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Photographic and acoustic tracking observations of the behaviour of the grenadier *Coryphaenoides (Nematonurus) armatus*, the eel *Synaphobranchus bathybius*, and other abyssal demersal fish in the North Atlantic Ocean

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Abstract. Using an autonomous free-fall vehicle (AUDOS), observations were made of demersal fish attracted to baits and baited acoustic transmitters at two stations in the North Atlantic Ocean. A comparison was made between Station PAP (48°50′N; 16°30′W), 4800 m deep on the Porcupine Abyssal Plain which is relatively eutrophic, and Station MAP (31°N; 20°W), 4900 m deep on the Madeira Abyssal Plain, which is oligotrophic. Experiments were conducted during summer, in 1989 and 1990. Four species of fish were observed at Station MAP, the grenadier, *Coryphaenoides (Nematonurus) armatus*, the eel, *Synaphobranchus bathybius*, and the ophidiids *Spectrunculus grandis*, and *Barathrites* sp. At Station PAP, *C. (N.) armatus* and *H. (S.) bathybius* were attracted to bait on all deployments and only two other individuals of different species, probably ophidiids, were seen. The mean first grenadier arrival time was 30 and 138 min at Stations PAP and MAP, respectively. Mean first eel arrival time was 29 and 151 min at Stations PAP and MAP, respectively. Estimated population densities of fish were 167 grenadiers km^{-2} and 180 synaphobranchid eels km^{-2} at Station PAP and 8 grenadiers km^{-2} and 7 eels km^{-2} at Station MAP. Only the grenadier *C. (N.) armatus* definitely ingested transmitters, and this species dominated fish activity around the baits. Mean time of departure of grenadiers with transmitters in their stomachs across an acoustic horizon at 1000 m range was 371 and 488 min at Stations PAP and MAP, respectively. Grenadiers had a longer mean staying time at the food source at the more oligotrophic Station MAP (364 min) than at Station PAP (141 min). This corresponds with predictions of optimal foraging theory.

Introduction

Ecology of abyssal fish is poorly understood, since obtaining data from the deep ocean environment is extraordinarily difficult. Trawling techniques can be employed at abyssal depths (e.g. Stein 1985), and have been the usual method for sampling deep-sea fish. A technique for supplementing trawl data is to attract fish to bait in view of a camera vehicle (Isaacs and Schwartzlose 1975). This can allow identification of fish, estimates of population densities and observations of feeding behaviour of those species that arrive at the bait (Isaacs and Schwartzlose 1975, Lampitt et al. 1983, Wilson and Smith 1984, Desbruyères et al. 1985, Priede et al. 1990).

Some fish will ingest acoustic transmitters embedded in baits deployed close to the sea-floor (Priede and Smith 1986, Armstrong and Baldwin 1990). This has allowed acoustic tracking systems to follow movements of fish as they depart from a bait source (Priede et al. 1990). In the North Pacific Ocean, two species of grenadiers have been tracked in this way: *Coryphaenoides (Nematonurus) armatus* and *C. (N.) yaguinae*. These are the only fish species that routinely appear at baits deployed at abyssal depths in the North Pacific Ocean (Wilson and Smith 1984).

Priede et al. (1990) and Armstrong et al. (1991) found differences in fish behaviour which were attributable to varying food availability in different parts of the North Pacific Ocean and at different times of the year. More recently, baited transmitters have also been deployed on the sea floor at locations between 4000 and 6000 m depth in the North Atlantic Ocean (Priede et al. 1991). It was observed that over large sectors of the Northern Hemisphere, baits placed at abyssal depths are rapidly detected, consumed and dispersed by grenadiers. These fish appear to play an important role in lateral dispersion of organic carbon in the deep ocean (Priede et al. 1991).

One of the main species observed to consume bait is *Coryphaenoides (Nematonurus armatus)*. This is the only grenadier present in each of the Pacific, Atlantic and Indian Oceans (Marshall 1979). Trawl catches have revealed spatial variation in the species composition of abyssal fish assemblages in the North Atlantic Ocean (Haedrich and Merrett 1988, 1990). Merrett (1987) recognised a faunal divide in the eastern North Atlantic at a

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latitude of 34–41 °N between high seasonal productivity in the north and non-seasonal production in the south, with low annual input of organic matter to the abyss.

In the present study, data was collected during the summer season in stations on either side of Merrett's (1987) faunal divide. The northern site, Station PAP (48°50′N; 16°30′W) at soundings of 4800 m on the Porcupine Abyssal Plain, is relatively eutrophic. The southern site, Station MAP (31°N; 20°W) at soundings of 4900 m on the Madeira Abyssal Plain, is relatively oligotrophic (Merrett 1987). Station MAP is situated west of the Saharan rise and is in an area subject to recurrent turbidite flows consisting of material originating from the NW African margin (Weaver and Kuijpers 1983). Turbiditic disturbance can be expected to reduce the biomass of benthic organisms, at least until re-colonisation, with a possible compounding reduction in food availability at Station MAP.

These two contrasting stations form a complementary pair to the two main stations investigated in the North Pacific Ocean, Station F (32°50′N; 124°W) and Station CNP (31°N; 159°W), which have been characterized as eutrophic and oligotrophic, respectively (Priede et al. 1990).

Materials and methods

Apparatus and experimental protocol

Data were collected using the free-fall vehicle AUDOS (Aberdeen University Deep-Ocean Submersible) (Bagley et al. 1990). The vehicle consisted of a tubular framework which supported an 800 frame 35 mm stills camera and flash unit (Camera Alive, CI800), an omnidirectional acoustic tracking system (ATEX), a test version of a directional tracking system (SCATEX), and two battery packs. The tracking data in this paper were obtained using an updated version of the ATEX system described by Priede et al. (1990). This system detects acoustic transmitters and allows an estimate of range from the decline in signal strength as fish move away; direction is not recorded. The performance of the ATEX detector used in this study was better than the original system due to an improved signal:noise ratio, and the nominal maximum range was 1000 m.

