fish locomotion behaviour

Some fishes are better adapted to carry out some particular modes of swimming than others (Videler, 1993). Lindsey (1978) defined 5 main modes of swimming in fish: *anguilliform, subcarangiform, carangiform, thunniform* and *ostraciiform*. Other sub-types were also described with regard to the utilisation of particular fins and amplitude of movements: *rajiform*, *diodontiform*, *labriform*, *amiiform* and *balistiform*. The classification of Lindsey (1978) is thought to be appropriate for shallow water fish and has helped us to understand their ecology. In contrast, very little information exists regarding locomotion in the deep sea. Although fin and body morphology are obviously adapted to the swimming mode (and vice-versa), we do not know how locomotory behaviour is related to habitat selection in deep-water fish.

1.5. Objectives of this study

The aim of this study is to reassess, characterize and explore the relationships between, benthos assemblages, environmental variables and the occurrence and behaviour of deep-water fish. The physical, geological and biological variables considered were measured during four dives performed by the submersible “Nautile” off the Bay of Biscay.

In the first part of the work quantitative multivariate analyses are performed to explore and test the associations between biotic and abiotic variables. Unlike other studies performed before the present observations were carried out at the individual (fish) level. It is shown that different fish are typically associated with specific environments. In the second part a qualitative study of locomotory behaviour is made, with basis on the classification developed for shallow water fish. This analysis has not been performed before for deep-sea fish and may help to understand what shapes their habitat selection and niche space.

2. Material and Methods

2.1. Dives, data collection and environments

The four dives analysed in this study were performed in 1998 by the submersible “Nautile” (Fig. 2) in the Bay of Biscay (Fig. 3). This vessel is operated by the IFREMER, which was one of the participants in the project OBERVHAL98. Table 1 summarizes the diving conditions. Preliminary screening of the cruise information showed that the selected dives differed in several factors such as depth range covered, temperature, current, bottom type and fish abundance (Latrouite et al., 1999; Lorance et al., 2002; Uiblein et al., 2002).

Fig. 2 - The Nautile is a manned submarine designed for observing and operating at depths reaching 6000 metres. The submersible capable of exploring 97% of the world's ocean floors (IFREMER).

The dives performed by the Nautilus served a number of different scientific and technical purposes, and were not specifically designed to produce information for the present study. The main objective of OBERVHAL98 was the assessment of demersal marine resources and deployment of experiments *in situ* for deep-sea fishing concerns.

The position of the submersible was established every 30 seconds by the support vessel “Nadir”, and charting was made along a metric X/Y grid in UTM projection (UTM= Universal Transverse Mercator). Although it was difficult to accurately define the position of the submersible this uncertainty did not affect the estimation of the crossed distance (Latrouite *et al.*, 1999). Underwater videos were recorded as the submersible navigated 1.5 m above the sea bottom at variable speed, but normally within the range 0.5-0.7 knots. Short stops along the diving transects were sometimes performed to carry out behavioural experiments or for technical reasons. The normal visual field was estimated by the pilot of the submersible to be about 5 m width and 10-15 m long (ahead), depending on the turbidity of the water, plankton density and seabed

topography (Lorance *et al*., 2000). During each dive two types of video cameras were operated: a fixed camera at the nose of the submersible and a mobile camera (remote).

Navigation and temperature data were previously processed by Lecornu, (2000) using ADELIE software. There were no specific logging devices for current velocity, but this information could be assessed from the recorded comments of the pilot and accompanying scientist (Table 1). Further characterization of the cruise can be found in the original diving report (Latrouite *et al*., 1999).

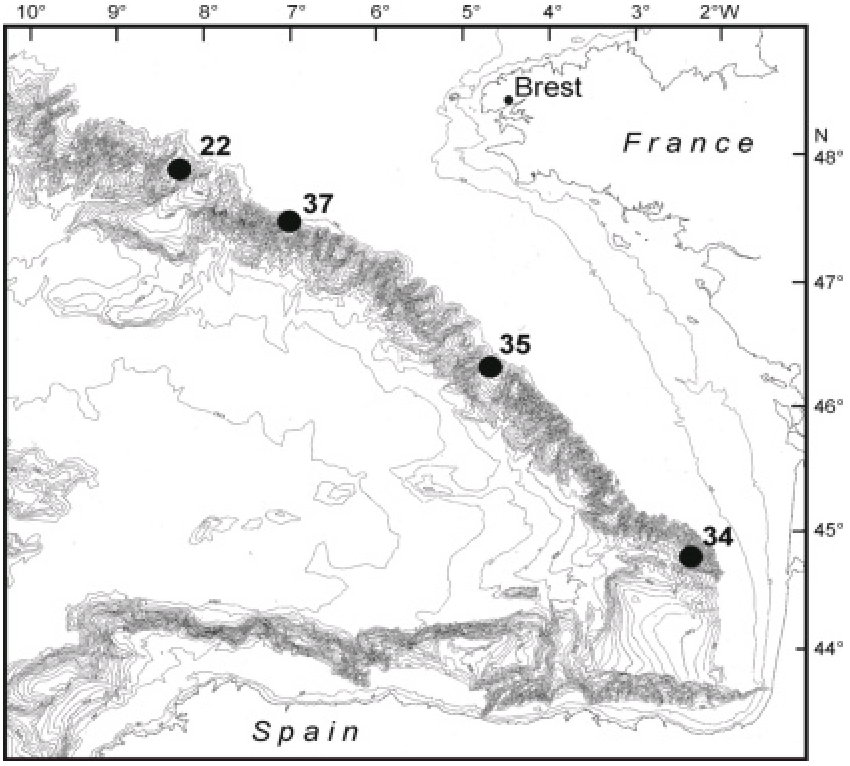


Fig 3. Map showing the four dive stations in the Bay of Biscay, NE Atlantic (Dives 22, 34, 35 and 37). Transects were performed perpendicular to the continental slope (Annex 2).

2.2. Video and data analysis

2.2.1. Video assessment and sampling units

The videotapes were analysed using a Panasonic NV-HS960 Super VHS video player and a large Trinitron screen. Some pictures and video sequences were also processed by means of computer video. Digital images were viewed using CorelDraw (version 9). When available 35 mm slides were used for illustrations as they provided higher picture definition.

In transect surveys a given stretch of seabed is normally considered to be the sampling unit (Malatesta *et al.*, 1992; Auster *et al.*, 1995). However, the sampling units in the present study were individual fish. The reason for this is that it was difficult to define crossed distances when the submersible was moving at variable speed. Further, the submersible performed stops and turns (or the mobile camera was turned sideways) along the transects. Characterisation of the fish and habitat started immediately after an individual fish appeared in a video sequence. If the submersible stopped or moved up away from the bottom this information was discarded from the habitat analysis. Traits such as size, shape and colour were important in the identification of both fish and bottom epifauna. The utilisation of colour was, however, particularly difficult owing to the different light conditions. In the case of fishes, their mimetic capacity was taken into consideration. However, many sedentary invertebrates live beneath the substrate and could not be easily detected or identified. In addition, organisms had to be large enough to be recognizable. Similar identification problems arouse when the water was turbid. Individual organisms or conspecific groups were identified to the lowest taxonomic level possible. In case of doubt photographs and videotape sequences were sent to experts for identification or crosschecking. Further, underwater videos and photographs taken during previous projects in the same area were used for training and comparison.

2.2.2. Microhabitats characterization

The microhabitat of each fish species was characterised according to different physical, geologic and biological factors (*e.g.* Greene *et al.*, 1999). Characteristics such as depth, temperature, slope inclination, bottom type and complexity, current velocity, temperature were coded as quantitative variables. The occurrence of conspicuous communities was coded qualitatively for presence or absence. In the case of the macro-benthos a subjective index of abundance was utilised since counting would be biased by the different diving conditions (visibility and angle of view) (Table 2). When there were no conspicuous epifauna associated with the fish the habitat was registered as “desert”. Utilisation of non-calibrated video data required certain assumptions such as that the video image was plane and that the camera angle remained constant. Therefore, cover analysis was merely semi-quantitative. Possible errors associated with these simplifying assumptions are likely to be of minor importance when the wide range of habitats covered in these dives is taken into account.

Table 2 - Categories used to define the microhabitats surrounding individual fish.

Depth	Depth in m
Temperature	º Celsius
Current	1. Absent or very low; 2. Low/moderate; 3. High/very high
Taxon	Species taxon (macronecton and benthos)
Slope inclination	1. Flat (0-5°); 2. Sloping (5-30°); 3. Steeply sloping (30-45°); 4. Steep (>45°)
Substracte Complexity	1. Flat; 2. Structured; 3. Complex
Ripple marks	0. None; 1. Some; 2. Very
Packing	1. well packed; 2. poorly packed
Bottom Structure	Percentage volume occupied by clast, rock or hard bottom: 1. (0-5%); 2. (5-25%); 3. (25-50%); 4. >50%
Benthos	Cover: 1. <5%; 2. 5-20%; 3. 20-70%; 4. >70%
Bioturbation	1. None; 2. Present
Water Visibility	G: Good; B: Bad; M: Medium

A large number of fish and epifaunal species were detected, but some of them were sparsely represented. For practical purposes the fish and benthic fauna were aggregated into major groups. The underlying principle was to reduce the number of observations to a treatable size while keeping taxonomic and ecological (functional) coherency. Only fish found on good/medium visibility conditions were selected for the microhabitat analysis.

For simplification in data analysis, species and taxa names were coded (Table 3)

Table 3 – Codes used for main demersal species (fishes and benthos).

Taxa	**Code**	**Taxa**	**Code**
Fishes		***Fishes (cont.)***	
Alephocephalidae	Ale	*Trachyscorpia cristulata*	Tra
Anguiliformes	Ang	Mesopelagic fishes	M
Beryx decadactylus	Ber		
Chimaerids	Chi	***Benthos***	
Coryphaenoides rupestris	Cor	Actinians	Act
Galeus melastomus	Gal	Asteroidea	Ast
Helicolenus dactylopterus	Hel	Pennatularians	Pen
Hoplostethus atlanticus	Hoa	Crinoids	Cri
Lepidion eques	Lep	Echinoids	Ech
Macrouridae (others)	Mac	Bryozoans	Bry
Mora moro	Mm	Hydroids	Hyd
Molva molva	Mol	Sponges	Spo
Moridae (others)	Mor	Scleractinians	Scl
Neocyttus helgae	Neo	Gorgonians	Gor
Notacanthus sp.	Not	Antipatharians	Ant
Sharks (others)	Sha	Sea Cucumbers	Sea
Synaphobranchus kaupi	Syn	**Desert**	Des

2.2.3. Grouping of variables

The complex set of observations collected in this study was organised into four major blocks: the major matrix of presence/absence of individual fish and three linked matrices describing accompanying epifauna, physical characteristics and locomotory behaviour for each particular fish. Quantitative, semi-quantitative and subjective methods were used to analyse these data.

2.2.4. Co-occurrence of fish and invertebrate fauna

A simple way to investigate the co-occurrence of fish and invertebrate fauna was to calculate and display the percentage of occurrence. Each individual fish was considered to be a sample and the index was calculated independently for each fish species as: fO % (frequency of occurrence of taxa f) = (Total number of fishes in co-ocurrence with benthonic taxa f / Total number of fishes). Usually this index does not reach 100% because some fishes are found on “desertic” bottoms and others are in association with several taxa at the same time, despite that the results were standardized: $100 \times fa / \Sigma f$, where f1, f2, f3 are the frequency of occurrence of taxa 1, 2, 3, etc.

2.2.5. Depth and temperature relationships

Boxplots were used to analyse the distribution of fish species in relation to depth and temperature. Boxplots are designed to display several descriptive statistics, including the quartiles of the distribution as well as the minimum and the maximum on a single chart. These distributions were further investigated using an analysis of variance (Anova: significance level set at alpha=0.05). Correlation between pairs of variables (*e.g.* depth and temperature) were tested using two different functions: Pearson’s correlation coefficient and (the non-parametric) Spearman’s Rank correlation coefficient (Zar, 1996).

2.2.6. Multivariate analysis

The analytical techniques described above allow a pair wise study of fish occurrence and epifaunal or physical characteristics associated with each species. In order to analyse the three matrices simultaneously, for all fish species, a multivariate technique was called upon. The main matrix of data consisted of binary data (fish presence or absence), and was extremely sparse in the statistical sense. Thus, each sample consisted of one presence (a single “1” value) and many absences (zeroes for all other fish species). The rest of the environmental variables were treated as quantitative (continuous) variables (see Table 2). The most appropriate tools to deal with this kind of multivariate data are those from the Correspondence Analysis (CA) family (Legendre & Legendre, 1998), and the CANOCO 4 software (ter Braak & Smilauer 1998) was utilised in the present investigation. Canonical correspondence analysis (CCA) and related methodology has found widespread use in aquatic sciences (ter Braak & Verdonschot, 1995). CCA is a multivariate method that helps to elucidate the relationships between biological assemblages and their environment, as well as to select environmental variables that affect community composition (ter Braak, 1986). It should be borne in mind, however, that the data contain no information about why a particular species is occurring more frequently in one habitat than in others (i.e. relationships disclosed are “correlational” rather than causative).

The first multivariate investigations conducted were independent dive analyses. The whole sets of biotic, geologic and physical data were examined independently for each of the four transects. Between 125-500 observations were available for the different dives. Secondly, a global dive analysis was performed, and data from all the dives were pooled and analysed together in one single multivariate model. The graphic software CANODRAW (4.1) that accompanies CANOCO sets, however, limitations to how many observations and variables can be handled and plotted in a single chart. Thus, the results from the global analysis are displayed for a sub-sample consisting of 500 observations. This sub-sample was taken randomly, with equal contribution from each transect (stratified sub-sampling). A third global analysis was performed to investigate the associations between benthos community composition and habitat (physical) characteristics, also by means of CCA. This analysis, which excluded the fish species matrix, was just performed for auxiliary purposes since the sampling design was not suitable to perform a proper community analysis of bottom epifauna. Followed by other two matrixes containing the values of all variables (quantitative and semi-quantitative, see Table 2) for that particular sample (fish individual).

The method was chosen based on the range of environmental variation in the sample set (ter Braak & Prentice, 1988). When length gradients are short (<3 SD) it was thought that most species would be better interpreted by the biplot rule and it implied species-sample plot of CCA (ter Braak & Smilauer, 1998).

In CCAs the eigenvalues measure the separation (values between 0 and 1) in the species data explained by the applied environmental variables of an ordination axis (ter Braak & Smilauer, 1998).

In all multivariate analyses the standard options of CCA in CANOCO were chosen: bi-plot scaling focused on inter-species distances. Furthermore, the effect of rare species was “Down-weighed” following a recommended option of CANOCO (ter Braak & Smilauer, 1998). Only the most meaningful axes were considered in the discussion of distribution patterns. The environmental variables were chosen by means of automatic forward selection using Monte-Carlo permutation tests (F-test: significance level set at alpha=0.05). A Monte-Carlo permutation test is a test of statistical significance obtained by repeatedly shuffling (permuting) the samples (ter Braak & Smilauer, 1998). This method separates the effects of variables of interest from those of co variables (option in CANOCO). For each test 1000 permutations were performed.

On the diagrams of CCA arrows represent the environmental variables. For an environmental variable the arrow points in the direction of maximum change of that variable (ter Braak, 1995). The optimum of the fish species along these arrows is projected in relation to the arrows.

2.2.7. Locomotory Behaviour

The study of the locomotory behaviour of fishes was based on an analysis of selected individuals. Only the best pictures, in terms of quality and field visibility were selected. It was equally important that the individuals studied did not show signs of unduly stress caused by the light projectors or submersible noise.

Each individual was observed while swimming and its behaviour registered. Films were observed at low frame rates giving a notion of the ability of fish swimming (*e.g.* Bone, 1971; Videler, 1993). A scale of locomotory categories was developed for the fish species. This scale was adapted from a previous qualitative study (Lindsey 1978) of fish locomotion for shallow waters. Other variables registered included distance off the bottom, swimming speed (measured qualitatively), fish orientation and reaction to disturbance (noise and light) (Table 4). For an easier comparison of the observations a final diagram was drawn illustrating the different modes of fish locomotion. This information was completed with a scheme containing concise information about each fish species. The fish drawings were hand-copied from identification books (*e.g.* Whitehead *et al*., 1984) and hence scanned and modified using Corel PHOTO-PAINT.

Table 4. Categories used to classify the locomotory behaviour of the fish.

Locomotion mode Lindsey (1978)	1. Subcarangiform; 2. Anguilliform; 3. Carangiform; 4. Diodontiform; 5. Balistiform; 6.Rajiform; 7. Ostraciform
Position in water column	1. attached to bottom; 2. slightly above bottom; 3. well above bottom
Activity level	1. inactive; 2. active; 3. disturbed arrival (burst swimming)
Flight response	1. no; 2. illumination by focus of front lights
Locomotion position	1. Horizontal; 2. Oblique; 3. Vertical
Speed swimming	1. slow; 2. medium; 3.fast

3. Results

3.1. General characterization of dives

3.1.1. Species richness, habitat types and sampling

The analyses of the video images indicated that the deep-sea habitats were highly diverse. Invertebrates were common and fish species were found associated with different types of habitat. Selected photographs of representative fish and microhabitats are shown in Figures 4 and 5. The number of individual fish sampled for the microhabitat analysis, global dive analysis and independent dive analysis, is shown by species in Figures 6 and 7. As a result of the different fish composition and density (Table 1), sample composition was unbalanced among the dives. The 26 fish taxa observed were aggregated into a less sparse matrix consisting of 19 fish groups – This included the following species or generic groups: Alephocephalidae, Anguiliformes, *Beryx decadactylus*, Chimaerids, *Coryphaenoides rupestris*, *Galeus melastomus*, *Helicolenus dactylopterus*, *Hoplostethus atlanticus*, *Lepidion eques*, Macrouridae (others), *Mora moro*, *Molva molva*, Moridae (others), *Neocyttus helgae*, *Notacanthus* sp., Sharks (others), *Synaphobranchus kaupi*, *Trachyscorpia cristulata* and Mesopelagic fishes. The bentho-fauna were aggregated into 12 major units (micro-habitat fauna) - Actinians, Asteroidea, Pennatularians, Crinoids, Echinoids, Bryozoans, Hydroids, Sponges, Scleractinians, Gorgonians, Antipatharians and Sea Cucumbers. Many other nektonic species (*e.g.* cephalopods and crustaceans) were observed on the tapes, but not in such density that could allow an appropriate habitat study.

