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# Mass deposition of jellyfish in the deep Arabian Sea

*D. S. M. Billett,*[1] *B. J. Bett, C. L. Jacobs, I. P. Rouse, and B. D. Wigham*[2]
National Oceanography Centre, Southampton, SO14 3ZH, United Kingdom

*Abstract*

In December 2002, large numbers of dead jellyfish, *Crambionella orsini*, were observed on the seabed over a wide area of the Arabian Sea off the coast of Oman at depths between 300 m and 3,300 m. Moribund jellyfish were seen tumbling down the continental slope. Large aggregations of dead jellyfish were evident within canyons and on the continental rise. At the deepest stations, patches of rotting, coagulated jellyfish occurred. The patches were several meters in diameter, at least 7-cm thick, and covered about 17% of the sediment surface. At other locations on the continental rise the seafloor was covered in a thin, almost continuous, layer of jelly "slime" a few millimeters thick or was littered with individual jellyfish corpses. Photographic transects were used to estimate the amount of carbon associated with the jelly detritus. The standing stock of carbon (C) varied between 1.5 g C $m^{-2}$ and 78 g C $m^{-2}$, the higher figure exceeding the annual downward flux of organic carbon, as measured by sediment traps, by more than an order of magnitude. The episodic nature of jellyfish blooms, which may be modulated by global change phenomena, provides a hitherto unknown mechanism for large-scale spatial and temporal patchiness in deep-sea benthic ecosystems.

Sudden population explosions of jellyfish are a feature of many parts of the world's oceans (Purcell et al. 2001) and cause large-scale ecosystem effects in surface waters (Axiak and Civili 1991; Mills 1995; Brodeur et al. 2002). The occurrences of jellyfish superabundances have the potential to change significantly the flux of organic matter to the seabed. Surprisingly, there are very few data on the effects of jellyfish blooms on carbon flux and on the seabed fauna.

In December 2002 during the RRS *Charles Darwin* cruise 143 (Jacobs 2003), large numbers of the scyphomedusan jellyfish *Crambionella orsini* (Vanhöffen 1888) were seen in surface waters across a wide area off Oman. Estimated visually, their abundance was typically about one individual per cubic meter, but very dense aggregations occurred at frontal systems. *C. orsini* is a native species of the Indian Ocean (Kramp 1961). The bell is 10–20 cm wide and is firm, smooth, and cartilaginous. The arms are about as long as the bell radius, making the total length of the medusa about 15 cm.

Whereas species of *Crambionella* are found in many areas of the Indian Ocean, they occur in large numbers only periodically. Off Oman, *C. orsini* was reported in the local press to have been superabundant only between 2001 and 2003 and not to have occurred in such numbers previously, at least in the recent past. Large and episodic increases in various taxa are a feature of the Arabian Sea, such as the superabundance of swimming crabs in surface waters in the early 1990s (van Couwelaar et al. 2001), many of which were deposited on the abyssal seafloor (Christiansen and Boetius 2000).

Gelatinous zooplankton play an important role in the transfer of organic matter to the seabed in fecal aggregates and mucous sheets (Wiebe et al. 1979; Robison et al. 2005). These sink rapidly to the deep seafloor and provide a labile food source for benthic organisms (Pfannkuche and Lochte 1991). However, the role played by the bodies of gelatinous zooplankton in the downward transport of carbon, as speculated from shipboard experiments by Moseley (1880), is less well documented. Cacchione et al. (1978) recorded salp carcasses rolling along the seabed in the Hudson Canyon at a depth of 3,400 m, and Wiebe et al. (1979) estimated that salp carcasses might provide more than half of the daily energy requirements of the bottom microfauna in the same general area. Elsewhere on the continental slope, remotely operated vehicle (ROV) and submersible observations have documented single occurrences of moribund scyphomedusans on the seabed (Jumars 1976; Miyake et al. 2002; Miyake et al. 2005). Distant from the continental slope, carcasses of the tunicate *Pyrosoma* have been observed in time-lapse photography of the Madeira Abyssal Plain seafloor (Roe et al. 1990). Remarkably, in shallow water, there has been no direct quantification of the deposition of jellyfish, even though a major input to the seabed has been suggested (Axiak and Civili 1991; Arai 1997; Kingsford et al. 2000).

