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Inter-relations of necrophagous amphipods, a fish predator, and tidal currents in the deep sea

R. S. Lampitt, N. R. Merrett and M. H. Thurston

Institute of Oceanographic Sciences; Brook Road, Wormley, Godalming GU8 5UB, Surrey, England

Abstract

Photographic and trap data obtained from the eastern North Atlantic Ocean in 1981 and 1978, respectively, have been combined to document the response of abyssal lysianassid amphipods to large food falls, and the predation on these amphipods by the fish *Paraliparis bathybius*. The use of a new camera/current meter system has demonstrated that overall numbers of amphipods and presence of fish were related to tidal currents. Species of *Paralicella* and *Orchomene* were the most abundant amphipods, and occurred in peak numbers during periods of low current velocity. Variation in abundance of *Eurythenes gryllus*, a larger species, which occurred in smaller numbers, was apparently not related to tidal currents. *Paraliparis bathybius* were present only during flood tides.

Introduction

For many years traps have been used to collect benthic organisms from the deep sea (see, for example, Richard, 1934). Early indications of the existence of a large, highly mobile element in the deep-sea benthos went largely unrecognised until the pioneering use of baited cameras by Isaacs (1969). The subsequent use of cameras and traps, either separately or together (Paul, 1973; Rannou and Nougier, 1974; Shulenberger and Hessler, 1974; Isaacs and Schwartzlose, 1975; Hessler *et al.,* 1978; Thurston, 1979; Stockton, 1982; Ingram and Hessler, in press) has shown these mobile necrophages to be abundant and ubiquitous at abyssal and hadal depths. Fish, particularly macrourids and ophidioids, and lysianassid amphipods dominate this part of the benthopelagic fauna.

Specimens from traps, together with photographs and current measurements have been obtained as part of a survey of the benthic fauna of the Porcupine Seabight (50°N; 13°W). Some of these data are here combined to elucidate behavioural relations between tidal currents, appearance of necrophagous amphipods at bait, and predation on these amphipods by a fish species.

Materials and methods

Data for this study were obtained from a prototype free-fall fish trap (Discovery Station 9756#8: 49°54.4′N, 13°56.3′W; 3 852 m; 13 April 1978) and a free-fall camera and current meter system (Challenger Station 51215: 49°52.7′N, 14°08.3′W; 4 009 m; 27 September 1981). The fish trap (Thurston, 1979) was equipped with a time-lapse camera system (Rice *et al.,* 1979) and two small auxilliary traps. All traps were baited with carcasses or fillets of the freshly trawled fish *Coryphaenoides (Nematonurus) armatus* (Hector, 1875). The small traps were 500 mm lengths of 70 mm diam plastic pipe closed at each end with 500 μm mesh and with 20 mm entrance holes near one end. They were located 1.2 m apart on the top and bottom bars of the main trap. The camera was set to take photographs at 8 min intervals. Photographs were taken during descent and ascent as well as on the bottom, but a fault developed in the timing system which resulted in unknown intervals between exposures. There is, however, no reason to believe that long periods elapsed during which no photographs were taken.

Bathysnap, the time-lapse camera and current meter system (Lampitt and Burnham, in press), photographed bait and 2 m^2 of the surrounding sea bed at 4 min intervals. The bait was also freshly trawled *Coryphaenoides (Nematonurus) armatus,* but enclosed in fine-mesh cotton gauze to resist consumption by fish. The amphipods on the bait were counted in each frame and plotted as the average of 5 successive frames (20 min).

Results

No animals were apparent in photographs taken during the descent of the fish trap. While on the bottom, 331 frames were exposed and these showed a gradual build-up of amphipods on the bait. Also present were a number of fish, some frames showing as many as 9 specimens of a small dark species. On recovery of the trap, a single mature female *Paraliparis bathybius* (Collett, 1879) of 115 mm SL was collected, thus confirming the identity of the small fish seen in the photographs. In addition, the trap contained 2 *Coryphaenoides (Nematonurus) armatus* and 41 lysianassid amphipods. The single *P. bathybius* and the low number of amphipods obtained by the trap contrasts with the photographic evidence. This discrepancy is, in all probability, attributable to the coarse mesh of the upper walls and roof of the trap, resulting in considerable loss of specimens during recovery. In all, 131 frames (40%) pictured *P. bathybius.* Single specimens were present in most of the pictures, but in 30% of the frames showing *P. bathybius,* 2 to 9 individuals were visible. In most cases, the fish appeared to be browsing over the bait (Fig. 1 A–C). Due to the fault in the timing system, a detailed analysis of arrival rates and build-up in numbers of amphipods and fish is not possible. There was, however, a distinct trend for *P. bathybius* to be present in more frames and in greater numbers towards the end of bottom-residence time than early in the drop.