The fish groups *Coryphaenoides rupestris*, *Lepidion eques* and Macrouridae (other species) dominated the samples in dive 22. *Synaphobranchus kaupi* were the dominant fish in dive 34. Chimaerids, *Helicolenus dactylopterus* and *Molva molva* were well represented in dive 37, and *Hoplostethus atlanticus* was the most abundant species in dive 35 (Fig.7).

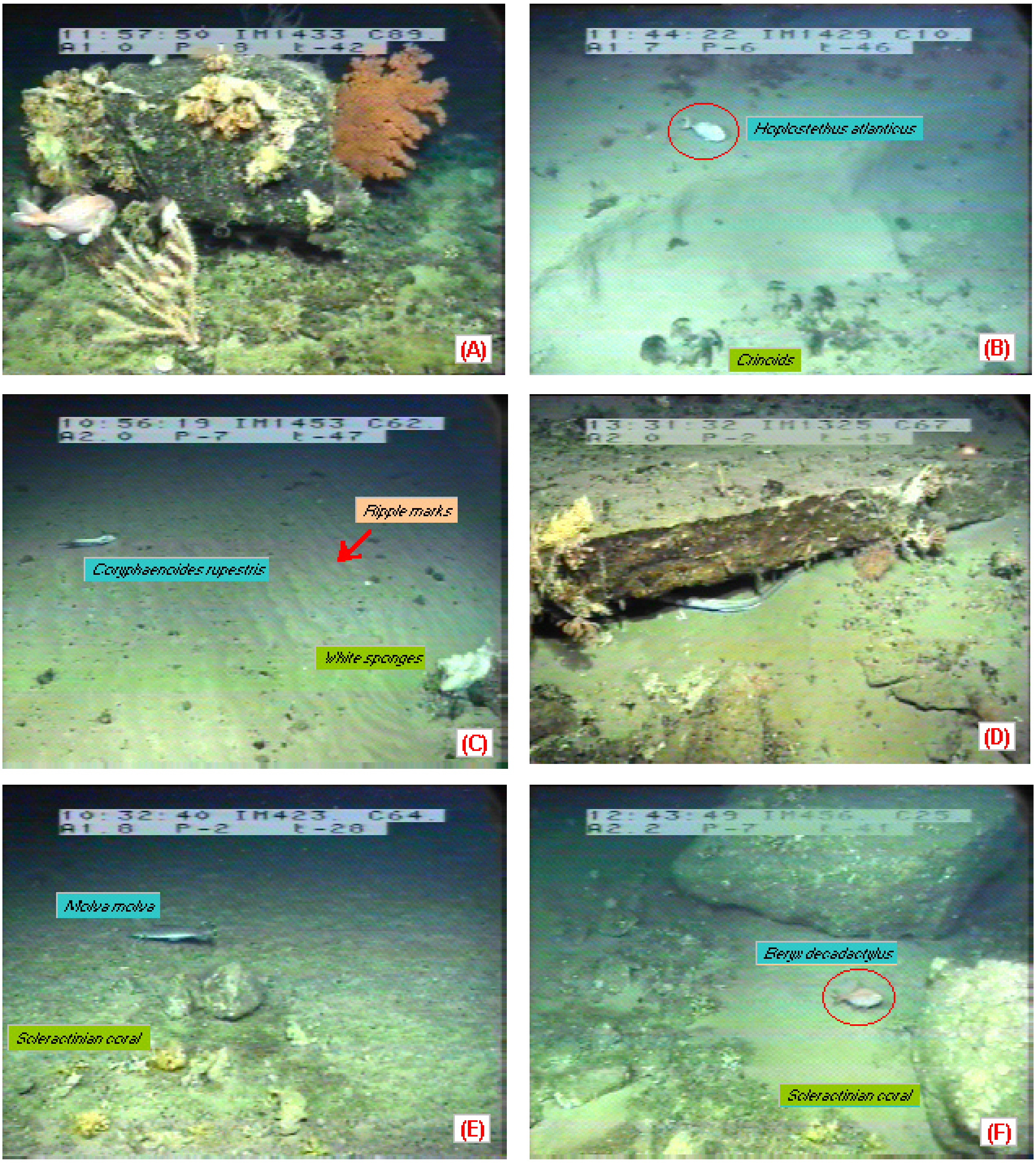


Fig 4 – (A) *Hoplostethus atlanticus* and diverse coral fauna (dive 35); (B) *Hoplostethus atlanticus* in crinoids' ground (dive 35); (C) *Coryphaenoides rupestris* and white sponges, with bottom showing the presence of several ripple marks (dive 35); (D) *Synaphobranchus kaupi*, rocky reef with gorgonians and antipatharians in background (dive 35); (E) *Molva molva* and scleractinian coral (dive 37); (F) *Beryx decadactylus* and scleractinian coral, in complex rocky reef (dive 37).

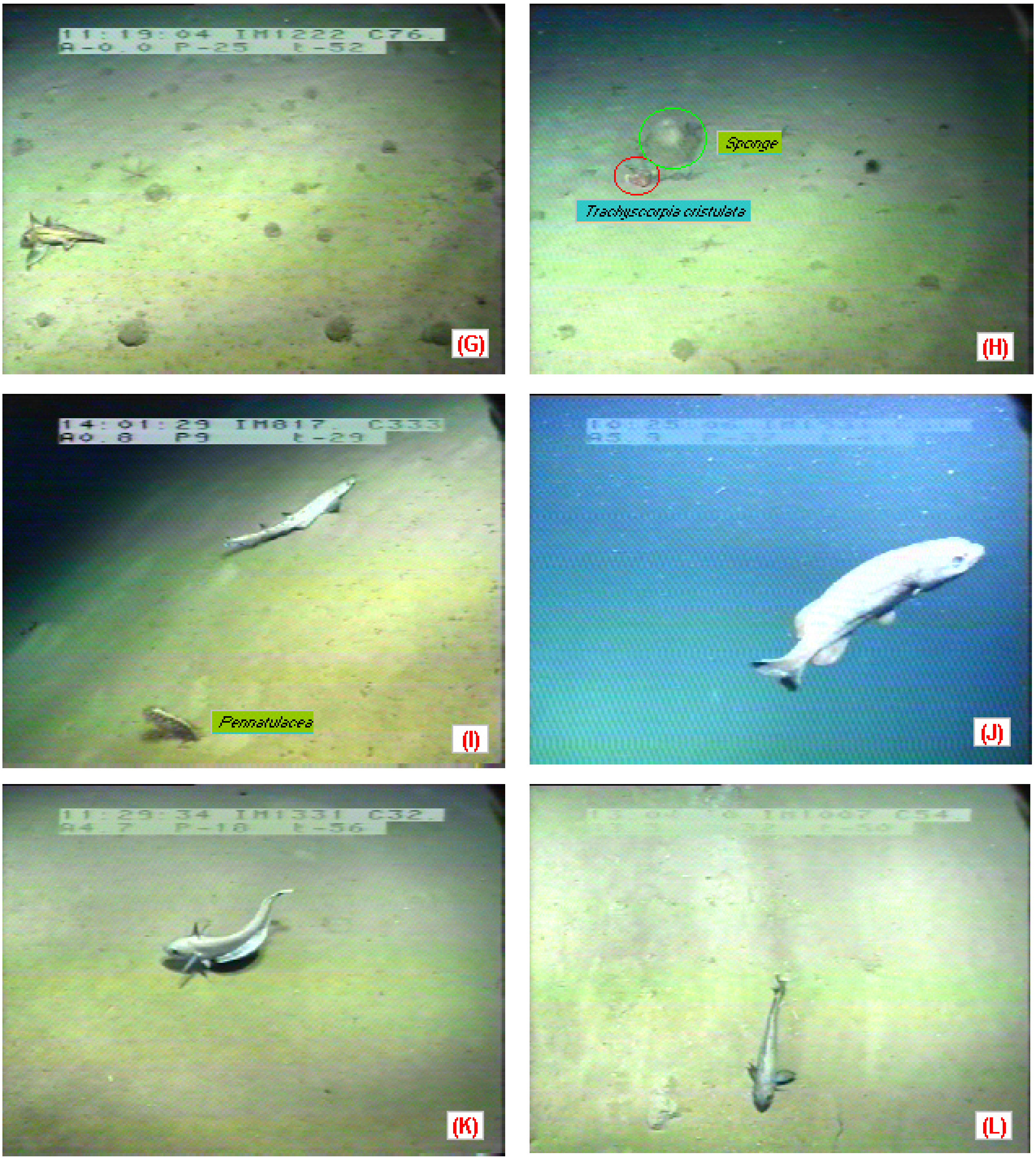


Fig 5 – (G) Chimaera and sea star (dive 22); (H) *Trachyscorpia cristulata* and “volcanic like” sponge (dive 22); (I) *Galeus melastomus* and pennatularian (dive 34); (J) Alepocephalidae, swimming in the water column (dive 34); (K) *Coryphaenoides rupestris* on desert bottom (dive 34); (dive 34); (L) *Mora moro* on desert bottom (dive 34).

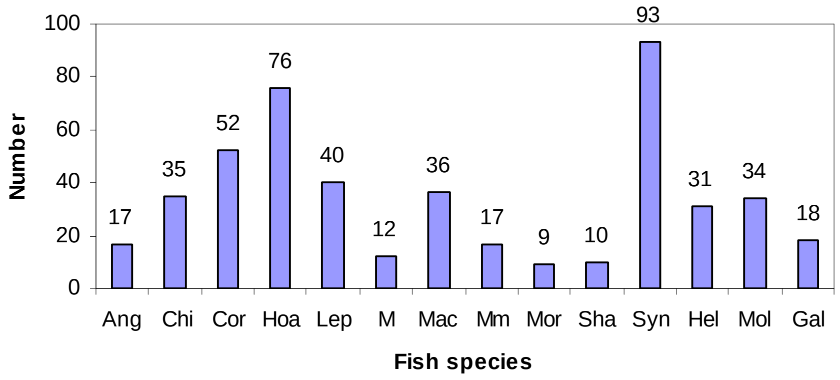


Fig. 6 – Number of fish sub-sampled for the global (pooled dive) analysis (n= 480 individuals), discriminated by species / taxon. The species names are coded for simplification, and their full names are found in Table 3 ’methods’.

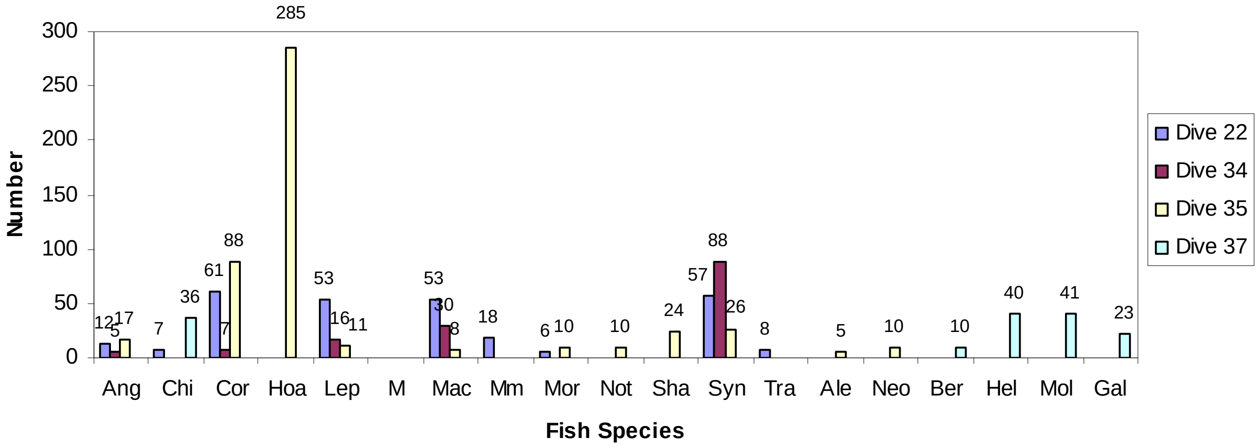
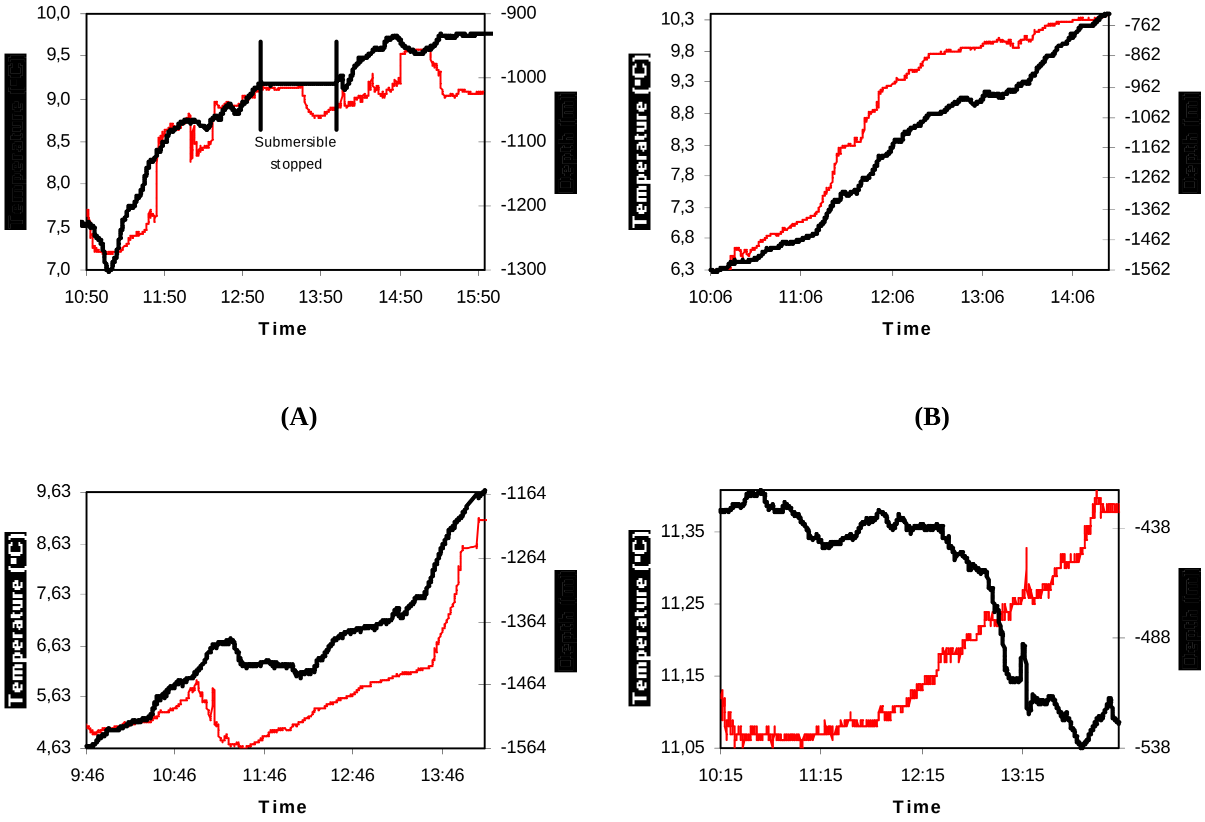


Fig. 7 – Number of fish sampled in individual transects for the independent microhabitat analysis (dive 22, n=268; dive 34=124; dive 35 n=475; dive 37 n=150).

3.1.2. Diving profiles, depth and temperature

The study area was heterogeneous with respect to bathymetric relief. Dives 22, 34 and 35 (Fig. 8A, 8B & 8C, respectively) were the deepest transects, and showed wide ranges of temperature (4-5ºC) and relatively low temperatures. In these transects a positive correlation (Table 20 in annex) between the negative of depth and temperature was observed, i.e. deeper areas were cooler. The diving transect performed in shallower water masses (dive 37) (Fig. 8D) presented the highest temperatures and had only a minor variation (< 1ºC). Temperature inversion with depth was observed.

The bottom substrate varied in composition from soft sediment to hard sediment. The distribution of major substrate types was often patchy. Dives 22 and 34 were characterised by the frequent soft sediments. Dives 35 and 37 were classified as more complex habitats, with hard and well-structured bottoms. Water current varied from relatively slow in dives 22, 34 and 37, to high and variable in dive 35 (Table 1).



(A) (B)

(C) (D)

Figure 8 – Depth and temperature profiles for the four transects, depth (black line) and temperature (red line): (A) Dive 22; (B) Dive 34; (C) Dive 35; (D) Dive 37.

3.1.3. Fish distribution according to depth and temperature

Bathymetric and thermal distribution of the fish taxa are presented in Fig. 9 and Fig. 10, respectively. The boxplots, display several of the important statistics. Significant differences were found among taxa regarding bathymetric and thermal distribution (Anova; in all cases P<0.05). Taxonomic groups Alephocephalidae, *Hoplostethus atlanticus*, *Neocyttus helgae*, *Notacanthus* sp. and Sharks were commonly found in deeper waters. Anguiliformes, Chimaerids, *Coryphaenoides rupestris*, *Lepidion eques*, Mesopelagic fishes, Macrouridae (others), *Mora moro*, Moridae, *Synaphobranchus kaupi* and *Trachyscorpia cristulata* were encountered in intermediate depths whilst *Beryx decadactylus*, *Galeus melastomus*, *Helicolenus dactylopterus* and *Molva molva* were more associated with shallower waters. An identical pattern was found with regard to temperature range. Anguiliformes, *Coryphaenoides rupestris* and Macrouridae were observed at most temperatures.

