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Baited camera observations of deep-sea demersal fishes of the northeast Atlantic Ocean at 15–28°N off West Africa

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Abstract For the first time the autonomous free-fall vehicle AUDOS was deployed at low latitudes in the northeast Atlantic Ocean. Observations of deep demersal fishes attracted to baited cameras were made at three stations near upwelling areas off West Africa: Canaries (27°20'N, 16°59'W), Cape Verde Terrace (17°45'N, 20°30'W), and Cape Verde Abyssal Plain (15°00'N, 20°30'W). The grenadier *Coryphaenoides (Nematonurus) armatus* was the main species attracted to the bait. Other fish species observed at bait were the eel *Histiobranchus bathybius*, a zoarcid, and the ophiidiids *Barathrites iris* and *Spectrunculus grandis*. A comparison was made between this study area and the stations Porcupine Abyssal Plain (48°50'N, 16°30'W), which is eutrophic, and Madeira Abyssal Plain (31°00'N, 20°00'W), which is oligotrophic. These are situated on either side of a proposed faunal divide at 40°00'N with a high abundance of large species of rattails to the north and lower biomass of smaller fish species to the south. This study revealed a high abundance of large *C. (N.) armatus* at 17°00'N, which is a violation of this putative zoogeographic divide. It is suggested that high primary productivity and upwelling off West Africa sustain this assemblage of deep demersal fishes.

Introduction

Life in the deep-sea is almost entirely dependent on organic matter derived from primary production in the surface layers of the ocean. A significant proportion of this reaches the sea floor in the form of food falls or carrion (Britton and Morton 1994) to which are attracted scavenging fishes and invertebrates of the benthic

boundary layer (Isaacs and Schwartzlose 1975). Priede et al. (1991) showed that there is a relationship between surface primary production and the rate at which deep-sea fishes living below these regions intercept such food falls. The mean first arrival time of fish varied between 16 min at 4,400 m depth under the California Current (Priede et al. 1990) and over 138 min in the oligotrophic area of the Madeira Abyssal Plain at 4,900 m (Armstrong et al. 1992). In temperate regions of the northern hemisphere at depths greater than 2,500 m interception and consumption of food falls is dominated by the grenadier *Coryphaenoides (Nematonurus) armatus*, replaced in the central North Pacific Ocean at depths greater than 5,000 m by the congener *C. (N.) yaquinae* (Priede et al. 1990). *C. (N.) armatus* was first described off New Zealand (Hector 1875) and is thought to occur throughout the world's oceans. Evidence has suggested that it might not be such an important species in the deep sea of tropical regions. Based on trawl samples, Merrett (1987) proposed a deep demersal ichthyofaunal divide at latitudes 34–41°00'N in the northeast Atlantic between assemblages characteristic of temperate regions with seasonal production to the north and tropical non-seasonal conditions to the south. Large rattails *C. (N.) armatus*, *C. (C.) leptolepis*, and *C. (C.) profundicola* dominated the fauna to the north, whereas to the south the small species *Bathymicrops regis* and *Bathypterois longipes* were dominant. This hypothesis was further supported by the observation in studies on scavenging species that abundance of *C. (N.) armatus* decreased from 877 km⁻² in the Porcupine Seabight and 167 km⁻² on the Porcupine Abyssal Plain (48°50'N) to only 8 km⁻² on the Madeira Abyssal Plain at 31°00'N. Studies in the Arabian Sea at depths of 3,190–4,420 m at latitudes of 10–20°00'N showed dominant fish species at abyssal food falls to be the ophiidiids *Barathrites iris* and *Holycomycteropus aequatorius* and a zoarcid *Pachycara* sp. Only a single macrourid, *C. (N.) armatus*, was observed in an extensive series of film sequences (Witte 1999; Janßen et al. 2000).

The aim of the present study was to make the first baited camera observations of deep-sea demersal

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scavengers at low latitudes in the northeast Atlantic, south of the faunal divide proposed by Merrett (1987), which was based on evidence from trawl data. Artificial small food falls were deployed on the sea floor at latitudes 14°00' and 27°00'N, at 3,200–4,040 m depth (Fig. 1) using the AUDOS Mk IIIb (Aberdeen University Deep Ocean Submersible), a free-fall lander vehicle equipped with a time-lapse camera, acoustic doppler current meter, and tracking system (Priede and Bagley 2000). A standard bait comprising a single mackerel as used in previous studies in the North Pacific (Priede et al. 1990) and Atlantic Oceans (Priede et al. 1994) was placed on the sea floor within the centre of the field of view of the camera.

Materials and methods

Data were collected during R.R.S. "Discovery" cruise 243 using the free-fall vehicle AUDOS. The tubular framework of the vehicle supported an 800 frame stills camera (Ocean Instrumentation M7) with two 200 J flashlights, a Sentsortek acoustic doppler current meter, twin acoustic ballast releases (MORS AR and RT), an alkaline battery pack, and a short baseline fish-tracking sonar system. This tracking system is used in conjunction with ingestible transponders to study the behaviour of fish departing from the bait source (Priede and Bagley 2000).

The AUDOS was deployed as a mooring comprising, from the top downwards, pick-up float, mast buoy with flag, radio beacon and strobe light, Trimsyn float (CRP Marine), syntactic foam block, AUDOS frame, cruciform reference scale, and 80 kg ballast.

On each deployment a 500 g mackerel was used as bait. The muscle tissue was shredded and divided into four mesh bags, which were attached to the arms of the scale cross within the centre of the field of view of the downward looking AUDOS camera. The remainder of the fish was attached to the centre of the cross.