During the RRS *Charles Darwin* cruise 143 the seabed was observed using real-time video and still photography. In the course of the work between 350 m and 3,300 m, many jellyfish were seen rolling along the seabed. It became clear that very large numbers of jellyfish were being transported rapidly to the deep-sea floor. In this article, we describe how jellyfish gather on the deep-sea floor, and we estimate the standing stock of carbon in jelly detritus deposited on the seabed. We speculate on what the

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[1] Corresponding author (dsmb@noc.soton.ac.uk).

[2] Present address: Department of Zoology, University of Aberdeen, Main Street, Newburgh, Aberdeenshire AB41 6AA, United Kingdom.

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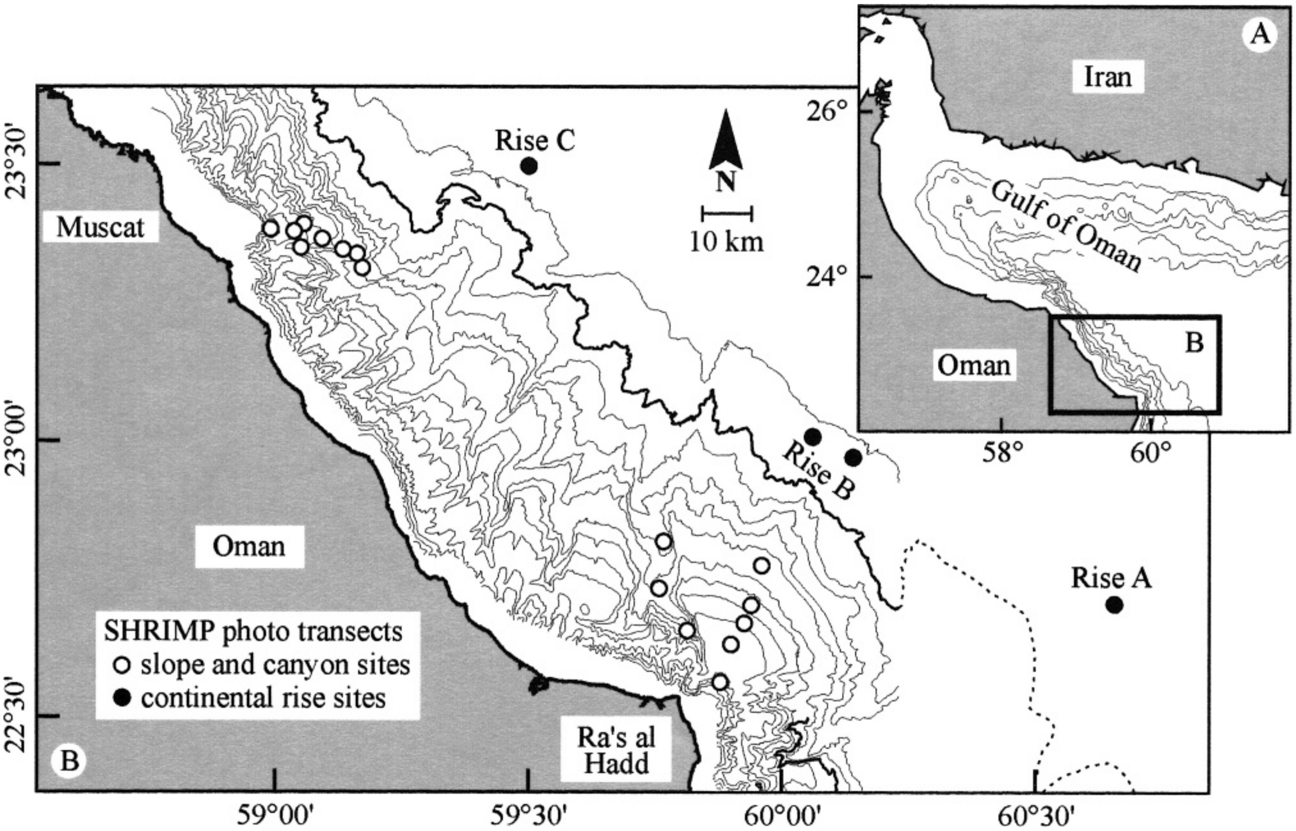


Fig. 1. (A) The Gulf of Oman and the location of the study area. (B) Detailed bathymetric chart of the Oman margin between Muscat and the Ra's al Hadd headland showing the location of seabed high-resolution imaging platform (SHRIMP) photographic observations and continental rise areas (A, B, and C) referred to in the text.

consequences might be for the deep-sea benthos and suggest that the episodic and long-term variation in jellyfish blooms in surface waters will introduce similar spatial and temporal variability to deep-sea benthic communities.