AUDOS was deployed as an autonomous mooring which comprised, from the bottom upwards: disposable ballast, a cruciform reference scale in view of the camera, a back-up magnesium/iron electrolytic decay release, an acoustic release (I.O.S.D.L. type), the AUDOS frame, glass buoyancy-spheres (Benthos Co.), a mast assembly, and pick-up float. The scale was attached above the ballast and was baited to attract scavenging fish. On deployment, the mooring descended to the sea-floor and AUDOS was suspended at a height of 2.4 m above the ballast with the camera angled toward, and centred on, the scale cross. For two deployments at each station, the strop connecting camera to release was shortened to allow close-up photographs or fish for more detailed checking of species identification. On termination of the experiment, the release was acoustically commanded to drop the ballast and the vehicle floated to the surface for recovery. Location on the surface was aided by a radio beacon, strobe flasher and large flag which were incorporated into the mast assembly.

The total quantity of bait used on each deployment was a standard mackerel of approx 0.5 kg. Most of the mackerel flesh was incorporated into baited transmitter packages, with the remainder of the carcass tied to the centre of the scale cross. Up to three acoustic transmitters per deployment were tied to the arms of the scale by fine thread. The transmitters for each deployment were all tuned to the same frequency (ca. 75 kHz) and matched to the receiver tuning to obtain maximum sensitivity of detection by ATEX.

Twin flash heads with a nominal output of 200 J were used with a camera aperture of f5 and 35 mm colour transparency film (Kodak Ektachrome 200 ASA nominal) loaded in 30 m lengths on each deployment, giving 750 to 800 available frames. The camera and flash were triggered by a timer. The timer interval was varied from 80 to 320 s, depending on the length of deployment. Standard frame intervals of 90 or 180 s intervals were chosen for all work following initial experimental adjustments on the first cruise. In the first part of the deployment, a 90 s interval was used followed by 180 s in the later stages; this permitted extended monitoring when the bait had been ingested and fish activity was reduced.

On retrieval of the system after each deployment, a sample of film was processed at sea (Ektachrome processing kit: Photocolor Chrome Six, Photo Technology Ltd.) to check operation of the equipment and to obtain preliminary data for planning of subsequent deployments. The bulk of the film was developed and analysed on shore.

Current speed at Station MAP was measured using a rotational vane meter (Andeera RCM 8) mounted above the AUDOS frame. Current direction close to the sea floor was determined by means of tell-tale ribbons on the arms of the scale cross. A compass was mounted within view of the camera for reference. Current data at Station PAP was recorded on a separate mooring deployed by the I.O.S. Deacon Laboratory at the time of this study (A. Rice personal communication)

Experiments

Deployments were made on two cruises of the RRS "Discovery" in 1989 and 1990. On Discovery Cruise 185, AUDOS was deployed nine times at Station PAP during August and September 1989 (Table 1) at depths of 4843 to 4851 m. On Discovery Cruise 194, ten deployments were completed at Station MAP during August 1990 (Table 2) at depths ranging from 4856 to 4947 m.

Species identification

Films from each deployment were viewed with a micro-film enlarger (REGMA LR6). Fish were identified on the basis of a comparison of gross morphology with that of the range of species caught at abyssal soundings in the North Atlantic and identified in the hand by specialists (e.g. Haedrich and Merrett 1988).

Results

Photographic data

Fish fauna: Porcupine Abyssal Plain

Two main species were distinguishable in photographs from Station PAP. Grenadiers were most frequently observed (Fig. 1). In all cases where there was a good view of the grenadier, they were identified as *Coryphaenoides (Nematonurus) armatus*. Their length-frequency distribution was measured from the photographs as total body length. The mean length was 68.7 cm ($n=158$, SD $= 9.4$) and the distribution is uni-modal (Fig. 2), consistent with the presence of only one species. The possibility that other grenadier species were present cannot be ruled out; however, it is clear that *C. (N.) armatus* was the only grenadier attracted to baits in significant numbers.

Table 1. Summary of deployments of autonomous fish tracking and camera vehicle "AUDOS" and of arrival times of the first grenadier (1st arriv.), peak grenadier numbers (max. nos.) and acoustic tracking data at Station PAP (48°50′N; 16°30′W). No. depl.: no. of transmitters deployed; ingestion times were recorded where transmitters were seen to have been taken; t_{max}: time of last acoustic contact. Times are all expressed in minutes after vehicle touchdown time; * denotes estimated touchdown time (no photographic record); dashes indicate no data

Serial No.	Station No.	AUDOS touchdown		Camera data		Acoustic transmitter data						
		Date (1989)	Time (hrs)	1st arriv.	max. nos.	No. depl.	Ingestion time (min)			t_{max} (min)		
							(1)	(2)	(3)	(1)	(2)	(3)
1	11908-08	24 Aug.	23.10	33	7	2	–	–		–	–	
2	11908-15	27 Aug.	02.06*	–	–	3	–	–	–	320	320	–
3	11908-21	29 Aug.	02.08	37	14	3	–	–	–	–	–	–
4	11908-32	1 Sept.	13.05	16	7	3	21	203	–	–	–	–
5	11908-36	3 Sept.	16.19	27	9	3	53	53	–	184	488	–
6	11908-43	5 Sept.	15.02	15	9	3	120	–	–	752	–	–
7	11908-49	7 Sept.	14.54	45	15	2	52	104		424	–	
8	11908-56	9 Sept.	14.28	40	13	3	59	83	89	224	312	312
9	11908-65	11 Sept.	03.23	25	14	3	32	32	81	–	–	–
Mean				29.8	11.0			75.5			370.7	
(SD)				(10.9)	(3.3)			(48.2)			(169.7)	
[*n*]				[8]	[8]	25		[13]			[9]	