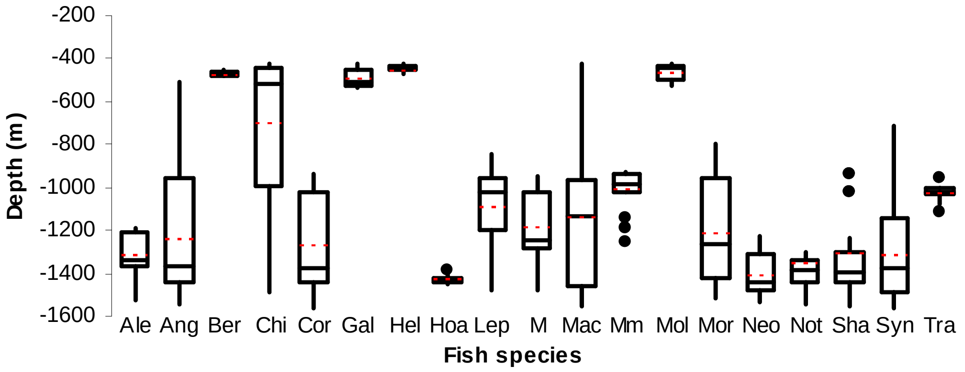


Figure 9 – Bathymetric distribution of the fish taxa selected. The median is represented by the middle horizontal line (not dotted) and the average by dotted red line. The species names are coded for simplification, and their full names are found in Table 3 'methods'.

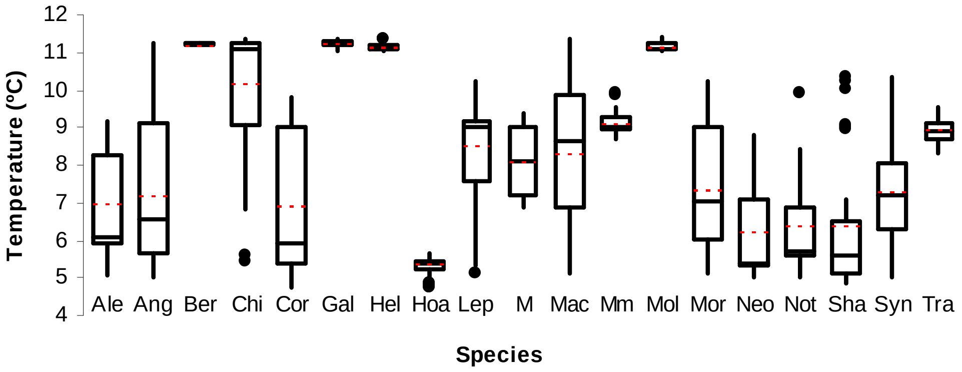


Figure 10 – Distribution of the fish taxa selected, according to the temperature.

3.2. Habitat use

3.2.1. Independent dive analysis

3.2.1.1. Canonical Correspondence Analysis (CCA), Dive 22

A considerable association of environmental parameters (in general) with the distribution of the fish was observed in dive 22. A high percentage of the variation in the species-environment relationship was explained (cumulative percentages of 38.3 and 60% for axes 1 and 2, respectively) (Table 12 in annex). The first canonical axis was statistically significant as well as the relation between species and the environmental variables (P-value=0.005).

Table 5, shows the conditional effects of the environmental variables in order of their inclusion in the model. The additional variance explained by each variable at the time it was included (lambda-A) is also shown. Results of the MonteCarlo tests show the significance of every variable at that time (P-value) together with its test statistics (F-value). The variables Temperature, Sponges, Pennatularians, Echinoids, Asteroidea and Depth contributed significantly (at the 5% significance level) to the model.

Fig. 11 illustrates the canonical correspondence analysis ordination of dive 22, which provided the following interpretation. Axis 1 divided two main fish groups, the ones positively associated with high temperatures and shallower areas (Moridae, *Mora moro*, *Trachyscorpia cristulata* and *Coryphaenoides rupestris*) from others more typically associated to deeper areas and lower temperatures (*Synaphobranchus kaupi*, Chimaerids and Macrouridae). Following gradient of axis 2, the latest group considered, in addition with *Coryphaenoides rupestris* (species presenting the highest weighed average with respect to sponges) showed strong association with respect to Asteroidea. In contrast, the group composed by Moridae, *Mora moro*, *Trachyscorpia cristulata*, Anguilliformes and *Lepidion eques* was more frequently associated with Actinians. In addition, *Synaphobranchus kaupi* presented the strongest gradient with respect to pennatularians and echinoids.

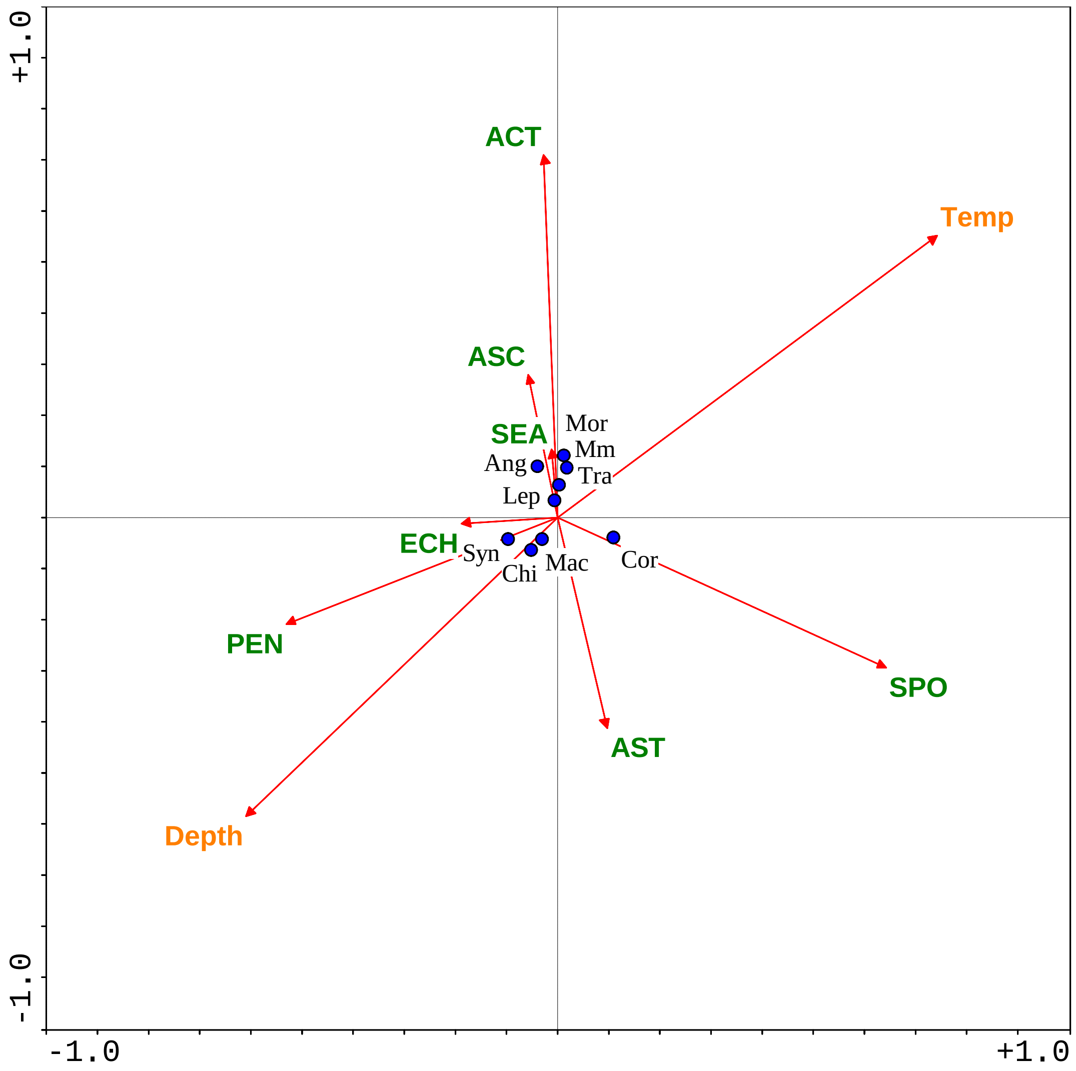


Figure 11. Canonical correspondence analysis (CCA) ordination diagram of dive 22 showing fish species (blue circles) and environment variables (arrows); first axis is horizontal, second axis vertical. The fish species are: Mor=Moridae, Mm=*Mora moro*, Tra=*Trachyscorpia cristulata*, Cor=*Coryphaenoides rupestris*, Ang=Anguilliformes, Lep=*Lepidion eques*, Syn=*Synaphobranchus kaupi*, Chi=Chimaerids, Mac=Macrouridae. The environmental variables are: ACT=Actinians, ASC=Ascidea, SEA=Sea Cucumber, Temp=Temperature, ECH=Echinoids, PEN=Pennatularians, Depth=Depth, AST=Asteroidea, SPO=Sponges.

Table 5. Monte Carlo test of significance of the environmental variables in dive 22. The environmental variables are: ACT=Actinians, ASC=Ascidea, SEA=Sea Cucumber, Temp=Temperature, ECH=Echinoids, PEN=Pennatularians, Depth=Depth, AST=Asteroidea, SPO=Sponges.

Variable	Var.N	LambdaA	P-value	F-value
Temp	10	0.23	0.005	7.10
SPO	9	0.13	0.005	3.82
ECH	5	0.10	0.020	3.13
PEN	7	0.10	0.010	3.02
ASC	3	0.08	0.155	2.41
AST	4	0.07	0.020	2.36
Depth	1	0.07	0.050	2.08
ACT	2	0.03	0.420	1.05
SEA	8	0.03	0.400	0.83

3.2.1.2. Canonical Correspondence Analysis, CCA Dive 34

All fit statistics indicated a strong association of environmental parameters (in general) with the distribution of the fish species. A high percentage of the variation in the species-environment relationship was also explained (cumulative percentages of 47.1 and 76% for axes 1 and 2, respectively) (Table 13 in annex). Both the trace of the CCA and the first canonical axis were statistically significant, as well as the relation between species and the environmental variables (P-value=0.015). Table 7 shows conditional effects, and the environmental variables in order of their inclusion in the model. Variables Temperature and Substrate contributed significantly (at the 5% significance level) to the model.

As reflected in Fig 12, Axis 2 showed a strong separation of *Coryphaenoides rupestris* from the other species analysed. This species was strongly associated with respect to Sponges. *Synaphobranchus kaupi* was more associated to the environmental variables Desert and Ripple marks. Fish groups Anguilliformes and *Lepidion eques* were more associated to higher Slopes, occurrence of Gorgonians and complex Substrates. Axis 1, showed a clear gradient of depth and temperature. *Coryphaenoides rupestris*, Macrouridae, anguilliformes and *Lepidion eques* related to shallower and warmer habitats in opposition to *Synaphobranchus kaupi* more represented in deeper and colder habitats.

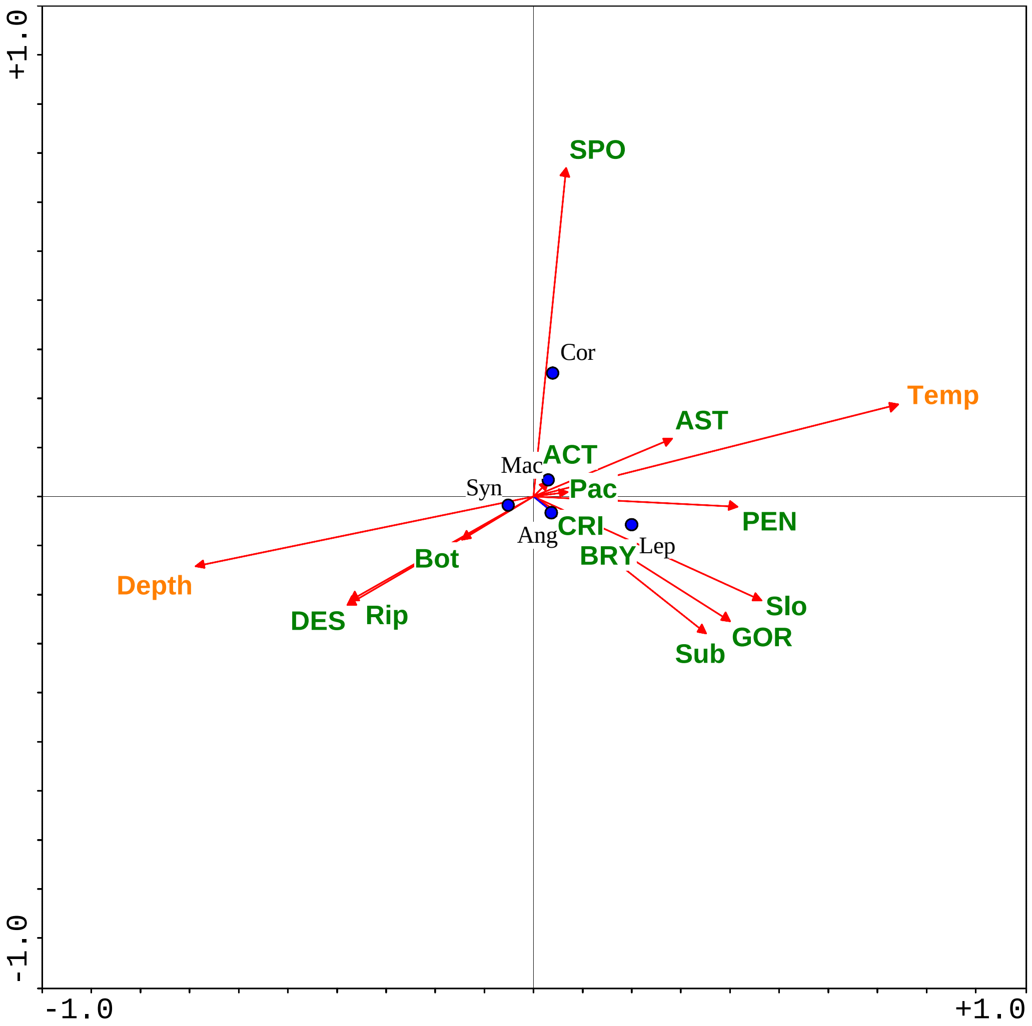


Figure 12. Canonical correspondence analysis (CCA) ordination diagram of dive 34 with fish species (blue circles) and environment variables (arrows); first axis is horizontal, second axis vertical. The fish species are: Cor=*Coryphaenoides rupestris*, Ang=Anguilliformes, Lep=*Lepidion eques*, Syn=*Synaphobranchus kaupi*, Mac=Macrouridae. The environmental variables are: ACT=Actinians, Temp=Temperature, PEN=Pennatularians, Depth=Depth, AST=Asteroidea, SPO=Sponges, DES=Desert, Rip=Ripple marks, Bot=Bottom texture, BRY=Bryozoans, CRI=Crinoids, Sub=Substrate, GOR=Gorgonians, Slo=Slope, Pac=Packing, AST=Asteroidea.

Table 7. Monte Carlo test of significance of the environmental variables in dive 34. The environmental variables are: ACT=Actinians, Temp=Temperature, PEN=Pennatularians, Depth=Depth, AST=Asteroidea, SPO=Sponges, DES=Desert, Rip=Ripple marks, Bot=Bottom texture, BRY=Bryozoans, CRI=Crinoids, Sub=Substrate, GOR=Gorgonians, Slo=Slope, Pac=Packing, AST=Asteroidea.

Variable	Var.N	LambdaA	P-value	F-value
Temp	15	0.27	0.005	10.30
SPO	9	0.13	0.075	5.40
Sub	11	0.10	0.020	3.81
Slo	12	0.09	0.110	3.89
DES	6	0.04	0.210	1.55
Depth	1	0.04	0.165	1.64
PEN	8	0.04	0.100	1.88
Bot	13	0.03	0.245	1.35
AST	3	0.03	0.345	1.21
ACT	2	0.05	0.085	1.90
BRY	4	0.02	0.260	1.07
Pac	14	0.02	0.420	0.80
Rip	10	0.01	0.700	0.56

3.2.1.3. Canonical Correspondence Analysis, CCA Dive 35

All the fit statistics indicated an evident association of environmental parameters (in general) with the distribution of the fish species for this dive. A high percentage of the variation in the species-environment relationship was explained (cumulative percentages of 44.3 and 65.5% for axes 1 and 2, respectively) (Table 14 in annex).

Both the “Trace” (P-value=0.005) and the first canonical axis were statistically significant as well as the relation between species and the environmental variables (P-value=0.015).

Table 8, shows the environmental variables in order of their inclusion in the model (conditional effects). The variables Ripple marks, Temperature, Current, Desert, Pennatularians, Actinians, Asteroidea, Antipatharians, Depth, Substrate and Sponges, contributed significantly (at the 5% significance level) to the model.

Table 8. Monte Carlo test of significance of the environmental variables in dive 35. The environmental variables are: ACT=Actinians, Temp=Temperature, PEN=Pennatularians, Depth=Depth, AST=Asteroidea, SPO=Sponges, Cur=Current, Rip=Ripple marks, Slo=Slope, Pac=Packing, HYD=Hydrozoans, CRI=Crinoids, Bot=Bottom texture, Sub=Substrate, DES=Desert, ANT=Antipatharians, GOR=Gorgonians.