## Materials and methods

*Study area*—The Gulf of Oman, between Oman and Iran, is a deep amphitheatre-shaped embayment of the continental margin (Fig. 1A). The continental slope of the Oman margin between Muscat and the headland of Ra's al Hadd is deeply incised by a number of canyons running offshore (Fig. 1B). The mouths of the canyons open onto the continental rise at a depth of about 2,700 m, some 40 km offshore.

The Gulf of Oman is influenced by the northeast (NE) monsoon (December to March) and southwest (SW) monsoon (June to September). Strong winds associated with the SW monsoon lead to high primary productivity along the Oman coast because of the upwelling of nutrient-rich water (Wiggert et al. 2005). The subsequent heterotrophic utilization of the primary productivity coupled with slow ocean circulation leads to a permanent hypoxic layer of water (<0.5 mL $O_2$ $L^{-1}$), known as the oxygen minimum zone (OMZ), that is typical of the northern Arabian Sea between 100 m and 1,000 m (Demopoulos et al. 2003). On the Oman continental margin to the north of Ra's al Hadd, oxygen levels as low as 0.05 mL $O_2$ $L^{-1}$ were measured (Fig. 2). Between 450 m and 1,000 m there was little or no variation in the very low levels of oxygen.

*Imaging of the seafloor*—Photography of the seabed was carried out using a towed camera system (seabed high-resolution imaging platform [SHRIMP]). The vehicle was flown about 2–3 m above the seabed by reference to real-time imaging and telemetered altimeter data. Video footage was recorded continuously, and still photographs were taken every 12 s. Deployments lasted 30–360 min, with the vehicle traveling at about 0.5 knots over the seabed. At an altitude between 2 m and 3 m, individual photographs covered an area of the seabed between 2.5 $m^2$ and 5.6 $m^2$. A weight was suspended below the camera to aid the SHRIMP operators in maintaining a constant altitude. The weight was also used to test the softness of the sediment surface and to estimate the thickness of the jelly detritus.

Twenty-four SHRIMP deployments were completed at depths between 300 m and 3,300 m (Table 1). All images were taken about 2 months after the SW monsoon. The surveys included gently sloping sediments, rocky outcrops, canyon walls and channels, and the continental rise. Seabed photographic surveys were concentrated in two areas (Fig. 1B). An additional SHRIMP deployment was made