Table 2. Summary of deployments of autonomous fish tracking and camera vehicle "AUDOS" and of arrival times of the first grenadier (1st arriv.), peak grenadier numbers (max. nos.) and acoustic tracking data at Station MAP (31°N; 20°W). Further details as in legend to Table 1

Serial No.	Station No.	AUDOS touchdown		Camera data		Acoustic transmitter data						
		Date (1990)	Time (hrs)	1st arriv.	max. nos.	No. depl.	Ingestion time (min)			t_{max} (min)		
							(1)	(2)	(3)	(1)	(2)	(3)
1	12168-01	11 Aug.	17.02	309	2	3	350	356	–	–	–	–
2	12171-01	14 Aug.	00.49	10	2	3	–	461	–	352	–	–
3	12174-02	15 Aug.	22.20	120	3	3	–	–	–	504	–	–
4	12174-17	17 Aug.	22.02	38	1	3	46	118	190	168	168	168
5	12174-27	19 Aug.	22.42	90	1	3	194	–	–	536	–	–
6	12174-39	21 Aug.	20.37*	–	–	3	–	–	–	720	–	–
7	12174-53	23 Aug.	21.55	179	3	3	223	–	–	554	544	480
8	12174-71	26 Aug.	01.06	28	3	2	–	–	–	864	520	–
9	12174-81	28 Aug.	02.54	322	2	2	321	–		–	–	
10	12174-91	30 Aug.	04.11	146	2	2	190	–		1464	632	
Mean				138.0	2.1			244.9			488.2	
(SD)				(115.1)	(0.8)			(125.0)			(220.4)	
[*n*]				[9]	[9]	27		[10]			[12]	

Eels were present in low numbers in all deployments, all appeared identical in general body form, head shape and pectoral fin configuration, and were identified as *Synaphobranchus bathybius*, since this is the only species present in the area. Two other individual fish, possibly ophidiids, were also observed.

Fish fauna: Madeira Abyssal Plain

Four different species of fish were distinguishable in the photographs at Station MAP. These were identified as *Coryphaenoides* (*Nematonurus*) *armatus*, *Synaphobranchus bathybius* and the ophidiids *Spectrunculus grandis* and *Barathrites* sp. (e.g. Fig. 1). *C. (N.) armatus* was again present in highest overall numbers on the photographs, but *Synaphobranchus bathybius* was also present during all the deployments. Mean total body length of *C. (N.) armatus* was 70.2 cm ($n = 79$, SD $= 8.9$), and the frequency distribution was uni-modal, not significantly different from that at Station PAP (Fig. 2).

Spectrunculus grandis and *Barathrites iris* were easily distinguished in photographs from shape of the head and body. An anterior nostril ridge, and a distinct bi-morphic colour variation were noted for *S. grandis* and are characteristic of the species (Nielsen and Hureau 1980). The lighter morph was white and the darker morph brown in colour. *S. grandis* and *B. iris* were each present on 5 of the 9 films (the camera failed on Deployment #6).

