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Baited camera survey of deep-sea demersal fishes of the West African oil provinces off Angola: 1200-2500m depth, East Atlantic Ocean.

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Short title: Deep-Sea fishes of the West African Margin

Abstract

Deep-sea demersal fish surveys using baited cameras were undertaken in the West African oil provinces between 1297 m and 2453 m in 2002, 2005 and 2008. A total of 29 deployments amounting to 16,175 images encountered 31 species of bait attending deep-sea fish from 17 families. The extrapolated species richness was 34, indicating that the survey encountered over 90 % of bait attending fish species in this area. The dominant species in the area were the morid *Antimora rostrata*, the synphobranchids *Synphobranchus* cf. *kaupii* and *Simenchelys parasitica*, the somniosid *Centroscymnus coelolepis* and the zoarcid *Pachycara crassiceps*. An unusually high diversity of bait attending macrourids was observed in addition to patchy aggregations of zoarcids. This study serves as baseline survey data on which to base future long-term environmental monitoring of fish populations in the vicinity of the West African oil provinces.

1. Introduction

The global demand for hydrocarbons has extended subsea oil and gas extraction into deeper waters beyond the continental shelf, a trend that is likely to continue (Walls & Clarke 2005). From an ecological context, many of these deeper and newly exploited areas are relatively unexplored, poorly known to science, and therefore cannot be assessed by extrapolation or comparison with better-known shelf areas (Gage 2001). Sound knowledge on the composition, distribution and diversity of

species assemblages in these environments is of vital importance for the long-term monitoring and maintenance of this marine ecosystem. The introduction of anthropogenic activity into poorly studied deep-sea environments has the potential to affect marine communities (Olsgrad & Gray 1995; Jones et al. 2006, 2007, Jorissen et al. 2009), therefore environmental impact surveys (EIS) are required to meet the demands of modern environmental legislation.

One such EIS series, commissioned by BP Exploration (Angola) Ltd, commenced in Licence Block 31 off West Africa to investigate the deep-sea faunal diversity in an area prior to the installation of infrastructure and subsea oil extraction. The West African Equatorial margin off the coast of the Congo and Angola has now been recognised as an important area for oil and gas exploration and production, operating in the deep sea to bathyal depths (>3000 m).

Before the current study, surveys of the offshore environment in this area were undertaken to describe the physical oceanography (Shannon & Chapman 1991, Speer et al. 1995, Larqué et al. 1997, John et al. 2004), geology (Homes et al. 1996, Uenzelmann-Neben 1997, Lavier et al. 2001, Lucazeau et al. 2003) and sediment dynamics (Bernard et al. 1999). The ZaiAngo (Savoye et al. 2009) and BioZaire (Sibuet & Vangriesheim 2009) projects undertook the first multidisciplinary geological and biological surveys to characterise the sediment and benthic community structure in the area. Benthic invertebrate communities were included in these projects (Brind'Amour et al. 2009, Galéron et al. 2009, Van Gaever et al. 2009), but no data were collected on fishes. Merrett & Marshall (1981) undertook trawl surveys of deep-sea demersal fish off the West African coast north of the equator beyond the Angola currents and there are records from neighbouring regions off Namibia (Lloris 1984, 1986), Congo, Gabon (Bianchi 1992a) and the eastern central Atlantic (Fischer et al. 1981). These and other studies off Angola by Bianchi (1992b), Tweddle & Anderson (2008) and Sobrino et al. (2012), however, predominantly focussed on shallower continental shelf regions at depths of interest to commercial fisheries (<750 m). At greater depths, more recent video surveys of demersal fauna on the Angolan margin have observed scavengers attending large fish-falls (Higgs et al. 2014) as well as fauna observed in the vicinity of asphalt mounds (Jones et al. 2014).

Here we present information on deep sea demersal fishes of the mid-bathyal slopes off Angola at depths of 1297-2453 m. Data was collected by a free fall baited lander system which attracted fish into the field-of-view of a camera (Fig. 1). The use of baited time-lapse camera systems to monitor the deep-sea mobile fauna around areas of current or proposed anthropogenic impact is recommended by the International Seabed Authority (ISA, 2002). Baited cameras can be used in topographically complex environments and therefore permit future and directly comparable observations to be made

regardless of physical obstructions due, for example, to newly installed offshore infrastructures. The aim of the survey was to catalogue the bait-attending demersal fish fauna of the study area, Licence Block 31 (Fig. 2) and to describe bathymetric patterns of species composition, sizes and relative abundances in the area. Additional deployment data from 2002 and 2005 surveys conducted in Block 31 and the neighbouring Block 18, South East of Block 31, were also integrated in this study.

2. Materials and methods

2.1 Study sites

The main study area, Licence Block 31 (~6 - 6.6°S to 10 - 11°E), lies to the south of the Congo submarine canyon on the eastern peripheral of the southern fan (Droz et al. 2003) from depths of 1300 m to 2700 m (Fig. 2). This area is situated on the boundary between the tropical waters of the Gulf of Guinea to the north and the Benguela current off the Namibian coast to the south, which results in a highly productive upwelling zone and a cyclonic gyre in the surface waters (van Bennekom & Berger 1984). The vertical water masses are stratified with the South Atlantic Subtropical Surface water down to 200 m, the South Atlantic Central Water, Antarctic Intermediate Water and the Upper Circumpolar Deep water between 200 and 1400 m. Deeper than 1400 m is the North Atlantic Deep Water punctuated by Antarctic Water through gaps in the Walvis ridge and Romanche Fracture Zone and via the Namib Col Current System (Reid 1989, Shannon & Chapman 1991, Speer et al. 1995, Larqué et al. 1997).

The main topographical feature in the region is the Congo deep-sea fan, which comprises a submarine canyon connected to the Congo River followed by a deep-sea channel (Babonneau et al. 2002, Droz et al. 2003). A large volume of particulate and dissolved organic matter is supplied to the deep waters from the Congo River from both the surface waters and near the seafloor through turbidity flows via the Congo canyon (Sibuet & Vangriesheim 2009). The river discharges an estimated 55×10^6 ton yr⁻¹ of sediment (Wetzel 1993). The influence of the Congo River outflow can be detected up to 800 km from the coast (Van Bennekom & Berger 1984, Larqué et al. 1997). The West African margin is known to host chemosynthetic environments (Bouloubassi et al. 2009, Cambon Bonavita 2009, Warén, & Bouchet 2009), deep-water coral reefs (Le Guilloux et al. 2009) and geological features such as pock marks, salt diapirs and asphalt mounds (Olu-Le Roy et al. 2007, Savoye et al. 2009, Jones et al. 2014). Annual primary productivity in surface waters in this area is estimated to be over 200 g C m⁻² yr⁻¹ (Antoine et al. 1996; Behrenfeld & Falkowski 1997).

Since these demersal fish surveys were undertaken, subsea oil extraction has commenced at both sites; Block 18 became operational in 2007, and includes two permanent scientific observatory platforms (Walls et al. 2010, Vardaro et al. 2013), and Block 31 became operational in 2012.

2.2 Data collection

The RObusT BIODiversity (ROBIO) lander is a free-fall autonomous baited camera system rated to 4000 m depth that was commissioned in 2000 by BP emerging areas and designed and constructed by Oceanlab, University of Aberdeen, UK (Jamieson & Bagley 2004). The main survey was carried out in Block 31 in April 2008 from the Gardline Survey vessel MV *Sea Trident*. The ROBIO was deployed 18 times between 1297 m and 2453 m in Block 31 (Fig. 2). In the 2008 survey, deployment sites were selected so that they were distributed evenly along the depth gradients across the study area. Similarly, the 2005 deployments were spatially randomised between 1813 and 2058 m in Block 31 (six deployments) and 1473 and 1601 m in Block 18 (two deployments) (Fig. 2). The 2002 deployments were purposely targeted at geological features; the three deployments 1, 2 and 3 were located close to a salt diaper, a pockmark and within a canyon respectively. Refer to Table 1 for information on deployment times and number of images collected for each deployment.

The lander comprised four main components; an instrument frame containing the scientific equipment; a positively buoyant vertical array of flotation packages; an expendable negatively buoyant ballast weight and an acoustically activated ballast release system. The lander was deployed from a ship and descended to the seabed in free-fall. On arrival at the seafloor, the lander performed a pre-programmed sampling regime, in this case, time lapse digital still photography and CTD measurements. At the end of the survey period the lander ballast weights were jettisoned by acoustic command from the ship initiating an ascent to the surface.

The main components of the scientific payload were the 5 mega pixel digital camera and flash system (OE14-208 and OE11-242 respectively; Kongsberg Maritime, UK). The lander in the 2005 and 2008 surveys also had an ultrasonic current meter with CTD capabilities (UCM-60; Sensortec, Norway) that recorded pressure, temperature, current velocity and current direction at 60 s intervals. The camera was pre-programmed to take an image at 60 s intervals throughout the 2008 survey. The same camera was used in the 2005 survey but owing to an older battery of lower capacity, images were taken at either 1 or 2 min intervals and deployment times were therefore either shorter or comprised fewer images. In the 2002 survey the lander was equipped with a 35 mm film camera (M5; Ocean Instrumentation, UK). This camera was set to image at 1 and 2 min interval alternately throughout the deployment. To attract fish in view of the camera, a locally sourced single skipjack tuna

(*Katsuwonus pelamis*) was used in each deployment of the 2005 and 2008 surveys, whereas in the 2002 survey, two whole mackerels (*Scomber scombrus*) were used per deployment, in both cases the weight of the bait was ~ 1kg.

