The fate of cetacean carcasses in the deep sea: observations on consumption rates and succession of scavenging species in the abyssal north-east Atlantic Ocean

Emma G. Jones*, Martin A. Collins, Philip M. Bagley, Steven Addison and Imants G. Priede

Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

The fate of cetacean carcasses in the deep sea was investigated using autonomous deep-sea lander vehicles incorporating time-lapse camera systems, fish and amphipod traps. Three lander deployments placed cetacean carcasses at depths of 4000–4800 m in the north-east Atlantic for periods of 36 h, 152 h and 276 h before being recovered. The photographic sequences revealed that carcasses were rapidly consumed by fish and invertebrate scavengers with removal rates ranging from 0.05–0.4 kg h⁻¹. In the longest experiment the carcass was skeletonized within five days. In each deployment, approximately an hour after emplacement, the grenadier *Coryphaenoides* (*Nematonurus*) *armatus* and large numbers of lysianassid amphipods had arrived at the food-fall. The initially high numbers of grenadiers declined once the majority of the bait had been consumed and a variety of other fish and invertebrates were then observed, some taking up residence at the site. None of the fish species appeared to consume the carcass directly, but preyed upon amphipods instead. Funnel traps recovered with the carcass indicated a succession in the species composition of amphipods, with the specialist necrophages such as *Parallicella* spp. being replaced by more generalist feeders of the *Orchomene* species complex.

Keywords: food-fall; autonomous lander; scavengers; cetaceans; *Coryphaenoides* (*N.*) *armatus*; amphipod

1. INTRODUCTION

The abyssal sea floor covers 40% of the Earth's surface and represents a massive sink for passive fall-out of organic matter from the surface. In temperate latitudes, seasonally pulsed particulate organic matter is largely responsible for sustaining sediment community metabolism at these depths (e.g. Smith 1978*b*; Lampitt 1985; Honjo & Doherty 1988). This source of enrichment is effectively processed by microbial and detritivore activity within months of arrival (Turley & Lochte 1990; Pfannkuche 1993; Smith *et al.* 1997*a*).

A less predictable source of enrichment are nekton carcasses, varying in size from fish (mesocarrion) to whales (macro- and megacarrion), as defined by Britton & Morton (1994). Despite their probable rarity, food-falls represent a concentrated nutrient input into an otherwise food-poor environment, causing localized changes in the benthic community (Smith 1986). Baited traps and camera studies have demonstrated the existence of highly effective scavenging fauna that respond to baits placed at any depth (Dayton & Hessler 1972; Isaacs & Schwartzlose 1975; Thurston 1979; Stockton 1982). Whereas mesocarrion is removed and dispersed within hours (Smith *et al.* 1997*b*;

Collins *et al.* 1998), larger food-falls may produce more than a transitory localized habitat change.

There has been considerable speculation on the importance or otherwise of large food-falls (e.g. Stockton & Delacca (1982) and references therein) but little quantitative data exist. Occasionally, naturally occurring large nekton carcasses have been observed (Heezen & Hollister 1971; Jannasch 1978) the most spectacular being a number of intact whale skeletons found at 850–2000 m depth in the Pacific Ocean (Smith *et al.* 1989; Smith & Baco 1998). Anaerobic conditions had developed within these remains, supporting thriving communities with affinities to those found at hydrothermal vents. Smith (1989) proposed the theory that such food-falls may provide organically enriched 'stepping stones', enabling vent and seep fauna to disperse across an otherwise inhospitable habitat. Cetaceans represent a considerable source of large nekton-falls (Katona & Whitehead 1988; Britton & Morton 1994) with the potential for unique environmental perturbations. Therefore, the knowledge of processes by which such a massive enrichment is consumed, dispersed and colonized is of ecological relevance.

In this paper we report the first experiments in which cetacean carcasses have been deployed on the abyssal sea floor and subsequently recovered to investigate the immediate fate of large food-falls in the deep sea. The studies were carried out in the north-east Atlantic at

*Author for correspondence (e.g. jones@aberddeen.ac.uk).