The composition of catches of amphipods from the two small traps is roughly comparable, although no *Eurythenes gryllus* were taken in the lower one (Table 1). The absence of *E. gryllus* from the lower trap may be due to its vertical distribution in the water column. *E. gryllus* reaches its maximum density at 20 m above the bottom, whereas species of *Orchomene* and *Paralicella* with a primary range of 1 to 2 m, are largely confined to the Ekman layer (Ingram and Hessler, in press). The low overall numbers, relative abundance of *E. gryllus,* and absence of *Paralicella* spp. in the main trap contrast with counts from the small traps. This disparity is probably a function of different mesh sizes of small and large traps, and the fact that *E. gryllus* and *Orchomene cavimanus* var. (see Barnard, 1961) are stouter and more tenacious organisms than are species of *Paralicella.*

The stomach of the *Paraliparis bathybius* from the fish trap was packed with the remains of at least 69 amphipods and a few large fish scales, apparently from the bait. No flesh from the bait was found. Most of these amphipods belonged to the three species dominating the trap catches (Table 1). A comparison of species composition in the amphipod traps and fish stomach may indicate some selectivity by *P. bathybius* for *Orchomene cavimanus* var. and against *Paralicella* spp. The small mouth-gape of *Paraliparis bathybius* would preclude the ingestion of any but the smallest specimens of *Eurythenes gryllus.*

Bathysnap was on the bottom for over 39 h at Station 51215, but the photographic record ended after about 25 h. The camera was pointing in the direction 086° true. The first amphipod to arrive at the bait appeared in the third seabed photograph, i.e., within 12 min of bottom contact. The fluctuations in numbers over the subsequent 25 h together with the appearance of other taxa, are shown in Fig. 1A. The camera photographed nearly all of the exposed surface of the bait, so it is unlikely that the variations in amphipods counted were due to changes in their positions on the bait.

Although the quality of photographs obtained from Bathysnap is high, the specific identification of amphipods is, in general, not possible. Evidence from the fish trap at Station 9756 and other trap stations worked subsequently (Thurston, unpublished data) suggests that most individuals would have been *Eurythenes gryllus, Orchomene cavimanus* var. or *Paralicella* spp. A small proportion of photographed specimens can be assigned to *E. gryllus,* however, on the grounds of size, shape of pleon, and the reflectance of light by the eye. The trend exhibited by the *E. gryllus* counts (Fig. 2A), which are minimum, differs from that shown by the total number of amphipods present. Three periods, defined by the average number of *E. gryllus* per 5 frames, were apparent. The first period ended 7.5 h after first bottom contact, the second 18 h, and the third extended to at least the end of the photographic record 24.5 h after arrival on the bottom. Although these three periods appear to be distinct, they do not coincide with changes in any measured physical or biological parameter. This apparent difference between *E. gryllus* and the other amphipod species may be related to the previously mentioned differences in distribution (Ingram and Hessler, in press).

Of the other taxa occurring in photographs, small black fish (Fig. 1D) were most frequently recorded. In size, appearance and behaviour they closely resembled the fish caught and photographed in the fish trap, and they are tentatively identified as *Paraliparis bathybius.* The occurrences of these fish were confined almost entirely to two periods, 9.5 to 11 h and 21 to 24 h after bottom contact, and coincided with marked decreases in numbers of amphipods visible on the bait (Fig. 2). This coincidence could be the result of chance, or of physical disturbance of the amphipods by the fish. However, in view of the known predatory habits of *P. bathybius,* these causes seem improbable. It is perhaps significant that the rate of increase in amphipod numbers was no greater after the departure of *P. bathybius* than before their arrival. Had the reduction in amphipod numbers been due to physical displacement rather than predation, a more rapid build-up in numbers after the departure of the fish might have been expected. Most photographs of *P. bathybius* show the fish orientated head to current, in close contact with the bait, and probably feeding on amphipods.

