***In situ* comparison of activity in two deep-sea scavenging fishes occupying different depth zones**

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The activity of two scavenging deep-sea fishes occupying the same niche in overlapping depth zones were compared by *in situ* measurements of swimming speeds, tail-beat frequencies and by arrival time at baits. At 4800 m on the Porcupine Abyssal Plain, the grenadier *Coryphaenoides (Nematonurus) armatus* was the dominant scavenger, arriving at baits after 30 min, and swimming at relatively slow speeds of 0.17 body lengths (BL) sec⁻¹. At 2500 m in the relatively food rich Porcupine Seabight both *C. (N.) armatus* and the blue-hake, *Antimora rostrata*, were attracted to bait, but *A. rostrata* was always the first to arrive and most of the bait was consumed before the *C. (N.) armatus* arrived. *A. rostrata* swam at mean speeds of 0.39 BL sec⁻¹, similar to related shallow water species at equivalent temperatures. Observations on tail-beat frequency from video sequences confirmed the greater activity of *A. rostrata*. The data indicate that, given sufficient food supply, high pressure and low temperature do not limit activity levels of demersal deep-sea fishes. Low activity of *C. (N.) armatus* is an adaptation to poor food supply in the abyss, where these fishes dominate, but prevents it competing with the more active *A. rostrata* in shallower depths.

Keywords: *Coryphaenoides (Nematonurus) armatus*; *Antimora rostrata*; swimming speed; metabolism

1. INTRODUCTION

The deep ocean represents the largest single habitat on the planet, accounting for 62% of the surface and 79% of the volume occupied by life (Childress 1995; Somero 1991). Although rather uniform in nature the deep sea is characterized by distinct vertical gradients of pressure, temperature and light (Gage & Tyler 1991). Pressure increases with depth, while light and temperature decline from the surface down to *ca.* 1000 m, below which they remain constant. Food availability also declines with depth and distance from the coast (Childress 1995; Gage & Tyler 1991). As a consequence of these gradients the deep-sea benthic fauna change rapidly with depth down the continental margin (Gage & Tyler 1991; Haedrich 1997; Merrett & Haedrich 1997). This depth-related zonation in deep-sea benthic and benthic-pelagic fauna is not geographically fixed, indicating that bathymetric distribution patterns are the result of complex interactions of factors rather than depth alone.

The physical and biological characteristics of the deep sea mean that the fauna need to be specially adapted. These adaptations can be divided into resistance adaptations, that permit survival under high pressure and low temperature, and capacity adaptations that establish rates of activity appropriate to environmental conditions (Somero 1991). There are probably costs in terms of enzyme efficiency associated with pressure-resistance adaptations (Somero & Siebenaller 1979) which may

prevent pressure-adapted species from competing in shallow water.

The zonation patterns of much of the deep-sea fauna, including the demersal fishes, are characterized by a gradual reduction in metabolism with depth (Childress 1995; Childress & Somero 1979; Smith 1978; Smith & Hessler 1974; Somero *et al.* 1983; Sullivan & Somero 1980). This decrease in metabolism is greater than can be explained by a loss in the efficiency of enzyme systems associated with pressure and temperature adaptation, particularly when one considers that other phyla maintain high activity in the deepest parts of the ocean (Childress 1995; Childress & Thuesen 1993; Thuesen & Childress 1993). Food availability, which declines exponentially with depth, was proposed as the principal factor limiting the metabolism and activity of deep-sea animals (Smith & Hessler 1974; Somero *et al.* 1983). However, it has been argued that relaxed selection for locomotion, associated with a reduction in light, is the principal factor responsible (Childress 1995; Childress *et al.* 1980).

In the north-east Atlantic Ocean the scavenging fishes show distinct vertical zonation (Merrett & Haedrich 1997; Priede *et al.* 1994). At depths greater than 3000 m the grenadier *Coryphaenoides (Nematonurus) armatus* (Gadiformes: Gadidae) is the dominant scavenger, but at shallower depths it is replaced by the blue-hake, *Antimora rostrata* (Gadiformes: Moridae). In the present study we have measured the activity of these scavenging deep-sea fishes and considered the causes and implications of observed differences.