Table 1. *Large abyssal food-fall experiments in the north-east Atlantic, arranged in ascending order of duration*

	experiment 1 RRS <i>Challenger</i> 134/97/01	experiment 2 RRS <i>Challenger</i> 134/97/07	experiment 3 RRS <i>Discovery</i> 222a/96/05
dates	8 August–10 August 1997	11 August–17 August 1997	30 July–11 August 1996
position	49°59.9' N, 14°19.1' W	50°00.1' N, 14°19.3' W	48°36.1' N, 16°10' W
depth (m)	4000	4000	4800
lander	LAFF 2	LAFF 2	LAFF 1
photo interval (min)	10	15	10
bottom time (h)	36	152	276
species of bait used	<i>Phocoena phocoena</i>	<i>Phocoena phocoena</i> <i>Delphinus delphis</i>	<i>Lagenorhynchus acutus</i>
carcass length (m)	1.69	1.40 1.70	2.04
soft tissue weight deployed (kg)	53	100	58
soft tissue weight recovered (kg)	51	50	<1
consumption rate (kg h ⁻¹)	0.05	0.30	0.40

4000–4800 m depths of the Porcupine Abyssal Plain. This region has been well described and studied (Rice *et al.* 1994) and was also the site of previous comparable work using fish food-falls (Armstrong *et al.* 1992; Priede *et al.* 1994).

2. MATERIALS AND METHODS

Three experiments were carried out using two different designs of autonomous lander vehicles (large abyssal food-fall (LAFF) 1 and 2). One experiment was conducted from the RRS *Discovery* (Cruise 222a) during August 1996 in the centre of the Porcupine Abyssal Plain at a depth of 4800 m. The other experiments were deployed from RRS *Challenger* (Cruise 134) during August 1997 at a depth of 4000 m on the edge of the abyssal plain near the Porcupine Seabight (table 1). Carcasses of an Atlantic white-sided dolphin (*Lagenorhynchus acutus* Gray, 1820), two common porpoises (*Phocoena phocoena* Linnaeus, 1758) and a common dolphin (*Delphinus delphis* Linnaeus, 1758) were obtained from coastal strandings or accidental fishery kills. The fresh carcasses were stored frozen and thawed immediately before each experiment. Experiment 3 used a sagittally sectioned half of the Atlantic white-sided dolphin, whereas experiments 1 and 2 used whole carcasses, which had been incised for veterinary post-mortem examinations.

In each experiment the carcass was deployed on the sea floor on a sheet of netting suspended beneath the lander vehicle (Jones *et al.* 1996). A vertically orientated time-lapse camera monitored events from a height of 2.7 m, allowing the carcass to be viewed in full. The camera was programmed to take photographs at time intervals of either 10 or 15 min using Kodak Ektachrome 200 ASA colour transparency film. A pair of strobe flash bulbs (160J total) provided illumination. Tell-tale ribbons and a compass, in view of the camera, indicated bottom current direction, while a reference scale enabled the size of scavengers viewed to be estimated. LAFF 2 was equipped with a second slave camera, placed horizontally close to the sea floor and triggered simultaneously with the vertical camera. This provided detailed side views of activity surrounding the carcass. Furthermore, LAFF 2 was able to sample the larger mobile megabenthos in view of the camera using a box trap that closed over the carcass when triggered acoustically at the end of each

experiment. Baited funnel traps attached to both lander frames captured samples of amphipods for identification. Both vehicles worked on a 'pop-up principle', incorporating acoustic ballast releases and buoyancy spheres, which enabled the return of the lander to the surface on acoustic command from the ship. On retrieval, the carcass remains were weighed and photographed. Representative parts were then frozen or preserved in 10% formalin. All invertebrates collected from the carcass and traps were preserved. Fish caught in the box trap were identified, measured, and stomach contents were collected where possible.

On shore, the invertebrates were transferred to 70% ethanol and identified. Sections of cetacean vertebral bone were prepared for examination by light microscopy by decalcifying in EDTA and embedding in wax. Sections of 5 µm thickness were stained with Haematoxylin and Eosin or Van Gieson's stain, the latter allowing differentiation between connective and muscle tissue.

From the films, counts were made of all species of fish in each frame. Identification was made using relevant texts (e.g. Whitehead *et al.* 1989) and comparison with specimens caught in contemporary traps and trawls. Although confidence in identification of common species was high, the identity of rarer individuals must remain speculative. Total body lengths, from tip of snout to tail were recorded from fish in every third frame where they were in full view and close to the sea floor. This minimized inaccuracies and the possibility of individuals being measured repeatedly. These length frequencies were plotted for the dominant fish species. Current direction was noted in each frame and correlated with fish numbers.