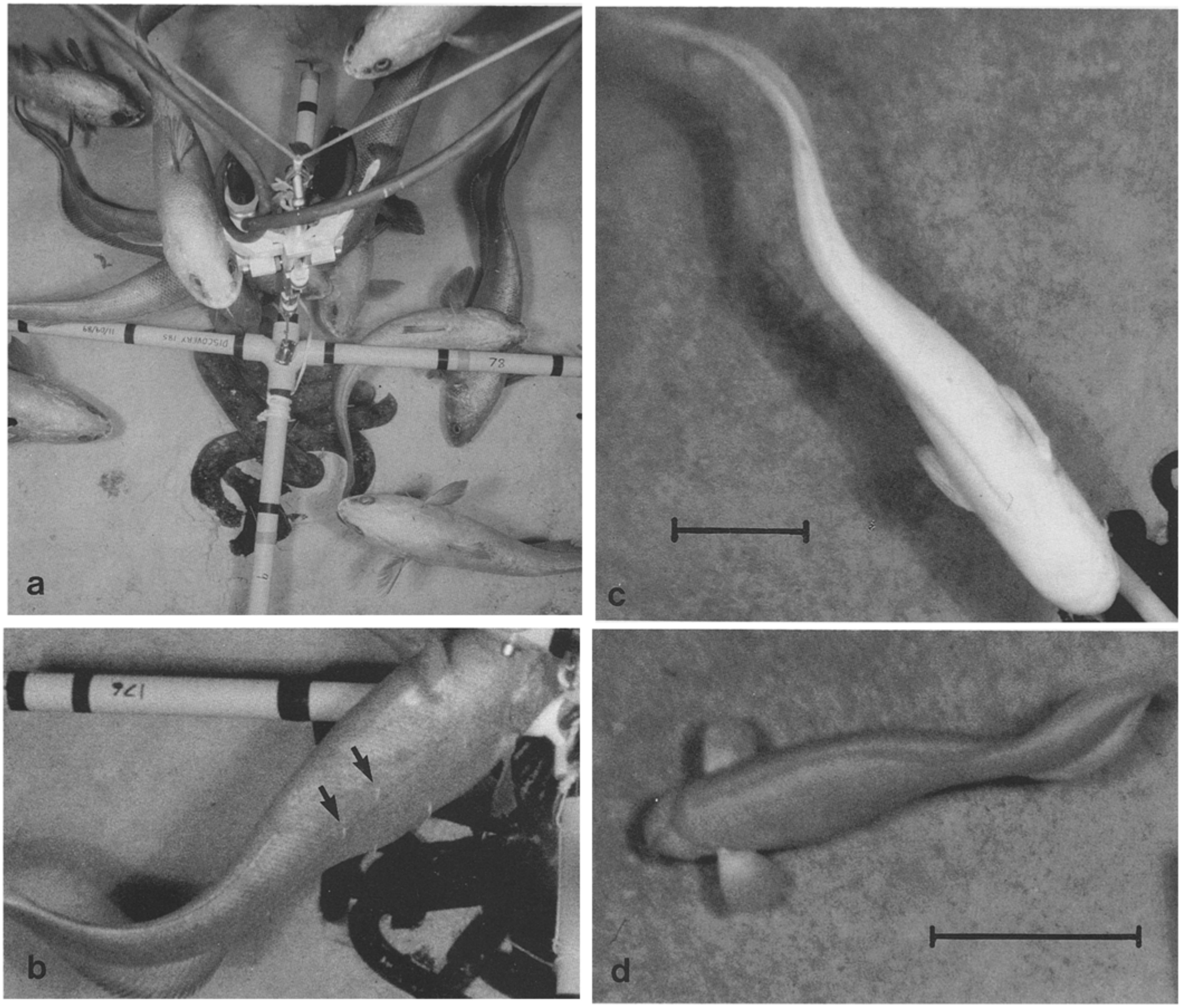

Fig. 1. Fish attracted to bait. (a) Grenadiers, *Coryphaenoides* (*Nematonurus*) *armatus*, at Station PAP (intervals between all black scale marks are 20 cm); (b) close-up of *C.* (*N.*) *armatus* at Station MAP, showing ecto-parasites (two are marked by arrows); (c) *Spectrunculus grandis* at Station MAP; (d) *Barathrites* sp. at Station MAP. [Scale bars in (c) and (d) = 20 cm]

Invertebrate fauna

In addition to the fish some observations were made of invertebrates. Large numbers of the amphipod *Eurythenes gryllus* were almost certainly attracted to the baits. These would be too small to be resolved in these photographs, except as unidentifiable spots, but they were present in large numbers in baits retrieved in other experiments carried out on these cruises (M. Thurston personal communication).

Ecto-parasites were observed on many grenadiers and ophidiids at Station MAP. These were less than 1 cm in length and were often noted as multiple infestations of up to at least five individuals per fish (Fig. 1b).

Prawns of the genus *Plesiopenaeus* were seen in many of the photographs. They were detected at the baits at Station MAP, particularly at times when no fish were present. Analysis showed that three of the transmitters deployed at Station MAP were removed by *Plesiopenaeus* spp. These transmitters were detected remaining static out of view of the camera but within range of acoustic detection when the AUDOS system was recovered. We presume that the prawns stripped off the edible part of the bait ball and left the transmitter lying on the sea floor.

First arrival times and fish numbers

Porcupine Abyssal Plain. There was no significant difference between the mean time that elapsed until first eel arrival (28.7 min, SD = 17.6) and first grenadier arrival (29.8 min, SD = 10.9). However, the patterns of change in numbers differed markedly thereafter (Fig. 3). For each film, the time scale was divided into 30 min intervals fol-

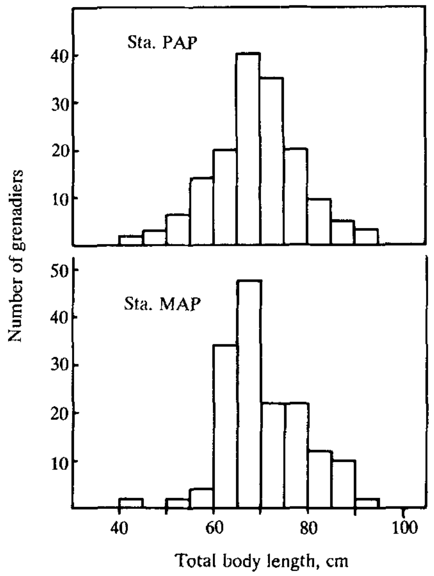

Fig. 2. *Coryphaenoides* (*Nematonurus*) *armatus*. Length-frequency distributions. Total body length from snout to tip of tail measured from photographs at Porcupine Abyssal Plain (48°50′N; 16°30′W), 4 800 m depth (Sta. PAP); and Madeira Abyssal Plain (31°N; 20°W), 4 900 m depth (Sta. MAP). (Unpublished data of B. Weitzel)

lowing vehicle touchdown t. The maximum number of fish visible during the 30 min was recorded. This follows the practice in previous analyses of video data in the Pacific Ocean (Priede et al. 1990). It eliminates the effect of frames with zero fish numbers and reflects the true number of fish attracted by the bait. Mean fish number at various times (N_t) is the arithmetic mean of all the individual maxima for each deployment at time t.

The maximum number of eels on any deployment was 3, and the peak mean number of 1.25 occurred at 0.5 to 1 h after vehicle touchdown time (Fig. 3). Mean number of grenadiers increased to a peak of 9.0 at 3 to 3.5 h after landing. After 1.25 h, the increase in grenadier numbers was accompanied by a concomitant decrease in the number of eels, so that after 3 to 3.5 h no more eels were recorded. After peaking, the mean number of grenadiers decreased to 1–3 fish within view of the camera, until monitoring ceased in the longest records at 14.5 h. By this stage, baits had invariably been consumed.