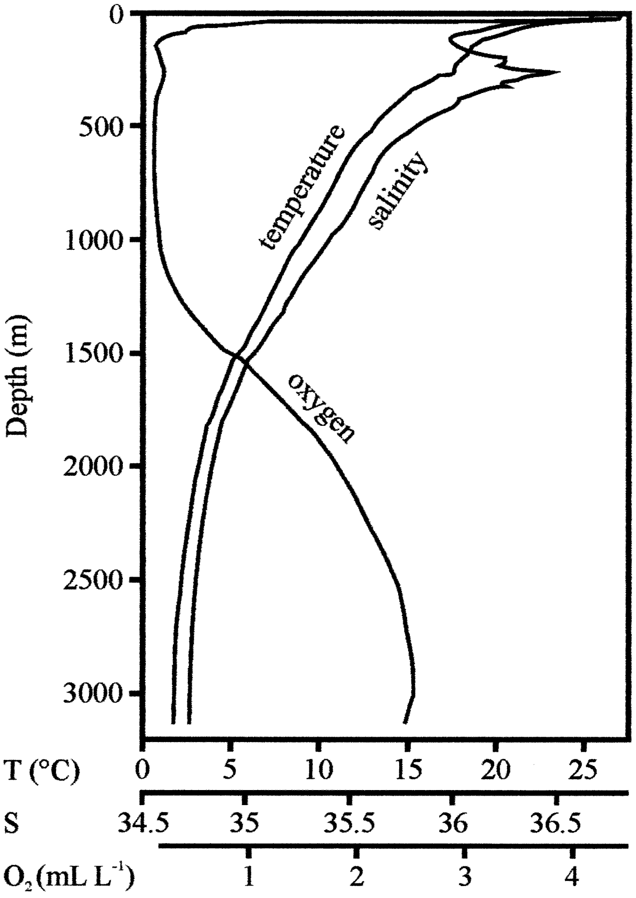


Fig. 2. Temperature, salinity, and oxygen profiles (oxygen sensor mounted on a conductivity, temperature, and depth probe and by Winkler oxygen titrations) of the water column (Stn. 55704#2, Table 1).

on the continental rise to the east of Ra's al Hadd (c. 3,200 m; Fig. 1B).

*Quantifying percentage cover, jelly detritus thickness, and carbon flux*—Using data on the percentage cover of jelly detritus from the photographic surveys and estimates of the thickness of the detritus, the standing stock of jellyfish, in terms of g C $m^{-2}$ of seabed, was calculated for the three continental rise areas. Photographic surveys were conducted in the mode of straight-line transects covering distances of between 0.3 km to 3 km at each station. From these transects the percentage cover of jelly detritus was estimated from every fifth photograph. An average altitude of 2.5 m was maintained during the phototransects, apart from short periods when the camera was taken to within 1 m of the seabed to determine the nature of the jelly detritus. By allowing the suspended weight to impact the seabed and reveal a section through the detritus or disappear into it, the thickness of the jelly layer could be estimated by reference to the known dimensions of the weight. The smallest dimension of the weight was used to estimate the thickness of the jelly detritus, and so estimates are conservative. From the percentage of cover and thickness, the volume and wet weight (assuming a specific gravity of 1) of jelly detritus were calculated. Wet weight data per unit area were converted to dry weight, then to grams of carbon using standard conversions for *Scyphomedusae*. Conversions of 5.2% for wet weight to dry weight and 12.9% for dry weight to carbon were used (Larson 1986).