3. RESULTS

(a) *Carcass consumption*

For convenience, these experiments are considered in rank order of duration (table 1). In experiment 1 (36 h), amphipods had penetrated the porpoise skin in places and ten grenadiers, *Coryphaenoides (Nematonurus) armatus* (Hector, 1875a), were captured in the box trap, but negligible tissue had been consumed. After 152 h in experiment 2, amphipods had entered through incisions and body openings or had made holes in the skin and tunnelled inside, preferentially ingesting muscle fibre but

Figure 1. Consumption of cetacean carcasses. (a) Cross-section through the vertebral column of the common dolphin carcass deployed for 152 h (experiment 2). (b) Cross-section of a neural process taken from the Atlantic white-sided dolphin skeleton after 276 h on the sea floor (experiment 3). The bone matrix (b) and oil-rich internal spaces (s) are shown. On the lower surface, in contact with the sediment, muscle tissue (m) and the periosteum (p) are still intact. (c) The full skeleton of the above dolphin after 276 h.

leaving connective tissue, skin and blubber largely uneaten. Most muscle tissue on the uppermost flank of the dolphin carcass had been consumed, exposing the vertebrae (figure 1a). Six grenadiers were captured in the box trap on this occasion. In experiment 3, the film sequence indicated that the half dolphin carcass was reduced to bare bones within 144 h. On retrieval after 276 h, 57% of the bone surface area had been stripped of all connective tissue, revealing the spongy matrix (figure

1b,c). The skin remained intact until swept clear of the skeleton after 5 days. Estimated soft tissue consumption rates are given in table 1.

(b) *Fish scavengers*

In all three film sequences, the grenadier *C. (N.) armatus* (figure 2a) was the first species to arrive (at 10–70 min) and overall, the most abundant fish encountered. In experiments 1 and 2, the carcasses were not fully

Figure 2. Photographic sequence showing different species of fish attracted to the dolphin carcass (D) during experiment 3. White arrows indicate the direction of current flow. (a) At 84 h, large numbers of *Coryphaenoides* (*Nematonurus*) *armatus* (C) were present. (b) At 115 h, the ophiidid *Spectrunculus grandis* (O) was present. (c) At 185 h, the carcass was stripped of soft tissue. A zoarcid, *Pachychara bulbiceps* (P), was resident near the skeleton. (d) At 208 h, a number of zoarcids (*P. bulbiceps* and *Lycenchelys/Lycodes* spp. (L)) and a galatheid crab, *Munidopsis* sp. (M), were resident.

consumed and grenadier numbers per frame fluctuated between 0 and a maximum of 22 for the duration of the deployments (figure 3*a,b*). In experiment 3, fish numbers reached 29 within 3 days (figure 3*ci*) and then decreased to a mean of 1–2 by day 6, when most soft tissue had been consumed.

Grenadiers approached the carcass from downstream, adjusting their orientation in accordance with tidal direction (e.g. figure 2*b*), which turned, on average, every 5–6.5 h. Although grenadier numbers fluctuated widely in experiments 1 and 2, the mean numbers present at the bait in each tidal phase were not significantly different: 9.8 (s.d.=2) with a westerly current, 9.7 (s.d.=4.2) with a north-easterly current and 9.4 (s.d.=3.6) during slack water. In experiment 3, fish numbers were not influenced by tidal flow either. Observing individuals with distinctive markings in this experiment gave an approximate mean staying time at the food-fall of 27 min ($n=43$, s.d.=33.6 min), with a maximum of 2 h 50 min. *C.(N.) armatus* individuals appear to arrive, feed and then depart when satiated.

In one instance a grenadier was seen directly consuming part of the exposed intestines of the carcass. Most fish

recovered with LAFF 2 had everted stomachs owing to pressure change, but stomach contents were retrieved from a single *C.(N.) armatus* from experiment 2. These consisted of a large, intact specimen of the amphipod *Eurythenes gryllus* (Lichtenstein, 1822) (95 mm) along with several smaller specimens and some unidentified fish remains.

A unimodal length frequency distribution, with a mean total length of 68 cm ($n=62$, s.d.=6.4 cm) was found for grenadiers observed in experiment 1 (figure 4*a*). In experiment 2, the distribution was wider, including individuals less than 40 cm, and the mean length was 61.5 cm ($n=77$, s.d.=10.2 cm) (figure 4*b*). These results were verified by measurements of specimens caught in the LAFF 2 box trap, with mean lengths of 70 cm ($n=10$, s.d.=0.4 cm) and 64 cm ($n=6$, s.d.=0.4 cm), respectively. The length frequency distribution in experiment 3 was similar to that in experiment 1, with a mean total length of 68.3 cm ($n=292$, s.d.=1.7 cm) (figure 4*c*).

In experiments 1 and 2, the liparid *Paraliparis bathybius* (Collett, 1879) was present in low numbers from about 3 h onwards. The ophiidid *Spectrunculus grandis* (Günther, 1877) was observed sporadically together with a single

Figure 3. Variation in number of fish per frame over the duration of each experiment.

(a) *Coryphaenoides (Nematonurus) armatus* numbers over 36 h (experiment 1).

(ai) Numbers of *Paraliparis bathybius* over the same time period. (b) *C.(N.) armatus* numbers over 115 h of the 152 h (experiment 2).