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2. MATERIAL AND METHODS

During August 1997 and September 1998 the Aberdeen University Deep Ocean Submersible (AUDOS) was deployed from the RRS *Challenger* and RRS *Discovery* at 2500 m in the Porcupine Seabight and at 4800 m on the Porcupine Abyssal Plain.

The AUDOS is an autonomous lander vehicle designed to photograph and track demersal deep-sea scavenging fishes (Collins & Bagley 1999). It consists of an aluminium frame onto which are mounted a downward-looking deep-sea camera (Ocean Instrumentation), a current meter (Sensortec) and twin acoustic releases (Mors) (Bagley & Priede 1997; Collins & Bagley 1999). The AUDOS is deployed by free-fall and is held in position on the sea-floor by 100 kg of ballast. The AUDOS frame is maintained 2 m above the ballast by syntactic foam buoyancy on a 50 m mooring line. Bait is attached to an aluminium graduated cross, tied to the ballast in the middle of the field of view of the camera and *ca.* 50 cm above the sea-floor. Following the experiment an acoustic signal, from the ship, triggers the release of the ballast and the AUDOS floats to the surface at a rate of 0.8 m s^{-1} under its own buoyancy. On the surface a marker buoy incorporating a VHF radio (Novatech), Argos satellite beacon (SIS) and a large pink flag, attached to the end of the mooring, aids recovery.

During each deployment the AUDOS was baited with a single 500 g mackerel (*Scomber scombrus*). Part of the mackerel was used to enclose code-activated transponders (CATs) (Bagley 1992), four of which were used on each deployment, attached to the apices of the cross. The CATs are miniature transponders that are readily swallowed by scavenging fishes and allow multiple fishes to be tracked simultaneously with a high degree of accuracy. Fishes taking the CATs were identified from photographs taken every minute, and positions of fishes that took the CATs were triangulated at one minute intervals using the differential arrival times of the return ping to a three hydrophone array (Collins & Bagley 1999). Swimming speeds were estimated, overground by interpolation between successive locations, and through the water by integrating synchronous current-meter data. The graduated cross, in the field of view, allowed the length of fishes, including those taking the CATs, to be measured.

Each AUDOS deployment lasted 12–14 h and took approximately 800 photographs. During one deployment at each location a video camera was added to the system and the fishes tail-beat frequencies were measured. The video recorder ran for 12 min during each deployment and the time taken for a complete tail-beat cycle was measured for all of the fishes seen.

3. RESULTS

(a) Porcupine Abyssal Plain (4800 m)

During three experiments at 4800 m on the Porcupine Abyssal Plain, the scavenging fauna were dominated by the grenadier *C. (N.) armatus*. *C. (N.) armatus* arrived at the bait, on average, 30 min after the AUDOS reached the sea-floor. More fish subsequently arrived, with numbers reaching a maximum of between eight and ten, for the three experiments (mean body length (BL) of 740 mm) within the 2.5 m^2 field of view after 200 min (figure 1a). Following the consumption of the bait the fish dispersed. The only other fish species attracted to bait at this depth

Figure 1. Ten minute running mean of fish numbers in view of the AUDOS camera. (a) Numbers of the grenadier *Coryphaenoides (Nematonurus) armatus* after the arrival of bait on the sea-floor at 4800 m on the Porcupine Abyssal Plain. (b) Numbers of the morid *Antimora rostrata* and (c) the grenadier *C. (N.) armatus* following the arrival of bait on the sea-floor during an experiment at 2500 m in the Porcupine Seabight.

was the eel *Histiobranchus bathybius*, which was only occasionally seen.

Four *C. (N.) armatus* ingested transponders and were tracked as they departed from the bait. Initially the grenadiers remained around the bait for up to 120 min after taking the transponder, swimming slowly within a 30 m radius of the bait. Once they had departed *C. (N.) armatus* followed a meandering path away from the bait, swimming across the prevailing current. Swimming speeds were calculated once each fish had left the immediate influence of the bait (range > 30 m). The mean swimming speed of *C. (N.) armatus* was 0.13 m s^{-1} (0.17 BL s^{-1}) as they swam out to the maximum range of detection (500 m). The maximum recorded speed in a one minute interval was 0.21 m s^{-1} (figure 2a). Mean arrival times, swimming speeds and mean sizes are detailed in table 1.