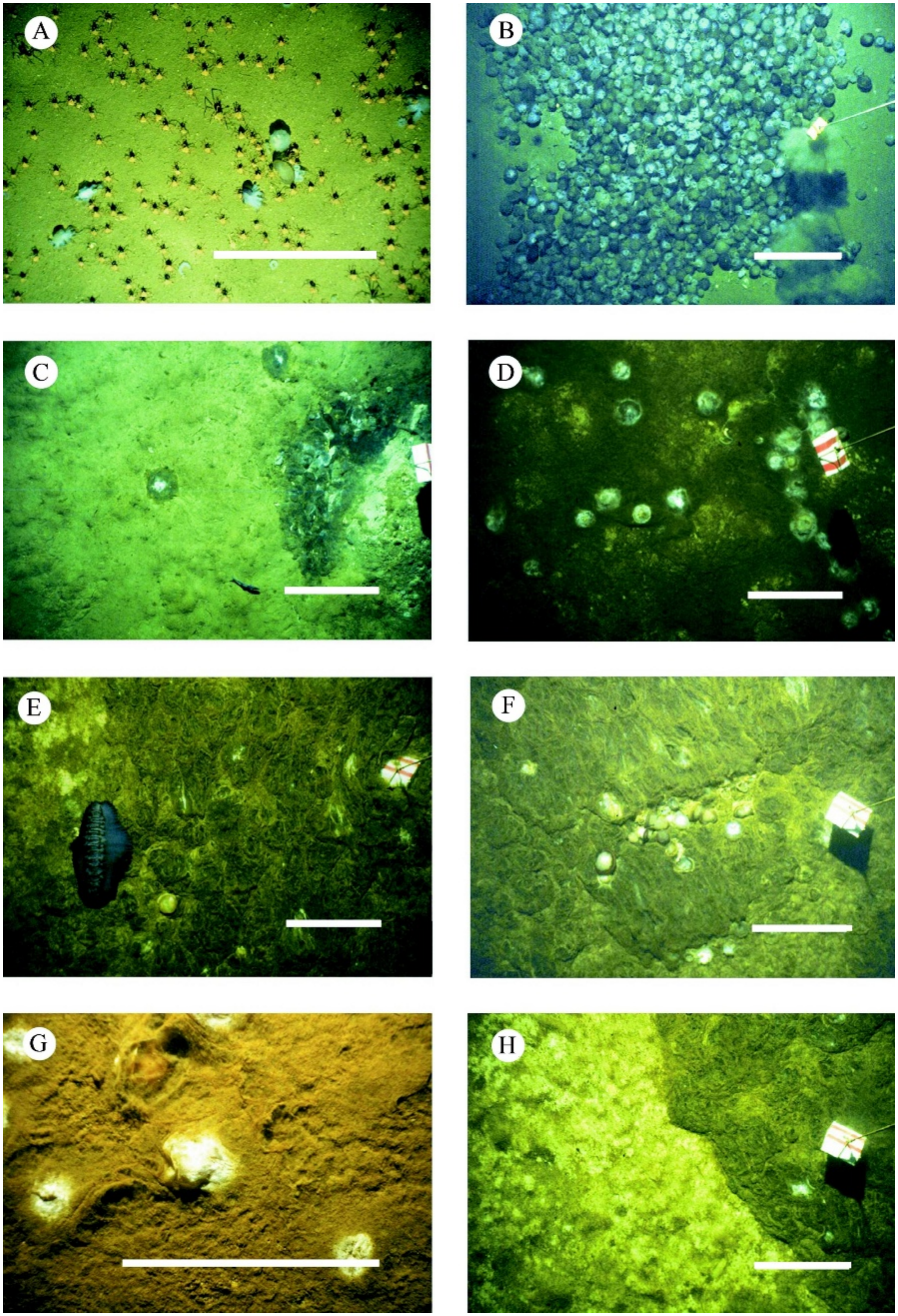
*Sampling of the seafloor*—Sediment samples were taken with a hydraulically damped Bowers and Connelly Megacorer (Gage and Bett 2005). The sediment surface was retrieved intact with essentially no disturbance. One sample was taken on the continental rise (Table 1) in an area in which jelly detritus had been seen in the video transects

Table 1. Station data for deployments referred to in the text (for the complete cruise listing see Jacobs 2003).*

| | | | | Position | | Depth (m) | | |
|---|---|---|---|---|---|---|---|---|
| Area | Station | Gear† | Date | Start (N) | Start (E) | Min. | Max. | Sample |
| Rise A | 55785#1 | SHR | 17 Dec 02 | 22°42.20′ | 060°39.05′ | 3,189 | 3,196 | 431 photos |
| Rise B | 55782#1 | SHR | 16 Dec 02 | 23°00.94′ | 060°03.13′ | 3,169 | 3,188 | 837 photos |
| Rise B | 55783#1 | AgT | 16 Dec 02 | 23°00.49′ | 060°03.77′ | 3,168 | 3,168 | Trawl catch |
| Rise B | 55784#1 | SHR | 17 Dec 02 | 22°58.59′ | 060°08.73′ | 3,157 | 3,170 | 542 photos |
| Rise B | 55788#1 | MgC | 18 Dec 02 | 23°01.00′ | 060°02.98′ | 3,185 | 3,185 | 11 cores |
| Rise C | 55704#2 | CTD | 29 Nov 02 | 23°29.57′ | 059°14.06′ | 0 | 3,101 | T, S, and $O_2$ profiles |
| Rise C | 55791#1 | SHR | 19 Dec 02 | 23°30.27′ | 059°29.91′ | 3,299 | 3,314 | 867 photos |
| Slope | 55734#1 | SHR | 06 Dec 02 | 22°35.19′ | 059°53.30′ | 307 | 902 | 1,220 photos |
| Slope | 55740#1 | SHR | 07 Dec 02 | 22°46.54′ | 059°57.70′ | 2,005 | 2,020 | 150 photos |
| Slope | 55741#1 | SHR | 07 Dec 02 | 22°42.21′ | 059°56.46′ | 1,495 | 1,521 | 128 photos |
| Slope | 55756#1 | SHR | 10 Dec 02 | 23°22.96′ | 058°58.91′ | 304 | 525 | 870 photos |
| Canyon | 55716#1 | SHR | 03 Dec 02 | 23°21.54′ | 059°10.34′ | 1,288 | 1,492 | 524 photos |
| Canyon | 55727#1 | SHR | 04 Dec 02 | 23°19.27′ | 059°02.51′ | 2,300 | 2,400 | 665 photos |
| Canyon | 55746#1 | SHR | 08 Dec 02 | 22°49.08′ | 059°45.88′ | 2,458 | 2,466 | 183 photos |
| Canyon | 55747#1 | SHR | 08 Dec 02 | 22°44.62′ | 059°45.52′ | 1,869 | 2,014 | 633 photos |
| Canyon | 55748#1 | SHR | 08 Dec 02 | 22°39.17′ | 059°49.11′ | 1,616 | 1,702 | 384 photos |