Variable	**Var.N**	**LambdaA**	P-val	**F-value**
Rip	12	0.54	0.005	27.92
Temp	17	0.29	0.005	15.47
Cur	11	0.11	0.005	6.12
DES	6	0.09	0.005	4.97
PEN	9	0.08	0.005	4.28
ACT	2	0.06	0.045	3.38
AST	4	0.05	0.010	2.56
ANT	3	0.04	0.015	2.25
Depth	1	0.03	0.040	2.09
Sub	13	0.04	0.050	1.88
SPO	10	0.03	0.040	1.99
HYD	8	0.03	0.170	1.71
Pac	16	0.03	0.155	1.45
Slo	14	0.02	0.230	1.34
GOR	7	0.03	0.275	1.21
Bot	15	0.01	0.670	0.77
CRI	5	0.01	0.720	0.74

From the analysis of the ordination diagram (Fig. 13) it can be inferred that *Hoplostethus atlanticus* was strongly associated with Gorgonians, Antipatharians and Asteroidea. Developed bottom structure and habitat complexity characterized the habitat of this species. In contrast, *Lepidion eques*, Chimaerids and Moridae were more strongly linked to warmer and shallower habitats (Fig 18 in appendix). The negative side of axis 2 was generally represented by deeper species. These were associated with several types of bottom structure and invertebrate fauna. *Synaphobranchus kaupi* showed the maximum weighted average with respect to light bottoms (poorly packed). Alepocephalidae, *Neocyttus helgae*, Macrouridae and Moridae represented the group more strongly associated with habitats of high currents, ripple marks, slope inclination and bottoms of desert type.

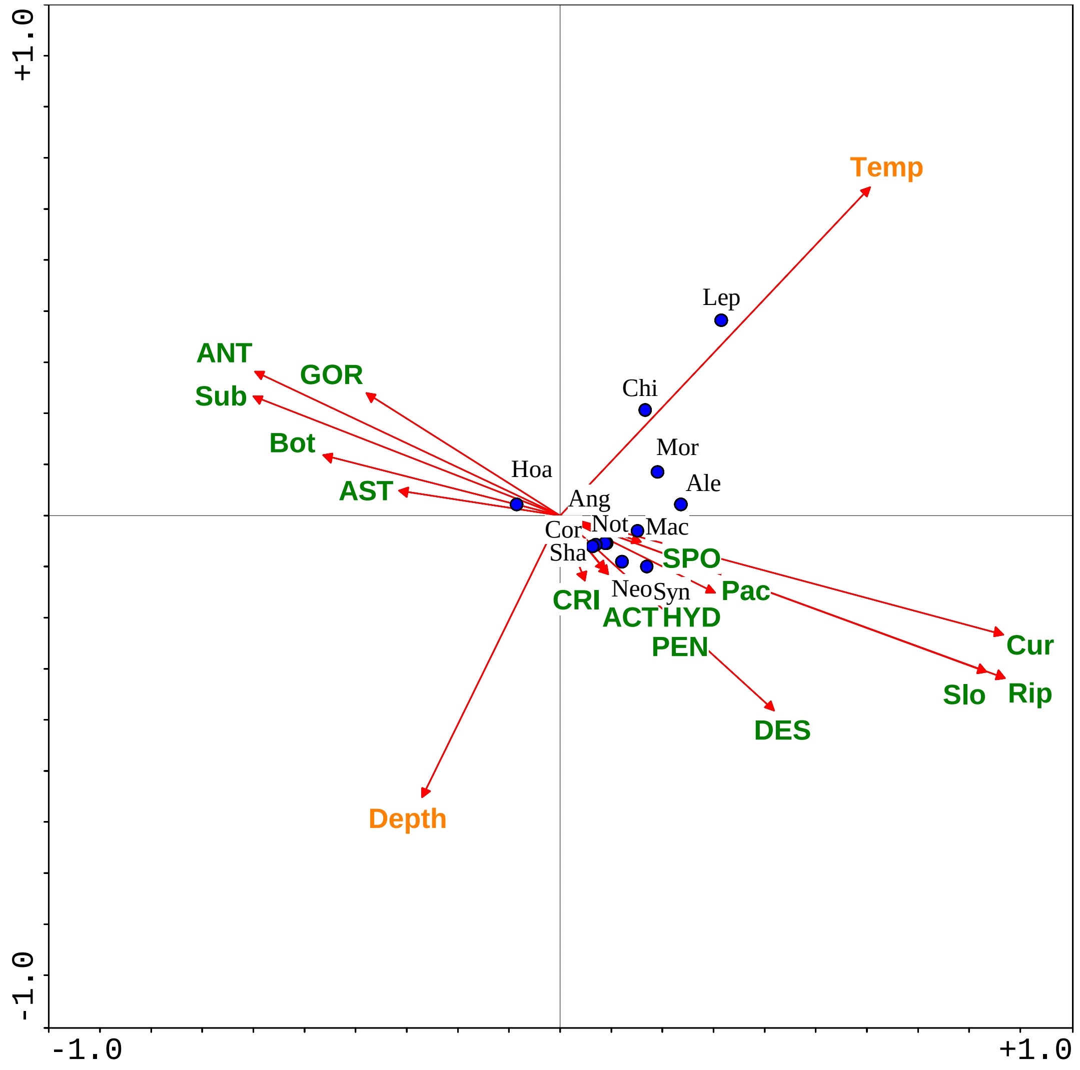


Figure 13. Canonical correspondence analysis (CCA) ordination diagram of dive 35 with fish species (blue circles) and environment variables (arrows); first axis is horizontal, second axis vertical. The fish species are: Cor=*Coryphaenoides rupestris*, Ang=Anguilliformes, Lep=*Lepidion eques*, Syn=*Synaphobranchus kaupi*, Chi=Chimaerids, Mac=Macrouridae, Ale= Alepocephalidae, Not= Notacanthus sp., Sha=Sharks, Hoa=*Hoplostethus atlanticus*, Mor=Moridae, Neo=*Neocyttus helgae*. The environmental variables are: ACT=Actinians, Temp=Temperature, PEN=Pennatularians, Depth=Depth, AST=Asteroidea, SPO=Sponges, Cur=Current, Rip=Ripple marks, Slo=Slope, Pac=Packing, HYD=Hydrozoans, CRI=Crinoids, Bot=Bottom texture, Sub=Substrate, DES=Desert, ANT=Antipatharians, GOR=Gorgonians, AST=Asteroidea, SPO=Sponges, Cur=Current, PEN=Pennatularians.

3.2.1.4. Canonical Correspondence Analysis, CCA Dive 37

Eigenvalues for the first two multivariate axes were 0.556 and 0.229, respectively, with the sum of canonical eigenvalues equal to 1.186 and the unconstrained eigenvalues equal to 5.0. All these values indicated a considerably association of environmental parameters (in general) with the distribution of the fish species. A high percentage of the variation in the species-environment relationship was explained (cumulative percentages of 46.9 and 66.2% for axes 1 and 2, respectively) (Table 15 in annex).

The value of “Trace” given by the results of the global permutation tests to judge the significance of the relation between species and environment was 1.186 (P-value=0.005). The first canonical axis was statistically significant as well as the relation between species and the environmental variables (P-value=0.005).

Table 9, shows the environmental variables in order of their inclusion in the model. The variables Substrate, Depth, Sponges, Sea cucumber, Scleractinians, Hydrozoans and Desert contributed significantly (at the 5% significance level) to the model.

Table 9. Monte Carlo test of significance of the environmental variables in dive 37. The environmental variables are: SEA=Sea Cucumber, Temp=Temperature, Depth=Depth, AST=Asteroidea, SPO=Sponges, Slo=Slope, Rip=Ripple marks, GOR=Gorgonians, Pac=Packing, HYD=Hydrozoans, DES=Desert, SCL=Scleractinians, Sub=Substracte.

Variable	Var.N	LambdaA	P-value	F-value
Sub	10	0.37	0.005	12.11
Depth	1	0.19	0.005	6.44
SPO	8	0.16	0.005	5.84
SEA	7	0.10	0.035	3.44
SCL	6	0.06	0.020	2.41
HYD	5	0.07	0.050	2.35
DES	3	0.07	0.045	2.57
AST	2	0.04	0.125	1.52
GOR	4	0.04	0.080	1.72
Temp	13	0.05	0.120	1.66
Rip	9	0.01	0.820	0.46
Pac	12	0.03	0.535	0.94

Canonical correspondence analysis (CCA) ordination of dive 37 showed a strong association of *Galeus melastomus* with respect to deeper and warmer habitats. Chimaerids were represented in similar habitat type but more strongly associated with Sponges. *Beryx decadactylus*, represented on the positive side of axis 1 of the diagram, was the most characteristic species with respect to the variables Scleractinians and Substrate complexity. The fish *Helicolenus dactylopterus* and Macrouridae were frequently associated with Hydrozoans and bottoms of desert type, usually found in shallower areas (negative side of axis 1 and 2) (Fig.14).

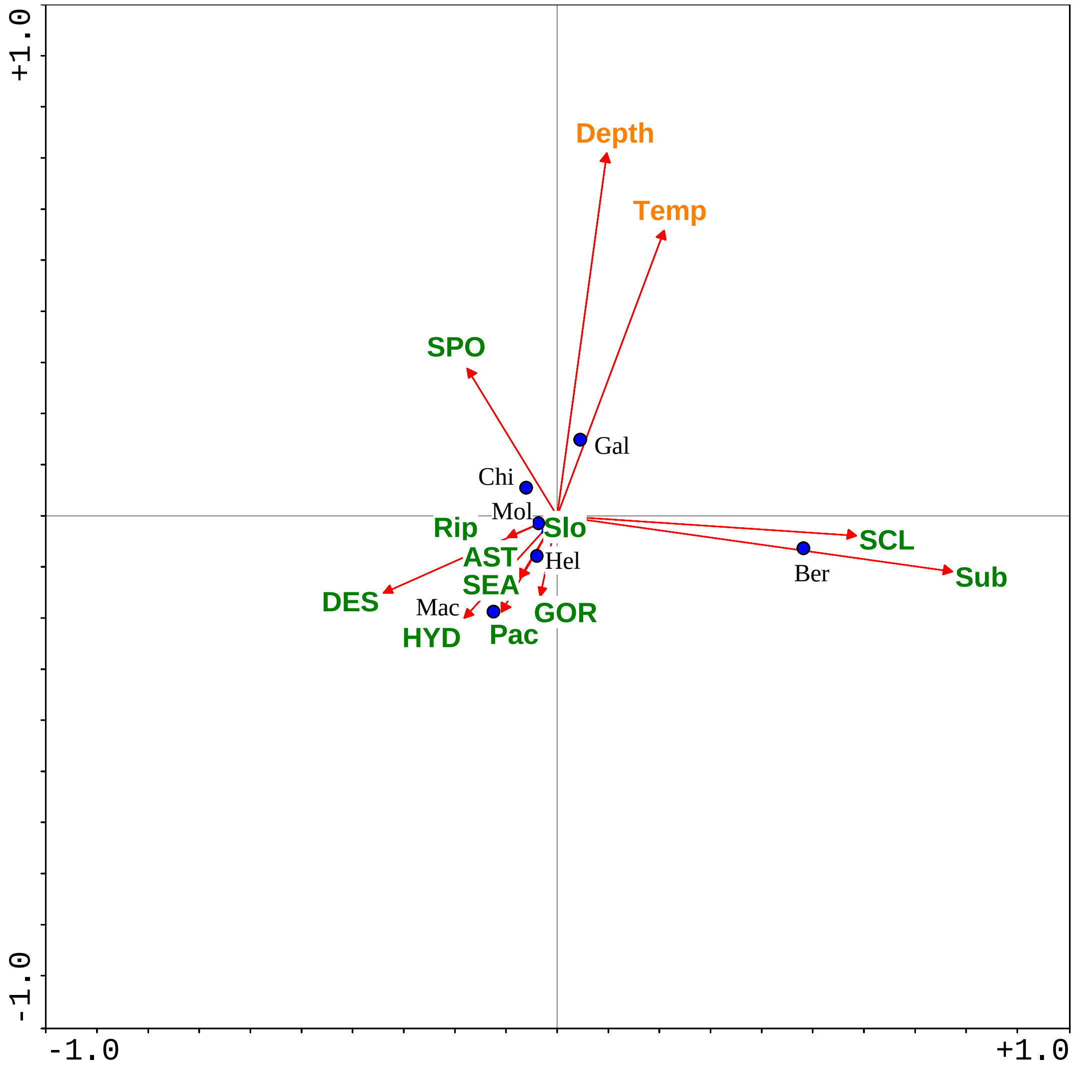


Figure 14. Canonical correspondence analysis (CCA) ordination diagram with fish species (blue circles) and environment variables (arrows); first axis is horizontal, second axis vertical. The fish speciesspecies are: Chi=Chimaerids, Mac=Macrouridae, Gal=*Galeus melastomus*, Ber=*Beryx decadactylus*, Mol=*Molva molva*, Hel=*Helicolenus dactylopterus*. The environmental variables are: SEA=Sea Cucumber, Temp=Temperature, Depth=Depth, AST=Asteroidea, SPO=Sponges, Slo=Slope, Rip=Ripple marks, GOR=Gorgonians, Pac=Packing, HYD=Hydrozoans, DES=Desert, SCL=Scleractinians, Sub=Substracte.

3.2.2. Canonical Correspondence Analysis (CCA), Global Dive Analysis

Eigenvalues for the first two multivariate axes were 0.693 and 0.520, respectively, with the sum of canonical eigenvalues equal to 1.186 and the unconstrained eigenvalues equal to 6.965. All these values indicated a considerably association of environmental parameters (in general) with the distribution of the fish species. A high percentage of the variation in the species-environment relationship was explained (cumulative percentages of 40.5% and 70.8% for axes 1 and 2, respectively) (Table 16 in annex).

The results of the global permutation tests to judge the significance of the relation between species and environment rising CCA showed a “Trace” of 3.301 (P-value=0.005). The first canonical axis was statistically significant as well as the relation between species and the environmental variables (P-value=0.005).

Table 10, shows the environmental variables in order of their inclusion in the model. Factors Depth, Slope, Bottom structure, Scleractinians, Sponges, Ripple marks, Current, Desert, Pennatularians, Substrate, Temperature, Hydrozoans and Antipatharians contributed significantly (at the 5% significance level) to the model.

Fig. 15 illustrates the canonical correspondence analysis ordination of the global dive analysis. The ordination of the fourteen fish species showed three main patterns of microhabitat association (black circles).

As represented on the upper side of axis 2 of this figure, *Hoplostethus atlanticus* was strongly defined by the association with Gorgonians, Antipatharians and bottoms containing ripple marks. The high complexity of its habitat and the separation from the other species were high. This species was generally found on areas of low current and low slope gradients. Axis 1 contrasted species found more often in deep areas and low temperatures with the ones associated to, and linked to, shallower and warmer areas.

Species Anguilliformes, Moridae, *Synaphobranchus kaupi*, *Lepidion eques* and *Mora moro* were positively associated with Actinians and free sediment (poorly packed bottoms). *Coryphaenoides rupestris* and Mesopelagic fishes were associated to

Pennatularians and Asteroidea. While the most representative species of bottoms characterized by sponges and Scleractinians were *Molva molva*, *Helicolenus dactylopterus*, *Galeus melastomus*, and Chimaerids, also weighted by a strong gradient of bottom structure (high percentage of clast or rock on the bottom).

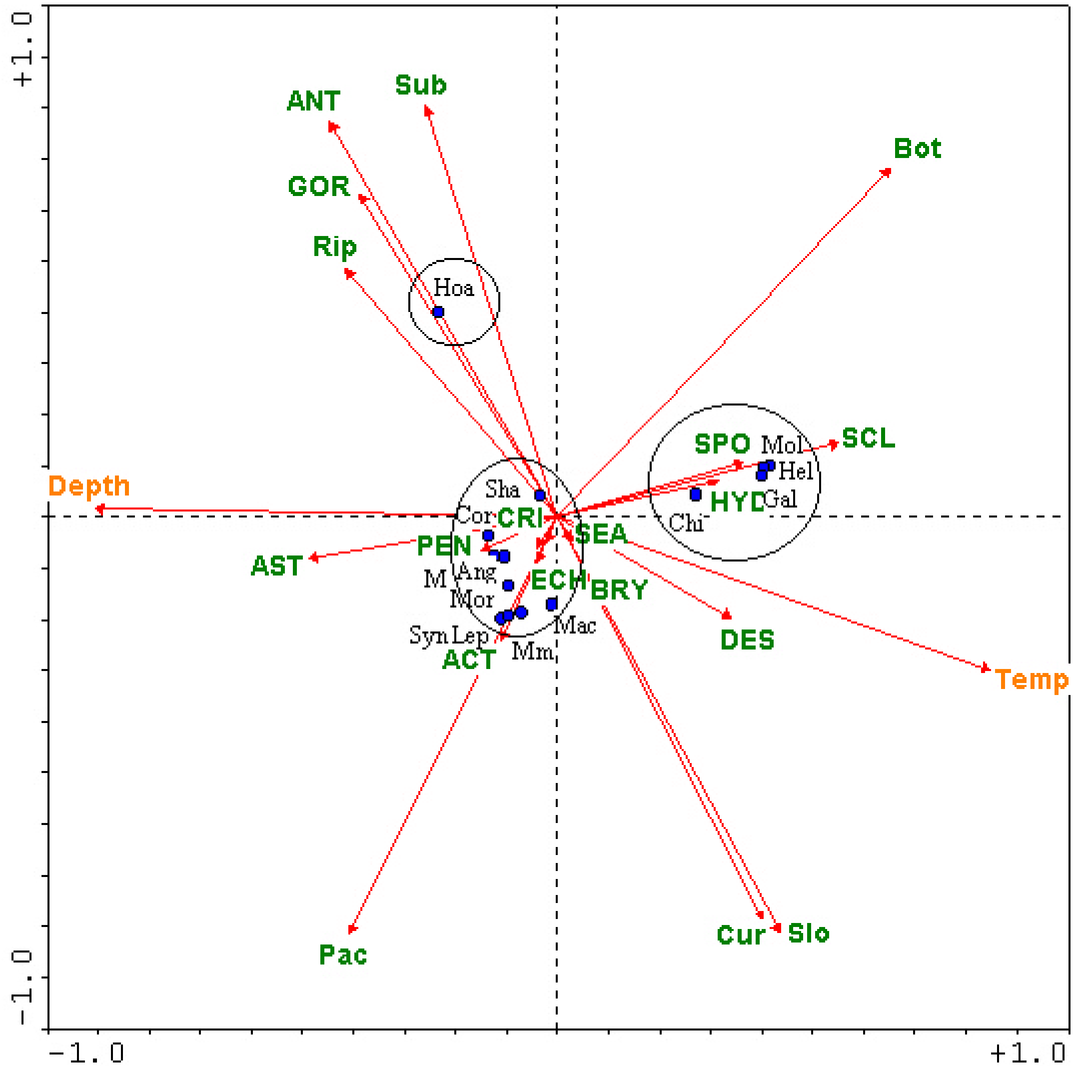


Figure 15. Canonical correspondence analysis (CCA) ordination diagram of all the dives with fish species (blue circles) and environment variables (arrows); first axis is horizontal, second axis vertical. The fish species are: Cor=*Coryphaenoides rupestris*, Ang=Anguilliformes, Lep=*Lepidion eques*, Syn=*Synaphobranchus kaupi*, Chi=Chimaerids, Mac=Macrouridae, Sha=Sharks, Hoa=*Hoplostethus atlanticus*, Mor=Moridae, M=Mesopelagic fishes, Mm=*Mora moro*, Gal=*Galeus melastomus*, Mol=*Molva molva*, Hel=*Helicolenus dactylopterus*. The environmental variables are: ACT=Actinians, Temp=Temperature, PEN=Pennatularians, Depth=Depth, AST=Asteroidea, SPO=Sponges, Cur=Current, Rip=Ripple marks, Slo=Slope, Pac=Packing, HYD=Hydrozoans, CRI=Crinoids, Bot=Bottom texture, Sub=Substrate, DES=Desert, ANT=Antipatharians, GOR=Gorgonians, Cur=Current, ECH= Echinoids, BRY=Bryozoans, SEA=Sea cucumber, SCL= Scleractinians.