The ROBIO lander was deployed in two modes: vertical and horizontal (Fig. 1). The vertical and horizontal refers to the orientation of the camera and resulting lander frame/ballast configuration. In horizontal mode the lander frame sat on a 25 mm thick 'Y'-shaped ballast plate, thus positioning the lander directly on the seafloor. The camera faced horizontally away from the lander towards bait that was positioned on a 1 m long bait arm protruding from the frame. Vertical mode had the ballast weight suspended 2 m below the frame. The main frame was therefore tethered between the ballast and buoyancy allowing the relatively small lander frame to image large areas of seafloor (and on uneven ground). The camera and flash were positioned looking vertically down with bait and a reference scale attached directly on top of the ballast (in the centre of the image). The horizontal mode imaged an area 55cm wide at the base of the field of view becoming wider to the horizon. The 2008 vertical mode images were of an area of seafloor 2.1 x 1.6 m (3.41 m²; 4:3 aspect ratio). In 2005 the field of view was 1.85 x 1.38 m (2.55 m²; 4:3 aspect ratio). The 35 mm film camera used in 2002 had a 1.95 x 1.3 m field of view (2.54 m²; 6:4 aspect ratio).

Horizontal mode produces close range images and was used for taxonomic purposes. Accurate identification to species level often requires a lateral or high-resolution image of the fish in question, which are not readily obtained from vertical photography. The vertical mode was used to observe fish communities within a standardised viewing area, in which identification to species level was possible for the more common fish present. The lander thus observed the succession and behaviour of fish species by simulating a natural food fall event. The species that intercept food falls are not necessarily obligate scavengers but potentially facultative scavengers, or predators that prey upon other fish or small scavenging crustaceans, and are therefore referred to hereafter as 'bait attending fish'.

2.3 Data analysis

All analyses were conducted post survey. Fishes were identified to the lowest possible taxonomic level from visible morphological characteristics using standard taxonomic texts for fish identification (Whitehead et al., 1984, 1986; Cohen et al., 1990). The 35 mm film from the 2002 survey, originally reported by Henriques (2004), was digitised. To avoid potential observer bias both the 2002 and 2005 images were re-analysed at the same time as the 2008 results using the same methods. Each fish in each frame from the vertical deployments were identified and counted manually. The horizontal deployments were used for species identification, behavioural observations or any details such as skin

conditions that are beyond the resolution of the vertical mode imaging. The arrival time for a given species (t_{arr}) was taken as elapsed time since touchdown of the lander until the first individual of that species appeared with the field of view. The maximum number (N_{max}) was the maximum number of simultaneous members of that species seen during each deployment. The body lengths of fish were measured using image processing software (ImageJ 1.42q, NIH, USA; Abramoff et al. 2004) calibrated against the scale bar in the field of view. Only fish from vertical mode deployments, that were adjacent to and at approximately the same altitude as the scale bar, were measured. To minimise the chance of measuring the same fish twice, species that were in high abundance were measured with a minimum of a 30 min interval between images. Fish that aggregated were measured from the image where most individuals occurred and fish that were rare and generally solitary were measured if individuality was determined by external morphology or distinguishing markings. Measurements for body lengths, t_{arr} and N_{max} were taken only from vertical deployments from the 2005 and 2008 surveys as the 2002 images were excessively dark owing to flash gun malfunction. Furthermore, the aspect ratio and field of view differed. Therefore the 2002 survey data and all horizontal deployment data were used only for calculating diversity of species.

Fish community structure was examined using Bray-Curtis similarity, based on square root transformed N_{max} for all species observed during the 2005 and 2008 deployments. Square root transformation prevented masking of species with low N_{max} by those with high N_{max} values. Hierarchical cluster analysis (hclust), using average linkage, was used to assess relative similarity between deployments. Significantly similar groups were identified using a similarity profile analysis (simprof) test using 999 permutations at the 1% similarity level. Deployment clusters based on relative similarity were visualised onto ordination plots, created using non-metric multidimensional scaling (metaMDS), with assessment of environmental vector regressions using envfit. The analyses were performed using the 'vegan' (Oksanen et al. 2008) and 'clustsig' (Whitaker & Christman 2014) packages in the R statistical environment version 3.3.1 (R Core Team 2016).

Trends in mean water temperature, salinity, current velocity as well as fish species richness per deployment were assessed in relation to depth gradients across the study area using univariate analyses. To estimate the total number of demersal fish species in the sample area, the rate of discovery of species with increasing number of lander deployments was examined. An averaged species accumulation curve was calculated for the lander data by using a randomisation procedure, in which the sample order was randomised 100 times and the mean species richness determined for each value of n (lander deployments $n = 1-29$) to produce a smoothed species accumulation curve (Colwell & Coddington 1994, Gotelli & Colwell 2001). Extrapolated species richness and its standard

error (s.e.) were estimated using the Chao estimation method (Chao 1987). These analyses were also performed using the 'Vegan' package in the R statistical programming environment.

For clarity and to facilitate comparison and avoid misinterpretation in future surveys, the fish species were sub-divided into three categories based on the number of deployments the species was encountered: frequently encountered (>20 deployments), intermediately encountered (between 5 and 20 deployment) and rarely encountered (<5 deployments).

For the 5 most frequently encountered fish species, linear regression analysis identified the role of the depth gradient in explaining the observed variation in maximum numbers (N_{max}), arrival time (t_{arr}) and body length. Both the N_{max} and t_{arr} data were square root transformed prior to the analysis to normalise and stabilise the variance. All statistical analyses were performed using R version 3.0.1 package (R Development Core Team 2013).

3. Results

3.1 Environmental data

The bottom sampling time averaged nearly 11.5 h per deployment (Table 1). The mean bottom temperature decreased linearly with depth ($n=17$, $F_{(1, 15)}=758.2$, $p<0.001$) from 4.6°C at 1297 m to 3.3°C at 2453 m (Fig. 3). Mean salinity decreased linearly with depth ($n=17$, $F_{(1, 15)}=126.3$, $p<0.001$) from 33.4 at 1297 m to 32.7 at 2453 m (Fig. 3). Mean current speed varied from 2.4 cm s⁻¹ to 11.8 cm s⁻¹ and was not correlated with depth (Fig. 3).

3.2 Fish community

Over the 18 deployments in 2008, ROBIO collected 12,215 images between 1297 m and 2453 m depth. A total of 30 species of fish were identified, spanning 16 families. The 2005 survey obtained 2331 images over 8 deployments and encountered 14 species. The three deployments in 2002 totalled 2039 images and 13 species were identified. In total 31 fish species from 17 families were identified from the 29 lander deployments (1297 to 2453 m) conducted between 2002 and 2008 in the study area (Table 2). The extrapolated species richness was 34 ± 3.2 (s.e.), indicating that this study reports ca. 91% of the bait attending fish species that can be observed using baited lander surveys in the study area (Fig. 4a). Across the study area a mean diversity of 11.7 species per deployment was found. No decrease in diversity with increasing depth was observed ($F_{(1,27)}=2.391$, $R^2=0.08$, $p=0.13$; Fig 4b).

Cluster analysis of the deployments based on V -transformed $N_{\max}$ data revealed a distinct faunal divide (Bray-Curtis dissimilarity = 60%) between 1813 and 1982 m depth. Simprof analysis revealed four significant clusters (A, B, C & D; Fig. 5). Year of deployment ($p=0.001$), depth ($p=0.001$) and current speed ($p=0.03$) were found to be a significant vectors within the ordination space. Cluster C was comprised exclusively of 2005 deployments. The deepest 2005 deployment, however, was included in cluster D with all other deep deployments. Clusters A and B included only 2008 deployments within Block 30, with cluster B comprised of the four shallowest deployments. Deployment duration was not a significant vector ($p=0.13$).

Details of the arrival times (min), maximum number present (and percentage of frames) as well as mean body lengths ($\pm$ S.D.) for all species are listed in Tables 3, 4 and 5, respectively.

3.3 Frequently encountered species

A total of five species were classified as ‘frequently encountered’: the Portuguese dogfish *Centroscymnus coelolepis* Barbosa du Bocage & de Brito Capello 1864 (Somniosidae), the subnose eel *Simenchelys parasitica* Gill 1879 (Synaphobranchidae), the cutthroat eel *Synaphobranchus cf. kaupii* spp. (Synaphobranchidae), the Blue Hake *Antimora rostrata* (Günther 1878) (Moridae), and the eelpout *Pachycara crassiceps* Roule 1916 (Zoarcidae) (Table 4; Fig. 6).