* Area is the physiographic setting. Station is the unique deployment identifier.

† AgT, Agassiz trawl; MgC, Megacorer; SHR, SHRIMP; CTD, conductivity, temperature, and depth probe with $O_2$ sensor.


A
B
C
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E
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Table 2. Summary of the mean area of seabed covered by jelly detritus at three locations on the Oman continental rise (Fig. 1B), average thickness of the deposit, and an estimate of the carbon standing stock of the jelly detritus. Mean values and confidence limits were calculated after arcsin-transformation of the data.

| Area | Rise A | Rise B | Rise C |
|---|---|---|---|
| Date | 17 Dec 02 | 17 Dec 02 | 19 Dec 02 |
| Number of photographs analyzed | 59 | 178 | 117 |
| Data range, jelly detritus cover (%) | 0–24 | 68–100 | 0–100 |
| Mean area covered by jelly detritus (%) (95% confidence limits) | 2.3 (1.8–2.9) | 93.4 (92.3–94.7) | 16.6 (10.7–23.4) |
| Thickness of jelly layer (mm) | 10 | 5 | 70 |
| Mean standing stock (g C $m^{-2}$) (95% confidence limits) | 1.5 (1.2–2.0) | 31.3 (31.0–31.8) | 78.0 (50.2–109.9) |

(Jacobs 2003). An Agassiz trawl was also used in close proximity to the SHRIMP photographic surveys in Area B (Fig. 1B) to collect voucher specimens for the identification of megafauna seen in photographs.

## Results

*Continental slope*—On the continental slope, many individual dead jellyfish were seen rolling along the seabed in the prevailing current (Fig. 3A). On the upper slope, within the OMZ, individuals tended to be in very good condition, although in many cases the swimming bell had become detached from the tentacles (Fig. 3A). There was little evidence that the larger benthic fauna fed upon the medusae. There was little evidence of bacterial breakdown of the jellyfish on the upper slope (shallower than 1,000 m).

*Canyon systems*—Within the upper reaches of the canyons, many dead jellyfish were seen tumbling downslope. At mid-slope depths in some canyons, where large boulders and rocks interrupted the down-canyon flow of jellyfish, large aggregations occurred (Fig. 3B). However, in the lower reaches of the canyons fewer individuals were seen, and generally they occurred in small aggregations covered by a white bacterial mat (Fig. 3C).

*Continental rise*—The greatest concentrations of decaying jellyfish were found at three locations on the continental rise. For ease of identification, these are referred to as areas A, B, and C (Fig. 1). All stations were surveyed within a few days of each other (Table 1). The appearance of the degrading jellyfish varied from single specimens covered by a white layer of presumed mat-forming bacteria (Fig. 3D) to patches of thick, coalesced jelly detritus (Fig. 3E). In the latter case, fresh jellyfish often occurred mixed in with the jelly patches (Fig. 3F). There was no evidence that the jelly detritus was being fed upon by larger animals.

The distribution and nature of the decaying jellyfish on the seabed differed at the three continental rise locations.

To the East, off Ra's al Hadd (area A, Fig. 1B), many individual jellyfish were seen decomposing on the seabed. There were some small aggregations, but generally the carcasses occurred separately (Fig. 3D). The mean area of the seabed covered by jellyfish carcasses was 2.3%. Using a conservative estimate of 10 mm as the average thickness of a decomposing jellyfish, based on the small amount of relief evident in individuals in each photograph, a mean standing stock value of 1.5 g C $m^{-2}$ was calculated (Table 2).