Madeira Abyssal Plain. At Station MAP the mean post-landing arrival time of the first grenadier (138.00 min, $n=9$, SD = 115.08) was not significantly different from that of the first eel (150.89 min, $n=9$, SD = 114.81). Both grenadier and eel numbers in view of the camera were generally much lower at Station MAP than at Station PAP (Fig. 4). A major difference between the stations was that eels were present at Station MAP on some deployments as long as 12 h after vehicle touchdown time.

Ingestion of transmitters

Baited transmitter packages could be clearly seen on the photographs unless masked by the rigging and release assembly. Ingestion time was identified from sequential

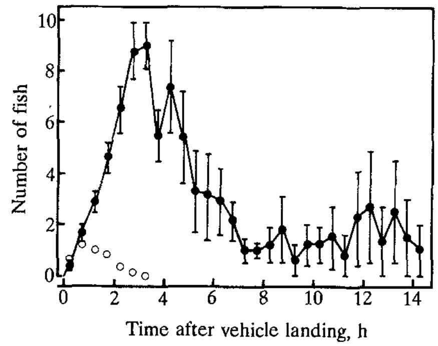

Fig. 3. *Coryphaenoides* (*Nematonurus*) *armatus* (•: means ±SE) and *Synaphobranchus bathybius* (o: means). Maximum numbers of fish within view of camera at 30 min intervals after vehicle touchdown time on Porcupine Abyssal Plain (48°50′N; 16°30′W)

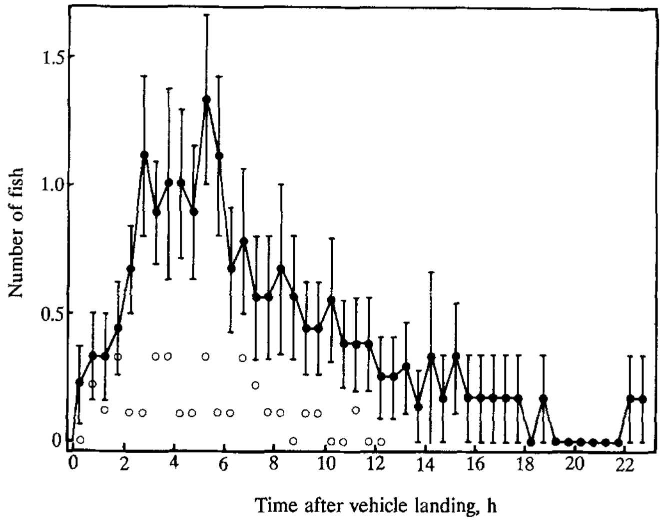

Fig. 4. *Coryphaenoides* (*Nematonurus*) *armatus* (•: means ±SE) and *Synaphobranchus bathybius* (o: means). Maximum numbers of fish within view of camera at 30 min intervals after vehicle touchdown time on Madeira Abyssal Plain (31°N; 20°W)

frames in which the transmitter was present and then absent. Transmitters were ingested at a mean time after vehicle touchdown of 75.53 min ($n=13$, SD = 48.23) at Station PAP, compared with 244.90 min ($n=10$, SD = 125.01) at Station MAP (Tables 1 and 2).

Curves fitted to numbers of grenadiers

Priede et al. (1990) showed that the number of fish visible at baits N_t could be described by the following pair of equations:

$$N_t = \begin{cases} \frac{\alpha_0}{x} e^{-xt}(e^{\beta x} - 1) & t > \beta \\ \frac{\alpha_0}{x}(1 - e^{-xt}) & t \leqslant \beta, \end{cases} \quad (1)$$

where t is time in minutes following vehicle touchdown time, α_0 is initial fish arrival rate (individuals/min), β is mean individual staying time at the bait (min), and x is a decay constant.

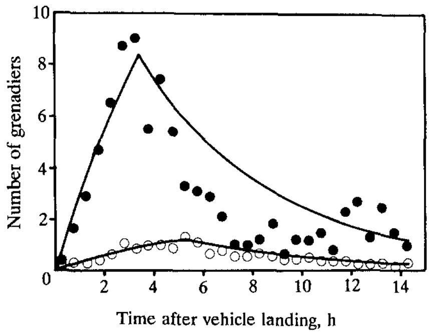

Fig. 5. *Coryphaenoides* (*Nematonurus*) *armatus*. Comparison of numbers of grenadiers attracted to bait on sea floor at Porcupine Abyssal Plain (●) and Madeira Abyssal Plain (o). Curves fitted using Priede et al. (1990) model. Grenadier arrival rate was faster and staying time shorter at Porcupine Abyssal Plain

The model was fitted to grenadier numbers at Stations PAP and MAP by setting β at the time of peak numbers (Priede et al. 1990) and then adjusting α_0 and x to produce the nearest approximation to the data points (Fig. 5). The best fit was achieved for Station PAP with $\alpha_0 = 0.055$, $\beta = 200$, $x = 0.003$; and for Station MAP with $\alpha_0 = 0.006$; $\beta = 310$, $x = 0.003$. Eq. (1) gave a good fit to the Atlantic data for the rising phase of the distributions. However, after peaking, the initial decline in fish numbers was more rapid than predicted from the model, suggesting a decline in staying time as bait was consumed.

Acoustic data

The acoustic tracking system provides approximate range estimates for transmitters as far as the limit of detection of 1000 m. The three transmitters that were taken by the crustacean *Pleisopanaeus* spp. at Station MAP and deposited on the sea-floor were excluded from the analysis. Other transmitters which were detuned and deployments where recording failed have also been excluded, giving totals of 9 and 12 fish tracked at Stations PAP and MAP, respectively.