The Portuguese dogfish *Centroscymnus coelolepis* was present at all sites except two (2215 and 2453 m) and were one of the most dominant species in Block 31 (Table 4). A significant increase in arrival time ($p<0.001$; Fig. 7F; Table 3, 6) and a decrease in maximum numbers with depth was found ($p<0.001$; Fig. 7A; Table 4, 6). Mean body lengths steadily increased with depth ($p<0.001$; Fig. 7K; Table 5, 6).

The subnose eel *Simenchelys parasitica* was seen between 1297 m and 2282 m (Table 2). Body lengths increased with depth ($p<0.01$; Fig. 7L; Table 5, 6). A significant decrease in maximum numbers with depth was found ($p=0.004$; Fig. 7B; Table 4, 6). No significant depth trend in arrival time with depth was found ($p = 0.15$; Fig. 7G; Table 3, 6).

The cutthroat eels may include both *Synaphobranchus kaupii* and *S. affinis*. While differentiation between these species is possible from the position of the dorsal fin origin relative to the anal fin, the feature is highly variable and assessment of dentition is required for a positive identification (Almeida et al. 2010). Images in which both the dorsal and anal fin origin were visible on the eels did not contain individuals which were clearly *S. affinis*. *Synaphobranchu cf. kaupii* was observed at 17 of the 29

deployments (all except 2215 and 2420 m). It was the most abundant species found in the area. The peak numbers ranged from 16 to 23 between 1297 and 1800 m and ranged from one to nine at deeper deployments. Maximum numbers observed decreased significantly with depth ($p < 0.0001$; Fig. 7C; Table 4, 6). At shallower sites between 1297 m and 2112 m, it had rapid arrival times of < 5 min, but this increased to 59, 8 and 406 min at 2263 m, 2282 m and 2453 m respectively (Table 3). However, more data collected at depths $> ca. 2200$ m would be required to establish a significant depth trend in arrival time for this species (Fig. 7H). The mean body size of this species increased markedly with depth ($p < 0.001$; Fig. 7M; Table 5, 6). Some individuals as large as 120 cm were seen at deeper sites.

The Blue Hake *Antimora rostrata* was the only fish present in all of the deployments, both vertical and horizontal. Maximum numbers were between two and three < 1800 m and between four and six > 1800 m and increased significantly with depth ($p = 0.001$; Fig. 7E; Table 4, 6). Mean body length increased significantly with depth ($p < 0.001$; Fig. 7O, Table 5, 6). *Antimora rostrata* was observed regularly making contact with the bait and the horizontal camera confirmed they directly but only occasionally ate bait. No significant relationship with arrival time and depth was found ($p = 0.07$; Fig. 7J; Table 3, 6).

The eelpout *Pachycara crassiceps* Roule 1916 was recorded in 14 of the 17 vertical deployments between 1297 m and 2282 m. Across this depth range the zoarcids mean body length increased with depth ($p = 0.004$; Fig. 7N; Table 5, 6). An abnormally large aggregation was observed at 1419 m whereby numbers accumulated to a maximum of 39 individuals at ~ 10 h. Otherwise, their maximum numbers showed a trend of increase from three at 1297 m to 14 at 1800 m and then decreased to three at 2282 m. A significant decrease in maximum numbers with depth was found ($p = 0.03$; Fig. 7D; Table 4, 6). The 2005 deployments recorded zoarcids at 1803 and 2033 m in Block 31 and at 1601 m in Block 18. The relatively low numbers at 2033 m (B31) and the apparent absence at 1473 m (B18) can be attributed to short deployment times (4 h 49 min and 5 h 5 min respectively) relative to the zoarcids rate of aggregation. However, in contrast to the 2008 survey (excluding the abnormal aggregation at 1419 m), where zoarcids appeared most abundant at 1800 m, the 1803 m deployment from 2005 observed an inexplicably low number of individuals with a maximum number of two. No significant relationship between arrival time and depth were found ($p = 0.15$; Fig. 7I; Table 3, 6).

3.4 Intermediately encountered species

Seven species of fish were categorised as 'intermediately encountered fish' (observed between 5 and 19 deployments) (Fig. 8): the white head hagfish, *Myxine ios* Fernholm 1981; the small eyed rabbit fish, *Hydrolagus affinis* (Capello 1868); the West African skate, *Bathyraja aff.*

276 *hesperaficana* Stehmann 1995; as well as four species of macrourid, *Coryphaenoides marshalli*, *C.*
277 *guentheri*, *C. thelostomus* and *C. rudis*.

278 The white head hagfish, *Myxine ios*, was observed at the six stations between 1419 and 1800 m (Table
279 2). The hagfish were present in relatively small numbers (maximum numbers: 5, 8, 11, from 1419-1480
280 m and 1 thereafter). The small eyed rabbit fish *H. affinis* was seen in 16 deployments between 1451
281 m and 2453 m with maximum numbers of 1-3 individuals (Table 4). A ray, *B. aff. hesperaficana* was
282 present between 1638 m and 2453 m. All encounters with this species were of solitary individuals
283 (Table 4).

284 Four species of macrourids were seen between 5 and 20 deployments: *C. marshalli* between 1297 and
285 1638 m (max. n = 1-2); *C. guentheri* between 1297 m and 1800 m (max. n =1-5); *C. thelostomus* at
286 three stations 1982 m, 2112 m and 2282 m (max. n = 1); *C. rudis* at 2282 m and 2420 m (max. n = 1)
287 (Table 4).

288 **3.5 Rarely encountered species**

289 There were 18 species classified as being 'rarely encountered' (Fig. 9) in that they were observed in
290 fewer than 5 deployments, often observed as single individuals or in pairs.

291 Among the rarely observed species were three squalid sharks; two individual *Centrophorus squamosus*
292 (Bonnaterre 1788) at 1297 m, a solitary *Dalatias licha* (Bonnaterre 1788) at 2282 m and an extremely
293 large individual of what is tentatively identified as *Somniosus microcephalus* (Bloch & Schneider 1801)
294 observed at 1597 and 2033 m (Table 5). The body length exceeded the field of view of the camera and
295 therefore not measured.

296 The African softnose skate *Bathyraja smithii* (Müller & Henle 1841; Family: Rajidae) was seen at 1297
297 and 1452 m. Both incidences were of solitary individuals (Table 4).

298 There were three sightings of a halosaurid, *Aldrovandia* sp., at 1297 m and two at 2112 m. None of
299 them appeared to show interest in the bait and appeared to be simply swimming through the field of
300 view. The possibility of the sightings being different species of halosauridae could not be confidently
301 ascertained.

302 A bathydemersal slickhead *Alepocephalus aff. bairdii* Goode & Bean 1879 was seen in two
303 deployments; 2282 m and 2453 m (Table 4). The dorsal fins of all Alepocephalids seen were infested
304 with external parasites, possibly copepods (Fig. 9E).

305 The tripod fish *Bathypterois phenax* Parr 1928 was seen at 1927 m on the horizontal camera. It was
306 present for four minutes and sat on the seafloor with its sensory pectoral fins forward in front of its
307 head over the bait.

308 Three species of Ophidiidae (cusk-eels) were observed in the area. An individual *Bassozetus* (sp. A)
309 was present for over ~9 hr at 2453 m and observed at 2215 m. A second unidentified *Bassozetus* (sp.
310 B) was observed at the horizontal camera at 1597 m circling the lander about 1 metre distance. An
311 unidentified Ophidiid (Ophidiid A) was also seen in at 1638 m. The bythitid *Cataetyx* aff. *laticeps*
312 (Koefoed 1927) was observed in vertical images at 1601 m, 1800 m, and 1813 m and at the horizontal
313 camera at 1861 m. Each encounter was of a solitary individual lying on the bottom (although not
314 stationary) around the periphery of the field of view probably feeding on crustaceans (Saldanha 1994).

315 The Psychrolutid *Cottunculus* aff. *thomsonii* Günther 1882 was observed briefly in two of the 2002
316 deployments in Block 18 (1451 and 1477 m). On these occasions it remained stationary on the
317 periphery for three and four frames before exiting.

318 Between 1297 m and 1800 m, three species of the family Liparidae (snailfish) were observed; two
319 from the genus *Paraliparis* and one from the genus *Careproctus*. None of the liparids were observed
320 in the lander horizontal mode images and therefore identifications should be considered tentative.
321 The two species belonging to the *Paraliparis* genus are thought to be of the *Paraliparis copei* complex;
322 *Paraliparis nigellus* sp. nov. (Chernova & Møller 2008) and *Paraliparis copei wilsoni* Richards 1966
323 (pers. comm. N. Chernova). With the exception of the 1297 m site where the maximum number was
324 two, they were only present individually. *Paraliparis copei wilsoni* Richards 1966 was seen at 1419,
325 1480, 1638 and 1800 m but most prevalent at 1297 m, reaching a maximum of three.