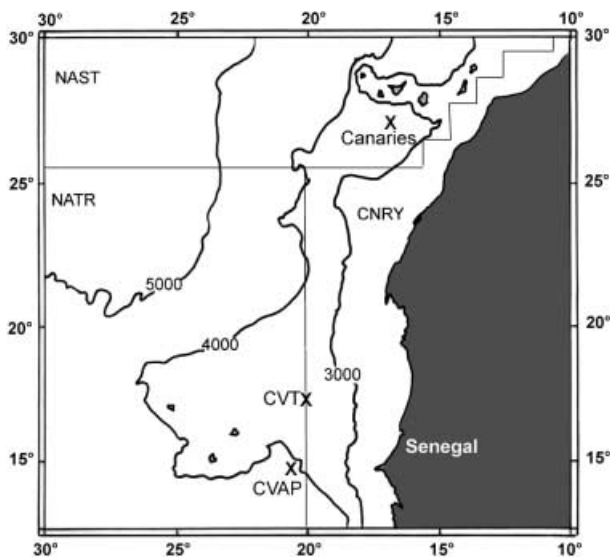


Fig. 1. Map of study area indicating the positions of the stations in relation to the bathymetry and to the biogeographic zones identified by Longhurst et al. (1995). Stations: Canaries, CVT Cape Verde Terrace, CVAP Cape Verde Abyssal Plain. Biogeographic zones: NAST North Atlantic Subtropical Gyral Province, NATR North Atlantic Tropical Gyral Province, CNRY Eastern Canary Coastal Province. The Guinea Current Coastal mentioned in the text lies to the south of this map following the coastline

In total, 11 deployments were achieved: 1 south of the Canary Islands (27°43'N, 16°59'W) at a depth of 3,350 m, 7 on the Cape Verde Terrace (17°40'N, 20°00'W) at 3,200 m, and 3 on the Cape Verde Abyssal Plain (15°00'N, 20°30'W) at 4,000 m (Fig. 1).

The AUDOS vehicle remained on the sea floor for periods of 7.5–22.5 h before ballast was released by acoustic command from the ship. The lander rose to the surface by virtue of positive buoyancy and was recovered.

The camera was programmed to take photographs at 1 min intervals using Kodak E200 Ektachrome color reversal film. Short strips of film (approximately 40 frames) were developed onboard ship (Photocolor Chrome-6) to check system function. The majority of the film was developed onshore. Film was then viewed using a microfilm enlarger (REGMA LR6).

Species identification was made based on morphological characters from photographs and specimens caught at abyssal soundings using the OTSB (Otter trawl semi-balloon) net.

Results

Coryphaenoides (Nematonurus) armatus (Macrouridae) was the main scavenger attracted to the bait. Other scavenging fishes photographed at the bait were *Barathrites iris* and *Spectrunculus grandis* (Ophiidiidae), *Histiobranchus bathybius* (Synphobranchidae), *Pachycara* spp. (Zoarcidae), and another macrourid, probably *Echinomacrurus mollis*. The invertebrate fauna observed included the crustaceans *Plesiopenaeus armatus* (Aristeidae) and *Munidopsis* spp. (Galatheididae) and unidentifiable amphipods, the holothurian *Enyppiastes* and unidentifiable ophiuroids.

Arrival times, maximum number of fish, and percentage of frames with visible fish were recorded for every fish species and are shown in Table 1, along with the mean current speeds of all deployments. Analysis of data from deployments on the Cape Verde Terrace revealed higher numbers of *C. (N.) armatus* and a higher number of species present than on the Cape Verde Abyssal Plain. The dominance of *C. (N.) armatus* is obvious from its presence in every deployment and a fairly strong presence of *B. iris* was noted at the deeper Cape Verde Abyssal Plain station. The macrourid *Echinomacrurus mollis* (Fig. 2D) was seen in two deployments but on only one frame each time.

The experiment at station 13666 attracted most species in the Cape Verde Terrace and is illustrated in greater detail by Fig. 3. Initially when the AUDOS reached the sea floor the current was flowing in a westwards direction at a velocity of approximately 90 mm s⁻¹. This progressively changed to a northwards direction, which predominated until 6 h after touchdown. The direction then changed to the south and the current decreased to 50–60 mm s⁻¹. The current rotated back to the westwards direction 10–11 h after touchdown, thus completing the tidal cycle we presume to be prevalent at this depth. *H. bathybius* (Fig. 2A) was the first fish to arrive, 26 min after vehicle touchdown, and it was only seen at the bait three times during the first half of the deployment. The next scavenger to appear at the bait was *B. iris* (Fig. 2B), 43 min post touchdown; all its occurrences were also in the first half of the deployment. *C. (N.) armatus* (Fig. 2A)

Table 1. Mean current speeds and summary data of fish occurrences from all AUDOS deployments