All tagged fish had moved out of range of the ATEX tracking system within 13 and 25 h at Stations PAP and MAP, respectively. Fig. 6 shows in cumulative form the exit times of fish across the 1000 m acoustic horizon. The curves show similar dispersal patterns, except that the Station MAP distribution is shifted to the right due to a delay in ingestion and departure. Mean radial velocity (V_r) after tag ingestion over the 1000 m range of the tracking system can be calculated using values for mean ingestion time (t_{ingest}) and mean time of last contact (t_{max}) (Tables 1 and 2):

$$V_r = 1100/(t_{max} - t_{ingest}). \tag{2}$$

V_r was 6.21 and 5.77 cm s^{-1} at Stations PAP and MAP, respectively. This confirms that, having ingested transmitters, fish at both stations swam away at very similar velocities. The measured radial velocity is probably lower than the true speed through the water, since vertical or horizontal meandering would add to the distance travelled.

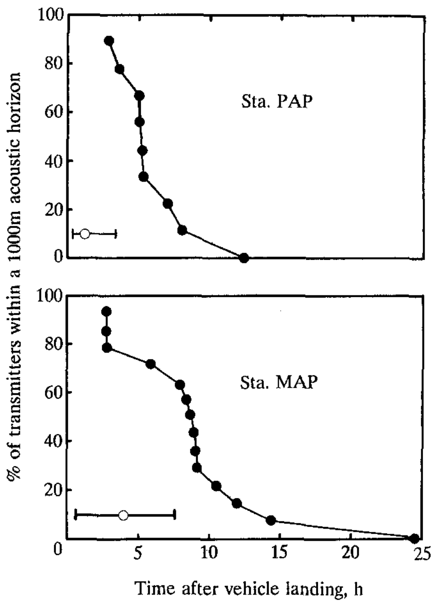

Fig. 6. *Coryphaenoides* (*Nematonurus*) *armatus*. Dispersal of fish that swallowed acoustic transmitters at the Porcupine Abyssal Plain (PAP) and Madeira Abyssal Plain (MAP) stations. All fish at both stations moved out of the 1 000 m range of acoustic detection. Open circle and horizontal bars: mean and range of transmitter ingestion times

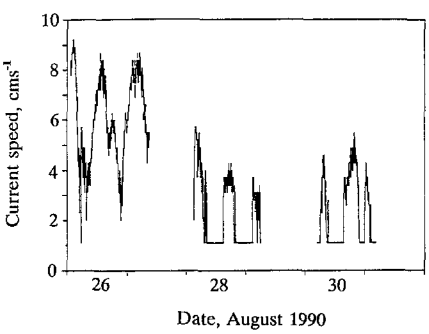

Fig. 7. Recordings of current speed from current meter mounted on autonomous free-fall vehicle (AUDOS) on Madeira Abyssal Plain at 4 900 m depth from 26–31 August 1990; breaks in record occurred when vehicle was recovered and re-deployed. Locations of the three successive deployments were within 10 nautical miles of each other, but may not have sampled same tidal stream

Current velocities

Current at Station MAP varied between <1.1 and 9 cm s^{-1}, with a semi-diurnal rhythmicity (Fig. 7). Similar velocities and rhythm were observed at Station PAP (A. Rice personal communication).

Discussion

These results show that, as in the North Pacific Ocean (Priede et al. 1990, Armstrong et al. 1991), unprotected bait parcels are rapidly detected, consumed and dispersed by scavenging grenadiers. The same species, *Coryphaenoides* (*Nematonurus*) *armatus*, that is dominant over a wide range in the Pacific Ocean is also largely responsible for this phenomenon in the North Atlantic Ocean. The major difference from the North Pacific is the observation of fish of genera other than *Coryphaenoides* (*Nematonurus*).

There were clear differences in the numbers and species of fish attracted to the artificial food falls at the two stations. *Coryphaenoides* (*Nematonurus*) *armatus* and *Synaphobranchus bathybius* were observed on all deployments at both stations, and their co-occurrence and wide distribution is in agreement with trawl catches in the North Atlantic (Haedrich and Merrett 1988). Ophidiids were only seen regularly at food-falls at the southern site, where they were represented by *Spectrunculus grandis* and *Barathrites* sp.

Only *Coryphaenoides* (*Nematonurus*) *armatus* was seen feeding directly on the bait. Ophidiids were frequently observed stationary in a fixed position over several successive frames (3 to 5 min), apparently not responding to the bait. Similar behaviour has been observed by Isaacs and Schwartzlose (1975). It is possible that these fish were feeding on invertebrates, e.g. the amphipod, *Eurythenes gryllus*, which appear in large numbers at protected baits in the abyssal North Atlantic (Thurston 1990). Lampitt et al. (1983) also observed that the fish *Paraliparius bathybius* browsed on lysianassid amphipods at a bait rather than feeding directly on the carrion. On no occasion were the ophidiids seen tearing at the flesh or feeding on transmitter packages.

Ecto-parasites were observed on grenadiers at Station PAP and on grenadiers and ophidiids at Station MAP. Limitations in resolution of the photographs precludes positive identification of the parasites. They are probably crustaceans, copopods, or possibly the amphipod *Eurythenes gryllus*, which is abundant in both areas and is known to attack restrained deep-water fish (Templeman 1967). Benefits to crustacean parasites could accrue through direct feeding on the host, through low-cost long-distance transport, and by using the fishes' ability to rapidly locate food-falls. This would reduce the metabolic costs associated with detection and location of food (Smith and Baldwin 1982). *Coryphaenoides* (*Nematonurus*) *armatus* is known to feed on amphipods (Mauchline and Gordon 1984), so opportunistic ecto-parasitism may involve a degree of risk to the amphipods.