Sightings of *P. bathybius* (+) and *S. grandis* (filled triangles) are also indicated. (ci) *C.(N.) armatus* numbers over 262 h (experiment 3).

(cii) Zoarcid numbers, *P. bulbiceps* and *Lycodes/Lycenchelys* spp., experiment 3. (ciii) Ophidiid numbers, *Spectrunculus grandis* and *Barathrites iris*, experiment 3.

sighting of the macrourid *Coryphaenoides (Chalinura) profundicolus* (Nybelin, 1957) during experiment 2. In experiment 3, four putative species of fish from two families were identified: two ophidiids, *S. grandis* (figure 2b,c) and *Barathrites iris* (Zugmayer, 1911) and the zoarcids, *Pachycara bulbiceps* (German, 1899) and a *Lycenchelys* or *Lycodes* sp. (figure 2c,d).

In experiment 3, a change in species composition was observed over the 276 h duration. Grenadiers constituted 98% of the fish in the first 24 h (figure 3ci). Ophidiids were present in low numbers between 12 h and 200 h, with a mean staying time of 51 min (figure 3ciii). From 18 h onwards, zoarcids began to take up residence at the food-fall, eventually replacing the grenadiers as the dominant fish scavengers (figure 3cii). The behaviour of zoarcids was distinctive, being apparently negatively buoyant, staying close to the sea floor, moving slowly at a

rate of 0.4 m h^{-1} or remaining motionless over periods of hours to days. The abdomens of some individuals became visibly swollen, presumably with food, over the course of the film.

(c) Invertebrate scavengers

Although individuals could not be resolved, the lysianassid amphipods were the first and most abundant invertebrates, in terms of numbers, to arrive at the food-fall. In experiment 2, the galatheid crab *Munidopsis* arrived after 106 h. A number of gastropods, identified as *Colus sabini* (Gray, 1824), were observed after 12 h and one individual was retrieved in the trap. The ophiuroid *Ophioplecton hastutum* (Lyman, 1878), was also retrieved. In experiment 3, the decapod *Pleisiopenaeus armatus* (Bate, 1881) was observed once within the first 12 h and a number of *Munidopsis* spp. took up residence after 200 h (figure 2d).

Figure 4. Percentage frequency distribution of total body length of *C. (N.) armatus*, showing tendency for larger fish to arrive first. (a) Experiment 1, August 1997. (b) Experiment 2, August 1997; note occurrence of smaller fish in this longer experiment. (c) Experiment 3, August 1996, distribution reflects depth and distance from slope regions where smaller fish are found. (d) August 1989 (data from Armstrong *et al.* 1992); note similarity with 1996 data. (e) April 1994 (data from Smith *et al.* 1997b), shows much smaller fish are present at this depth earlier in the year.

Table 2. *Percentage composition of lysianassid amphipods collected from funnel traps and carcasses of large food-fall experiments*

experiment number	1		2		3	
duration	36 h		152 h		276 h	
trap/carcass	traps	carcass	traps	carcass	traps	carcass
species						
<i>Eurythenes gryllus</i>	0	39	12	46	6	6
<i>Paralicella caperesca</i>	0	12	43	28	0	0
<i>Paralicella tenuipes</i>	8	21	7	10	11	0
<i>Paracallisoma</i> spp.	70	19	22	1.5	0	11
<i>Orchomenella</i> (<i>O.</i>) <i>gerulicorbis</i>	3	3	0	0.5	83	44
<i>Orchomene chevreuxi</i>	19	6	16	14	0	0
<i>Abyssorchomene abyssorum</i>	0	0	0	0	0	33
<i>Valettietta gracilis</i>	0	0	0	0	0	6
total number (<i>n</i>)	37	67	349	212	46	18

After every deployment a varying number of amphipods were collected from the funnel traps and carcass remains, clinging to the skeleton or burrowing into the soft tissue. Species composition varied considerably

between deployments (table 2). Amphipods collected from the shorter experiments, 1 and 2, were dominated by *Paracallisoma* spp., *Eurythenes gryllus* and species of *Paralicella*. However, in experiment 3, after the longest

time-period, these species together totalled less than 20% of the individuals collected from traps and the carcass. The dominant species were *Orchomenella* (*Orchomenopsis*) *gerulicorbis* (Schulenberger and Barnard, 1976) and *Abyssorchomene abyssorum* (De Broyer, 1984).