Location	Canaries 27°23'N, 16°59'W	Cape Verde Terrace 17°45'N, 20°30'W							Cape Verde Abyssal Plain 15°00'N, 20°30'W				
Depth	3,350 m	3,200 m							4,000 m				
Station no.	13635	13639 ^a	13644	13663	13666	13668	13671	13676	Mean	13646	13650	13654	Mean
Date	21 Oct 1999	28 Oct 1999	30 Oct 1999	9 Nov 1999	10 Nov 1999	11 Nov 1999	12 Nov 1999	14 Nov 1999		1 Nov 1999	3 Nov 1999	4 Nov 1999	
Touchdown time	2328 hours	2232 hours	1913 hours	2026 hours	2144 hours	1451 hours	1036 hours	1032 hours		0858 hours	1052 hours	2033 hours	
Deployment duration	7 h 28 min	22 h 16 min	10 h 59 min	11 h 51 min	11 h 15 min	10 h 47 min	11 h 57 min	10 h 40 min		11 h 29 min	11 h 31 min	11 h 32 min	
Mean current speed (mm s ⁻¹)	40.51	43.07	45.95	58.11	73.61	58.61	62.65	51.03	57.08 ^b	39.21	43.85	57.1	44.71 ^a
Standard deviation	19.79	18.59	17.73	21.34	21.11	15.12	23.83	20.93	22.28	14.4	17.83	21.39	19.55
<i>Coryphaenoides armatus</i>													
First fish arrival (min)	13	6	32	44	44	58	35	42	37.3 ^c	44	26	79	49.7
Max no. fish	3	4	3	3	6	6	6	4	4.6	2	4	5	3.7
% frames with visible fish	21.21	8.94	33.23	22.22	35.11	27.30	37.90	20.63	26.47	12.14	17.51	23.04	17.56
<i>Histiobranchus bathybius</i>													
First fish arrival (min)					26		136	109	90.33			74	74
Max no. fish					1		1	1	1			1	1
% frames with visible fish		0	0	0	0.74	0	0.76	0.31	0.26	0	0	1.18	0.390
<i>Barathrites iris</i>													
First fish arrival (min)					43				43	39	97		68
Max no. fish					1				1	2	1		1.5
% frames with visible fish		0	0	0	4.44	0	0	0	0.63	17.48	22.29	0	13.26
<i>Spectrunculus grandis</i>													
First fish arrival (min)	198			577	480				418.33				
Max no. fish	2			1	1				1.33				
% frames with visible fish	5.54	0		0.42	0.15	0	0	0	0.87				
Zoarcid													
First fish arrival (min)				299	211				255				
Max no. fish				1	1				1				
% frames with visible fish		0	0	49.51	4.89	0	0	0	7.77				
<i>Echinomacrus mollis</i>													
First fish arrival (min)		1244	393						818.5				
Max no. fish		1	1	0	0	0	0	0	1				
% frames with visible fish		0.07	0.3	0	0	0	0	0	0.053				

^a Time lapse camera set on 2 min intervals

^b Mean of full data set, not mean of means

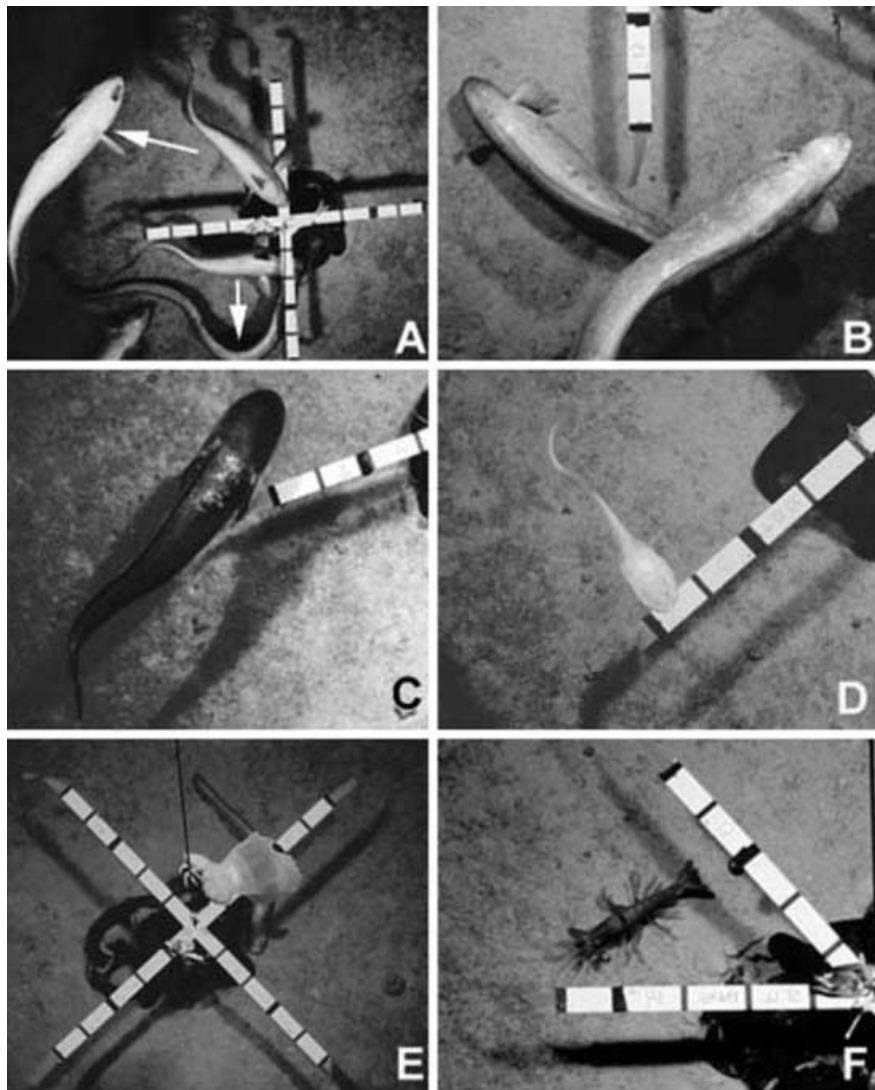
^c Excluding value for station 13639

arrived only 1 min after *B. iris*. Although various individuals, up to a maximum of six per frame, approached the bait throughout the entire experiment, the highest numbers were observed during the first 380 min. For the rest of the time only one fish was seen per frame. The zoarcid (Fig. 2E) appeared 211 min after touchdown and from the photographs it seems that the same individual stayed around the bait for 37 min. The ophidiid *S. grandis* (Fig. 2C) came to the bait 480 min post touchdown and was only observed on one photograph.