Table 10. Monte Carlo test of significance of the environmental variables in all dives. The environmental variables are: ACT=Actinians, Temp=Temperature, PEN=Pennatularians, Depth=Depth, AST=Asteroidea, SPO=Sponges, Cur=Current, Rip=Ripple marks, Slo=Slope, Pac=Packing, HYD=Hydrozoans, CRI=Crinoids, Bot=Bottom texture, Sub=Substrate, DES=Desert, ANT=Antipatharians, GOR=Gorgonians, ECH= Echinoids, BRY=Bryozoans, SEA=Sea cucumber, SCL= Scleractinians.

Variable	**Var.N**	**LambdaA**	**P-value**	**F-value**
Depth	1	0.75	0.005	21.76
Slo	20	0.59	0.005	17.47
Bot	21	0.28	0.005	8.59
SCL	15	0.24	0.005	7.26
CRI	11	0.18	0.010	5.70
SPO	9	0.18	0.005	5.64
Rip	18	0.17	0.005	5.36
Cur	17	0.13	0.005	4.11
DES	12	0.12	0.005	3.71
PEN	7	0.09	0.015	2.72
Sub	19	0.07	0.005	2.34
Temp	16	0.07	0.010	2.22
ECH	5	0.07	0.085	2.27
HYD	13	0.06	0.025	2.17
ANT	10	0.07	0.045	1.99
AST	4	0.05	0.075	1.67
GOR	6	0.04	0.145	1.49
Pac	22	0.05	0.155	1.46
ACT	2	0.04	0.210	1.29
SEA	8	0.02	0.385	0.89
BRY	14	0.03	0.385	0.83

3.3. Locomotory Behaviour: species comparison

Modes of forward swimming, orientation and speed of selected fish species are illustrated in Fig.16 and described in Table 11. Characterisation of swimming mode was adapted from the classification for shallow water species made by Lindsey (1978). The thirteen (13) fish species showed considerable variability in swimming modes. The two extreme modes of propulsion observed were “anguilliform” and “ostraciiform”.

Synaphobranchus kaupi, *Notacanthus* sp. and *Galeus melastomus* were well characterized by the “anguilliform” style where movement of the trunk is an essential feature. *Coryphaenoides rupestris*, *Molva molva*, *Lepidion eques* and *Mora moro* were placed on an intermediate position of the diagram, classified as sub-carangiform. *Coryphaenoides rupestris*, *Beryx decadactylus* and Alepocephalidae were classified as purely ostraciiform in their locomotory mode. Some fish taxa assumed particular or mixed modes of locomotion. Thus, *Aphanopus* were observed to utilise both anguilliform and ostraciiform propulsion. Chimaerids can probably be classified into the diodontiform mode of Lindsey (1978), owing to the dependence on their pectoral fins. *Necocyttus helgae* showed strong activity of the anal and dorsal fins, a characteristic of the balistiform mode.

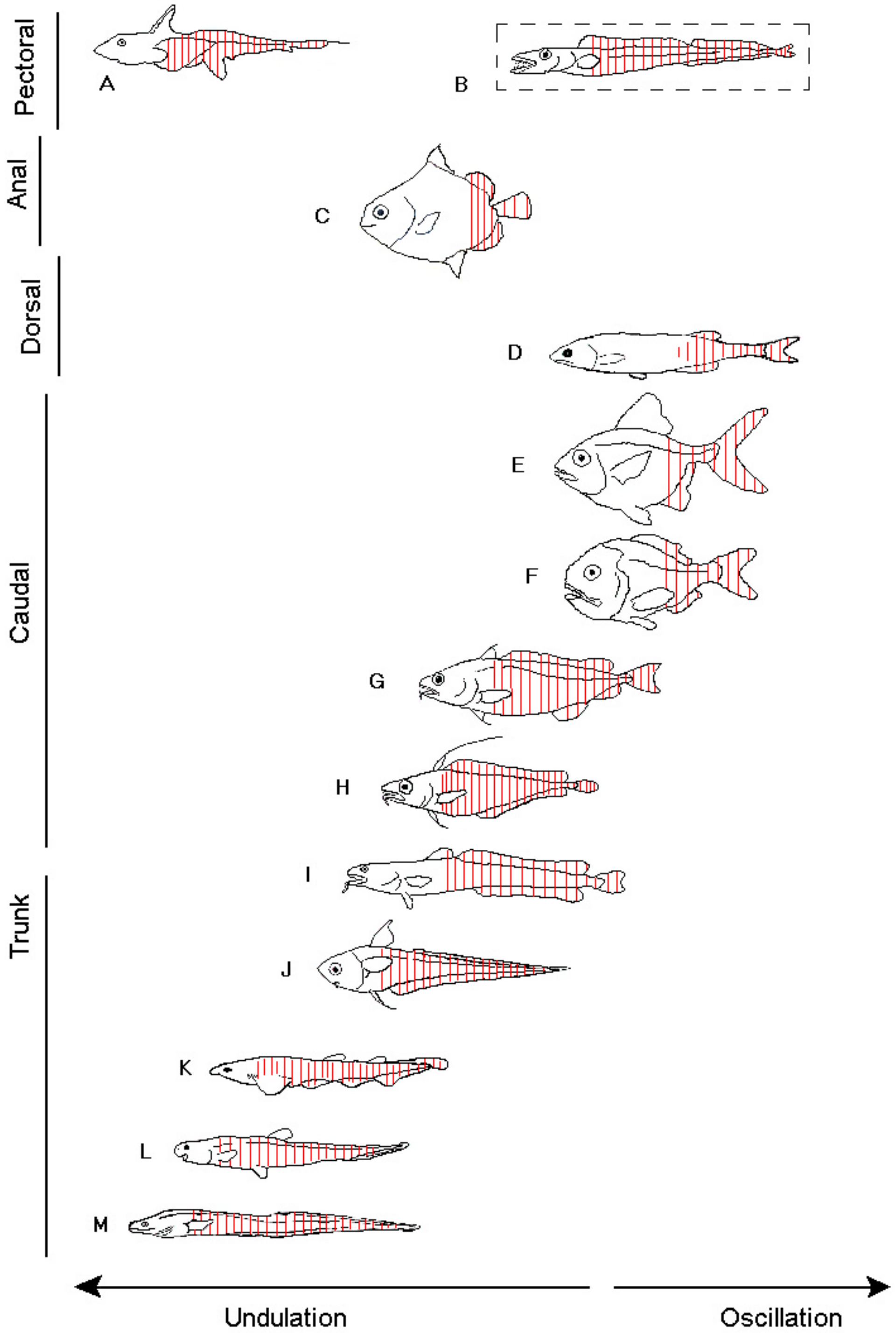


Figure 16 – Observed modes of forward swimming of some demersal fish. The different species are arranged along the vertical axis according to the propulsive mode of body and fins, and along the horizontal axis according to a scale running from serpentine undulation to oscillation (according to the classification scale of Lindsey, 1978). Species illustrated are: (A) Chimaerids, (B) *Aphanopus carbo*, (C) *Neocyttus helgae*, (D) Alepocephalidae, (E) *Beryx decadactylus*, (F) *Hoplostethus atlanticus*, (G) *Mora moro*, (H) *Lepidion eques*, (I) *Molva molva*, (J) *Coryphaenoides rupestris*, (K) *Galeus melastomus*, (L) Notacanthus sp., (L), and (M) *Synaphobranchus kaupi*.

4. Discussion

The deep-sea habitats investigated were highly diverse (Table 1), and fish occurrence showed species-specific patterns in response to physical, geological and biological characteristics (*e.g.* Figures 4, 5 and 15). Diversity of deep-sea benthic communities is generally high in terms of taxa (Hessler & Sanders, 1967; Grassle *et al*., 1975; Grassle, 1989; Cailliet *et al*., 1999). Diversity patterns of demersal fish assemblages can generally be comprehended in terms of interrelationships of predation, competition, environmental heterogeneity, and trophic level (Haedrich *et al*., 1980).

The emphasis of the present study was placed, however, on environmental heterogeneity, at a micro-habitat level, as a determinant of fish occurrence. Thus, important behavioural traits such as social interaction of conspecifics, and inter-specific avoidance or aggregation were not taken into consideration. The major reason for this was the difficulty to handle several sources of information simultaneously. This included information on species occurrence, micro-habitat, physical variables and behaviour (four data matrices, in statistical vocabulary). Advances in statistical theory, including the recent approach to the “4-th corner problem” (Legendre & Legendre, 1998) will facilitate this type of analysis in the future.

Another limitation of the present study was the sampling design. The aim of the survey was multi-purpose. Thus, unlike most fishery surveys, it did not aim exclusively at disclosing spatial patterns of distribution. Ecological and fishery studies normally rely on quadrate counts (*e.g.* swept-area surveys performed along linear transects), and the sampling unit is a stretch of seabed (or “station”). This methodology is prone to describe general patterns of fish association better. However, many different micro-habitats might go un-noticed in a long stretch of seabed. Thus, the detail of the present study might be larger, because it was performed at the individual fish level. However, general patterns of association might have been missed or biased. For instance, if two conspecifics were observed in the immediate vicinity of each other their occurrence, and that of the common micro-habitat, was recorded as two independent events. Fish species (and associated micro-habitats) that were detected in large frequencies became, thus, clearly over-represented.

The ordination methods used in the data analysis of the dives showed that the environmental variables related strongly to the two first ordination axes (Table 10). Therefore, these variables seemed to be sufficient to predict the main part of variation in the species composition (ter Braak, 1986). It was inferred that these axes provided information of patterns of habitat use and on gradients of fish distribution. Heterogeneity was found within a same dive transect and among different transects. Some of the aspects of fish-micro-habitat association described here were consistent with prior findings obtained with data collected in the same cruise (*e.g.* Lorance *et al.*, 2002; Uiblein *et al in press*).

Canonical correspondence analysis (CCA) performed on pooled data from the four dives seemed to provide adequate representation of the general habitat structure of the slope of the Bay of Biscay (Figure 15). One of the main vantages of using multiple ordination methods was that it was possible to have the perception of the importance of all the habitat components together in a single diagram. Nevertheless, it should be borne in mind that ordination techniques are only empirical visualisations of data and lack an underlying causative model. Thus, these techniques cannot explain why a particular species was not observed. Some species were relatively rare or absent in the pooled model (Table 1), and therefore independent dive analysis was needed.

The fish species analysed in the present study showed different distributions according to depth and temperature (Fig. 9 and 10, respectively), but this was also a reflection of the different characteristics of the four dives. Dive 37 was *e.g.* particularly shallow and warm (Fig. 8D). It is well known that species habiting the deep-sea are zoned with depth: different fish communities can be encountered over a change in depth of just a few hundred meters (Bianchi, 1992; Uiblein *et al.*, 1998; Haedrich *et al.*, 2001; Hareide & Garnes, 2001). As noticed by Uiblein *et al* (*in press*), total fish density varied among the dives considered in this study, but did not seem to follow any depth gradient. Previous studies of habitat use suggested that nekton respond similarly to environmental variables in different depths of the same continental slope (Felley & Vecchione, 1995; Uiblein *et al in press*). No single environmental parameter was found to consistently influence microhabitat selection. (Figure 15; Table 10) although many of these variables were related to depth. Fish species were most likely not responding to singular specific characteristics such as depth, temperature or sediment type, but to the general environment that constitutes their habitats (“trade-off”).

Current flow is known to be uneven in the seabed resulting in a patchy distribution of the food (Grassle & Grassle, 1992). Water current was qualitatively measured in two different ways, “current velocity” and “current temporal characteristics”. Occasionally organisms typical of fast currents, such as gorgonians and antipatharians, were frequent in habitats showing relatively low currents. Thus, caution was warranted in the utilisation of current as explanatory variable of fish or micro-habitat occurrence. For example, current was unstable in some parts of the diving transect 35 (Table 1). This was also reflected in its temperature profile (Fig. 8C). High hydrological activity due probably to up- or down-welling, or tidal effects might have occurred in this area (Lorance *et al*., 2002; Uiblein *et al in press*). The deepest (dive 34) and shallowest (dive 37) dives showed constant hydrological conditions (Fig. 8B and 8D, respectively). Dive 22, showed high current temporal characteristics reflecting strong tidal or internal wave effects in that area (Pingre *et al*., 1984; New & Pingree, 1990; Pingre & New, 1995). Different organisms provided very useful information with regard to the current system prevailing in their habitats (Kaufmann *et al*., 1989). In the case of benthos, gorgonians (on the edge of the rocks) and crinoids (above the viscous sublayer of the benthic boundary layer) were clear indicators of current flow (Tyler & Zibrowius, 1992). The most frequently species in dive 22 were *Coryphanoides rupestris*, *Lepidion eques* and *Synaphobranchus kaupi*. Dive 34 presented high density of *Synaphabranchus kaupi*, while an enormous concentration of *Hoplostethus atlanticus* occurred in dive 35. *Helicolenus d. dactylopterus* was a more coastal species (dive 37) (Table 1). A more comprehensive sampling grid would be required to undertake a biogeographical analysis, but this type of intensive surveys are difficult to perform in the deep sea. The occurrence of the different fish species seemed to reflect local geological and hydrological conditions rather than meso geographic gradients (*e.g.* North-South).

4.1. Species-specific patterns and habitat use

Hoplostethus atlanticus was highly represented in this study by dive 35 (Fig. 7). However, most of these specimens were sampled in a specific zone of the diving transect (Table 1, *see* dive 35 part B). This was a zone of high hydrological activity (Fig. 13 and 15), rich in corals, as gorgonians and antipatharians, and hard and complex bottoms. As pointed out by Lorance *et al* (2002), these fish are probably associated with areas of high water mass movements and mixing, and adopt calm current areas when recovering between foraging trips. Spawning aggregations are also frequent (Pankhurst, 1988; Kloser *et al.*, 1996). However, the present observations were made outside the spawning season (January-February) (Lorance *et al.*, 2002). Strong evidence linking these aggregations to feeding was that these fish were seldom observed in the “desert” type of habitat (Figure 18 in annex). These findings are in agreement with those made in the seamounts of New Zealand by Clark (1999).

Areas of strong hydrological conditions could provide for the appearance of plankton prey (Mortensen, 2000; Uiblein *et al in press*), and these organisms can in turn attract the prey of orange roughy, including prawns, amphipods, mesopelagic fish and mysids (Gordon & Duncan, 1987; Rosecchi *et al.*, 1988). *H. atlanticus* is known to have relatively high rates of food consumption and metabolism (Bulman & Koslow, 1992). Sea fans and corals (Heezen & Hollister, 1971; Tyler & Zibrowius, 1992), fan-shaped gorgonians (Tyler & Zibrowius, 1992) and other suspension feeders are common at sites of flow acceleration (Genin *et al.*, 1986). The association of orange roughy to these organisms suggests feeding concentrations rather than predator defence, which was the behaviour suggested by Koslow (1995) for fish occurring in seamounts.

Synaphobranchus kaupi preferred areas associated to currents, low subtract complexity and soft bottoms populated by asteroids (Fig.13 and 15). According to Uiblein *et al* (2002), *S. kaupi* responds behaviourally to different habitat conditions. This can probably be explained by its adaptive adjustment of habitat selection and foraging behaviour. The presence of currents on its habitat can probably improve the strategy of food search through the canalisation of odour plumes from food sources (Uiblein *et al.*, 2002; Uiblein *in press*). Asteroids do not usually show selective patterns with depth (Carey, 1972). Most asteroids are carnivorous and feed upon on almost any sessile animal, mainly molluscs and other echinoderms (Heezen & Hollister, 1971). The diet of *S. kaupi* is broad and typical of carnivorous (Saldanha, 1980) and scavenger species (Priede *et al*., 1994; Gordon & Mauchline, 1996). However there is no strong evidence in this study suggesting availability of these types of prey. It is also known that when predators are generalists their distribution ranges may be wide rather than restricted (Haedrich *et al*., 1980). In all the dives *S. kaupi* appeared associated to cooler and deeper habitats, and this is in agreement with other studies for the depth range considered (Fig. 9) (Merret & Domanski, 1985; Gordon & Mauchline, 1990; Uiblein *et al*., 2002). This is probably because of decreased predation risk and energy savings in those areas (Torres *et al*., 1979; Uiblein *et al*., 2002). Therefore, depth and current are considered likely to exert a combined influence on its microhabitat distribution. Association of *S. kaupi* with benthic fauna seemed to be strong, especially with respect to pennatulids (Fig. 11, Table 5; Fig. 13, Table 8). Beds of pennatularians are strong indicators of more eutrophic conditions (Tyler & Zibrowius, 1992).