Figure 2. (a) Frequency distributions of swimming speeds of the grenadier *Coryphaenoides (Nematonurus) armatus* at 4800 m on the Porcupine Abyssal Plain. (b) Frequency distributions of swimming speeds of the blue-hake *Antimora rostrata* at 2500 m in the Porcupine Seabight.

Video sequences of *C. (N.) armatus* at the bait were used to estimate tail-beat frequency. *C. (N.) armatus* were seen swimming slowly around the bait and tugging at the bait bags containing the transponders. The mean tail-beat frequency was 0.5 Hz, and the maximum tail-beat frequency, when tugging at bait, was 1 Hz (figure 3a).

(b) Porcupine Seabight (2500 m)

The six experiments in the Porcupine Seabight, attracted a greater diversity of scavengers. The first species to arrive at the bait was always the blue hake, *Antimora rostrata*, which arrived, on average, after 15 min. More *A. rostrata* arrived in rapid succession to reach maximum numbers, between the six experiments, of four to six (mean length 550 mm) within view 30 min after AUDOS touchdown (figure 1b); they consumed most of the bait, including the transponders. The bait was always consumed within two hours of touchdown, and the *A. rostrata* dispersed. The other species of fishes regularly seen at the bait were the grenadier *C. (N.) armatus*, the ophiidiid *Spectrunculus grandis*, the ray *Bathyrhaja richardsoni*, the shark *Centroscymnus coelolepis* and the eel *H. bathybius*. *C. (N.) armatus* (mean size, 524 mm) arrived on average after 50 min, by which time most of the bait, including the transponders, had been consumed. Numbers of *C. (N.) armatus* subsequently rose to a maximum of three to four after 200 min (figure 1c), depending on the amount of bait which remained. *S. grandis* were seen around the bait in small numbers during most experiments (a maximum of three in one frame), the other species were only occasionally seen.

Six *A. rostrata* swallowed the CATs and were tracked. In some cases the *A. rostrata* remained around the bait after swallowing the transponder, but more typically the fish

departed the bait area soon after. The mean along-track overground swimming speed of *A. rostrata*, measured when they were more than 30 m from the bait, was 0.21 m s^{-1} (0.39 BL s^{-1}), twice as fast as *C. (N.) armatus* performing the same task at 4800 m (figure 2b). Swimming speed through the water was slightly faster (0.24 m s^{-1} , 0.44 BL s^{-1}) since the *A. rostrata* typically departed against the current. The maximum overground recorded swimming speed of *A. rostrata* was 0.63 m s^{-1} (1.13 BL s^{-1}). Arrival times, swimming speeds and mean sizes are summarized in table 1.

Analysis of video sequences at 2500 m allowed tail-beat frequencies of both *A. rostrata* and *C. (N.) armatus* to be measured. Tail-beat frequencies of *C. (N.) armatus* were not significantly different between 4800 m ($n=27$) and 2500 m ($n=23$) (Student's *t*-test $p>0.1$) and the *C. (N.) armatus* data are pooled in figure 3. Tail-beat frequencies of *A. rostrata* were on average 1.0 Hz, twice as fast as *C. (N.) armatus* (figure 3).

4. DISCUSSION

To date, studies of activity of deep-sea animals have used proxies such as muscle enzyme activity (e.g. Childress & Michel 1985; Childress & Somero 1979; Siebenaller & Somero 1982; Siebenaller *et al.* 1982; Somero 1982; Sullivan & Somero 1980) and metabolic rates, measured in constrained animals (Childress 1971; Smith 1978). Autonomous landers, such as the AUDOS provide a platform for obtaining direct measurements of unconstrained activity *in situ*. This study highlights important differences in the activity of two phylogenetically related species of fishes occupying similar niches in overlapping depth zones, and provides important clues to the factors that control the bathymetric distribution of demersal deep-sea fishes. In all three measures of activity, arrival at the bait, tail-beat frequency and departure swimming speeds, the bathyal species, *A. rostrata*, was more active than the abyssal species, *C. (N.) armatus*.