The data from station 13650 are shown in Fig. 4 as an example of an abyssal plain deployment with a high occurrence of *B. iris*. The current regime was more variable than observed on the Cape Verde Terrace. Over the first half-hour after the AUDOS reached the sea floor the current was very weak, running at 20 mm s⁻¹ in a southwards direction. This changed to north and westerly currents of up to 55 mm s⁻¹ up to 4 h after touchdown. From 5 h after touchdown the current changed to a predominantly southwards current with a

Fig. 2A–F. Photographs of the vertebrate and invertebrate fauna observed at the AUDOS baits. Markings on cross are at 10 cm intervals for scale.

A Four *Coryphaenoides (Nematonurus) armatus* and one eel, *Histiobranchus bathybius*. Station 13654, 4,000 m at CVAP, 3.05 h after touchdown. **B** Two *Barathrites iris*. Station 13646, 4,000 m at CVAP, 2.44 h after touchdown. **C** One *Spectrunculus grandis*. Station 13639, 3,000 m at CVT, 13.50 h after touchdown. **D** One *Echinomacrurus mollis*. Station 13644, 3,000 m at CVT, 10.15 h after touchdown. **E** One zoarcid, one holothurian, *Enypniastes* sp., and one decapod, *Munidopsis* sp. Station 13663, 3,000 m at CVT, 3.58 h after touchdown. **F** One *Plesiopenaeus armatus*. Station 13646, 4,000 m at CVAP, 38 min after touchdown



maximum velocity of 77 mm s^{-1} with an important westerly component at times.

The first fish to arrive at the bait was a *C. (N.) armatus* at 44 min after vehicle touchdown; by 96 min there were four of this species present. From 110 min onwards there was generally only one *C. (N.) armatus* present, but on four occasions two or three individuals were visible. One *B. iris* arrived 97 min after touchdown and one member of this species (we cannot be certain if it was the same individual) was present in most photographs until 350 min after touchdown. Overall *B. iris* was present in more frames, 22.3%, than the more abundant *C. (N.) armatus*, 17.5%.

C. (N.) armatus

This species was found in all the baited deployments and owing to the large sample size data can be analysed in more detail than for the other species. Measures of total

body length were taken from photographs and expressed as frequency distribution histograms (Fig. 5). Fish at Cape Verde Terrace are smaller, in the range of 40–95 cm with a mean length of 67.9 cm compared to a range of 50–110 cm and mean length of 83.3 cm at Cape Verde Abyssal Plain. In both cases the distribution is unimodal as was expected from the presence of only one species of grenadier. Maximum number of *C. (N.) armatus* in every 30 min period was recorded following the method of analysis previously used for the Porcupine and Madeira Abyssal Plains (Armstrong et al. 1992) and a curve was then fitted to this data using the model proposed by Priede et al. (1990; Fig. 6). This is shown by the following relationship:

$$N_t = \alpha_0/x \cdot e^{-xt} (e^{\beta x} - 1) \quad \text{if } t > \beta \text{ or} \\ N_t = \alpha_0/x (11 - e^{-xt}) \quad \text{if } t \leq \beta \quad (\text{a})$$

where N_t is number of fish present at time t (in minutes) after the bait reaches the sea floor, α_0 is initial arrival

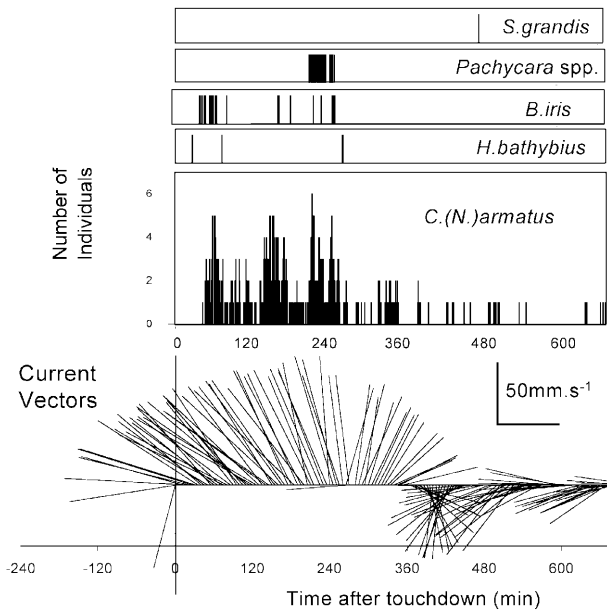


Fig. 3. Data from AUDOS deployment at station 13666 at 3,200 m depth on the Cape Verde Terrace. The lower panel shows the current speed (denoted by length of the vector line) and direction (denoted by the angle of the line) at 5 min intervals. North is upwards, parallel to the y -axis. The upper panels show the numbers of fish of each species within view of the AUDOS camera

rate of fish, β is mean fish staying time, and x is the bait decay constant.