326 A commensal relationship between an undescribed liparid of the *Careproctus* genus and the lithodid
327 crab *Lithodes ferox* (Crustacea: Lithodidae) was observed at 1452 m. Presumably the liparid laid its
328 eggs in the branchial chamber of the crab for protection, and remaining in relatively close proximity
329 (Hunter 1969, Stein 1980, Love & Shirley 1993, Somerton & Donaldson 1998, Yau et al. 2000). The
330 *Careproctus* observed in this study was 22 cm in length and appeared either attached to, or in close
331 proximity to the crab in 40 of the 56 frames (56 min) in which the crab was present. With a dorsal
332 carapace 21 cm wide by 24 cm long and mean leg length of 47 cm $\pm$ 2 S.D., this crab was abnormally
333 large for its species in this area (Abelló & Macpherson 1991, 1992).

334 Four species of macrourids were seen in the rare category (1-5 deployments). With the exception of
335 *Coryphaenoides leptolepis*, it was not possible to positively identify them. *Coryphaenoides leptolepis*

was seen between 1638 m and 2453 m (max. n = 1). *Coryphaenoides* sp. A, B and C were seen at 1297 and 1480 m, 2112 m and 2282 m, and 2453 m, respectively (Table 4).

4. Discussion

4.1 Demersal community

The fish assemblages within this area show little or no overlap with shallower studies, for example Bianchi (1992a) trawled over a million specimens comprising 354 species to a depth of 500 m of which there was no species correlation with this study. Similarly, Tweddle & Anderson (2008) recovered 1704 specimens of 277 species from 20-800 m and only the hagfish *Myxine ios* appeared in that study and the baited camera in this study. No Macrourid species were found in common between this study and sampling undertaken off Angola down to 800 m depth (Sobrinho et al. 2012). The nearest baited camera deployments to this area (Henriques et al. 2002) reported only six species at 3200-3350 m and three species at 4000 m off Cape Verde, none of which were found in this slightly shallower study. However, most scavenging fish species that were observed at manta ray carcasses found at ca. 1200 m depth in the region (Higgs et al. 2014) have been reported in this study. In addition to this, some overlap of fish species observed by ROV over soft sediments in Block 31 (Jones et al. 2014) are also reported here.

A distinct bathymetric divide was identified at ca. 1900 m depth. Several species were present in the shallower group that were not present in the deeper group, such as *M. ios*, *C. guentheri* and the *Paraliparis* spp. In addition to this, several species that reached high $N_{\max}$ in the shallower group were not observed in such high numbers in the deeper group (Table 4), including *C. coelolepis*, *S. parasitica* and *S. kaupii*. Conversely, some species appear almost exclusively in the deeper group, in particular several macrourid species, and species such as *A. rostrata* and *H. affinis* have higher $N_{\max}$ compared to the shallower group. In some cases the reason for the differences between the two groups relate to the depth range of certain species, as in the case of *M. ios*. In addition to depth there may be other environmental factors, such as oxygen concentration, that influence the structure of the faunal community. Some evidence for temporal variation was found within the < 1900 m sites, with deployments undertaken in autumn 2005 forming a distinct group from the spring 2008 deployments. However, further sampling would be required to determine the differences resulting from seasonal and inter-annual variation. Seasonality in the production of phytoplankton at the sea surface creates a seasonal pulse in the flux of organic material to deeper waters (Rowe 2013). Inter-annual variation in primary production will also influence the availability of food in the deep, influencing the amount

and type of prey available to demersal fishes. In the sampled region off Angola, a major factor driving temporal variation is likely to be fluctuation in the Congo River outflow (Spencer et al. 2016).

The environmental conditions of the West equatorial African margin appear to support a rich and diverse fish assemblage. Observing 31 species of fish using a baited camera represents a relatively large faunal community compared with other deep-sea baited camera work (Priede et al. 2010). This is, however, enhanced by the comparatively larger number of deployments across a relatively small depth range. By comparison to better known deep Atlantic sites such as the Porcupine Sea Bight, Porcupine Abyssal Plain (Priede et al. 2010) and the Mid-Atlantic Ridge (King et al. 2006), the bathyal bait-attending fish diversity off Angola appears high. Priede et al. (2010) reported that of the 108 demersal fish species, 22 are known to attend baited cameras, however this study does incorporate a wider depth range of 240 to 4865 m (a total range of 4625 m). On the Mid-Atlantic Ridge (MAR), the same lander used in this study was deployed 17 times and observed 22 species, again over a wider depth range of 924 to 3420 m (a total of 2496 m; King et al. 2006). The comparative species accumulation curves shown in Figure 4A show the higher rate of species discovery per unit effort observed on the Angolan margin, despite the reduced depth range (1156 m). Extracting data from the MAR study for the equivalent depth range to this study results in a total of 19 species over nine deployments. Similarly, extracting the equivalent depth data from Priede et al. (2010) there are 15 species known in the Atlantic over seven deployments.

The high diversity of bait-attending species in our study can partly be attributed to a large number of rarities accumulated as a result of a high sample number: 58 % of species (18 species) were observed in less than five deployments whereas 26 % of species (8 species) were observed from 5 to 20 deployments and 16 % (5 species) were observed in 20 deployments or more. By examining the feeding strategies of each species a clear trend appears. The most dominant species, which tend to arrive first with greater maximum numbers, were scavengers (Fig. 6), whereas the rare species, that arrive later in lower numbers, were indifferent to the bait (Fig. 9). Indeed only 32 % (10 species) were scavengers compared to 26 % of species (eight species) which appeared to prey upon small crustaceans. Forty two % of species observed (13 species) were indifferent and therefore are perhaps simply chance observations.

By examining the most frequently encountered species and species specific bathymetric ranges, it is clear from this survey that the dominant and key species in this area are *Antimora rostrata*, *Synaphobranchus* cf. *kaupii*, *Simenchelys parasitica*, *Centroscymnus coelolepis*, and *Pachycara crassiceps*. Other species such as *Bathyraja* sp. and *Hydrolagus affinis* are quite conspicuous but given

their tendency to arrive in single numbers, presence or absence in future surveys could be misinterpreted. Caution must also be taken in the use of the Zoarcid *P. crassiceps* as a key species, as their maximum number and arrival times are entirely dependent on deployment duration owing to their aggregating behaviour (Table 7). Short deployments (as was the case in some of the 2005 deployments) under represent this species. We therefore recommend that *A. rostrata*, *S. kaupii*, *S. parasitica* and *C. coelolepis* are sufficiently dominant to be interpreted as key species in future environmental surveys in this area.

Increasing the number of deployments to accumulate further species encounters will simply add more rarities to the range of species observed. Comprehensively cataloguing every species in the area is of course a useful exercise from a marine census perspective, and more useful in terms of other sampling methods, such as trawl surveys. However, these rarities are not especially functional in the long-term monitoring of fish populations using baited cameras, as they represent unpredictable chance encounters from which few conclusions can be drawn. For example, the absence of the tripod fish *Bathypterois phenax* from a future baited camera survey from the same season will not indicate its extinction from the area as it was only seen in 4 out of 12215 images from the 2008 survey. Whereas any future absence from a baited camera survey of the eel *Synaphobranchus* cf. *kaupii* which was seen in 4920 out of 12215 images, will surely indicate a significant shift in the scavenging community, and will therefore require immediate attention. Based on the findings reported here, a reasonable recommendation for future baited camera surveys would be at least 10 deployments, evenly spread over a similar depth range of approximately 1200 – 2200 m. Ten deployments appear sufficient to observe the most conspicuous fishes at an adequate range of depths and at a frequency on which conclusions can be drawn.

4.2 The Zoarcid anomaly

The zoarcids are one of the more successful fish to inhabit muddy bottoms of continental shelves and slopes of boreal regions (Anderson 1994). In the 2008 survey, the zoarcids peaked at 1800 m, with lower numbers at the shallower and deeper sites, with none present at the deepest two sites. Arrival patterns were consistent at all sites present; a continuous increase in numbers with low fluctuations in the number of individuals, indicating long residence times (an aggregation). This pattern is typical of zoarcids at baited landers (Witte 1999, Janßen et al. 2000, Kemp et al. 2008; Table 7).

In contrast to this general trend was an abnormally large aggregation at 1419 m where the maximum number of aggregating zoarcids was 39 over a deployment lasting 12 h. The arrival pattern was typical for zoarcids but at a much greater aggregation rate. At this site the aggregation rate was 3.9 ind.h⁻¹

compared to 0.1-1.4 ind.h⁻¹ at other depths (our study, Witte 1999, Janßen et al. 2000, Kemp et al. 2008). Lander experiments using larger or multiple baits have shown zoarcids taking up temporary residence in ever increasing numbers after relatively long arrival times (>3 h ; Witte 1999, Janßen et al. 2000, Kemp et al. 2008). Both Janßen et al. (2000) and Witte (1999) observed aggregations of ~15-20 individuals after 24 h and ~40 individuals after 48 h at the same site one year apart whilst lower numbers at neighbouring sites at similar depths (~4000 m) were observed. This suggests that zoarcid populations are permanently denser in some areas than others inferring a specific habitat driven distribution rather than a uniform distribution.