Coryphaenoides rupestris inhabited similar habitats, depth and temperature ranges as *S. kaupi* (Figures 9 and 10). This species showed a general tendency to environments containing pennatularians, asteroidea, as well as bottoms characterized by poorly packed sediment (Figures 13 and 15) and sponges (Figures 11 and 12). Cailliet *et al* (1999) noted similar fauna associated to this species off central California at depths of 2000-3000m. There is, however, strong evidence related to its benthopelagic mode of life and foraging flexibility. *Coryphaenoides rupestris* feeds upon on zooplankton and small mesopelagic fishes (Mauchline & Gordon, 1984). This species seems to be rather more influenced by hydrological and dietary factors than by bottom structure.

Macrouridae (others), followed the same habitat use patterns as *Coryphaenoides rupestris*, probably due their biological affinities. Further identification down to species level would be needed for a more specific discussion of these taxa. Their association to bottom structure did not seem to follow specific gradients. Macrourids are generally known to have a rhythmic and active feeding behaviour, affected by the tide and transport of food (Guennegan & Rannou, 1979).

The two-scorpaenid species considered in this study *Helicolenus dactylopterus dactylopterus* (*person observ*; Fig.15) and *Trachyscorpia cristulata* (Fig. 5H, 18 and 19D) were found associated with sponges. Scorpaenid fishes were observed and documented associated to sponges by Smith & Hamilton (1983) in the Santa Catalina Basin using the submersibles Alvin and Sea Cliff. On the continental shelf off southwestern Norway, Fossa (*pers. obs. in* Husebo *et al.*, 2002) noted a similar association for *Sebastes* spp.: fish were often observed beside large sponges, resting or hiding in their concavities, and among stone features. Sponges have been documented as providing small niches for small cryptofaunal as colonial zoanthids and other suspension feeders (Beaulieu, 2001). Nevertheless, this association seems to be better explained by the sheltering provided by these organisms, rather than the special nature of this organisms (Husebo *et al.*, 2002). Hydroids were occasionally associated to the microhabitat of *Helicolenus dactylopterus dactylopterus* (Fig. 14), but due their small sizes and forms, accurate measurement of coverage was particularly difficult.

Molva molva, *Galeus melastomus* and Chimaerids dwelled in a similar habitat type to *H. dactylopterus dactylopterus* (Figure 15). Within these fish groups, Chimaerids were less associated to complex bottoms (Figure 14), and this is probably explained by their feeding behaviour, benthic affinity and active mode of life (Lorance *et al.*, 2000). The swimming pattern of *G. melastomus* indicated an active foraging behaviour and exploitation of the bottom (*pers. observ.*). These fish are known to live in energetically poor environments (Lorance *et al.*, 2000). Their diet is typical of a predator, feeding mostly on fish and euphausids (Santos & Borges, 2001).

Several arguments have been postulated to affect the habitat use of gadiforms. According to Cohen *et al* (1990), *Molva molva* has a strong benthic affinity, occurs mainly on rocky bottoms and feeds principally on fish (cod, herring, flatfish), lobsters, cephalopods and starfishes. As noted by Husebo *et al* (2002) *Molva molva* tends to be larger on the reef areas than in non-coral habitats. Evaluation of this fact was particularly difficult in this study because no specific devices (*e.g.* laser beams) were available to measure fish. If this was due to feeding conditions provided by the reef zones or to large fish being more fitted to hunt on coral habitat remains to be explained.

Little is known about the ecology of *Lepidion eques* (Magnússon, 2001). It has a diet typical of a euryphagic predator, with a wide variety of prey as amphipods, decapods, copepods and mysids (Mauchline & Gordon 1980). Inhabiting a similar habitat (Figures 11 and 15) *Mora moro*, Moridae (others) and *Lepidion eques* are known to have similar station holding behaviours (Uiblein *et al in press*). Diet of *Mora moro* from the deep of the Catalan Sea was analysed by Carrassón *et al* (1997) evidencing a diet based on benthic prey, chiefly epibenthic and suprabenthic prey (crustaceans, fishes, and cephalopods). Distributional responses evidences to small-scale habitat variability by juvenile gadoids (*Merluccius bilinearis*) were shown by Auster *et al* (1991, 1997). These fish seemed to choose interstices of the substrate as shelter from predators, and at larger sizes tend to occur in more diverse habitats. Complex microhabitats may be also functional foraging sites. Silver hakes were observed to keep station on the downcurrent side of crests where they ambushed demersal zooplankton (Auster *et al*., 1991). Competition for space or foraging positions (partitioning of food resources) are likely factors to explain the distribution of this species.

When compared with the other species analysed in the dive 37, *Beryx decadactylus* seemed to prefer areas of high substrate complexity (Figure 14; Table 9), mainly formed by small reefs of scleractinians and small rocky formations (*e.g.* Figure 4f). Similar reasons as the ones suggested above to *H. atlanticus* (its parental specie), could possibly explain its association to complex reefs. Feeding habits of this species are only documented by Durr & González (2002) off the Canary Islands. It is known to feed upon on small fishes, crustaceans and cephalopods.

Neocyttus helgae is another species strongly associated with “reefs” (*personal observation*; Table 11). Habitat conditions presenting strong currents and slope inclination were strong, and separated well this species from others analysed. *Neocyttus helgae* was frequently found associated with deep-sea slopes and coral reefs in the seamount ‘Mont Theresa’ (NE Atlantic) by Dekindt (2001).

One of the main difficulties in the assessment of habitat preferences is the evaluation of environmental parameters, especially the topographical ones (*e.g.* La Mesa, 2002). In the present study identification of microhabitats such as biogenic depressions (burrows) was particularly difficult owing to visibility conditions. These structures can be useful as indicators of prey availability in the inner the sea bottom and their faunal distributions (Malatesta *et al*., 1992). Further, the dive transects were often not rectilinear, and this made difficult the study of demographic responses to specific parameters. Another important factor to take into consideration in future experiments is the size of the fishes. This was not evaluated here, especially when considering different depth ranges. Depth-body size relationships have been studied before, and specific distribution patterns seem to exist (*e.g.* Uiblein *et al*., 1998).

One of the limitative constraints in the investigation of the deep ocean is the inevitable bias imposed by the sampling instruments. The lights and sounds produced by the submergible can attract or scare the fish in a selective form (Merrett & Haedrich, 1997). Other factors that could have influenced data collection were sea floor relief, profusion of suspended particles and consequent visibility conditions, size of organisms (Else *et al*., 2002), and occurrence of mimetic species, like flatfishes (Lorance *et al*., 2000). Combined fish faunal surveys using trawl and submersibles, might be useful in the future to provide additional ecological and physiological information (Cailliet *et al*., 1999).

4.2. Locomotory Behaviour

The suite of swimming modes described by Lindsey (1978) for shallow water species seemed to be appropriate for the demersal environment off the Bay of Biscay (Figure 16). In the case of *Aphanopus carbo*, the analysis was based upon one singular individual, and was thereby particularly limited. During the first contact with the submersible, the fish was vertically oriented, holding position in the ostraciiform mode. When disturbed by the submersible, it used the anguiliform for a better acceleration. As pointed out by Bone (1971), this fish shows a design appropriate for low-speed swimming. The vertical position could probably be adopted for drifting. It is known that fish may opt for a particular swimming strategy for energetic or range increase advantages (Blake, 1983). Its unusual ventral position of the lateral line (Bone, 1971) can be a special adaptation to this swimming mode.

Synaphobranchus kaupi, *Notacanthus* sp. and *Galeus melastomus* were better characterized by the anguilliform style. Anguilliform is a completely undulatory swimming mode, and it involves the whole body. The swimming amplitude is large along the whole body, increasing towards the tail. In general the caudal fin is small and sometimes absent (Lindsey, 1978). In parallel with other shallow water relatives (other gadiforms) *Coryphaenoides rupestris*, *Molva molva*, *Lepidion eques* and *Mora moro* were classified on a more intermediate mode of swimming, the subcarangiform.

Compared with the anguilliform mode, the subcarangiform mode has small amplitude of undulations at the anterior half of the body.

The Lateral line system is particularly well developed in grenadiers and notacanthiformes (described above) that have cavernous regions of the head housing specialized canals lined with sensory detectors (Merret & Haedrich, 1997). This is probably a significant factor that has led to the co-evolution of the elongate body form in many of the deep-sea demersal fishes (*e.g.* chimaeras, eels, notacanthiformes, spiny eels, and grenadiers) (Merret & Haedrich, 1997). Most Chimaeras observed seemed quite sensitive to the submersible disturbance. Their swimming was characterized by the flapping of the pectoral fins (diodontiform/rajiform mode), and this was not entirely in agreement with the observations made by Lindsey (1978).

Hoplostethus atlanticus, *Beryx decadactylus* and Alepocephalidae were classified as using the carangiform mode of swimming. In the carangiform mode, only the posterior portion of the body is capable of wide flexibility. The undulations are reserved to the last part of the fish, and the power force drives the tail (Lindsey, 1978). The first two species were found frequently associated to complex habitats, and Alephocephalidae were associated with less complex and packed bottoms (Figure 13). Thus, a common swimming strategy might be employed in habitats characterised by different current conditions.

Neocyttus helgae was closer to the balistiform mode characterised by undulation of the dorsal and anal fins. This species was often observed in horizontal and oblique positions (Table 11) and was particularly associated with slopes, reefs of rocks and gorgonians. Its “gently” mode of swimming, also documented by Desbruyères & Segonzac (1997), seems to be well adapted to spatially complex environments. Manoeuvring experts like the angelfish have diamond-shaped body: their short, deep-bodies make very short turns possible (Videler, 1993).

Due to the multiple objectives of the dives under consideration, the study of locomotory behaviour was primarily qualitative in nature. However, it provided some novel information that might be relevant for future studies. More quantitative data are needed, regarding e.g. undulation, wavelength, wigwag motion, and acceleration (*e.g.* Cohen, 1977) in order to achieve an accurate view of the locomotion process.

5. Conclusion

Deep-sea fish showed specific patterns of micro-habitat and environmental association. At the micro-scale level there were important biological indicators of habitat use, particularly the presence of deep-water coral reefs of gorgonians and scleractinians. The occurrence of sponges and pennatularians were valuable indicators of different hydrological conditions. The most important physical characteristics determining fish occurrence were depth, temperature and current. Geological factors were likely important, as for *e.g.* the substracte complexity, bottom structure and ripple marks. Species such as *Hoplostetus atlanticus* and *Beryx decadactylus* were clearly associated with complex bottoms, including coral reefs. Others, such as *Coryphaenoides rupestris* and *Synaphobranchus kaupi*, were more flexible to adjust to different environments. These findings have relevance for understanding the consequences of inadequate fishing practices on deep-sea habitats.

No clear geographic trends of fish micro-habitat distribution could be obtained from this study. However, local physical characteristics (current, steepness of slope and depth) rather than long-range gradients seemed to correlate with the occurrence of individual fish species.

The main swimming strategies used in shallow waters are also used in the demersal environment. Convergences were frequent even in taxonomically remote groups. For instance, *Galeus melastosmus* (sharks) and *Synaphobranchus kaupi* (eels) use the same “anguiliform” mode of swimming. Convergence is, thus, not an exception of shallow water species. Novel observations regarding swimming modes were also made, as e.g. for *Aphanopus* sp. Some species seem to adapt different swimming modes depending on the local habitat and environment. These qualitative findings help to understand the eco-physiology of deep-sea fish.

6. References

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Annex

Table 12. Results of ordination by Canonical correspondence analysis (CCA) (see Fig.11) of dive 22.

Axes	1	2	3	4	Total inertia
Eigenvalues:	0.320	0.181	0.140	0.110	7.982
Species-environment correlations:	0.567	0.426	0.375	0.333	
Cumulative percentage variance					
of species data:	4.0	6.3	8.0	9.4	
of species-environment relation:	38.3	60.0	76.8	90.0	
Sum of all unconstrained eigenvalues					7.982
Sum of all canonical eigenvalues					0.835

Table 13. Results of ordination by Canonical correspondence analysis (CCA) (see Fig.12) of dive 34.

Axes	1	2	3	4	Total inertia
Eigenvalues:	0.412	0.253	0.146	0.065	4.000
Species-environment correlations:	0.642	0.503	0.382	0.254	
Cumulative percentage variance					
of species data:	10.3	16.6	20.3	21.9	
of species-environment relation:	47.1	76.0	92.6	100.0	
Sum of all unconstrained eigenvalues					4.000
Sum of all canonical eigenvalues					0.875

Table 14. Results of ordination by Canonical correspondence analysis (CCA) (see Fig. 13) of dive 35.

Axes	1	2	3	4	Total inertia
Eigenvalues:	0.662	0.317	0.194	0.141	10.000
Species-environment correlations:	0.813	0.563	0.441	0.375	
Cumulative percentage variance					
of species data:	6.6	9.8	11.7	13.1	
of species-environment relation:	44.3	65.5	78.5	88.0	
Sum of all unconstrained eigenvalues					10.000
Sum of all canonical eigenvalues					1.493

Table 15. Results of ordination by Canonical correspondence analysis (CCA) (see Fig. 14) of dive 37.

Axes	1	2	3	4	Total inertia
Eigenvalues:	0.556	0.229	0.215	0.123	5.000
Species-environment correlations:	0.746	0.479	0.464	0.350	
Cumulative percentage variance					
of species data:	11.1	15.7	20.0	22.5	
of species-environment relation:	46.9	66.2	84.4	94.7	
Sum of all unconstrained eigenvalues					5.000
Sum of all canonical eigenvalues					1.186

Table 16. Results of ordination by Canonical correspondence analysis (CCA) (see Fig. 15) of all dives (global analysis).

Axes	1	2	3	4	Total inertia
Eigenvalues:	0.693	0.520	0.313	0.117	6.965
Species-environment correlations:	0.892	0.759	0.651	0.458	
Cumulative percentage variance					
of species data:	10.0	17.4	21.9	23.6	
of species-environment relation:	40.5	70.8	89.1	96.0	
Sum of all unconstrained eigenvalues					6.965
Sum of all canonical eigenvalues					1.713

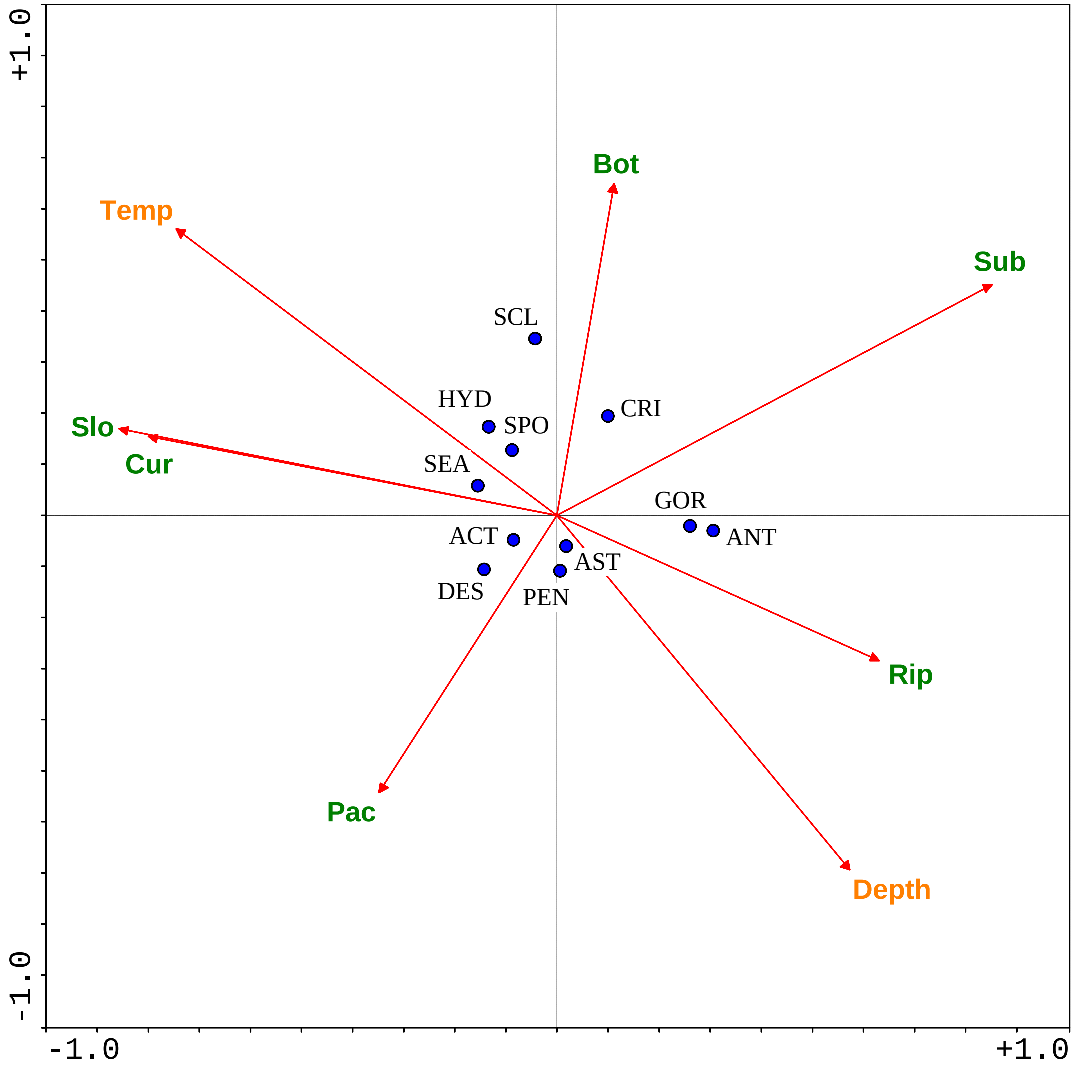


Fig. 17. Canonical correspondence analysis (CCA) ordination diagram with benthonic species (blue circles) and environment variables (arrows); first axis is horizontal, second axis vertical. The benthonic species are: ACT=Actinians, PEN=Pennatularians, AST=Asteroidea, SPO=Sponges, HYD=Hydrozoans, CRI=Crinoids, ANT=Antipatharians, GOR=Gorgonians, ECH= Echinoids, BRY=Bryozoans, SEA=Sea cucumber, SCL= Scleractinians. The environmental variables are: Temp=Temperature, Depth=Depth, Cur=Current, Rip=Ripple marks, Pac=Packing, Slo=Slope, Bot=Bottom texture, Sub=Substrate, Cur=Current.