By adjusting staying time to the time of maximum numbers and then arrival rate and bait decay to fit the data, the best fit for Cape Verde Terrace was obtained with $\alpha_0 = 0.033$, $\beta = 120$, $x = 0.003$; and for Cape Verde Abyssal Plain with $\alpha_0 = 0.025$, $\beta = 130$, $x = 130$. Error bars are shown for each observed value (Fig. 6).

Invertebrates

Plesiopenaeus armatus (Fig. 2F) was present in every deployment and *Eynpiastes* spp. (Fig. 2E) was present in all Cape Verde Terrace deployments but was never seen in the Cape Verde Abyssal Plain. The squat lobster, *Munidopsis* spp. (Fig. 2E), appeared in a series of photographs from stations 13635 and 13639 and the ophiuroids were seen in stations 13639 and 13644. It is likely that amphipods were attracted to the bait. However, their small size means they would not be resolved in these photographs but would appear as a blurry spot. Some grenadiers showed ecto-parasites of up to 1 cm in length.

Discussion

This study of deep demersal fishes at low latitudes in the northeast Atlantic revealed the presence of a large population of *Coryphaenoides (Nematonurus) armatus*, which is also the dominant species, attracted to bait. This is

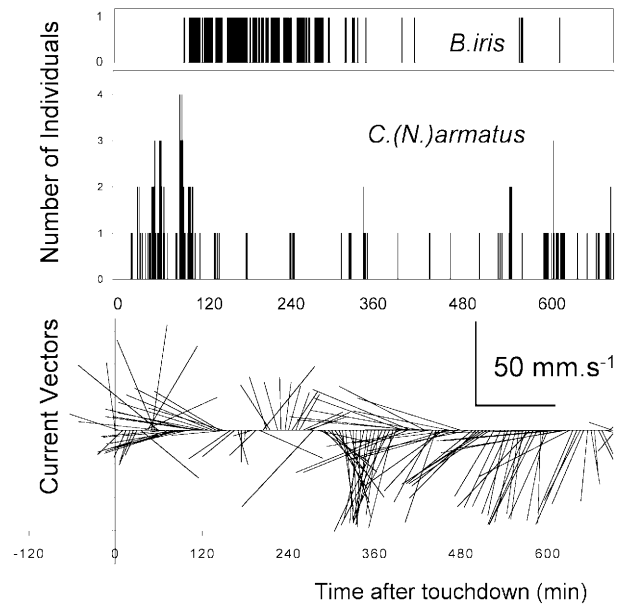


Fig. 4. Data from the AUDOS deployment at station 13650 at 4,000 m on the Cape Verde Abyssal Plain. Key as for Fig. 3

remarkably similar to the high abundance and rapid arrival of *C. (N.) armatus* observed at temperate latitudes, 48–50°00' in the northeast Atlantic (Priede et al. 1991). *C. (N.) armatus* is assumed to be well adapted to exploitation of organic matter fallout from the surface, either through direct consumption of carrion or through feeding on benthic and epibenthic fauna (Priede and Bagley 2000). We hypothesise that this abundance of *C. (N.) armatus* off West Africa is sustained by fallout from high surface productivity in an upwelling region.

Priede et al. (1990) showed that the arrival time of the first *C. (N.) armatus* is governed largely by population density in accordance with an inverse square relationship:

$$N = C/t_{\text{arr}}^2 \quad (\text{b})$$

where N is the number of fish per square kilometre and t_{arr} is the time delay (in seconds) between the bait landing on the sea floor and arrival of the first fish. C is a constant, the value of which depends on the water velocity (V_w) current dispersing the odour from the bait and the velocity of the fish (V_f) approaching the bait. Following Priede and Bagley (2000), $C = 0.3848(1/V_f + 1/V_w)$.

Applying $V_f = V_w = 50 \text{ mm s}^{-1}$ to fish arrival data over a wide area of the North Atlantic Ocean, Priede and Merrett (1998) found a good correlation with trawl estimates of abundance of this species. However, Yau et al. (2000) analysed errors associated with these assumed values of V_f and V_w and showed that errors are greatest at the lowest speeds. For the present study (C. Wylie, unpublished) we have measured the mean swimming speed of *C. (N.) armatus* in situ departing from the bait as 77 mm s^{-1} . This departure velocity can be taken as a possible estimate of V_f . Furthermore, we have measured current speeds in situ and can assume

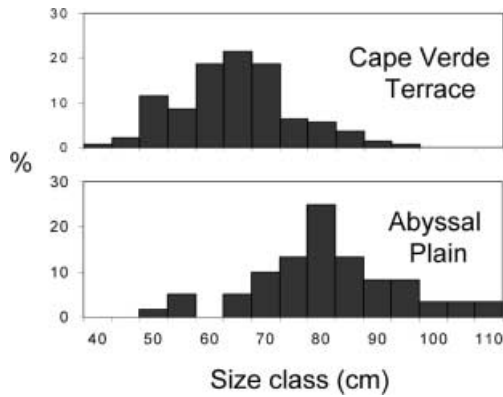


Fig. 5. Comparison of the length frequency distribution of *C. (N.) armatus* observed at the AUDOS baits in the present study on the Cape Verde Terrace, depth 3,200 m (mean total length 67.9 cm, SD = 10.98, $n = 120$) and the Cape Verde Abyssal Plain (mean total length 83.3 cm, SD = 12.75 cm, $n = 60$)