4. DISCUSSION

This study indicates that, at abyssal depths, vertebrate and invertebrate scavengers remove soft tissue from cetacean food-falls at rates comparable with studies on large fish carcasses at bathyal depths (Smith 1985) and shallow water observations (Minshall *et al.* 1991; Elliot 1997). Given these consumption rates, a small cetacean carcass (50–100 kg) would typically be reduced to a skeleton within 15 days. For larger carcasses, scavenging and decomposition may remove 1 kg h^{-1} , equivalent to *ca.* 9 t yr^{-1} ($1 \text{ t}=10^3 \text{ kg}$) and sufficient to skeletonize small whales within one year.

The assemblage of scavengers attracted was characterized by a fish species succession from the mobile grenadier, *C. (N.) armatus*, to zoarcids and liparids taking up residence among the bones in the later stages. Evidence of a possible switch in dominant amphipod species was also observed. This assemblage was quite different to the hagfish and ophiuroids, which were found to dominate at shallower bathyal depths in the eastern Pacific (Smith 1985).

The initial dominance by *C. (N.) armatus* was very similar to previous experiments, with small fish food-falls in the same area (Armstrong *et al.* 1992; Priede *et al.* 1994; Thurston *et al.* 1995; Smith *et al.* 1997b). However, there were some significant differences. Excluding experiment 2, which was placed directly over the site of the previous experiment 1, arrival of fish was somewhat slower at cetacean carcasses and the eel *Histiobranchus bathybius* (Günther, 1877) was never observed. *C. (N.) armatus* readily consumed the entire mackerel bait in previous studies. In these experiments only one instance of a grenadier directly ingesting cetacean tissue (exposed intestines) was observed. Consumption was apparently indirect, through ingestion of amphipods, which were able to preferentially 'mine' the softer muscle tissue. This appeared to be confirmed by the one instance of a *C. (N.) armatus* captured with amphipods in its stomach. It is speculated that the skin and blubber layer was less palatable and hindered direct consumption of the carcass by fish scavengers, resulting in a shift in terms of the local food chain.

Grenadiers tend to swim against or across the current direction in search of food odour plumes (Priede *et al.* 1991) and this was reflected in the direction of arrival of fish in the present experiment. Guennegan & Rannou (1979) and Desbruyeres *et al.* (1985) related grenadier numbers at baits to changes in tidal currents, but we found no such correlation. Furthermore, *C. (N.) armatus* did not take up residence at the food-fall. It seems possible that, given their slow metabolism (Smith 1978a), digestion of the meal may require in excess of a week. Remaining at the food-fall during that time may have incurred predation risks from other grenadiers and amphipods (Walker 1907; Armstrong *et al.* 1992).

The length frequency distributions of the *C. (N.) armatus* observed in the different experiments contain some

interesting information. In experiments 1 and 2, closest to the Porcupine Seabight, a significant fraction of grenadiers were less than 50 cm long (figure 4b). This reflects the proximity of continental slope regions where smaller fish tend to occur (Merrett *et al.* 1991a,b). Comparing the size spectra in experiment 1 and 2, which were 36 h and 152 h in duration (figure 4a,b), there is a tendency for large individuals to arrive first at the food-fall. The size frequency distribution observed in experiment 3, at the centre of the Porcupine Abyssal Plain (figure 4c) was similar to that observed previously at this location at the same time of year (Armstrong *et al.* 1992) (figure 4d). However, Smith *et al.* (1997b), found smaller fish to be present in April (figure 4e) and suggested that this was the result of seasonal migrations from the ocean margins. The present data provide further circumstantial evidence that such a migration may be seasonal. This implies that soft tissue material ingested from a food-fall may be dispersed over much larger areas than the magnitude of tens or hundreds of metres as suggested by Smith (1985).

The ophidiid family is second only to the macrourids in terms of percentage contribution to total number of species at abyssal depths (Merrett & Haedrich 1997), but few were seen at the cetacean carcass. Zoarcid numbers increased once grenadier numbers declined and these fish remained for extended periods. Both the zoarcids and *P. bathybius* were thought to be preying on amphipods. This is supported by previous evidence from stomach contents of these species (Lampitt *et al.* 1983; L. W. Bullough, personal communication).

The abundant lysianassid amphipods appeared to be the main direct consumers of the carcasses. The species compositions found in the shorter deployments were in agreement with previous work using short-term baited traps at abyssal plain depths of 4000 m plus (Thurston 1979, 1990). A time-related rather than a depth-related trend is therefore postulated for the shift in species dominance observed after 276 h. This was thought to be a consequence of variations in scavenging behaviour between species. *Eurythenes gryllus* and *Paralicella* spp. are known to be highly specialized necrophages processing food at high assimilation efficiencies (Schulenberger & Barnard 1976; Dahl 1979; Thurston 1979; Hargrave 1985; Sainte-Marie 1992), whereas *Orchomene* species are less efficient, generalist feeders (Thurston 1979; Smith & Baldwin 1982; Sainte-Marie *et al.* 1989; Sainte-Marie 1992). Other invertebrates attracted in lower numbers included decapods, a gastropod, and an ophiuroid.