The lifestyle characteristics and general traits are thought to be uniform in Zoarcidae (Brodte et al. 2006). Although some zoarcids are thought to directly consume bait (Witte 1999), benthic fauna are their main prey (McAllister et al. 1981, Houston & Haedrich 1986), particularly small crustaceans such as amphipods (Ferry 1997, Janßen et al. 2000, Lipski 2001, Sancho et al. 2005). In our study there is little evidence to suggest that the zoarcids were consuming bait and their posture and distribution around the bait favours a grazing predatory strategy. Zoarcid fishes are commonly found in sulfide-rich habitats such as mud volcanoes (Milkov et al. 1999), hydrothermal vents and cold seeps (Rosenblatt & Cohen 1986, Sibuet & Olu, 1998, Biscoito et al. 2001, 2002, Shillito et al. 2008) and are even thought to play a significant role in determining the biological structure of vent habitats (Sancho et al. 2005). Dense populations of benthic zoarcids are known to occur around pockmarks (Hovland et al. 2005) which, are common to this study site (Olu-Le Roy et al. 2007, Savoye et al. 2009).

The number of zoarcids aggregating at 1419 m in our study far exceeds any other deployment and even that of the larger baits in previous studies over the same time period (Witte 1999, Janßen et al. 2000, Kemp et al. 2008) which, could suggest that this unusually dense population is a result of its proximity to a habitat feature such as a pockmark. However, there are no pockmarks known to exist closer to that site than any of the surrounding sites (unpublished data, BP) and this site and the 1297 m, 1452 m, 1480 m and 1638 m sites are all within a 20 km radius of each other. Furthermore, the 1477 m deployment from 2002 was directly on top of a pockmark and obtained just 21 sightings of individual zoarcids over 15 h, entirely contradictory to a pockmark preference. Likewise, the 2002 deployment on a salt diaper showed a low number of zoarcids relative to the 2008 survey despite longer deployment durations. Therefore this large aggregation may be attributable to either uncharted geological features (e.g. a cold seep) or an ephemeral habitat such as a whale fall. There are some reports of zoarcids associating themselves with whale-falls (Goffredi et al. 2004, Lundsten et al. 2010). The West African margin is also known to host a variety of large cetaceans (Weir 2007, 2008) and is a humpback whale over-winter breeding ground (Best et al. 1995). Areas of deep-water

underlying whale migration corridors increase the likelihood of ephemeral whale fall habitats (Smith & Baco 2003), which would not appear in geological surveys. The extremely large aggregation at 1419 m may therefore be a chance landing in close proximity to an unknown geological or larger biological feature such as a whale or other large food fall, such as those found in the area by Higgs et al. (2014). Either way it is important for future surveys to account for considerable patchiness of Zoarcidae to prevent the overestimation of populations at a given depth.

The behaviour of zoarcids should be considered in future surveys as the results are greatly affected by deployment duration and population patchiness. Had the 2008 survey simply deployed at 1419, 1800 and 2453 m a reasonable conclusion of extremely high to low to zero densities across these depths could have been reached, which clearly is not the case. Similarly, using maximum numbers as a proxy for abundance does not apply to zoarcids as their maximum number is subject to deployment duration. The short durations of the 2005 surveys yielded far lower numbers and the numbers observed using larger baits over longer durations show even higher numbers (Witte 1999, Janßen et al. 2000,).

4.3 Macrourid diversity

In the West Equatorial African margin, Tweddle & Anderson (2008) reported that no macrourids were recovered from trawling between 20-800 m, Bianchi (1992ab) found three macrourid species shallower than 500 m, and Sobrino et al. (2012) reported 11 trawled macrourid species to a depth of 750 m. However, none of these reported species were found in the present study. The most comprehensive data set on which to compare is that of Merrett & Marshall (1981) who reported on 4600 specimens of 148 species between 261 and 6059 m off the coast of northwest Africa. In our study the macrourids are tentatively attributed to eight species all belonging to the *Coryphaenoides* genus whereas Merrett & Marshall (1981) recorded 26 macrourids, of which 15 were found at the equivalent depth range of our study. Of those 26 macrourids, 12 were *Coryphaenoides*, with seven *Coryphaenoides* whose depth ranges matched the depths of this study. The only cross correlated species between our study and Merrett & Marshall (1981) are *C. lepolepis*, *C. guentheri* and *C. rudis* (the latter documented by Merrett & Marshall (1981) as *C. macrocephalus*). In addition to these, three macrourids were unidentifiable from the images.

Aside from specific identification, the diversity of macrourids attending the baited camera appears unusually high. Using the same lander vehicle as in our study, King et al. (2006) found two species (*Coryphaenoides armatus* and one unidentified *Coryphaenoides*) and some unidentified juveniles from 1124 to 3420 m on the Mid-Atlantic Ridge. Similarly, King et al. (2008) reported only one macrourid

(*Trachyrincus scabrus*) slightly shallower (911-920 m) and only *Coryphaenoides armatus* slightly deeper (3455 to 4437 m). Priede et al. (2010) reported just two baited camera attending macrourids (*Coryphaenoides armatus* and *Trachyrincus* sp.) across the Porcupine Sea Bight and Abyssal Plain (NE Atlantic) of which there are 17 macrourid species known from trawl sampling (11.7 % of macrourid species attended the baited lander). By using the nearest comparable trawl data to this study area (Merrett & Marshall 1981), where 15 macrourids were trawled from equivalent depths to our study, then 53 % of the macrourids attended the baited lander.

5. Conclusion

These survey results suggest that to truly categorise bait-attending fish assemblages using baited cameras then a high number of deployments will yield the best results as they are numerous rarely seen species that may not be observed from limited observations. However the number of achievable deployments is in reality driven by time and cost limitations and achieving greater than, for example, 30 deployments would require significant financial backing and effort probably beyond the resources available in the oil provinces when prioritised against industrial activity. One solution would be to deploy multiple camera vehicles simultaneously, but again at further financial cost and with additional issues surrounding multiple odour plumes interacting with one another. In the framework of providing useful and comprehensive environmental surveys to provide a baseline on which to draw conclusions and apply policy, it is the identification and quantification of key species that is important, in this case *Antimora rostrata*, *Synaphobranchus* cf. *kaupii*, *Simenchelys parasitica* and *Centroscymnus coelolepis*. Although the zoarcid *Pachycara crassiceps* represents a dominant bait-attending fraction, their tendency to aggregate over time and their apparent patchy distribution is vulnerable to misrepresentation and must therefore be interpreted with caution. Another major dominant fraction is the macrourid family which are not as readily identified from photography as most other families (Jamieson et al. 2012). To accurately identify each species of macrourid and ultimately resolve macrourid diversity in the area, a collection campaign for voucher specimens via trawling or traps is paramount to create a baseline archive of specimens on which to interpret images in the future. In the presence of complex sub-sea infrastructure, traps (including cameras) would pose the most ideal solution compared to bottom trawling, however catch rates are lower. Therefore, comparative trawling campaigns may have to take place on the periphery of the oil provinces. Alternatively this may be the ideal application in which to adopt environmental DNA methods (e.g. Thomsen et al., 2016). In conclusion, this study provides useful baseline data in a poorly studied deep-water environment in the midst of industrialisation and provides information on little known fish assemblages present at depths where scientific research capabilities are limited.

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745

Fig. 1. Two operational modes of the ROBIO lander. Horizontal mode (a); sitting directly on the seafloor with camera and flash facing horizontally out over baited area. Vertical mode (b); the lander is tethered 2-metres above its ballast and bait with camera and flash focused vertically downwards. The white and yellow arrows represent the camera and flash optical paths respectively.

Fig. 2. Map of the study site off West Africa with deployments marked: 2008 (circles), 2005 (Triangles) and 2002 (Squares). Latitude ($^{\circ}$ S) and longitude ($^{\circ}$ E). Black symbols represent vertical deployments, white represent horizontal deployments.

Fig. 3. Environmental data from Block 31 (squares) and 18 (triangles) surveys: mean temperature, salinity and current speed.

Fig. 4. A Species accumulation curve for bait attending fish in the West African oil provinces (Depth range: 1419 to 2453 m) (solid line) with comparative curves for the Mid-Atlantic Ridge (Depth range: 924 to 3420 m; King et al. 2006) (dashed line) and the NE Atlantic (Depth range: 240 to 4865 m; Priede et al. 2010) (dotted line). **B** Total number of species observed as a function of depth from Block 31 (squares) and 18 (triangles).

Fig. 5. Output from hierarchical cluster analysis with $\sqrt{v}$ -transformed maximum numbers ($N_{\max}$). **A** Bray-Curtis dissimilarity dendrogram, with clusters A, B, C and D indicated. **B** NMDS ordination plot with 95% confidence ellipses for clusters A, B, C and D. Significant environmental vectors are shown, with arrows pointing to the direction of most rapid change and the length of the arrow proportional to the correlation between the ordination and the environmental variable.

771

772 **Fig. 6.** Frequently encountered species. **A** *Centroscyrnus coelolepis*, **B** *Synaphobranchus* cf. *kaupii*, **C**
 773 *Antimora rostrata*, **D** *Pachycara crassiceps*, **E** *Simenchelys parasitica*.