that the mean current velocity for the first 30 min of each deployment is equal to V_w . Table 2 compares estimates of abundance of *C. (N.) armatus* using the different assumptions regarding V_f and V_w . Use of the observed swimming speed of 0.077 m s^{-1} decreased the abundance estimates. (Data from station 13639 with a very short arrival time was excluded from this analysis since the inverse square law gives a disproportional bias in the results). Taking into account relatively slow water velocities measured in situ greatly increased the abundance measurements at the abyssal stations. Priede and Merrett (1996) found 213 fish km^{-2} at 4,050 m depth and 247 fish km^{-2} at 3,500 m in the Porcupine Seabight, northeast Atlantic. Priede et al. (1990) reported 601 fish km^{-2} at 4,100 m in the eastern North Pacific Ocean. We conclude that abundance of *C. (N.) armatus* off Cape Verde is comparable to, or lower than, that found in temperate deep ocean margin conditions at similar depths and much higher than the 9 fish km^{-2} found on the Madeira Abyssal Plain (Armstrong et al. 1992). We only have a few measurements on the Cape Verde Abyssal Plain and their standard deviation is high, so we cannot determine whether any difference in abundance with depth is significant.

There is a clear trend of bigger *C. (N.) armatus* living deeper (Fig. 5), a general phenomenon wherever this species occurs. We have applied these size–frequency

Table 2. Estimates of abundance and biomass of *C. (N.) armatus* calculated from first fish arrival times. Numbers in parentheses are standard deviations

Velocity (m s^{-1})	Cape Verde Terrace		Cape Verde Abyssal Plain	
	$n = 6$		$n = 3$	
	Abundance ($n \text{ km}^{-2}$)	Biomass (kg km^{-2})	Abundance ($n \text{ km}^{-2}$)	Biomass (kg km^{-2})
$V_f = V_w = 0.05^a$	105 (41)	160	123 (117)	390
$V_f = 0.077, V_w = 0.05^b$	71 (28)	108	83 (79)	263
$V_f = 0.077, V_w = \text{actual speeds}^c$	88 (47)	134	185 (227)	587

^a Standard values for water and fish velocities

^b Values of fish speed measured in the Cape Verde region

^c Best available actual values of fish and water velocity

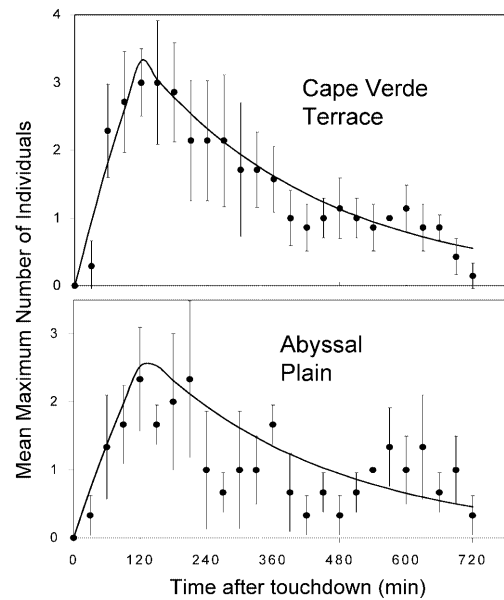


Fig. 6. Comparison of numbers of *C. (N.) armatus* as a function of time after touchdown of bait on the sea floor on the Terrace (3,200 m) and the Abyssal Plain (4,000 m) near Cape Verde. Points indicate the mean maximum number of fish observed within each 30 min period at the two locations; $n = 7, n = 3$, respectively. The vertical bars are ± 0.5 standard deviations. The fitted curves are based on the equations of Priede et al. (1990) (see text)

distributions and converted the lengths to wet weights using the relationship $W = 5 \times 10^{-9} \times L_{\text{total}}^{3.3413}$ derived from analysis of trawl catches of this species from the northeast Atlantic Ocean (D. Bailey, unpublished data; W is wet weight in kilograms and L_{total} is total length in millimetres). Resulting biomass estimates are given in Table 2. This suggests that biomass of *C. (N.) armatus* was much higher on the abyssal plain than on the Cape Verde Terrace. Whereas the water-velocity-corrected abundance estimates show a twofold difference, the biomass difference was more than fourfold.

Longhurst et al. (1995) have subdivided the world's oceans into biogeographic zones (Fig. 1) based on surface primary production as measured by satellite remote sensing techniques. Since Priede et al. (1991) suggested that patterns of distribution of *C. (N.) armatus* in the abyss are related to patterns of surface productivity this raises the question as to whether the biogeographic differences identified by Longhurst et al. (1995) are