After 276 h, erosion of the skeleton was visible, exposing the oil-rich spongy interior of the bones to dissolution. Cetacean bone typically accounts for 5% of the carcass weight and contains 10% lipid and 25% protein (Honda *et al.* 1984) which, for experiment 3, gives an estimated 500 g of organic carbon, equivalent to 325 years worth of average daily background flux of carbon per square metre to this area, as given by Lampitt *et al.* (1995). This would provide a local enrichment, possibly resulting in a reduced environment in the sediment (Kitazato & Shirayama 1996).

The ageing of food patches has been suggested to increase spatial and temporal microheterogeneity in macrofauna (Snelgrove *et al.* 1996). At cetacean carcasses, this process would persist for a year or more. Furthermore,

by acting as a focus for aggregations of normally widely dispersed benthic species, food-fall sites may have significant roles in certain aspects of life histories (Smith 1985). We suggest that the close juxtaposition of gastropods, fish and crustacea may facilitate completion of parasite life cycles such as that of the digeneans (Campbell *et al.* 1980) known to occur in *C. (N.) armatus*.

In the North Pacific a density of one gray whale carcass every 300 km² was estimated (Smith *et al.* 1989), but the ocean-wide frequency of cetacean carcasses as food-falls is unknown. Nevertheless, based on estimates of populations and natural mortality, the contribution of whale-falls to the overall vertical carbon flux to the deep sea has been estimated at two-to-three orders of magnitude less than the dominant source, phytodetritus (Jelmert & Oppen-Berntsen 1996). However, the significance of these events lies not with their total contribution to downward carbon flux, but with their creation of long-sustained point sources of energy and nutrients. Such unique habitat islands may play a significant role in influencing species diversity and community structure in the deep sea. These experiments have highlighted aspects of the early stages of this process and clear differences between cetaceans and other food-fall sources. Finally, the use of lander vehicles that can operate autonomously for long periods of time and retrieve carcasses with other samples is a promising technique for future research.

This work was supported by a NERC grant, GR3/10162, and a European Commission MAST 3 contract, CT950010, to I.G.P., and a NERC research studentship held by E.G.J. We thank the ships' companies of the R.R.S. *Discovery* (Cruise 222a) and *Challenger* (Cruise 134) for making this work possible. We thank Bram Couperus (RIVO, Ijmuiden), Mike Collins (Immingham), Emer Rogan (U.C. Cork), Morgan Goodlad (NAFC, Shetland) for help in obtaining cetacean carcasses and Bill Edwards for patience with bone sectioning. Nigel Merrett and Mike Thurston gave invaluable assistance with specimen identification and, along with Cynthia Yau and an anonymous referee, commented on the manuscript.