C. (N.) armatus is a ubiquitous species occurring at abyssal depths (2000–5000 m) throughout the world's oceans. The data from this and previous studies show that *C. (N.) armatus* is a roving scavenger, with a behaviour pattern designed to maximize the probability of encountering relatively rare feeding opportunities (Armstrong *et al.* 1992; Bagley *et al.* 1994; Collins *et al.* 1998; Priede *et al.* 1991; Smith *et al.* 1997). The present study indicates that routine swimming speeds are low, although *C. (N.) armatus* does have higher muscle enzyme activities than lethargic species from similar depths (Siebenaller *et al.* 1982; Sullivan & Somero 1980). The observations on tail-beat frequency confirm the low activity of *C. (N.) armatus* and even when tugging at bait the maximum tail-beat frequency observed was 1.0 Hz. Assuming that this species swims at 0.7 BL per tail beat (Wardle & Videler 1980), this equates to 0.5 m s^{-1} , which may be the maximum possible speed.

In contrast to *C. (N.) armatus*, the swimming speeds of *A. rostrata* were high, similar to those of related shallow water species such as cod (*Gadus morhua*) performing an equivalent task at similar temperatures (Lokkeborg 1998) (see table 1), and demonstrate that high hydrostatic pressure does not prevent high activity. The rapid arrival at the bait

Table 1. *Details of arrival times, swimming speeds and mean lengths of fish tracked during the present study and previous work*

(Dashes indicate no available data; PSB, Porcupine Seabight; PAP, Porcupine Abyssal Plain.)

	location	depth (m)	temperature (°C)	arrival time (min)		fish length (mm)		weight of mean- sized fish (g)	swimming speed (m s ⁻¹)	
				mean	range	mean	s.d.		maximum	mean
<i>Antimora rostrata</i>	PSB	2500	2.5	14.3	11–18	550	45.8	1343	0.633	0.213
<i>Coryphaenoides</i> (<i>Nematonurus</i>) <i>armatus</i>	PSB	2500	2.5	50	34–79	524	75.8	527	—	—
<i>Coryphaenoides</i> (<i>Nematonurus</i>) <i>armatus</i>	PAP	4800	2.2	30	16–38	740	91.9	2163	0.229	0.137
<i>Coryphaenoides</i> (<i>Nematonurus</i>) <i>armatus</i> (Bagley <i>et al.</i> 1994; Priede <i>et al.</i> 1994)	PSB	2500–4050	—	24	13–40	425	11.2	342	0.210	0.088
<i>Coryphaenoides</i> (<i>Nematonurus</i>) <i>armatus</i> (Smith <i>et al.</i> 1997)	PAP	4800	2.2	28	7–63	543	17.0	767 ^a	0.193	0.088
<i>Gadus morhua</i> (Lokkeborg 1998)	Norway	35–85	2.5	—	—	400–550	—	—	0.540	0.116

^a 376 g value published by Smith *et al.* (1997) is incorrect. Figure 3. (a) Tail-beat frequency of grenadier *Coryphaenoides* (*Nematonurus*) *armatus* at 2500 m and 4800 m. (b) Tail-beat frequency of the blue-hake *Antimora rostrata* at 2500 m.

and tail-beat frequencies confirm the high activity. A previous report of a single *A. rostrata* followed by a submersible (Cohen 1977) had suggested that this species may be capable of high sustained speeds. However, measurements of low muscle enzyme activities in comparison with other demersal deep-sea fishes led to the suggestion that *A. rostrata* is a passive drifter (Sullivan & Somero 1980), a direct contradiction of *in situ* observations.

Differences in swimming ability in these species are a consequence of differences in morphology and metabolism. The morphology of the two species is different (see the

inserts in figures 1–3) and the video sequences show the tapered *C. (N.) armatus* swimming with anguilliform locomotion, compared with the sub-carangiform movement of *A. rostrata*. However, these differences are unlikely to account for a twofold variation in speed, particularly when one considers the larger size of *C. (N.) armatus* tracked at 4800 m. The data thus indicate that the routine metabolic rate of *A. rostrata* is higher than that of *C. (N.) armatus*, a finding confirmed by the relative heart weights of 0.12% and 0.09% body weight, respectively (M. A. Collins, unpublished data from *Challenger* cruise 134). *In situ* measurements of resting oxygen consumption (Smith 1978) also demonstrated the low metabolism of *C. (N.) armatus*.