reflected in the deep demersal ichthyofauna. The Cape Verde study areas in this article can be considered to correspond to the eastern margin of the North Atlantic Tropical Gyre (NATR), which has an overall average primary production of $106 \text{ g C m}^{-2} \text{ year}^{-1}$. However the study sites are within the influence of the coastal domains Canary Current Coastal (CNRY) and Guinea Current Coastal (GUIN), which are characterised by seasonally varying primary production associated with upwelling, amounting to 732 and $495 \text{ g C m}^{-2} \text{ year}^{-1}$, respectively (Longhurst et al. 1995). We hypothesise that some of this fixed carbon is transported down the slope to bathyal and abyssal depths and becomes available to the deep-sea ichthyofauna. Figure 7 compares the present data on *C. (N.) armatus* with information from the Porcupine and Madeira Abyssal Plains (Armstrong et al. 1992). The Porcupine Abyssal Plain is within the area known as the North Atlantic Drift (NADR) with a primary production rate of $240 \text{ g C m}^{-2} \text{ year}^{-1}$ and the Madeira Abyssal Plain lies within the area known as the North Atlantic Subtropical Gyre, East (NASE), with a primary production rate of $122 \text{ g C m}^{-2} \text{ year}^{-1}$ as defined by Longhurst et al. (1995). Armstrong et al. (1992) hypothesised that the very low abundance of *C. (N.) armatus* at Madeira Abyssal Plain reflected the oligotrophic conditions of this area with insufficient organic matter fallout from the surface to support an active scavenging fish population. Figure 7 clearly shows that the profile of numbers of fish appearing at baits in the present study is intermediate between the values from the Madeira and Porcupine stations, with the rising first part of the curve closer to the values at Porcupine Abyssal Plain than at Madeira Abyssal Plain. This correlates with the comparatively high abundance of *C. (N.) armatus* in the Cape Verde area. The time of peak numbers β , which is equal to the mean fish staying time, is approximately 2 h. As a broad generalisation in food-rich areas, numbers of *C. (N.) armatus* are high and their staying time at food patches, such as bait, is short since in accordance with optimal foraging theory alternative feeding opportunities are numerous. The staying time in this study is approximately half the expected value predicted using the fitted equation of Priede and Merrett (1998) for the relationship between fish abundance and staying time. This indicates that in the present study area the *C. (N.) armatus* are behaving as if they have abundant food resources available. We conclude therefore that the presence of an active population of *C. (N.) armatus* in this tropical region is sustained by high primary production associated with upwelling off the west coast of Africa. The data from station 13635 off the Canary Islands indicate that this phenomenon is latitudinally quite extensive.

The absence of small *C. (N.) armatus* from photographs could be explained by a difference in the feeding habits of the younger, smaller fish. The rostrum of *C. (N.) armatus* bears lateral line pores and probably taste buds, and as the fish grows it becomes shorter and blunter, becoming less important for detecting prey by

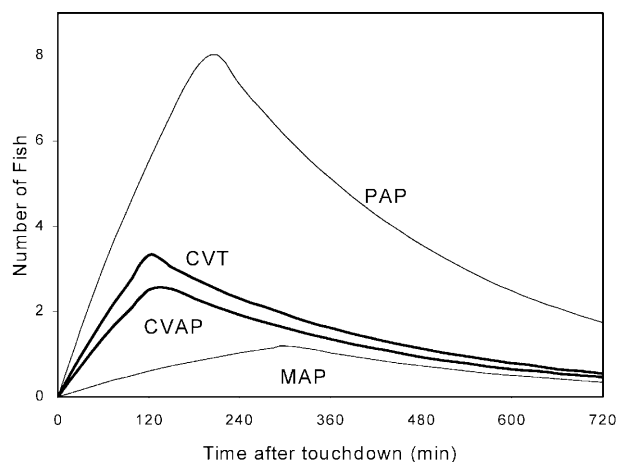


Fig. 7. Comparison of fitted curves of numbers of *C. (N.) armatus* at different stations in the northeast Atlantic Ocean. *PAP* Porcupine Abyssal Plain, $48^{\circ}50'N$ 4,800 m depth; *MAP* Madeira Abyssal Plain, $31^{\circ}00'N$ 4,900 m depth (Armstrong et al. 1992); *CVT* Cape Verde Terrace, $17^{\circ}40'N$ 3,200 m depth; *CVAP* Cape Verde Abyssal Plain, $15^{\circ}00'N$ 4,000 m depth. Note that the time of peak numbers, indicative of fish staying time, is shorter at Cape Verde than at the more northerly stations. Arrival rate, indicative of species abundance, at Cape Verde is intermediate between the values found at *PAP* and *MAP*

contact (McLellan 1977). If young *C. (N.) armatus* are not sensitive to odour plumes but find their prey by contact, this would explain their absence from photographs with baited cameras. Another possibility is that they are feeding further up in the water column, although this goes against existing evidence of benthic invertebrates in stomach contents of 10 to 29 cm specimens (Pearcy and Ambler 1974).

Amongst the other fishes observed in this study, the eel *Histiobranchus bathybius*, (previously referred to as *Synaphobranchus bathybius*) is also common to more northerly stations at Madeira Abyssal Plain and Porcupine Abyssal Plain, where it was also only seen as solitary individuals, often arriving early in the bait observation sequence and then departing on arrival of other species (Armstrong et al. 1992). The ophidiids *Barathrites iris* and *Spectrunculus grandis*, however, were only found as far north as Porcupine Abyssal Plain attracted to long-term cetacean carcasses (Jones et al. 1998), but both were recorded by Armstrong et al. (1992) at Madeira Abyssal Plain attracted to AUDOS fish baits. These are species with a more tropical distribution so they can be regarded as a deep demersal fish characteristic of south of the $40^{\circ}00'N$ faunal divide. Armstrong et al. (1992) commented that on no occasion were ophidiids seen tearing at the flesh or consuming bait. In this study *B. iris* did feed actively at baits. One zoarcid scored a very high percentage presence in the photographic frames at Station 13663 and another individual was seen at Station 13666. These fish have been observed at experimentally placed cetacean carcasses at Porcupine Abyssal Plain, where they arrived long after *C. (N.) armatus* had abandoned the skeleton and took

up residence amongst the bones, moving very little for hours at a time (Jones et al. 1998). This inactive lifestyle was also evident in this study. *Echinomacrurus mollis* showed apparently accidental transits through the field of view of the camera, appearing just in single frames with no behaviour indicating attraction to the bait. Apart from the presence of the holothurian *Eynpniastes* spp., the invertebrate fauna observed was very much like that from studies at Porcupine and Madeira Abyssal Plains and in the Arabian Sea.