Fig. 7. A-E Linear regression analysis of $\sqrt{N_{\max}}$ with depth for the five most frequently encountered species. F-J Linear regression analysis of $\sqrt{t_{\text{arr}}}$ with depth for these species. K-O Linear regression analysis of mean body length with depth for these species. Solid lines show linear regression where significant with 95% confidence intervals (dotted lines).

780

781 **Fig. 8.** Intermediately encountered species. **A** *Myxine ios*, **B** *Bathyraja aff. hesperaficana*, **C**
 782 *Hydrolagus affinis*, **D** *Coryphaenoides marshalli*, **E** *Coryphaenoides guentheri*, **F** *Coryphaenoides*
 783 *thelastomus* **G** *Coryphaenoides rudis*.

784

785 **Fig. 9.** Rarely encountered species. **A** *Dalatias licha*, **B** *Centrophorus squamosus*, **C** *Somniosus*
 786 *microcephalus*, **D** *Bathyraja* aff. *smithii*, **E** *Alepocephalus* aff. *bairdii*, **F** *Aldrovandia* sp. **G** *Bathypterois*
 787 *phenax* **H** *Bassozetus* sp. A, **I** *Cottunculus* aff. *thomsonii*, **J** *Bassozetus* sp. B, **K** *Cataetys* aff. *laticeps*, **L**
 788 *Paraliparis copei wilsoni*, **M** *Paraliparis nigellus* **N** *Careproctus* sp. with litholid crab **O** *Coryphaenoides*
 789 *leptolepis* **P** macrourid A, **Q** macrourid B, **R** macrourid C.

DEP#	Station#	Date	Block	Latitude (°E)	Longitude (°S)	Depth (m)	Lander mode	Bottom time (hh:mm)	Total image #	Camera Interval (min)
2008 Survey										
1	R-12	20-Apr	31	11.06810	6.60643	1297	V	10:14	614	1
2	R-01	30-Mar	31	11.03082	6.62542	1419	V	11:54	715	1
3	R-05	19-Apr	31	10.97080	6.42764	1452	V	10:51	651	1
4	R-11	31-Mar	31	11.12652	6.83899	1480	V	12:03	723	1
5	R-T1	01-Apr	31	10.99999	6.82045	1597	H	12:09	729	1
6	R-02	02-Apr	31	10.89213	6.67115	1638	V	13:31	811	1
7	R-T9	18-Apr	31	10.85659	6.41574	1684	V	10:34	634	1
8	R-T14	13-Apr	31	10.79151	6.10660	1800	V	11:20	680	1
9	R-T10	14-Apr	31	10.68335	6.40499	1927	H	10:59	659	1
10	R-03	04-Apr	31	10.78582	6.79989	1982	V	15:20	918	1
11	R-06	12-Apr	31	10.63607	6.12361	2070	H	12:01	721	1
12	R-04	05-Apr	31	10.73853	6.81492	2112	V	14:01	841	1
13	R-T4	16-Apr	31	10.69692	6.68699	2215	H	01:26	86*	1
14	R-10	06-Apr	31	10.60997	6.79525	2263	V	14:02	842	1
15	R-08	11-Apr	31	10.50427	6.19192	2282	V	11:58	718	1
16	R-09	10-Apr	31	10.47751	6.28068	2410	H	12:45	765	1
17	R-T15	15-Apr	31	10.63054	6.52258	2420	V	05:24	324*	1
18	R-T16	09-Apr	31	10.55110	6.49770	2453	V	13:04	784	1
2005 Survey										
1	RO1	20- Oct	18	11.85341	7.82839	1473	V	05:05	305	1
2	RO3	24- Oct	18	11.94324	7.95699	1601	V	08:46	263	2
3	RO5	29- Oct	31	10.65272	6.22396	1813	V	05:58	358	1
4	RO7	02-Nov	31	10.78573	6.21467	1861	H	06:24	384	1
5	SV9	28- Oct	31	10.71788	6.15287	1964	H	06:48	204	2
6	RO4	26- Oct	31	10.73776	6.25721	2033	V	11:20	340	2
7	PO1	26- Oct	31	10.68768	6.30342	2001	H	02:24	144	1
8	RO6	31- Oct	31	10.74761	6.31134	2058	H	11:06	333	2
2002 Survey										
1	501	04-Feb	18	12.00337	7.91142	1451	V	14:00	565	1-2 altn
2	502	06-Feb	18	12.06503	7.91854	1477	V	18:11	728	1-2 altn
3	504	08-Feb	18	12.30979	7.99063	1442	V	18:38	746	1-2 altn

791 **Table 1.** Deployment details of the baited camera deployments. * indicates technical fault resulting
792 in reduced number of images. 'atln' indicates images were taken at 1 and 2 minute intervals
793 alternately. Lander mode: Vertical (V); Horizontal (H).

Order	Family	Species	Authority	Max./Min. Depth (m)	Mean Length (cm) (± S.D.)
Myxiniformes	Myxinidae	<i>Myxine ios</i> ^a	Fernholm 1981	1419-1800	43± 15
Chimaeriformes	Chimaeridae	<i>Hydrolagus affinis</i> ^a	(de Brito Capello 1868)	1638-2453	122±18
Squaliformes	Centrophoridae	<i>Centrophorus squamosus</i> ^c	(Bonnaterre 1788)	1297	121±12
	Somniosidae	<i>Somniosus microcephalus</i> ^c	(Bloch & Schneide, 1801)	1597-2058	461
		<i>Centroscymnus coelolepis</i> ^a	Barbosa du Bocage & de Brito Capello 1864	1297-2420	58±12
		<i>Dalatia licha</i> ^c	(Bonnaterre 1788)	2282	104
Rajiformes	Rajidae	<i>Bathyraja aff. smithii</i> ^b	(Müller & Henle 1841)	1297-1452	69±6
		<i>Bathyraja aff. hesperaficana</i> ^b	Stehmann, 1995	1638-2453	113±24
Elopiformes	Halosauridae	<i>Aldrovandia</i> sp. ^c	-	1297-2212	30±10
Anguilliformes	Synphobranchidae	<i>Simenchelys parasitica</i> ^a	Gill 1879	1297-2282	43±7
		<i>Synphobranchus</i> cf. <i>kaupii</i> ^a	Johnson 1862	1297-2453	62±20
Argentiniformes	Alepocephalidae	<i>Alepocephalus</i> aff. <i>bairdii</i> ^b	Goode & Bean 1879	2282-2453	74±1
Aulopiformes	Ipnopidae	<i>Bathypterois phenax</i> ^b	Parr 1928	1927	-
Gadiformes	Macrouridae	<i>Coryphaenoides marshalli</i> ^c	Iwamoto 1970	1297-1638	53±9
		<i>Coryphaenoides guentheri</i> ^c	(Vaillant 1888)	1297-1861	54±6
		<i>Coryphaenoides leptolepis</i> ^a	Günther 1877	1638-2453	54±9
		<i>Coryphaenoides thelestomus</i> ^a	Maul 1951	1861-2410	107±15
		<i>Coryphaenoides rudis</i> ^a	Günther 1878	1831-2282	97±23
		Macrourid A ^c	-	1297-1480	44±7
		Macrourid B ^c	-	2070-2282	-
		Macrourid C ^c	-	2453	-
	Moridae	<i>Antimora rostrata</i> ^a	(Günther 1878)	1297-2453	49±9
Ophidiiformes	Ophidiidae	<i>Bassozetus</i> sp. A ^c	-	2215-2453	53
		<i>Bassozetus</i> sp. B ^c	-	1597	-
		<i>Ophidiid</i> A ^c	-	1638-1813	48±11
	Bythitidae	<i>Cataetys</i> aff. <i>laticeps</i> ^c	(Koefoed 1927)	1601-1861	53±1
Scorpaeniformes	Psychrolutidae	<i>Cottunculus</i> aff. <i>thomsonii</i> ^c	Günther 1882	1451-1477	-
	Liparidae	<i>Careproctus</i> sp. ^c	-	1452	22
		<i>Paraliparis copei wilsoni</i> ^b	Richards 1966	1297-1800	18±4
Perciformes	Zoarcidae	<i>Paraliparis nigellus</i> ^b	Chernova and Møller 2008	1297-1452	27±4
		<i>Pachycara crassiceps</i> ^b	Roule 1916	1297-2410	48±15

Table 2: List of species observed by the ROBIO lander in the 2002, 2005 and 2008 fish surveys of Block31 and Block 18 in the West Equatorial African Margin derived from both the horizontal and vertical imaging. Scavengers, predators and ‘unknown from this study’ and denoted by a, b and c respectively.