Current velocities at 1.3 m above the sea floor were obtained by Bathysnap (Fig. 2B), and clearly demonstrated a tidal cycle (Fig. 3). Three complete cycles were recorded. The third, with two well-defined current maxima, resembled the first cycle rather than the second. It is also clear that amphipod abundances and the appearances of *Paraliparis bathybius* were related to these tidal currents. During the first tidal cycle, peaks in the numbers of amphipods on the bait coincided with periods of lower current velocities. Fluctuations in velocities during the second cycle were less clear cut, as were the

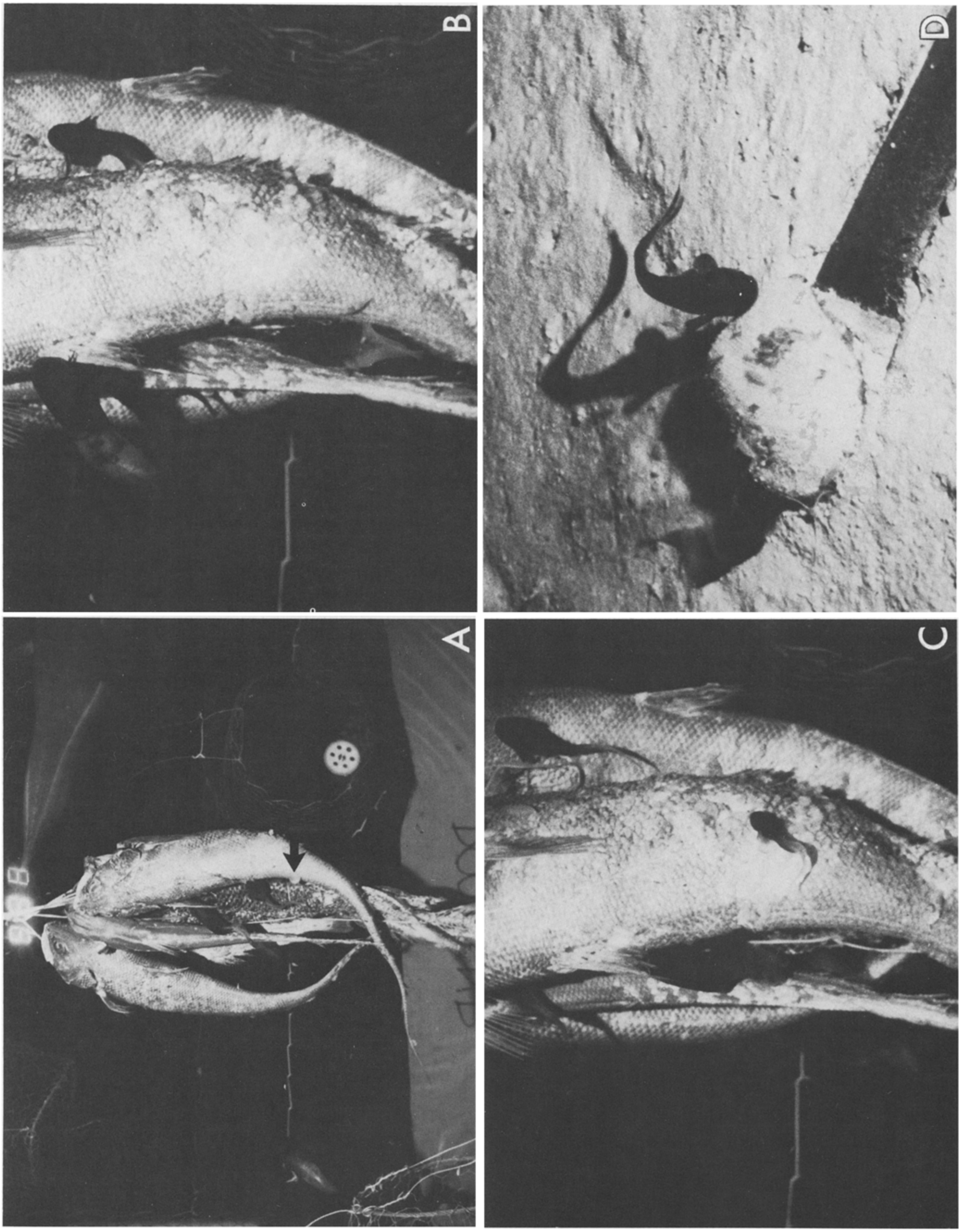

Fig. 1. Amphipods and fish (probably *Paraliparis bathybius*) at bait. (A)–(C) Station 9756 #8, 3 852 m (arrow in "A" points to one of the more conspicuous amphipods); (D) Station 51215, 4 009 m (fish standard length ca. 110 mm)