All photographs of *Eynpniastes* spp. obtained in this study show this medusa-like sea cucumber hovering above the bottom. Seabed photographs of the species *E. eximia* off eastern Japan show that it spends part of its time on the bottom, probably feeding on surface deposit (Ohta 1985). Because *Eynpniastes* spp. at Cape Verde Terrace was observed hovering in all deployments this may indicate high numbers of this organism rather than an attraction to the bait. Observations from the Arabian Sea show the peak number of the prawn *Plesiopenaeus armatus* to be eight individuals per frame (Witte 1999); this compares to two at Cape Verde Terrace and Cape Verde Abyssal Plain. *P. armatus* was observed particularly at times when fish were absent, as was the case at station Madeira Abyssal Plain (Armstrong et al. 1992).

The 40°00'N faunal divide for deep demersal fishes proposed by Merrett (1987) in the northeast Atlantic corresponds approximately to the boundary between areas NADR and NASE proposed by Longhurst et al. (1995) based on primary production characteristics. The presence of large populations of *C. (N.) armatus* at 17°00'N appears to be a violation of this putative zoogeographic divide. However the presence of upwelling off West Africa appears to be able to fuel a relatively abundant assemblage of deep demersal fishes and this zone may act as a bridge between populations living in the northern and southern hemispheres.

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References

- Armstrong JD, Bagley PM, Priede IG (1992) Photographic and acoustic observations of the behaviour of the grenadier *Coryphaenoides (Nematonurus) armatus*, the eel *Synaphobranchus bathybius*, and other abyssal demersal fish in the North Atlantic. *Mar Biol* 112:535–544
- Britton JC, Morton B (1994) Marine carrion and scavengers. *Oceanogr Mar Biol Annu Rev* 32:369–434
- Hector J (1875) Descriptions of five new species of fishes obtained in New Zealand Sea by H.M.S. "Challenger" Expedition. *Ann Mag Nat Hist* 4 15:78–82
- Isaacs JD, Schwartzlose RA (1975) Active animals of the deep-sea floor. *Sci Am* 233:85–91
- Janßen F, Treude T, Witte U (2000) Scavenger assemblages under differing trophic conditions: a case study in the deep Arabian Sea. *Deep-Sea Res II* 47:2999–3026
- Jones EG, Collins MA, Bagley PM, Addison S, Priede IG (1998) The fate of cetacean carcasses in the deep sea: observations on consumption rates and succession of scavenging species in the abyssal northeast Atlantic Ocean. *Proc R Soc Lond B* 265:1119–1127
- Longhurst A, Sathyendranath S, Patt T, Caverhill C (1995) An estimate of global primary production in the ocean from satellite radiometer data. *J Plankton Res* 17:1245–1271
- McLellan T (1977) Feeding strategies of the macrourids. *Deep-Sea Res* 24:1019–1036
- Merrett NR (1987) A zone of faunal change in the assemblages of abyssal demersal fish in the eastern North Atlantic: a response to seasonality in production. *Biol Oceanogr* 5:137–151
- Ohta S (1985) Photographic observations of the swimming behaviour of the deep-sea pelagothuriid holothurian *Eynpniastes* (Elasipoda, Holothurioida). *J Oceanogr Soc Jpn* 41:121–133
- Pearcy WG, Ambler J (1974) Food habits of deep-sea macrourid fishes off the Oregon coast. *Deep-Sea Res* 21:745–759
- Priede IG, Bagley PM (2000) In situ studies on deep-sea demersal fishes using autonomous unmanned lander platforms. *Oceanogr Mar Biol* 38:357–392
- Priede IG, Merrett NT (1996) Estimation of abundance of abyssal demersal fishes: a comparison of data from trawls and baited cameras. *J Fish Biol* 49 [Suppl A]:207–216
- Priede IG, Merrett NR (1998) The relationship between numbers of fish attracted to baited cameras and population density: studies on demersal grenadiers *Coryphaenoides (Nematonurus) armatus* in the abyssal NE Atlantic Ocean. *Fish Res* 36:133–137
- Priede IG, Smith KL, Armstrong JD (1990) Foraging behaviour of abyssal grenadier fish: interference from acoustic tagging and tracking in the North Pacific Ocean. *Deep-Sea Res* 37:81–101
- Priede IG, Bagley PM, Armstrong JD, Smith KL Jr, Merrett NR (1991) Direct measurement of active dispersal of food-falls by deep-sea demersal fishes. *Nature* 351:647–649
- Priede IG, Bagley PM, Smith A, Creasey S, Merrett NR (1994) Scavenging deep demersal fishes of the Porcupine Seabight, north-east Atlantic: observations by baited camera, trap and trawl. *J Mar Biol Assoc UK* 74:481–498
- Witte U (1999) Consumption of large carcasses by scavenger assemblages in the deep Arabian Sea: observations by baited camera. *Mar Ecol Prog Ser* 183:139–147
- Yau C, Priede IG, Collins MA (2000) Estimation of abundance of deep-sea fishes: telemetry and the problem of measuring swimming speed. In: Moore A, Russell I (eds) *Advances in Fish Telemetry*. Proceedings of the 3rd Conference on Fish Telemetry in Europe. CEFAS, Lowestoft, pp 159–164