	Depth (m)																
Species	1297	1419	1452	1473	1480	1601	1638	1684	1800	1813	1982	2033	2112	2263	2282	2420	2453
<i>Myxine ios</i>	-	86	45	-	27	-	165	303	258	-	-	-	-	-	-	-	-
<i>Hydrolagus affinis</i>	-	-	-	-	-	-	384	-	247	-	28	-	510	82	288	68	371
<i>Centroscymnus coelolepis</i>	13	11	9	87	5	16	5	5	34	82	21	38	144	570	467	183	-
<i>Centrophorus squamosus</i>	121	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Dalatia licha</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	662	-	-
<i>Bathyraja aff. smithi</i>	174	-	147	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bathyraja aff. hesperaficana</i>	-	-	-	-	-	-	392	-	-	-	164	150	46	161	225	76	218
<i>Alrovandia sp.</i>	8	-	-	-	-	-	-	-	-	-	-	-	40	-	-	-	-
<i>Simenchelys parasitica</i>	105	28	228	166	123	122	58	58	2	38	128	-	318	-	442	-	-
<i>Synaphobranchus cf. kaupii</i>	4	3	4	4	3	1	3	3	0	6	4	10	3	59	8	-	406
<i>Alepocephalus aff. bairdii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	378	-	42
<i>Coryphaenoides marshalli</i>	10	250	57	-	141	-	114	-	-	-	-	-	-	-	-	-	-
<i>Coryphaenoides guentheri</i>	29	58	13	35	102	-	253	89	50	-	-	-	-	-	-	-	-
<i>Coryphaenoides leptolepis</i>	-	-	-	-	-	-	336	219	18	-	16	-	40	-	66	23	712
<i>Coryphaenoides thelostomus</i>	-	-	-	-	-	-	-	-	-	-	84	-	467	-	375	-	-
<i>Coryphaenoides rudis</i>	-	-	-	-	-	-	-	-	-	388	-	-	-	-	222	81	-
<i>Macrourid A</i>	88	561	117	-	660	-	-	-	-	-	-	-	-	-	-	-	-
<i>Macrourid B</i>	-	-	-	-	-	-	-	-	-	-	-	-	541	-	619	-	-
<i>Macrourid C</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	19
<i>Antimora rostrata</i>	9	47	39	64	66	1	185	147	53	1	14	5	7	4	8	7	14
<i>Bassozetus sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	168
<i>Unidentified Ophidiid</i>	-	-	-	-	-	-	305	-	-	114	-	-	-	-	-	-	-
<i>Cataetys aff. laticeps</i>	-	-	-	-	-	122	-	-	237	178	-	-	-	-	-	-	-
<i>Careproctus sp.</i>	-	-	590	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paraliparis copei wilsoni</i>	63	52	-	-	102	-	63	-	1	-	-	-	-	-	-	-	-
<i>Paraliparis nigellus</i>	325	50	248	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pachycara crassiceps</i>	138	141	301	-	50	32	135	180	28	232	188	247	30	481	402	-	-

801 **Table 3.** Arrival times (min) of species attracted to bait between 1297 m and 2453 m in the West African Oil provinces. All data taken from
802 vertical deployments from the 2005 and 2008 surveys.

	Depth (m)																
Species	1297	1419	1452	1473	1480	1601	1638	1684	1800	1813	1982	2033	2112	2263	2282	2420	2453
<i>Myxine ios</i>	-	5 (44.3)	8 (43.9)	-	11 (57.1)	-	1 (1.7)	1 (3.5)	1 (7.8)	-	-	-	-	-	-	-	-
<i>Hydrolagus affinis</i>	-	-	-	-	-	-	1 (0.98)	-	1 (2.5)	-	2 (15.5)	-	1 (5.74)	2 (12.46)	3 (17.37)	2 (25)	1 (2.38)
<i>Centroscymnus coelolepis</i>	6 (62.9)	9 (52.6)	6 (53.3)	2 (21.1)	8 (69.5)	1 (5.3)	6 (47.5)	7 (32.6)	6 (35.6)	5 (14.9)	2 (16.4)	1 (1.0)	2 (11.2)	1 (0.3)	2 (7.6)	1 (5.2)	-
<i>Centrophorus squamosus</i>	1 (0.33)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Dalatia licha</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1 (1.96)	-	-
<i>Bathyraja aff. smithi</i>	1 (0.49)	-	1 (1.08)	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bathyraja aff. hesperaficana</i>	-	-	-	-	-	-	1 (0.84)	-	-	-	1 (1.26)	1 (3.4)	1 (0.14)	1 (0.42)	1 (1.68)	1 (1.23)	1 (0.84)
<i>Alrovandia sp.</i>	1 (0.49)	-	-	-	-	-	-	-	-	-	-	-	1 (0.28)	-	-	-	-
<i>Simenchelys parasitica</i>	2 (11.4)	3 (8.8)	2 (6.3)	2 (17.2)	3 (21.4)	2 (5.3)	5 (40.2)	5 (42.6)	6 (41.9)	7 (24.4)	1 (3.2)	-	2 (16.8)	-	1 (1.7)	-	-
<i>Synaphobranchus cf. kaupii</i>	21 (92.5)	25 (93.7)	16 (97.2)	11 (95.5)	22 (97.2)	13 (98.1)	23 (88.1)	19 (66.9)	22 (67.2)	11 (38.4)	5 (35.5)	2 (30.7)	9 (44)	2 (7.6)	3 (31)	-	1 (1.3)
<i>Alepocephalus aff. bairdii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1 (0.42)	-	1 (2.1)
<i>Coryphaenoides marshalli</i>	2 (11.4)	1 (2.5)	2 (4.8)	-	1 (0.3)	-	1 (0.3)	-	-	-	-	-	-	-	-	-	-
<i>Coryphaenoides guentheri</i>	5 (45.2)	2 (8.4)	4 (35.5)	1 (1.6)	1 (2.5)	-	1 (0.1)	1 (1.3)	1 (0.4)	-	-	-	-	-	-	-	-
<i>Coryphaenoides leptolepis</i>	-	-	-	-	-	-	1 (3.6)	1 (0.9)	1 (1.5)	-	1 (0.1)	-	2 (3.4)	-	1 (1.8)	2 (9.0)	1 (0.3)
<i>Coryphaenoides thelostomus</i>	-	-	-	-	-	-	-	-	-	-	1 (1.7)	-	1 (4.8)	-	1 (0.4)	-	-
<i>Coryphaenoides rudis</i>	-	-	-	-	-	-	-	-	-	1 (1.2)	-	-	-	-	1 (4)	1 (1.5)	-
<i>Macrourid A</i>	1 (0.7)	1 (0.3)	1 (1.4)	-	1 (0.1)	-	-	-	-	-	-	-	-	-	-	-	-
<i>Macrourid B</i>	-	-	-	-	-	-	-	-	-	-	-	-	1 (0.1)	-	1 (0.6)	-	-
<i>Macrourid C</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1 (0.4)
<i>Antimora rostrata</i>	3 (32.5)	2 (14.4)	2 (11.5)	3 (23.1)	2 (7.7)	1 (7.1)	3 (25.9)	3 (14.5)	3 (16.2)	2 (13.7)	5 (47.2)	2 (16.4)	6 (54.1)	6 (56.3)	6 (66.1)	5 (49.1)	4 (55.3)
<i>Bassozetus sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1 (29.3)
<i>Unidentified Ophidiid</i>	-	-	-	-	-	-	1 (0.28)	-	-	1 (2.1)	-	-	-	-	-	-	-
<i>Cataetys aff. laticeps</i>	-	-	-	-	-	1 (0.4)	-	-	1 (3.68)	1 (0.9)	-	-	-	-	-	-	-
<i>Careproctus sp.</i>	-	-	1 (6.14)	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paraliparis copei wilsoni</i>	3 (41.6)	2 (3.56)	-	-	1 (4.48)	-	1 (0.7)	-	1 (1.32)	-	-	-	-	-	-	-	-
<i>Paraliparis nigellus</i>	2 (8.78)	1 (0.98)	1 (0.31)	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pachycara crassiceps</i>	3 (65.9)	39 (74.3)	6 (41)	-	7 (38.9)	4 (67.3)	8 (77)	9 (62)	14 (89)	2 (20.8)	5 (57.1)	1 (1.7)	3 (49.4)	2 (11.)	3 (24)	-	-

803 **Table 4.** Maximum number (and percentage of frames) of species attracted to bait between 1297 m and 2453 m in the West African Oil provinces. All data
804 taken from vertical deployments from the 2005 and 2008 surveys.