Table 1. Numbers of amphipods collected from traps and from *Paraliparis bathybius* stomach contents

Amphipod species	Fish trap		Small traps				*P. bathybius*	
	No.	%	Bottom No.	Top No.	Total No.	%	No.	%
Eurythenes gryllus	32	78.0	0	6	6	2.5	1	1.4
Orchomene cavimanus var.	8	19.5	13	2	15	6.2	29	42.0
Paracallisoma alberti	1	2.4	0	0	0		0	–
aff. *Paracallisoma*							2	2.9
Paralicella caperesca	0	0	155	62	217	90.0	37	53.6
Paralicella tenuipes	0	0	3	0	3	1.2	0	–
Total	41	99.9	171	70	241	99.9	69	99.9

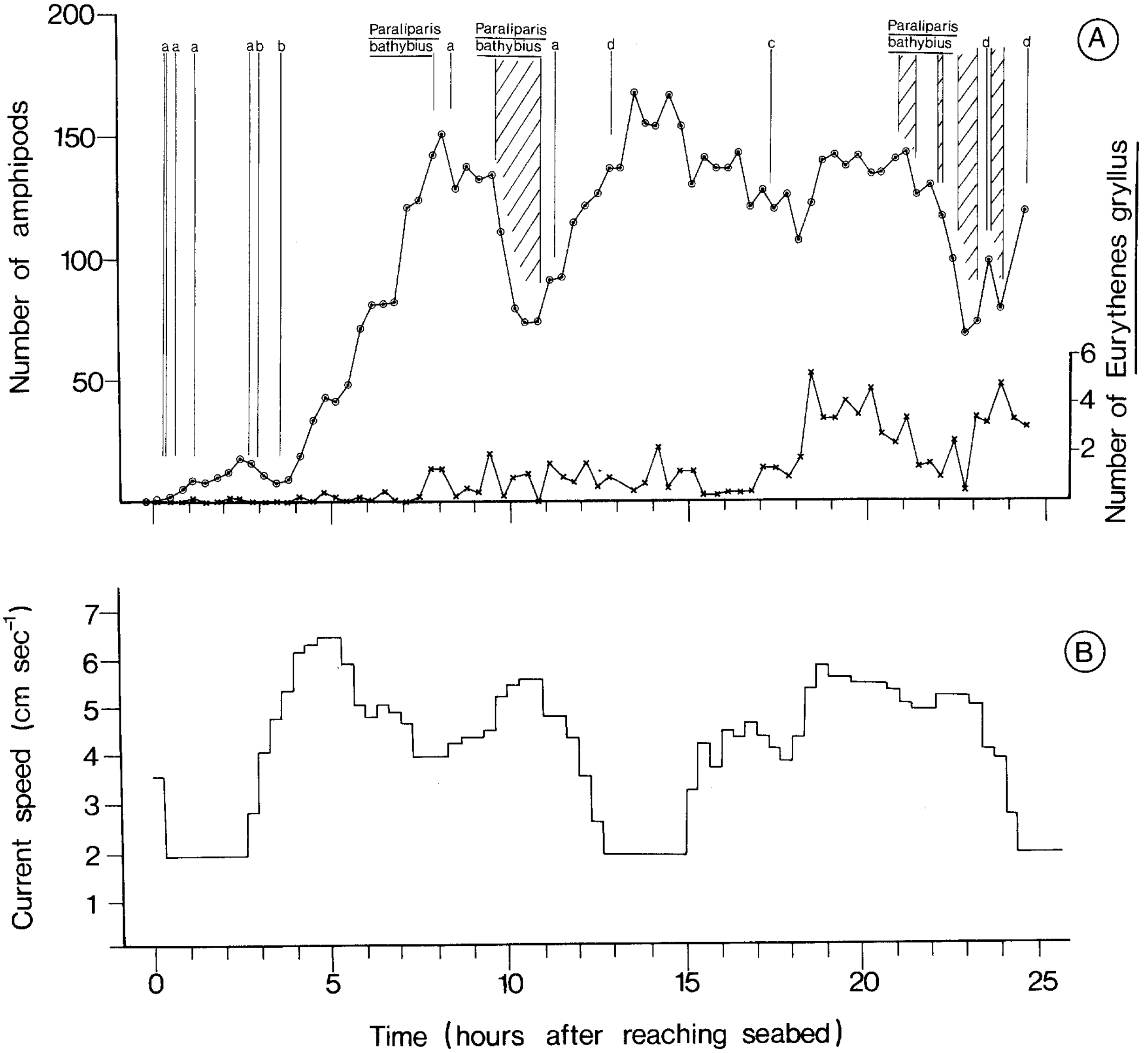

Fig. 2. Station 51215. (A) Numbers of all amphipod specimens and of *Eurythenes gryllus* visible on bait, and occurrences of *Paraliparis bathybius* and other organisms in photographs (graphs represent average numbers per 5 frames; hatched areas show main periods of occurrence of *P. bathybius*): a, *Coryphaenoides (Nematonurus) armatus*; b, *Echinomacrurus mollis* (fish); c, small silver-blue fish (unidentified); d, *Pleisiopenaeus edwardsianus* (natantian decapod). (B) Current velocities (apparent constant current velocities at 0 to 3, 13 to 15 and 24 to 25 h are artefacts of current-meter sensitivity)