Barathrites iris has previously been recorded near Station MAP, but at soundings from 5033 to 5285 m (Nielsen 1986); the observations from the present study suggest that the depth range may extend to at least 4900 m. *Spectrunculus grandis* has been recorded in the North Atlantic at a maximum depth of 4255 m (Vaillant 1888, Nielsen and Hureau, 1980) and more recently in an extensive trawl survey at 4222 m (Merrett et al. 1991). In the Pacific Ocean, the photographic records indicate that the depth range extends down to at least 6273 m (Machida et al. 1987). Photographic observations in the present study suggest that *S. grandis* is not uncommon at depths of at least 4900 m in the Atlantic Ocean, so the distribution extends beyond that apparent from trawl surveys.

Haedrich and Merrett (1988) recorded 32 species of demersal fishes at abyssal depths (>4500 m) in the North Atlantic Ocean. The species attracted to the baits in the present experiments constitute a small fraction of this fauna. At Station PAP, *Corphaenoides* (*Nematonurus*) *armatus* was the most abundant species in both trawl and camera samples and generally exceeded 50% of a trawl catch (N.R. Merrett personal communication). *Synaphobranchus bathybius* also occurred in both trawl and camera samples, but *C.* (*Chalinura*) *leptolepis*, although relatively abundant in trawls, was never seen in the photographic record. Camera samples at Station MAP were dominated by *C.* (*N.*) *armatus* and *S. bathybius*, but these were a minor component of the trawled fish fauna. It is evident that the baited camera technique selectively samples active carrion feeders or browsers which are attracted by baits. Fish such as *Bathypterois* spp. which feed on the epibenthic microfauna, would not be expected to appear at large baits. An exception to the concept that the baited camera samples are a sub-set of the demersal trawlable fauna are the ophidiids. These were recorded frequently on camera deployments, but have not been recorded from trawl studies at these depths although *Spectrunculus grandis* is readily captured by trawl at shallower depths (Merrett et al. 1991). The species is either rare at Station MAP or behaves differently, perhaps foraging away from the sea-floor and so avoiding trawls.

It is possible to estimate population density of fish species that appear routinely and rapidly at baits. Population density can be expected to be inversely proportional to the arrival time of the first fish (Wilson and Smith 1984). Priede et al. (1990) used an inverse square relationship:

$$N \cdot m^{-2} = C/t_{\mathrm{arr}}^2, \tag{3}$$

where N is number of fish, t_{arr} is time of arrival of the first fish following vehicle touchdown (min), and C is a constant. C depends on the rate at which odour is dispersed by the bottom current (V_w) and swimming speed of the fish as they approach the bait (V_f), m s^{-1}:

$$C = \frac{1}{3(1/(1/V_f + 1/V_w))^2}. \tag{4}$$

Using typical bottom current speeds, $V_w = 0.05$ m s^{-1} and fish swimming speed, V_f, $= 0.05$ m s^{-1}, this gives a values of C for a typical deep-water location of 5.333×10^2. Substituting a value of 5.333×10^8 into Eq. (3) then gives the result in numbers of fish per km^2. At Station PAP, the estimates are 167 grenadiers km^{-2} and 180 eels km^{-2}. This is lower than, but of the same order of magnitude as, the 601 grenadiers km^{-2} estimated for a eutrophic station in the North Pacific (Station: F 32°50′; 124°W) underlying the California Current (Priede et al. 1990). At Station MAP, the estimates are 8 grenadiers km^{-2} and 7 eels km^{-2}, much lower than the oligotrophic Central North Pacific (Station CNP; 31°N; 159°W), where grenadier number has been estimated as 78 km^{-2} (Priede et al. 1990)[1] and 154 km^{-2} (Armstrong

[1] The population densities in Priede et al. (1990) are erroneously given as ten times the correct value

et al. 1991). It is interesting to note that at both Atlantic stations the theoretical population density of eels is equal to the theoretical population of grenadiers.

The observation that there were many more grenadiers than eels on the photographic record is a reflection of differences in the behaviour of the species at a bait. Whilst population densities of grenadiers and eels, as quantified by first-fish arrival times, are similar, the build-up in grenadier numbers to a higher peak value can be attributed to a longer mean staying time (Priede et al. 1990). Low eel numbers during periods of high grenadier numbers may result in part, from competitive exclusion at the bait. *Coryphaenoides* (*Nematonurus*) *armatus* is apparently a voracious predator and the eels may be showing avoidance behaviour.

Population densities at the PAP station, estimated using trawls, are 270 km^{-2} for grenadiers (3 trawls, 52 fish) and 100 km^{-2} for eels (3 trawls, 13 fish) (Priede et al. 1991, N.R. Merrett personal communication). These estimates compare well with those from the first-fish arrival times. Merrett et al. (1991) consider that shallow-water trawls tend to under-estimate population density but that deep-water trawl catches are more representative of true values. Sibuet and Segonzac (1985) trawled at BIOGAS Station 4 (46.5–47.5°N; 10–11°W; 4149 to 4700 m depth), near PAP, and estimated grenadier abundance as 750 fish km^{-2}. The discrepancy between this and the other estimates is not large, considering the low sample sizes and spatial separation of sites.