Species	Depth (m)																
	1297	1419	1452	1473	1480	1601	1638	1684	1800	1813	1982	2033	2112	2263	2282	2420	2453
<i>Myxine ios</i>	-	44 ± 22	35 ± 14	-	43 ± 15	-	45	52	54 ± 6	-	-	-	-	-	-	-	-
<i>Hydrolagus affinis</i>	-	-	-	-	-	-	118 ± 13	-	135	-	113 ± 25	-	121 ± 11	123 ± 24	135 ± 12	117 ± 24	122 ± 18
<i>Centroscymnus coelolepis</i>	46 ± 6	49 ± 9	55 ± 8	55 ± 10	55 ± 8	49 ± 10	63 ± 9	61 ± 11	63 ± 8	55 ± 9	74 ± 15	69	73 ± 10	63	63 ± 5	67 ± 4	-
<i>Centrophorus squamosus</i>	121 ± 12	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Dalatia licha</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	104	-	-
<i>Bathyraja aff. smithi</i>	74	-	65	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Bathyraja aff. hesperaficana</i>	-	-	-	-	-	-	106	-	-	-	122	100	-	81	128 ± 36	-	111 ± 27
<i>Alrovanidia sp.</i>	30 ± 10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Simenchelys parasitica</i>	46 ± 6	34 ± 7	42 ± 2	46 ± 2	40 ± 9	41 ± 4	44 ± 3	40 ± 7	46 ± 6	44 ± 4	49 ± 6	-	47 ± 6	-	53 ± 3	-	-
<i>Synaphobranchus cf. kaupii</i>	55 ± 9	49 ± 14	55 ± 17	55 ± 16	50 ± 15	57 ± 12	54 ± 20	63± 21	67 ± 18	74 ± 13	86 ± 14	86 ± 12	80 ± 16	84 ± 8	86 ± 9	-	81 ± 6
<i>Alepocephalus aff. bairdii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	74 ± 1
<i>Coryphaenoides marshalli</i>	52 ± 6	57 ± 16	57 ± 3	-	40 ± 7	-	54 ± 3	-	-	-	-	-	-	-	-	-	-
<i>Coryphaenoides guentheri</i>	55 ± 5	49 ± 4	55 ± 4	43	53 ± 3	-	-	51 ± 7	37 ± 11	-	-	-	-	-	-	-	-
<i>Coryphaenoides leptolepis</i>	-	-	-	-	-	-	58 ± 10	65 ± 4	54 ± 6	-	-	-	57 ± 11	-	48 ± 2	41 ± 3	58
<i>Coryphaenoides thelostomus</i>	-	-	-	-	-	-	-	-	-	-	85 ± 11	-	116 ± 6	-	106	-	-
<i>Coryphaenoides rudis</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	101 ± 31	87	-
<i>Macrourid A</i>	49	54	42 ± 6	-	41	-	-	-	-	-	-	-	-	-	-	-	-
<i>Macrourid B</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Macrourid C</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Antimora rostrata</i>	41 ± 6	45 ± 8	44 ± 5	43 ± 5	44 ± 7	44 ± 2	43 ± 6	47 ± 8	45 ± 5	40 ± 6	45 ± 6	44 ± 6	51 ± 8	51 ± 8	54 ± 7	59 ± 8	47 ± 6
<i>Bassozetus sp.</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	53
<i>Unidentified Ophiidiid</i>	-	-	-	-	-	-	40	-	-	56	-	-	-	-	-	-	-
<i>Cataetys aff. laticeps</i>	-	-	-	-	-	52	-	-	55	54	-	-	-	-	-	-	-
<i>Cottunculus aff. thomsonii</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Careproctus sp.</i>	-	-	23	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Paraliparis copei wilsoni</i>	19 ± 5	17 ± 4	-	-	18 ± 4	-	18	-	12 ± 3	-	-	-	-	-	-	-	-
<i>Paraliparis nigellus</i>	28 ± 4	27 ± 4	25 ± 3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pachycara crassiceps</i>	43± 6	35 ± 8	40 ± 6	-	50 ± 20	38 ± 4	49 ± 13	59 ± 4	53 ± 16	58 ± 9	66 ± 5	59	50 ± 19	54 ± 26	66 ± 6	-	-

805 **Table 5.** Body lengths (cm ± S.D.) of species attracted to bait between 1297 m and 2453 m in the West African oil province. All data taken from vertical
806 deployments from the 2005 and 2008 surveys.

807

808 **Table 6.** Results from linear regression analysis of of $\sqrt{V}$ -transformed maximum numbers ($N_{\max}$), $\sqrt{V}$ -arrival time (t_{arr}) and mean body length (cm) with depth for
809 the five most frequently encountered fish species.

810	Measurement	F-statistic	R²	P-value	Slope	Intercept
811	<i>Centroscymnus coelolepis</i>					
812	$\sqrt{V}T_{arr}$	$F_{(1,14)}=19.7$	0.58	$p<0.001$	0.015	-18.78
813	$\sqrt{V}N_{\max}$	$F_{(1,14)}=20.44,$	0.58	$p<0.001$	-0.0017	4.94
814	Mean body length	$F_{(1, 14)}=19.23$	0.58	$p<0.001$	0.02	26.9
815	<i>Simenchelys parasitica</i>					
816	$\sqrt{V}T_{arr}$	$F_{(1,11)}=2.425$	0.18	$p = 0.15$		
817	$\sqrt{V}N_{\max}$	$F_{(1,15)}=11.29$	0.43	$p=0.004$	-0.0015	4.12
818	Mean body length	$F_{(1, 11)}=9.477$	0.46	$p<0.01$	0.01	25.2
819	<i>Synaphobranchus cf. kaupii</i>					
820	$\sqrt{V}T_{arr}$	$F_{(1,11)}= 8.673$	0.34	$p = 0.34$		
821	$\sqrt{V}N_{\max}$	$F_{(1,15)}=53.04$	0.78	$p<0.0001$	-0.0037	9.89
822	Mean body length	$F_{(1, 14)}=66.21$	0.83	$p<0.001$	0.04	0.90
823	<i>Antimora rostrata</i>					
824	$\sqrt{V}T_{arr}$	$F_{(1,15)}=3.72,$	0.20	$p=0.07$		
825	$\sqrt{V}N_{\max}$	$F_{(1,15)}=14.56$	0.49	$p=0.001$	-0.0008	0.28

826	Mean body length	$F_{(1, 15)}=17.94$	0.54	$p<0.001$	0.01	28.6
827	<i>Pachycara crassiceps</i>					
828	νT_{arr}	$F_{(1,12)}=2.331$	0.16	$p=0.15$		
829	νN_{max}	$F_{(1,15)}=5.348$	0.26	$p=0.03$	-0.002	5.86
830	Mean body length	$F_{(1, 12)}=13.02$	0.52	$p=0.004$	0.02	12.02
831						

Table 7. Species specific behaviour of fish species at the ROBIO baited lander.

Species	Behaviour
<i>Simenchelys parasitica</i>	Both vertical and horizontal deployment modes showed <i>S. parasitica</i> boring its head into the bait and remaining stationary for up to 10 min, interspersed with periods of circling the bait in close proximity. The horizontal camera revealed the dorsal surfaces of <i>S. parasitica</i> to be heavily scratched with some marks resembling bite marks.
<i>Synaphobranchus</i> cf. <i>kaupii</i>	Generally, <i>S. kaupii</i> arrived at the bait very quickly and despite showing interest in the bait, did not engage in feeding bouts (indicated by a peak in numbers and sediment disturbance) until shortly after the Portuguese dogfish <i>Centroscymnus coelolepis</i> removed a significant piece of bait allowing them access to the softer flesh (a detailed analysis of this behaviour is reported in Jamieson <i>et al.</i> 2011).
<i>Pachycara crassiceps</i>	Zoarcids are grazing predators which appeared to aggregate in the vicinity of the bait to exploit the higher densities of scavenging amphipods. Both the vertical and horizontal images showed this species sitting stationary for long periods of time, some even positioning themselves on top of the bait itself.
<i>Myxine ios</i>	This species of hagfish aggregated in close proximity to the bait and covered the bait with mucus. The mucus was observed trailing up to at least a metre and out of the field of view. Occasionally some buried their head and tail in the sediment and remained stationary for short periods of time.
<i>Hydrolagus affinis</i>	Generally, <i>H. affinis</i> appeared on the periphery of the field of view, but occasionally made contact with the bait, and on one occasion an individual was observed directly removing bait.
<i>Bathyraja</i> aff. <i>hesperaficana</i>	This species was also observed on some of the horizontal deployments. They were mostly seen traversing the 'horizon' at a distance of ~2 m. The horizontal images show that <i>Bathyraja</i> aff. <i>hesperaficana</i> circles the lander a few times before making an attempt to reach the bait, which is typified by a large sediment cloud shortly after.
<i>Bathypterois phenax</i>	<i>B. phenax</i> remained positioned on the seafloor with its sensory pectoral fins forward in front of its head over the bait, presumably to lure prey. It is assumed that the fish wandered into the field of view and was not attracted by the odour plume produced by the bait.
<i>Paraliparis nigellus</i>	<i>P. nigellus</i> were seen to adopt occasional snout-down and tail-up feeding bouts at the bait, although whether they removed bait or preyed on small crustaceans could not be ascertained

<i>Paraliparis copei wilsoni</i>	These liparids were frequently observed within 20 cm of the bait in feeding bouts, but as with <i>P. nigellus</i> the exact food source (bait or prey) could not be determined.
<i>Cataetyx aff. laticeps</i>	This species remained lying on the bottom (although not stationary) around the periphery of the field of view, probably feeding on crustaceans (Saldanha 1994).
<i>Cottunculus aff. thomsonii</i>	This species remained stationary on the periphery for three and four frames before exiting.
<i>Careproctus sp.</i>	Remained in relatively close proximity to the litholid crab, <i>Lithodes ferox</i> . The liparid had possibly laid its eggs in the branchial chamber of the crab for protection (Hunter 1969, Stein 1980, Love & Shirley 1993, Somerton & Donaldson 1998, Yau et al. 2000).