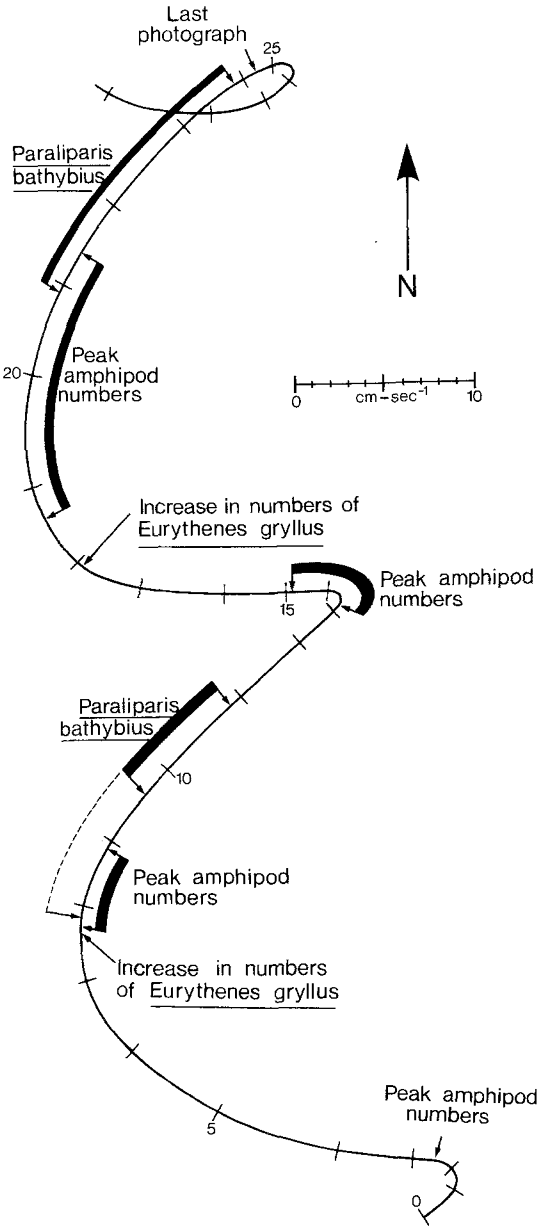

Fig. 3. Station 51215. Progressive vector diagram of tidal currents, illustrating periods during which amphipod numbers were most abundant and when *Paraliparis bathybius* were present. Also shown are approximate times when numbers of *Eurythenes gryllus* appeared to increase

variations in amphipod numbers. There does not appear to be any relationship between current direction and amphipod numbers. Appearances of *P. bathybius* followed peaks in amphipod numbers, but were confined to periods of what are probably flood tides. Such appearances are unlikely to be related directly to peak amphipod numbers, as *P. bathybius* were not recorded at 14 h after touchdown, when amphipods reached maximum numbers (Fig. 2A). Presence of *P. bathybius* does not appear to be related to current velocity, but there does appear to be a relation with current direction. All records of *P. bathybius* occurred when the direction of water movement was close to 040° true. It may be significant that at Station 51215 such a flow is perpendicular to the contours, and up slope.