Metabolic differences in these species are likely to be an adaptation to environmental gradients. Between 2500 m in the Porcupine Seabight and 4800 m on the abyssal plain the principal environmental gradients are depth (pressure) and food availability. Light and temperature levels are relatively constant at these depths. The difference in the metabolic rate of the two species could be a consequence of extreme pressure adaptation in *C. (N.) armatus*, resulting in a loss of enzyme efficiency (Somero 1991; Somero & Siebenaller 1979; Somero *et al.* 1983). However, most of the direct pressure effects on marine animals occur from the surface to 800 m (Childress 1995); there is only a twofold increase in pressure from 2500–4800 m and many species can maintain a high metabolism despite high pressure (Childress & Michel 1985; Childress & Thuesen 1993). Food availability, however, shows a distinct decline. Taking megafaunal biomass as a proxy for food availability, there is a 32-fold decline between 2500 m and 4000 m in the Porcupine Seabight (Lampitt *et al.* 1986). The low metabolism of *C. (N.) armatus* must therefore be an adaptation to the low food supply to the abyss, allowing it to dominate the scavenging fauna in the abyssal areas of the world's oceans. Only in the highly oligotrophic central North Pacific is the dominance of *C. (N.) armatus*

challenged, by replacement with *Coryphaenoides* (*Nematonurus*) *yaquinae* (Wilson & Waples 1983), and this species may have an even lower metabolism than *C. (N.) armatus*.

Differences in routine metabolism will have profound effects on the distribution of the two species. For a scavenging species the ability to rapidly locate and obtain food is clearly an advantage, so the lowered metabolism and hence swimming speed of *C. (N.) armatus* puts it at a competitive disadvantage at the depths where it overlaps with the more active *A. rostrata*. Thus at 2500 m it appears that *C. (N.) armatus* is unable to compete with the more active *A. rostrata*, which is capable of intercepting a food-fall, consuming it and dispersing to 500 m in the time taken for *C. (N.) armatus* to arrive. The low food supply on the abyssal plain is probably insufficient to support the higher routine metabolism of *A. rostrata* and this prevents it from competing with *C. (N.) armatus* at abyssal depths.

Both *A. rostrata* and *C. (N.) armatus* display a larger-deeper trend (Merrett & Haedrich 1997), so at 2500 m the size of the *C. (N.) armatus* is smaller than those tracked at 4800 m. The smaller size and perhaps lower abundance account for the longer mean arrival time of *C. (N.) armatus* at 2500 m, compared to 4800 m. Martin & Christiansen (1997) showed that smaller-sized *C. (N.) armatus* are not as reliant on scavenging as the larger fish, possibly because by living in shallower water they cannot compete, as scavengers, with *A. rostrata*. The question remains as to what prevents *A. rostrata* extending its bathymetric range into shallower water. It is possible that adaptation to pressure does have costs in terms of enzyme efficiency (Somero & Siebenaller 1979), preventing it from competing with more efficient or faster swimming species in shallow water, or that visually oriented scavengers rather than olfactory scavengers predominate at shallower depths.

This study indicates that it is food supply and competition that define the boundary between the abyssal species *C. (N.) armatus* and the bathyal species *A. rostrata*, and that the low activity and metabolism of *C. (N.) armatus* is a capacity adaptation to the deep sea rather than a consequence of efficiency loss in resistance adaptation. The reduction in metabolism seen in many other deep-sea species is probably a consequence of many factors. Childress (1995) argued that relaxed selection for locomotion was the principal reason for capacity adaptations of deep-sea animals, particularly in the pelagic realm, where the reduction of light negates the requirement to move rapidly either in pursuit of food or in avoiding predation. In scavengers, the ability to move rapidly remains important in obtaining rare food resources, and so other factors such as food availability are more important in determining capacity adaptations.

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