Desbruyères et al. (1985), using an odour-plume attraction model, estimated a grenadier density at BIOGAS Station 4 of 2000 km^{-2}, significantly higher than that achieved by the other methods. Sainte-Marie and Hargrave (1987), using a Guassian odour-plume model, also obtained high population density estimates of 1000 to 63 000 km^{-2} for the abyssal North Pacific Ocean using the data of Wilson and Smith (1984). The odour-plume models generally attempt to calculate the area covered by the plume at different time intervals, taking into account current velocity, boundary layer and dilution effects. It is assumed that fish are static until the plume arrives, whereupon they move upstream towards the bait. The model of Priede et al. (1990) does not attempt to simulate the hydrodynamics of the plume. It is assumed firstly that fish are uniformly spaced at the centres of hexagons of radius, r, and area, $3 \cdot r^2$. Secondly, it is assumed that each fish can detect odour impinging on any part of its hexagon, i.e., two adjacent fish would not miss a food source if the odour plume passed between them. This requires either plume-spreading at a wide angle or fish movement to enhance encounter probability. It is now known that grenadiers are not static and that there is a significant tendency to move across-current (Priede et al. 1991). This suggests that the model of Priede et al. (1990) may be reasonably realistic, the spacing of fishes being part of a constantly moving dynamic pattern. Further comparative studies using trawls and cameras would enable more precise calibration of the method.

The finding that population densities of grenadiers and eels are lower at Station MAP than at Station PAP is consistent with the lower food availability in this area (Merrett 1987) and is in agreement with the trends observed in the Pacific Ocean (Priede et al. 1990).

Analysis of the temporal change in number of grenadiers (Fig. 5) revealed important differences between the two stations. The arrival rate, α_0, can be expected to be correlated with population density, being approximately the reciprocal of t_{arr}, the first arrival time. The α_0 value at the eutrophic Station PAP (0.055) is less than that at the eutrophic Pacific Station F (0.10), but is similar to that at the oligotrophic Station CNP in the Pacific where $\alpha_0 = 0.05$ to 0.06 (Priede et al. 1990, Armstrong et al. 1991). The value of $\alpha_0 = 0.006$ at Station MAP is extraordinarily low compared with the oligotrophic Central North Pacific. The population density of fish at Station MAP is evidently much lower than would be expected in an undisturbed area of oceanic abyss in the Northern Hemisphere. This may reflect low food availability in this area resulting from the turbiditic disturbances to the benthic infauna (Weaver and Kuijpers 1983). Population densities of *Coryphaenoides* (*Nematonurus*) *armatus* at both stations in the North Atlantic may also be restricted through competition from other species for food. Whilst this study shows that the grenadiers dominate fish activity around carrion baits, it also appears that *Synaphobranchus bathybius* responds rapidly to available food and has a population density comparable with that of *C.* (*N.*) *armatus*. In contrast, grenadiers are the only fish seen at baits at abyssal depths in the North Pacific (Wilson and Smith 1984).

Priede et al. (1990) argued, based on optimal foraging theory (Stephens and Krebs 1987), that fish staying time at the bait source (β) depends upon the general availability of food in the environment; when food is scarce fish stay longer. The higher β value at Station MAP (310 min) compared with the relatively eutrophic Station PAP (200 min) is in accordance with this prediction.

The staying time at Station PAP (200 min) is longer than at a eutrophic location in the Pacific Ocean (Station F), where staying time is only 60 min (Priede et al. 1990). We conclude that both grenadier population density and general food availability are lower at the eutrophic station in the Atlantic (Station PAP) than at the eutrophic station in the Pacific (Station F).

The staying time at Station MAP (310 min) is longer than the mean for the oligotrophic Station CNP in the central North Pacific Ocean (261 min, Priede et al. 1991). This suggests that not only are numbers of scavengers low at Station MAP, but food availability is also lower there than at any locality we have investigated. However, seasonal changes have been observed at Station CNP (Armstrong et al. 1991), with staying time at Station CNP in summer/autumn extending to 400 min (Priede et al. 1990). This suggests that at certain times of the year food availability at Station CNP is even lower than at Station MAP. The presence of more than one species of scavenger and the extraordinarily low population density at Station MAP, however, limits our ability to compare these two stations using the optimal foraging theorem.

Synaphobranchus bathybius was not seen actively feeding on bait during this study, but stomach analyses have shown that this species does consume carrion directly

(Gordon and Duncan 1987). The absence of feeding observations probably results from a much lower number of total observations than those for *Coryphaenoides* (*Nematonurus*) *armatus*. The possibility that some of the transmitters were ingested by *Synaphopranchus bathybius* cannot be ruled out. However, in view of the numerical dominance of *C.* (*N.*) *armatus* at baits, and since *S. bathybius* was absent at most times when tags were seen to be ingested, we presume all fish tracks are of *C.* (*N.*) *armatus*.

All tagged fish dispersed rapidly from the tracking vehicle at both stations; this conforms with observations in the North Pacific (Priede et al. 1990). Furthermore, Priede et al. (1991) have shown that these fish do not simply drift but swim actively, independent of bottom currents. Sustained active swimming by grenadiers is to some extent at odds with the low metabolic activities of these fish (Smith 1978, Somero et al. 1983). It is clear that low-level continuous swimming makes modest physiological demands, as demonstrated for a shallow-water species (Brett 1964). Every indication in the present study suggests that Station MAP is extremely oligotrophic, and it is of note that even when food is apparently very scarce a sit-and-wait energy-conserving strategy is not favoured by grenadiers.

The radial dispersal velocities (V_r) probably underestimate the true velocity, since they do not take into account time spent near the bait after tag ingestion. A combined estimate for departure rates from data collected in this study and by Priede et al. (1990) suggests a mean dispersal velocity of 11 cm s^{-1} (Priede et al. 1991). A more detailed analysis of fish departure velocities in different areas requires the use of a more precise range-finding system using transponding acoustic transmitters. The present study has confirmed that baits deployed at abyssal depths are rapidly transported horizontally by grenadier fish even in apparently biologically impoverished locations such as the Madeira Abyssal Plain. These fish play an important role in dispersal of surface-derived organic carbon that reaches the seafloor.

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