Discussion

Evidence for semidiurnal and seasonal variations in biological activity (e.g. Geistdoerfer, 1979; Hureau *et al.*, 1979; Tyler and Gage, 1980; Gage and Tyler, 1982), together with reports of physical variations of an annual (Deuser *et al.*, 1981) and diurnal (Dickson *et al.*, 1982) nature, contrast with the concept of the deep sea as an area of environmental stability (Sanders, 1968; Grassle and Sanders, 1973). The present study suggests that *Paraliparis bathybius* is markedly influenced by tidal currents, and may not, therefore, be a strong swimmer, thus supporting anatomical evidence. Studies in the Bay of Biscay by Guennegan and Rannou (1979) showed a similar effect in that slow swimming macrourids and ophidioids fluctuated in abundance in response to tidal activity, whereas the stronger swimming sharks and Anguilliformes did not.

Data on swimming speeds of abyssal organisms are virtually non-existent. Cohen (1977) reported 392 mm s^{-1} as the maximum prolonged speed for the morid fish *Antimora rostrata* (Gunther, 1878). No information is available on swimming speeds of abyssal necrophagous amphipods, and very little on small marine crustaceans in general. Although speeds of 1 m s^{-1} have been recorded for copepods (Clutter and Anraku, 1968), such velocities are achieved only during escape reactions, and are unlikely to be maintainable for more than a few metres at most. Cruising speeds are much lower; values of 200 mm s^{-1}, having been recorded for euphausiaceans and mysidaceans (Clutter and Anraku, 1978). Laval (1974) found that the hyperiid amphipod *Vibilia armata* Bovallius, 1887 averaged only 117 mm s^{-1} and did not exceed 150 mm s^{-1} except for very short periods. If necrophagous amphipods swim no faster than this, then the bottom currents in excess of 60 mm s^{-1} experienced at Station 51215 would have a significant effect on over-the-ground progress and could lead to the observed fluctuations in amphipod numbers. However, Wolff (1971) indicates that some, at least, of the abyssal near-bottom amphipods can swim rapidly.

Fluctuations in arrival rates will, in part, depend on foraging strategy. Amphipods arrive early at bait and clearly swim rather than crawl to food sources (Hessler *et al.*, 1972, 1978; Thurston, 1979). Wolff (1971) observed large numbers of amphipods within 2 m of the bottom in 4 160 m off Madeira, and Jumars and Gallagher (1982) have suggested that scavengers may spend much of their time hovering above the bottom. Hovering implies the ability to recognize a particular patch of sediment, and an energy expenditure to counteract water movements. As has been pointed out by Ingram and Hessler (in press), random swimming and drifting with the current would be simpler and energetically less expensive.

Data from both stations used in this study indicate that *Paraliparis bathybius* feeds on amphipods attracted to large food falls. Andriashev (1954) reported the hyperiid amphipods *Themisto oblivia* (Kröyer, 1838) and *T. libellula* (Mandt, 1822) to form a major part of the diet of

P. bathybius taken in the Norwegian Sea, but that mysidaceans, the lysianassid *Tmetonyx cicada* (Fabricius, 1780) (as *Hoplonyx*) and small benthic gastropods were also eaten. It is perhaps significant in connection with the present findings, that *T. cicada* is common at shelf and mid-to-upper-slope depths and is a known necrophage (Sars, 1890–1895; Chevreux, 1935). The presence of *Themisto* spp. does not preclude the possibility that *P. bathybius* leads a predominantly benthic existence. There is increasing evidence that benthic fish feed extensively on bathy- and abyssopelagic organisms in areas where the latter impinge on the continental slope or deep sea floor (e.g. Pearcy and Ambler, 1974; Marshall and Merrett, 1977).

Aggregations at food falls may increase risk of predation. There is evidence for cannibalism and possibly interspecific predation among amphipods at deep-sea food falls (Hessler *et al.*, 1978; Thurston, 1979; Ingram and Hessler, in press). Hessler *et al.* (1978) and Thurston (1979) have suggested that the absence of ovigerous amphipods at bait may reduce the risk of predation, but until now, no predator has been identified. Evidence that *Paraliparis bathybius* is such a predator adds weight to this suggestion.

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