REFERENCES

- Armstrong, J. D., Bagley, P. M. & Priede, I. G. 1992 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. *Mar. Biol.* **112**, 535–544.
- Britton, J. C. & Morton, B. 1994 Marine carrion and scavengers. *Oceanogr. Mar. Biol. A. Rev.* **32**, 369–434.
- Campbell, R. A., Haedrich, R. L. & Munroe, T. 1980 Parasitism and ecological relationships among deep-sea benthic fishes. *Mar. Biol.* **57**, 301–313.
- Collins, M. A., Priede, I. G., Addison, S. & Bagley, P. M. 1998 Acoustic tracking of the dispersal of organic matter by scavenging fishes in the deep-sea. *Hydrobiologia*. (In the press.)
- Dahl, E. 1979 Deep-sea carrion feeding amphipods: evolutionary patterns in niche adaptation. *Oikos* **33**, 167–175.
- Dayton, P. K. & Hessler, R. R. 1972 Role of biological disturbance in maintaining diversity in the deep-sea. *Deep-Sea Res.* **19**, 199–208.
- Desbruyeres, D., Geistdoerfer, P., Ingram, C. L., Khrapounoff, A. & Lagardère, J. P. 1985 Réparation des populations de l'épibenthos carnivore. In *Peuplements profonds du Golfe de Gascogne Campagnes BIOGAS* (ed. L. Laubier & C. Monniot), pp. 1–630. Brest: IFREMER.
- Elliot, J. M. 1997 An experimental study on the natural removal of dead trout fry in a Lake District stream. *J. Fish Biol.* **50**, 870–877.
- Guennegan, Y. & Rannou, M. 1979 Semi-diurnal rhythmic activity in deep-sea benthic fishes in the Bay of Biscay. *Sarsia* **64**, 113–116.
- Hargrave, B. T. 1985 Feeding rates of abyssal scavenging amphipods (*Eurythenes gryllus*) determined *in situ* by time-lapse photography. *Deep-Sea Res.* **32**, 443–450.
- Heezen, B. C. & Hollister, C. D. 1971 *The face of the deep*. Oxford University Press.
- Honda, K., Fujise, Y., Tatsukawa, R. & Miyazaki, N. 1984 Composition of chemical components in bone of striped dolphin, *Stenella coeruleoalba*: distribution characteristics of major inorganic and organic components in various bones, and their age-related changes. *Agric. Biol. Chem.* **48**, 409–418.
- Honjo, S. & Doherty, K. W. 1988 Large aperture time-series sediment traps; design objectives, construction and application. *Deep-Sea Res.* **35A**, 133–149.
- Isaacs, J. D. & Schwartzlose, R. A. 1975 Active animals of the deep-sea floor. *Scient. Am.* **233**, 85–91.
- Jannasch, H. W. 1978 Experiments in deep-sea microbiology. *Oceanus* **21**, 50–57.
- Jelmert, A. & Oppen-Berntsen, D. A. 1996 Whaling and deep-sea biodiversity. *Conserv. Biol.* **10**, 653–654.
- Jones, E. G., Collins, M. A., Addison, S. & Priede, I. G. 1996 A new lander vehicle for investigating the impact of large food-falls in the deep-sea. *J. Fish Biol.* **49**(Suppl. A), 339.
- Katona, S. & Whitehead, H. 1988 Are cetacea ecologically important? *Oceanogr. Mar. Biol. A. Rev.* **26**, 553–568.
- Kitazato, H. & Shirayama, Y. 1996 Rapid creation of a reduced environment and an early stage of chemosynthetic community on cattle bones in Sagami Bay, Central Japan. *Vie Milieu*. **46**, 1–5.
- Lampitt, R. S. 1985 Evidence for the seasonal deposition of detritus to the deep-sea floor and its subsequent resuspension. *Deep-Sea Res.* **32**, 885–897.
- Lampitt, R. S., Merrett, N. R. & Thurston, M. H. 1983 Interrelations of necrophagous amphipods, a fish predator and tidal currents in the deep sea. *Mar. Biol.* **74**, 73–78.
- Lampitt, R. S., Raine, R. C. T., Billett, D. S. M. & Rice, A. L. 1995 Material supply to the European continental slope: a budget based on benthic oxygen demand and organic supply. *Deep-Sea Res.* **42**, 1865–1880.
- Merrett, N. R. & Haedrich, R. L. 1997 *Deep-sea demersal fish and fisheries*. London: Chapman & Hall.
- Merrett, N. R., Gordon, J. D. M., Stehmann, M. & Haedrich, R. L. 1991a Deep demersal fish assemblage structure in the Porcupine Seabight (eastern North Atlantic): slope sampling by three different trawls compared. *J. Mar. Biol. Ass. UK* **71**, 329–358.
- Merrett, N. R., Haedrich, R. L., Gordon, J. D. M. & Stehmann, M. 1991b Deep demersal fish assemblage structure in the Porcupine Seabight (eastern North Atlantic): results of single warp trawling at lower slope to abyssal soundings. *J. Mar. Biol. Ass. UK* **71**, 359–373.
- Minshall, G. W., Hitchcock, E. & Barnes, J. R. 1991 Decomposition of rainbow trout (*Oncorhynchus mykiss*) carcasses in a forest stream ecosystem inhabited only by non-dramous fish populations. *Can. J. Fish. Aquat. Sci.* **48**, 191–195.
- Pfannkuche, O. 1993 Benthic response to the sedimentation of particulate organic matter at the BIOTRANS station, 47° N, 20° W. *Deep-Sea Res.* **40**, 135–149.
- Priede, I. G., Bagley, P. M., Smith, A., Creasey, S. & Merrett, N. R. 1994 Scavenging deep demersal fishes of the Porcupine Seabight, North-East Atlantic: observations by baited camera, trap and trawl. *J. Mar. Biol. Ass. UK* **74**, 481–498.