To the North of Ra's al Hadd (Area B, Fig. 1B), single decaying jellyfish and bacterial mats occurred, but close-up views of the seabed showed that most of the sediment surface was covered in a thin layer of slime (Fig. 3G). One deployment of a Megacorer was made in the vicinity. Eleven cores were retrieved from the deployment, all with a layer of jelly detritus about 10-mm thick. At a local scale, at least, this corroborates the photographic and video evidence that the vast majority of the sediment was covered in a thin layer of jelly detritus. In some cores, lumps of gelatinous detritus were noted. At the base of the jelly detritus there was a thin black layer overlying the sediment surface. On average, the photographs indicated that the jelly detritus thickness was <10 mm, so a conservative estimate of 5 mm was used. The jelly detritus covered an average 93.4% of the seabed, producing a mean standing stock of 31.3 g C $m^{-2}$ (Table 2). An Agassiz trawl deployed in the area retrieved a small sample containing

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Fig. 3. Seafloor photographs from the Oman margin. Scale bars refer to 50 cm in all cases. (A) Stn. 55734#1. Jellyfish carcasses at about 350-m depth within a depth zone occupied by many deep-sea spider crabs, *Encephaloides armstrongi* (Creasey et al. 1997). Although many jellyfish were intact, the oral arms had become detached from the swimming bell in some cases. (B) 55716#1. Mass accumulation of jellyfish on the seabed in a canyon at a depth of 1,400 m south of Muscat. (C) 55746#1. Decaying jellyfish patch at the base of a rock outcrop and individual decaying jellyfish at 2,460 m. (D) 55785#1. Continental rise area A. Decaying individual jellyfish and thick layer of phytodetritus. (E) 55791#1. Continental rise area C. Thick jelly detritus layer with the sea cucumber *Pelopatides mammillatus*. Note penetration of suspended weight top right. (F) 55791#1. Fresh and decaying jellyfish mixed with thick jelly detritus covering the entire seabed. (G) 55784#1. Continental rise area B. Thin layer of jelly detritus covering the entire seabed with individual decaying jellyfish carcasses at 3,160 m. (H) 55791#1. Jelly detritus patch (RHS) with a clear edge and the seabed with patches of phytodetritus (LHS).

several decomposing carcasses of *C. orsini*. The sample and the net had a powerful odor of what was assumed to be rotting jellyfish.

To the south of Muscat (Area C, Fig. 1B) fresh and decaying jellyfish were mixed with large patches of jelly detritus (Fig. 3F). The patches were several meters in diameter, often with a clearly defined edge (Fig. 3H), and had a conservatively estimated average depth of 70 mm, based on how deeply the weight suspended below the camera sank into the detrital layer (Fig. 3E). The jelly detritus patches covered a mean 16.6% of the seabed; this produced a mean standing stock value of 78.0 g C $m^{-2}$ (Table 2). When the weight suspended below the camera was dragged through the jelly detritus, the resuspended sediment was very black in color and different from sediments disturbed in areas clear of jelly detritus.

## Discussion

Jelly detritus in the Arabian Sea provides a new major transport pathway for carbon into the deep ocean. Whereas observations made during the *Challenger* expedition indicated that salp carcasses could be transported rapidly to abyssal depths and might act as a good food source for benthic fauna (Moseley 1880), evidence that the carcasses of dead animals provide a significant transport pathway for carbon in the oceans has been rather slow in accumulating. Whale carcasses are notable exceptions (Smith and Baco 2003), but in terms of global significance to carbon cycling, fauna that occur in great abundance are potentially more significant. Yet, direct observations of a quantitative nature are scarce.