Table 17. Summary of the global permutation test of the relation between bentho-species and environment using Canonical correspondence analysis (CCA).

Summary of Monte Carlo test

Test of significance of first canonical axis: eigenvalue = 0.693
F-ratio = 54.281
P-value = 0.0050
Test of significance of all canonical axes: Trace = 1.713
F-ratio = 20.019
P-value = 0.0050

Table 18. Monte Carlo test of significance of the environmental variables of benthos (global analysis). The environmental variables are: Temp=Temperature, Depth=Depth, Cur=Current, Rip=Ripple marks, Pac=Packing, Slo=Slope, Bot=Bottom texture, Sub=Substrate, Cur=Current.

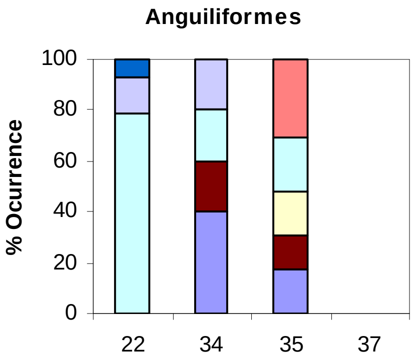
Variable	**Var.N**	**LambdaA**	**P**	**F**
Sub	5	0.62	0.005	49.03
Temp	2	0.49	0.005	41.65
Bot	7	0.16	0.005	13.88
Depth	1	0.20	0.005	17.86
Cur	3	0.15	0.005	13.30
Pac	8	0.03	0.005	3.51
Rip	4	0.03	0.015	2.71
Slo	6	0.03	0.035	2.81

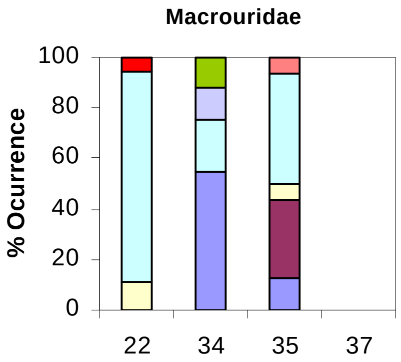
Table 19. Results of ordination by Canonical correspondence analysis (CCA) ordination of benthonic species (see Fig.17) of all dives (random).

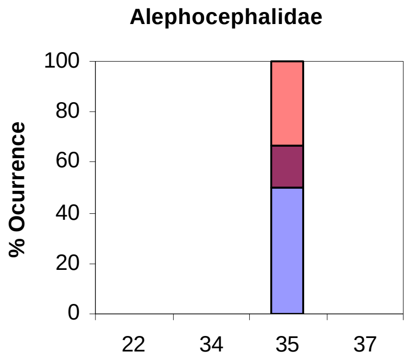
Axes	1	2	3	4	Total inertia
Eigenvalues:	0.878	0.742	0.349	0.310	18.000
Species-environment correlations:	0.937	0.861	0.591	0.557	
Cumulative percentage variance					
of species data:	4.9	9.0	10.9	12.7	
of species-environment relation:	26.6	49.1	59.6	69.0	
Sum of all unconstrained eigenvalues					18.000
Sum of all canonical eigenvalues					3.301

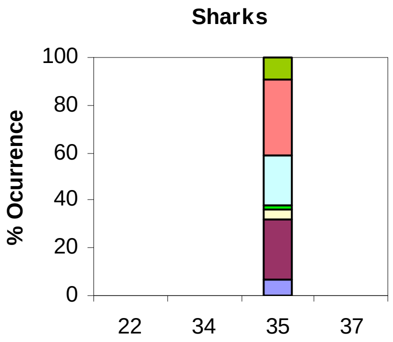
Table 20. Correlations and p-values between depth and temperature for all the dives.

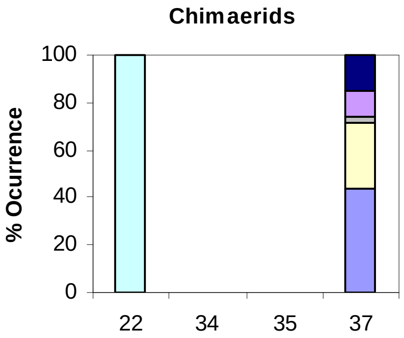
	Dives			
	22	34	35	37
Pearson’s r	0.94	0.98	0.84	-0.94
p-value	4.06E-116	2.6E-120	8.9E-132	1.71E-74
Spearman’s s	0.9	0.99	0.68	-0.9
p-value	7.19E-94	1.91E-152	2.3E-68	4.48E-57

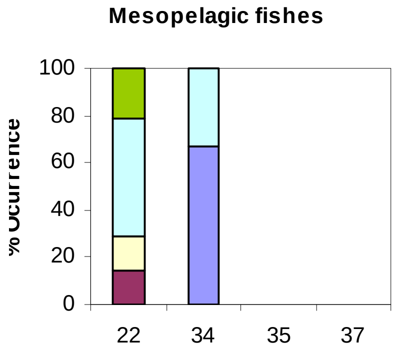

Anguiliformes

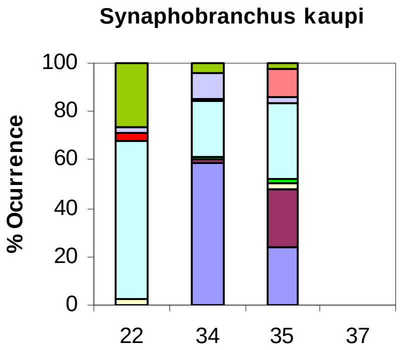

Macrouridae

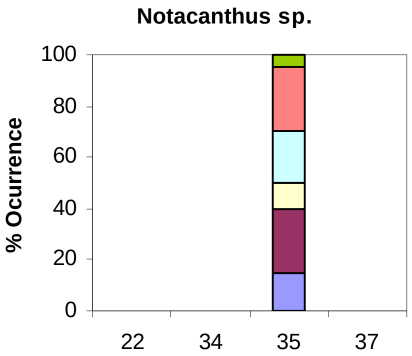

Alephocephalidae

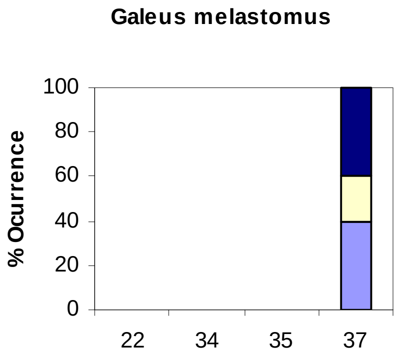

Sharks

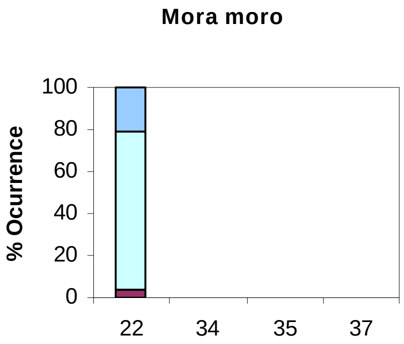

Chimaerids

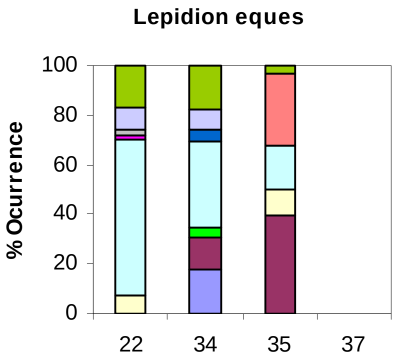

Mesopelagic fishes

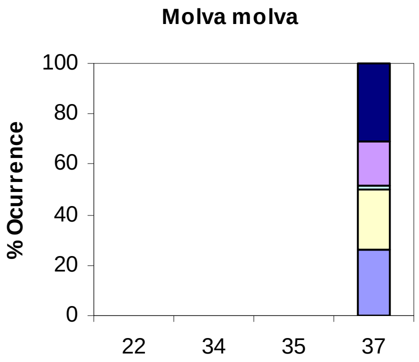

Synaphobranchus kaupi


Notacanthus sp.


Galeus melastomus


Mora moro


Lepidion eques


Molva molva

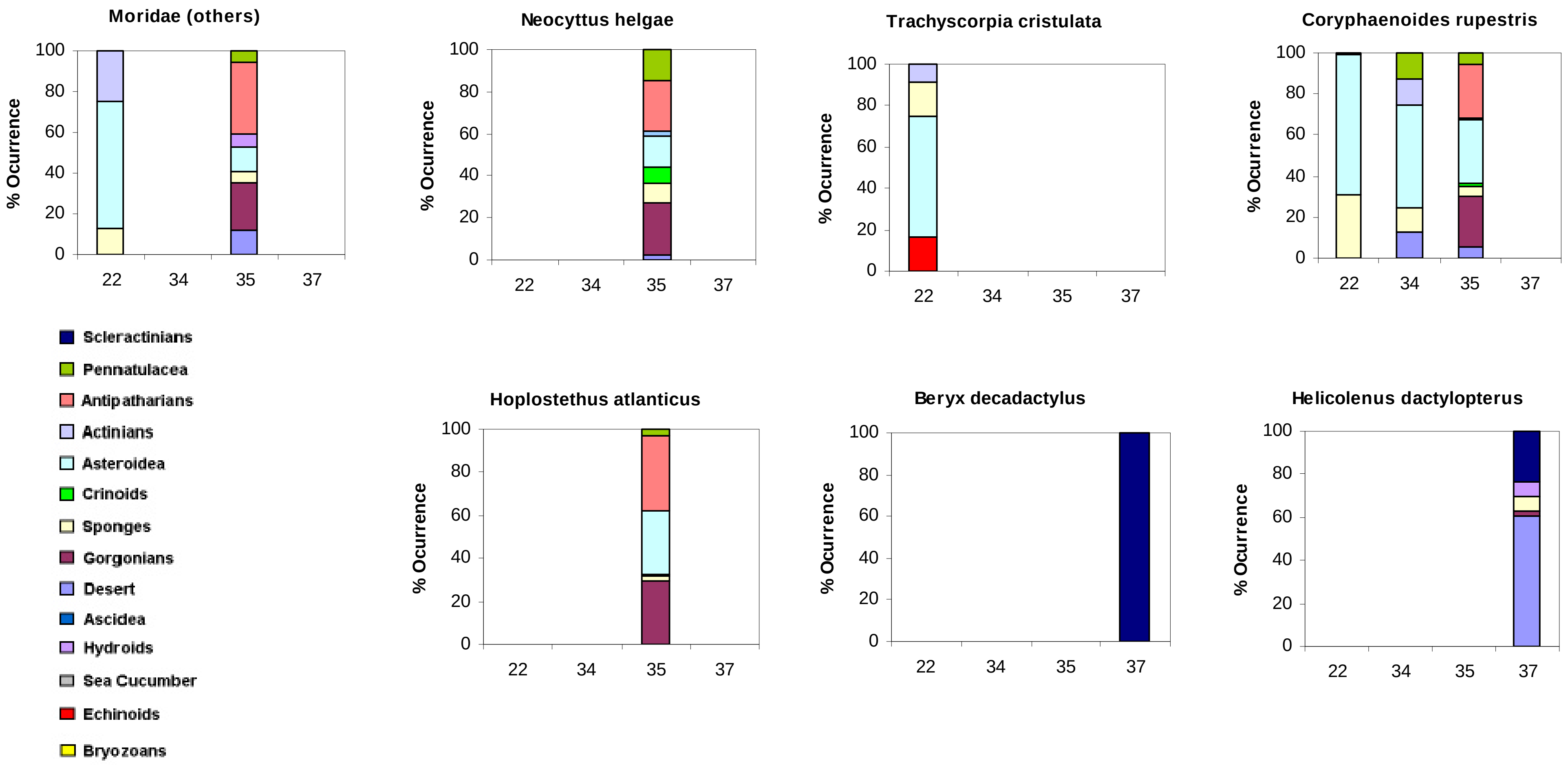
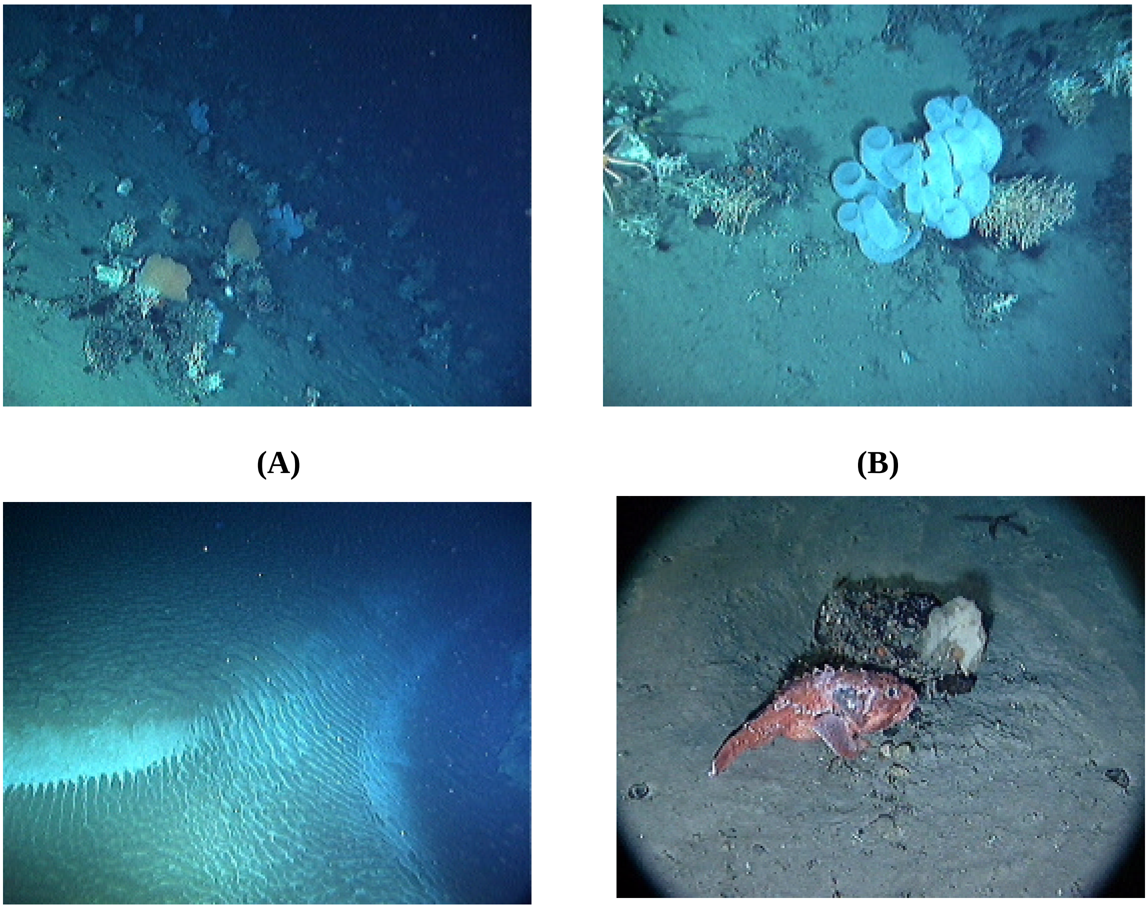


Figure 18 – Percentage of occurrence of the invertebrate fauna associated to the fish species microhabitats among the different dives (dives 22, 34, 35 and 37).