- Priede, I. G., Bagley, P. M., Armstrong, J. D., Smith, K. L. J. & Merrett, N. R. 1991 Direct measurement of active dispersal of food-falls by deep-sea demersal fishes. *Nature* **351**, 647–649.
- Rice, A. L., Thurston, M. H. & Bett, B. J. 1994 The IOSDL DEEPSEAS programme: introduction and photographic evidence for the presence and absence of a seasonal input of phytodetritus at contrasting abyssal sites in the North-Eastern Atlantic. *Deep-Sea Res.* **41**, 1305–1320.
- Sainte-Marie, B. 1992 Foraging of scavenging deep-sea lysianassoid amphipods. In *Deep-sea food chains and the global carbon cycle*, vol. 360 (ed. G. T. Rowe & V. Pariente), pp. 105–124. Dordrecht: Kluwer Academic Publishers.
- Sainte-Marie, B., Percy, J. A. & Shea, J. R. 1989 A comparison of meal-size and feeding rate of the lysianassid amphipods, *Anonyx nugax*, *Onisimus* (= *Pseudalibrotus*) *litoralis* and *Orchomenella pinguis*. *Mar. Biol.* **102**, 361–368.
- Schulenberg, E. & Barnard, J. L. 1976 Amphipods from an abyssal trap set in the North Pacific Gyre. *Crustaceana* **31**, 241–258.
- Smith, A., Matthiopoulos, J. & Priede, I. G. 1997a Areal coverage of ocean floor by the deep-sea elasipodid holothurian *Oneirophanta mutabilis*: estimates using systematic, random and directional search strategy simulations. *Deep-Sea Res.* **44**, 477–486.
- Smith, A., Priede, I. G., Bagley, P. M. & Addison, S. W. 1997b Interception and dispersal of artificial foodfalls by scavenging fishes in the abyssal North-East Atlantic: early-season observations prior to annual deposition of phytodetritus. *Mar. Biol.* **128**, 329–336.
- Smith, C. R. 1985 Food for the deep-sea: utilization, dispersal and flux of nekton falls at the Santa Catalina Basin floor. *Deep-Sea Res.* **32**, 417–442.
- Smith, C. R. 1986 Nekton falls, low-intensity disturbance and community structure of infaunal benthos in the deep sea. *J. Mar. Res.* **44**, 567–600.
- Smith, C. R., Kukert, H., Wheatcroft, R. A. & Jumars, P. A. 1989 Vent fauna on whale remains. *Nature* **341**, 27–28.
- Smith, K. L. 1978a Metabolism of the abyssopelagic rattail *Coryphaenoides armatus*, measured *in situ*. *Nature* **274**, 362–364.
- Smith, K. L. 1978b Benthic community respiration in the NW Atlantic Ocean: *in situ* measurements. *Mar. Biol.* **47**, 337–347.
- Smith, K. L. & Baldwin, R. J. 1982 Scavenging deep-sea amphipods: effects of food odour on oxygen consumption and proposed metabolic strategy. *Mar. Biol.* **68**, 287–298.
- Smith, S. E. & Baco, A. R. 1998 Whale-fall communities in the deep north-east Pacific: succession and species diversity. Abstract no. 0532H-3 in the 1998 Ocean Sciences Meeting, San Diego, CA. *Eos Trans. Am. Geophys. Union* **79**, 114.
- Snelgrove, P. V. R., Grassle, J. F. & Petrecca, R. F. 1996 Experimental evidence for aging food patches as a factor contributing to high deep-sea macrofaunal diversity. *Limnol. Oceanogr.* **41**, 605–614.
- Stockton, W. L. 1982 Scavenging amphipods from under the Ross Ice Shelf, Antarctica. *Deep-Sea Res.* **29**, 819–835.
- Stockton, W. L. & Delacca, T. E. 1982 Food falls in the deep-sea: occurrence, quality and significance. *Deep-Sea Res.* **29**, 157–169.
- Thurston, M. H. 1979 Scavenging abyssal amphipods from the North-East Atlantic Ocean. *Mar. Biol.* **51**, 55–68.
- Thurston, M. H. 1990 Abyssal necrophagous amphipods (Crustacea: Amphipoda) in the northeast and tropical Atlantic Ocean. *Progr. Oceanogr.* **24**, 257–274.
- Thurston, M. H., Bett, B. J. & Rice, A. L. 1995 Abyssal megafaunal necrophages: latitudinal differences in the eastern North Atlantic Ocean. *Int. Revue Ges. Hydrobiol.* **80**, 267–286.
- Turley, C. M. & Lochte, K. 1990 Microbial response to the input of fresh detritus to the deep-sea bed. *Palaeogeogr. Palaeoclimatol. Palaeoecol. (Global Planet. Change Sect.)* **89**, 3–23.
- Walker, A. O. 1907 Crustacea III. *Amphipoda*. *Natn. Antarct. Exped. 1901–1904, Nat. Hist. Zool. Bot.* **3**, 1–39.
- Whitehead, P. J. P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J. & Tortonese, E. (eds) 1986 *Fishes of the north-eastern Atlantic and the Mediterranean*, vols 1–3. Paris: UNESCO.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.