Robison et al. (2005) highlighted the importance of the mucous feeding nets of larvaceans in transporting carbon rapidly to the deep-sea floor. From a 10-yr time series of ROV observations off California, they calculated an average carbon flux of 7.6 g C $m^{-2}$ $yr^{-1}$ via abandoned larvacean "houses," roughly equivalent to the seafloor carbon flux at mid-slope depths in the same area (7.2 g C $m^{-2}$ $yr^{-1}$; Pilskaln et al. 1996). Wiebe et al. (1979) estimated a flux of 3.5 mg C $m^{-2}$ $d^{-1}$ in the dead bodies of the salps in addition to 12 mg C $m^{-2}$ $d^{-1}$ of fast-sinking fecal material from a salp bloom during a mid-summer period. This was corroborated by the observations of Cacchione et al. (1978) of dead salps rolling along the nearby outer Hudson Canyon during the same period. The longevity of the salp bloom was unknown, but taking the data of Wiebe et al. (1979) and estimating that the salp bloom lasted 2 months, the flux of salp feces/carcasses could have provided a carbon input of about 1 g C $m^{-2}$ over the 2 months. This is equivalent to about half the mean annual downward organic carbon flux in the area as measured by near-bottom sediment traps (Biscaye et al. 1988).

In the mid-1990s, Arabian Sea surface waters were notable for large numbers of the swimming crab *Charybdis smithii* (van Couwelaar et al. 1997). The carcasses of many of these crabs were deposited on the abyssal seabed. Seafloor photographic surveys estimated a standing stock of carbon in crab carcasses of about 1 g C $m^{-2}$ (Christiansen and Boetius 2000), similar to the lower values of carbon flux noted in jelly detritus (Table 2).

Total annual organic carbon fluxes as measured by sediment traps at 3,100 m off the coast southeast of Oman in the mid-1990s ranged between 4.3 g C $m^{-2}$ $yr^{-1}$ to 4.8 g C $m^{-2}$ $yr^{-1}$ (Honjo et al. 1999). Whereas the jelly detritus standing stock at area A (Fig. 1B) was about one-third of annual downward organic carbon flux, the standing stock of jelly detritus closer to the base of the continental slope (areas B and C, Fig. 1B) was an order of magnitude greater, indicating a mass deposition event in the deep sea far greater than anything witnessed before.

The causes of the spatial variation in jelly detritus from high levels in thick patches on the Oman continental rise just south of Muscat to intermediate levels as a "skin" of jelly over the sediment off Ra's al Hadd and (comparatively) low levels of individual jellyfish carcasses more distant from the continental margin are not clear. All the photographic observations were made within a few days of each other, so the differences in the nature of the jelly detritus were probably not related to regional-scale temporal variation. The occurrence of many jellyfish carcasses in canyon systems (Fig. 3B) might indicate the importance of canyon systems in the transport of jelly detritus, particularly since the greatest concentrations of jelly detritus were observed on the continental rise in close proximity to canyons. However, as large jellyfish aggregations were not seen in the deeper canyon areas, down-canyon flows of jelly detritus might be episodic in nature.

The relevance of the observations in the Gulf of Oman to other oceanic areas is uncertain. It is possible that the jelly detritus noted off Oman occurred only as a result of the intense OMZ. If OMZs are important in reducing the rate of degradation of jellyfish as they pass through the water column then it might be expected that the deposition of jelly detritus is more significant in OMZ regions. Jellyfish blooms, however, are widespread (Mills 2001). It is possible, therefore, that jellyfish carcasses, and indeed the bodies of other gelatinous zooplankton, are important vectors for carbon transport to the deep sea in many areas of the world ocean.

The episodic nature of *C. orsini* blooms and the periodic mass occurrences of swimming crabs (Christiansen and Boetius 2000), with the deposition of large numbers of carcasses in the Arabian Sea in both cases, indicate that population explosions at the sea surface have a significant, time-varying effect on the deep seabed. It is likely that the jelly detritus has a significant effect on the underlying sediment in much the same way as sediments in the vicinity of whale carcasses are perturbed significantly for extended periods (Smith and Baco 2003). However, although the nature of the disturbance by jelly detritus will be less intense locally, it will affect a far greater area of the seabed regionally. The patchiness of jelly detritus will form a myriad of enrichment patches over a large area, contributing a new mechanism for intermediate-scale patchiness in species distributions, and possibly diversity, in the deep sea (Grassle and Maciolek 1991). The legacy of *C. orsini* may persist in deep-sea sediments of the Arabian Sea for some time after the jellyfish have disappeared from surface waters.

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