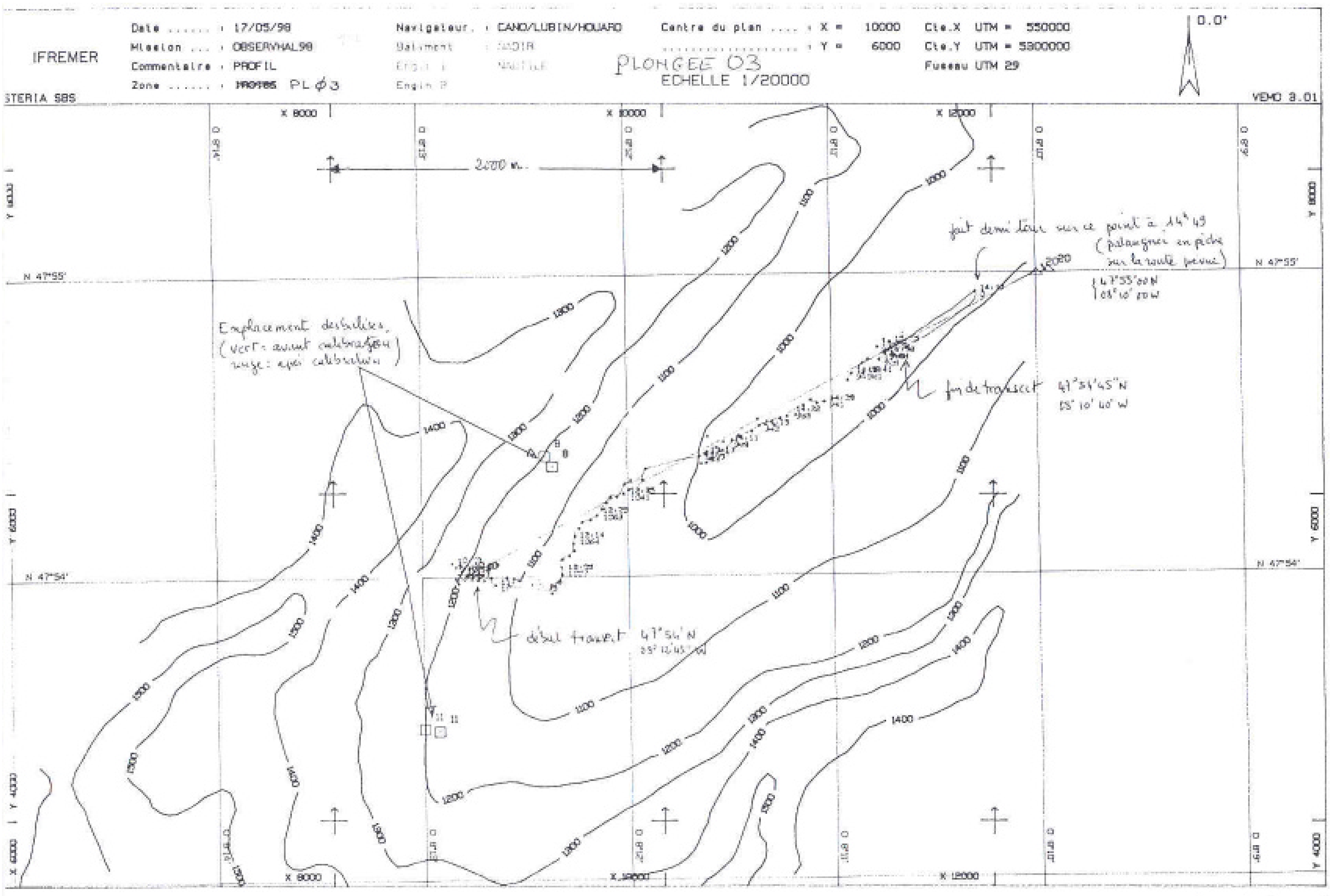


(A) **(B)**

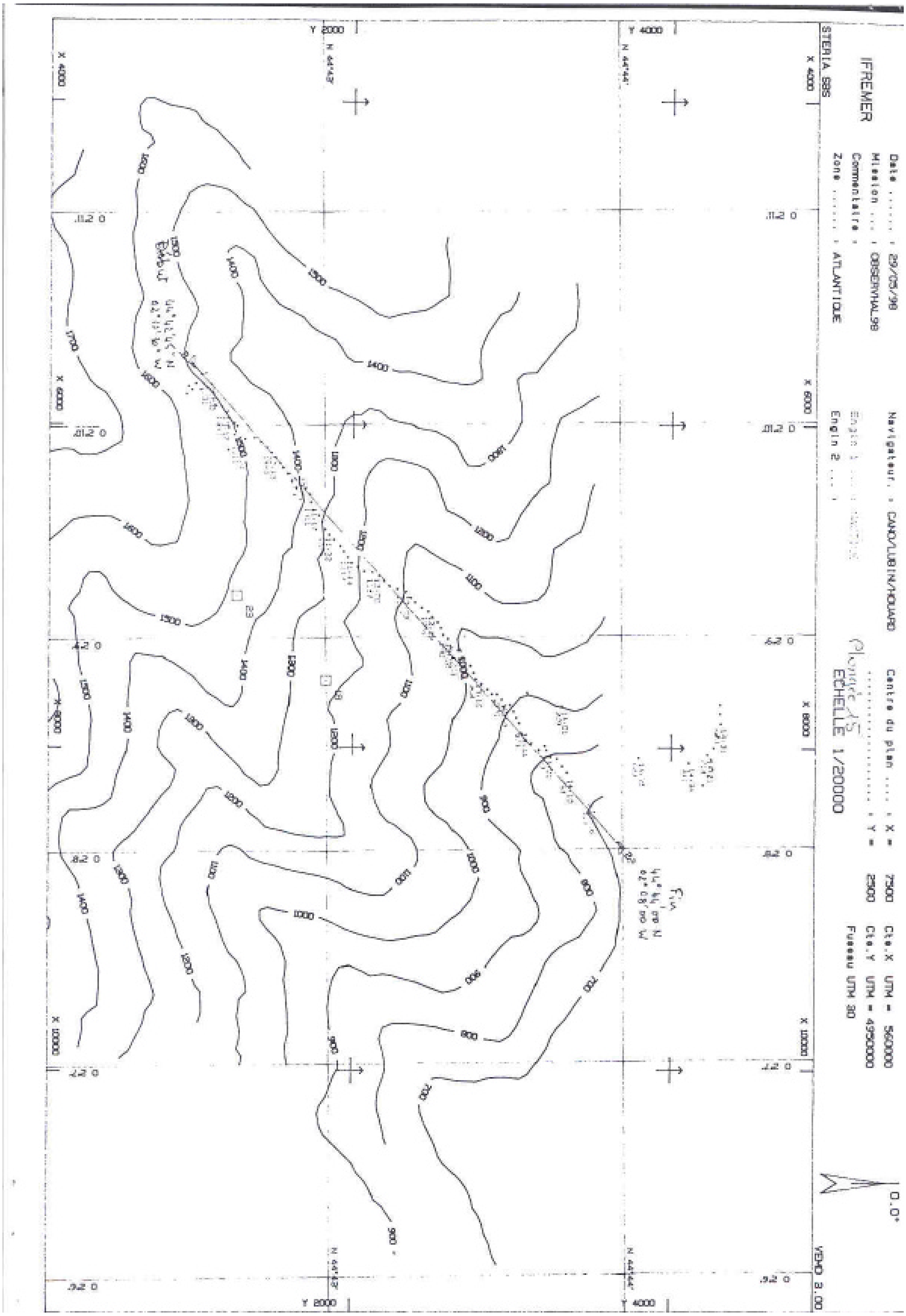
(C) **(D)**

Figure 19. (A) Deep-sea coral reef on a slope region; (B) White sponges and diverse coral fauna; (C) bottom showing the presence of several ripple marks; (D) *Trachyscorpia cristulata* beside a small rock with white sponge and sea star.

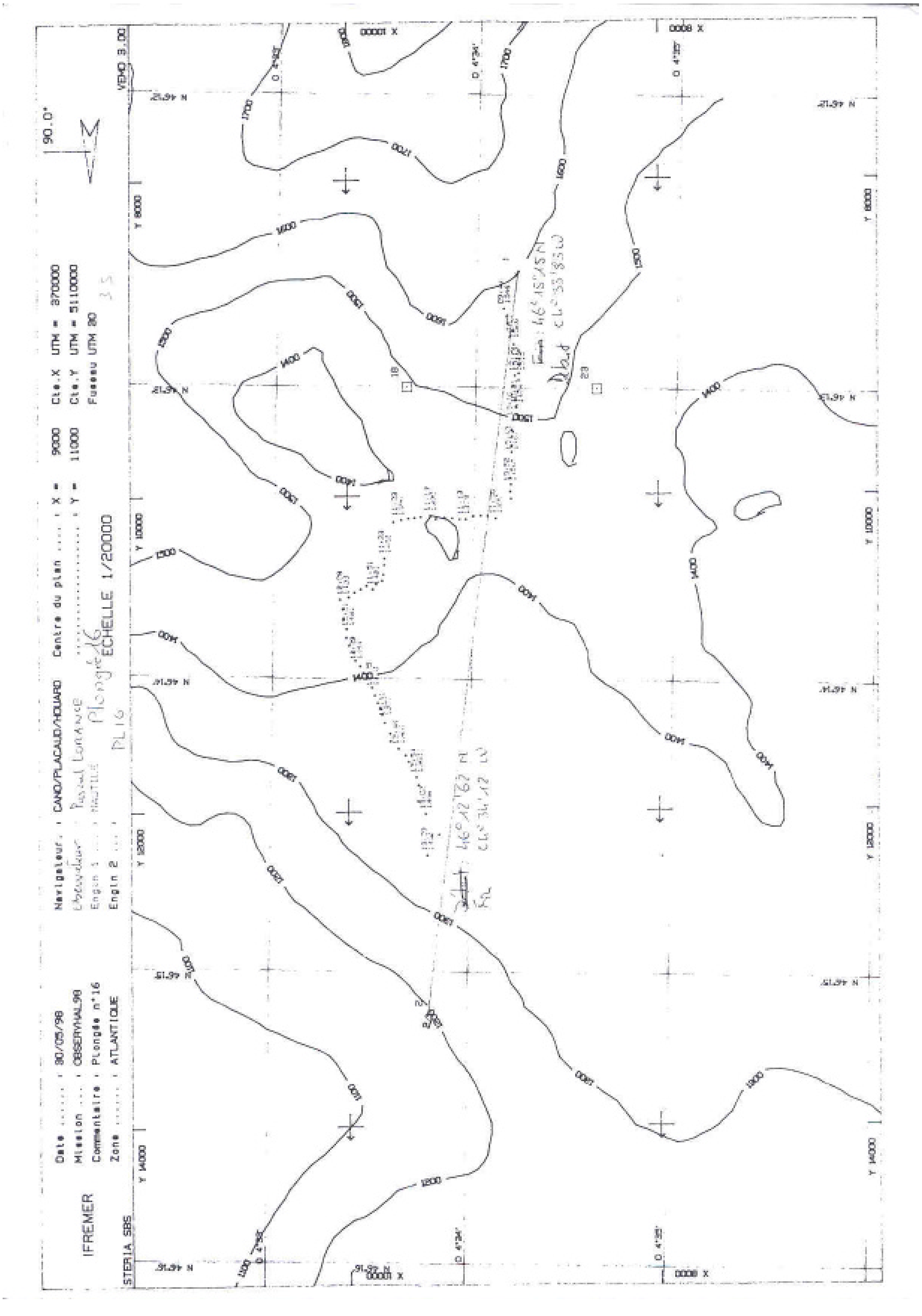
Dive transect 22



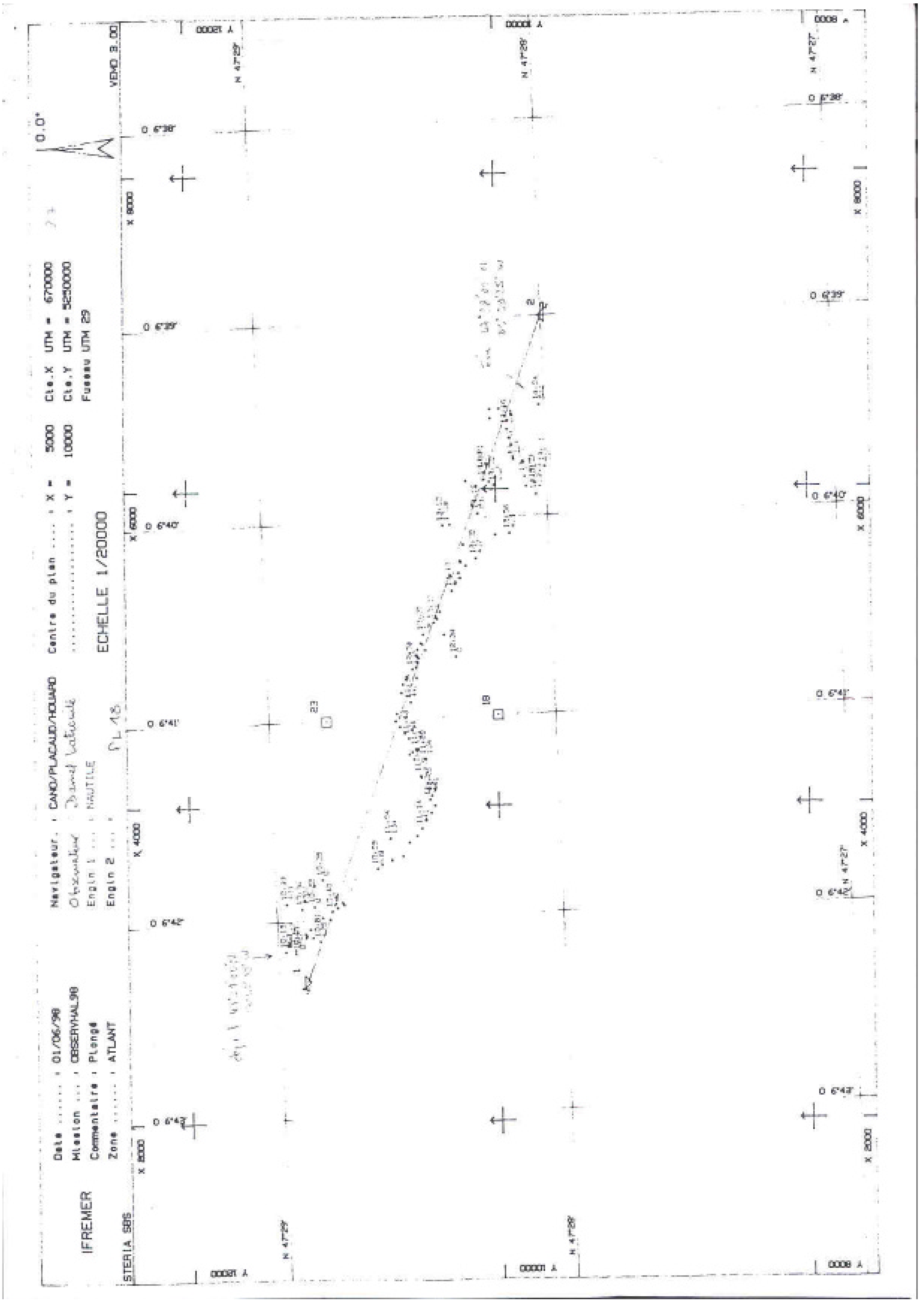
Dive transect 34



Dive transect 35



Dive transect 37



	Dive 22	Dive 34	Dive 35		Dive 37
Date	17/05/98	29/05/98	30/05/98		01/06/98
Position	47º54´N 0811´W	44º43´N 02º09´W	46º15´N 04º34´W		47º28´N 06º41´W
			(A)	(B)	
Distance crossed (meters)	3600	3800	5100	430	5270
Time (hours)	10:57-11:48	9:56-14:32	9:44-14:20	12:07-12:35	10:14- 14:20
Duration (minutes)	219	275	274	28	246
Dive conditions					
Depth (meters)	931-1301	710-1561	1153-1561	1442-1393	422-538
Dive-path inclination	Variable	High	Low	Low	Low/Medium
Bottom structure					
Bottom type	Soft sediment	Fine sediment	Hard, Highly structured	Hard, Highly structured	Soft mixed with hard, structured
Bioturbation	High	Medium	None	None	None
Ripples marks	None	Visible	Visible	Visible	None
Temporal conditions					
Current velocity ($m\ s^{-1}$)	<0.5	<0.1	0.1-1	0-0.1	0.3-0.5
Current temporal characteristics	Highly variable	Constant	Variable	Constant	Constant
Temperature range	7.185-9.578	6.232-10.373	4.730-9.100	5.06-5.59	11.057-11.403
Tide coefficient (AM/PM)[a]	66/61	89/83	77/71	77/71	53/49
Aphanopus carbo	-	-	1 [0.4]	-	-
Bathypterois sp.	1 [0.7]	11 [5.8]	-	-	-
Beryx decadactylus	-	-	-	-	10 [3.8]
Coryphaenoides rupestris	73 [50.3]	7 [3.7]	82 [32.2]	37 [172.1]	-
Galeus melastomus	-	-	-	-	30 [11.3]
Helicolenus d. dactylopterus	-	-	-	-	57 [21.5]
Hoplostethus atlanticus	1 [0.7]	3 [1.6]	24 [9.4]	351 [1632.6]	-
Lepidion eques	48 [33.1]	22 [11.6]	4 [1.6]	-	-
Merluccius merluccius	-	-	-	-	1 [0.4]
Molva molva	-	-	-	-	19 [7.2]
Mora moro	19 [13.1]	8 [4.2]	1 [0.4]	-	-
Neocyttus helgae	-	3 [1.5]	15 [5.9]	4 [18.6]	-
Notacanthus sp.	1 [0.7]	11 [5.7]	9 [3.5]	2 [9.3]	-
Phycis blennoides	-	-	-	-	46 [17.4]
Synaphobranchus kaupi	37 [25.5]	108 [56.8]	29 [11.4]	-	-
Trachyscorpia cristulata	6 [4.1]	1 [0.5]	1 [0.4]	-	-
Other fishes	43 [29.7]	66 [34.7]	94 [36.8]	16 [74.4]	56 [21]
Total fish	229 [157.9]	240 [126.3]	260 [102]	410 [1907]	219 [82.6]

[a] tide coefficient is an index of the amplitude of the astronomical tide

Table 11 – Locomotory behaviour observations on selected fish species.

Taxa	N	Swimming Mode	Orientation	Speed	Remarks
Alepocephalidae	4	Carangiform	Horizontal/Oblique	Medium	Always on the water column; far away from the bottom
Aphanopus carbo	1	Anguilliform and ostraciiform	Vertical	Slow	Rapid anguilliform movements when disturbed and ostraciiform mode when stalking
Chimaerids	15	Diodontiform and rajiform	Horizontal	Medium	Pectoral fins flapping (diodontiform/rajiform mode); strong reaction to the submersible
Synaphobranchus kaupi	27	Anguilliform	Horizontal	Variable	Low amplitude tail beats
Notacanthus *sp.*	8	Anguilliform	All	Variable	Undulating anal fin?
Galeus melastomus	4	Anguilliform	Horizontal	Slow/Medium	Wide undulations
Mora moro	6	Subcarangiform	Horizontal	Slow	Stationary on bottom
Lepidion eques	12	Subcarangiform	Horizontal	Slow	Stationary on bottom; variable
Molva molva	13	Subcarangiform	Horizontal	Variable	Mostly associated with rocky reefs
Coryphaenoides rupestris	22	Subcarangiform	Horizontal/ Oblique	Variable	Tail up; low amplitude tail beats
Neocyttus helgae	9	Balistiform	Oblique/Horizontal	Slow	Dorsal and anal fins very active; Head down; Associated with slopes and reefs of rocks and gorgonians
Hoplostethus atlanticus	15	Carangiform	Horizontal	Variable	Mostly stationary on bottom
Beryx decadactylus	8	Carangiform	Horizontal	Slow	Mostly associated with rocky reefs