

Mass deposition of jellyfish in the deep Arabian Sea

D.S.M. Billett, B.J. Bett, C.L. Jacobs, I.P. Rouse, B.D. Wigham¹

National Oceanography Centre, Southampton, SO14 3ZH, United Kingdom.

Corresponding author: dsmb@noc.soton.ac.uk

Running head: Deep sea mass deposition of jellyfish

¹ Present address. Department of Zoology, University of Aberdeen, Main Street, Newburgh,
Aberdeenshire AB41 6AA, United Kingdom.

1 **Acknowledgements**

2 We thank the Government of the Sultanate of Oman for permission to work in Oman
3 waters, and Ahmed Al Mazrooei, Director Marine Science Fisheries Centre, Oman and his
4 colleagues for their valuable support. We are grateful for information supplied by Mike
5 Dawson (University of New South Wales), Cathy Lucas (NOCS), an anonymous referee of
6 an earlier manuscript, and the referees of this paper. We thank the Master and crew of RRS
7 *Charles Darwin* for their support during the field expedition.

1 **Abstract**

2
3 In December 2002 large numbers of dead jellyfish, *Crambionella orsini* (Vanhöffen
4 1888), were observed on the seabed over a wide area of the Arabian Sea off the coast of Oman,
5 at depths between 350 and 3300 m. Moribund jellyfish were seen tumbling down the continental
6 slope. Large aggregations of dead jellyfish were evident within canyons and on the continental
7 rise. At the deepest stations, patches of rotting, coagulated jellyfish occurred. The patches were
8 several metres in diameter, at least 7 cm thick and covered about 17% of the sediment surface.
9 At other locations on the continental rise the seafloor was covered in a thin, almost continuous,
10 layer of jelly “slime,” a few millimetres thick, or was littered with individual jellyfish corpses.
11 Photographic transects were used to estimate the amount of carbon associated with the jelly
12 detritus. The standing stock of carbon varied between 1.5 and 78 g C m⁻², the higher figure
13 exceeding the annual downward flux of organic carbon, as measured by sediment traps, by more
14 than an order of magnitude. The episodic nature of jellyfish blooms, which may be modulated
15 by global change phenomena, provides a hitherto unknown mechanism for large-scale spatial
16 and temporal patchiness in deep-sea benthic ecosystems.

1 **Introduction**

2

3

4

5

6

7

8

9

10

11

12

13

14

15

16

17

18

19

20

21

22

23

24

25

26

Sudden population explosions of jellyfish are a feature of many parts of the World's oceans (Purcell et al. 2001). They cause large-scale ecosystem effects in surface waters (Axiak and Civili 1991; Mills 1995; Brodeur et al. 2002). The occurrences of jellyfish super-abundances 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 RRS *Charles Darwin* cruise 143 (Jacobs 2003), large numbers of the scyphomedusan jellyfish *Crambionella orsini* (Vanhöffen 1888) were seen in surface waters over a wide area off Oman. Estimated visually their abundance was typically about one individual per cubic metre, but very dense aggregations occurred at frontal systems. *Crambionella orsini* is a native species of the Indian Ocean (Kramp 1961). The bell is 10 to 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.

While 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 super-abundant 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 super-abundance 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 faecal 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

1 zooplankton in the downward transport of carbon, as speculated from shipboard experiments
2 by Moseley (1880), is less well documented. Cacchione et al. (1978) recorded salp carcasses
3 rolling along the seabed in the Hudson Canyon at a depth of 3400 m and Wiebe et al. (1979)
4 estimated that salp carcasses might provide over half the daily energy requirements of the
5 bottom microfauna in the same general area. Elsewhere on the continental slope, ROV and
6 submersible observations have documented single occurrences of moribund scyphomedusans
7 on the seabed (Jumars 1976; Miyake et al. 2002; Miyake et al. 2005). Distant from the
8 continental slope, carcasses of the tunicate *Pyrosoma* have been observed in time-lapse
9 photography of the Madeira Abyssal Plain seafloor (Roe et al. 1990). Remarkably, in
10 shallow water, there has been no direct quantification of the deposition of jellyfish, even
11 though a major input to the seabed has been suggested (Axiak and Civili 1991; Arai 1997;
12 Kingsford et al. 2000).

13 During RRS *Charles Darwin* cruise 143 we observed the seabed using real time video
14 and still photography. In the course of the work between 350 and 3300 m, many jellyfish
15 were seen rolling along the seabed. It became clear that very large numbers of jellyfish were
16 being transported rapidly to the deep-sea floor. In this paper we describe how jellyfish gather
17 on the deep-sea floor and we estimate the standing stock of carbon in jelly detritus deposited
18 on the seabed. We speculate on what the consequences might be for the deep-sea benthos
19 and suggest that the episodic and long-term variation in jellyfish blooms in surface waters
20 will introduce similar spatial and temporal variability to deep-sea benthic communities.

21 22 **Materials and methods**

23 24 *Study area*

25
26 The Gulf of Oman, between Oman and Iran, is a deep amphitheatre-shaped
27 embayment of the continental margin (Fig. 1A). The continental slope of the Oman margin
28 between Muscat and the headland of Ra's al Hadd is deeply incised by a number of canyons

1 running offshore (Fig. 1B). The mouths of the canyons open out onto the continental rise at a
2 depth of about 2700 m, some 40 km offshore.

3 The Gulf of Oman is influenced by the NE monsoon (December to March) and SW
4 monsoon (June to September). Strong winds associated with the SW monsoon lead to high
5 primary productivity along the Oman coast owing to the upwelling of nutrient-rich water
6 (Wiggert et al. 2005). The subsequent heterotrophic utilisation of the primary productivity
7 coupled with slow ocean circulation, lead to a permanent hypoxic layer of water ($<0.5 \text{ mL O}_2$
8 L^{-1}), the Oxygen Minimum Zone (OMZ), that is typical of the northern Arabian Sea between
9 100 and 1000 m (Demopoulos et al. 2003). On the Oman continental margin to the north of
10 Ra's al Hadd oxygen levels as low as $0.05 \text{ mL O}_2 \text{ L}^{-1}$ were measured (Fig. 2). Between 450
11 and 1000 m there was little or no variation in the very low levels of oxygen.

12 13 *Imaging of the seafloor*

14
15 Photography of the seabed was carried out using a towed camera system (SHRIMP -
16 Seabed High Resolution IMaging Platform). The vehicle was flown c. 2 to 3 m above the
17 seabed by reference to real-time imaging and telemetered altimeter data. Video footage was
18 recorded continuously and still photographs were taken every 12 seconds. Deployments
19 lasted 30 to 360 minutes, with the vehicle travelling at about 0.5 knots over the seabed. At an
20 altitude of between 2 and 3 m individual photographs covered an area of seabed between 2.5
21 and 5.6 m^2 . A weight was suspended below the camera to aid the SHRIMP operators to
22 maintain a constant altitude. The weight was also used to test the softness of the sediment
23 surface and to estimate the thickness of the jelly detritus.

24 Twenty four SHRIMP deployments were completed at depths between 300 and 3300
25 m (Table 1). All images were taken c. two months after the SW monsoon. The surveys
26 included gently sloping sediments, rocky outcrops, the walls and channels of canyons, and
27 the continental rise. Seabed photographic surveys were concentrated in two areas (Fig. 1B).

1 An additional SHRIMP deployment was made on the continental rise to the east of Ra's al
2 Hadd (c. 3200 m) (Fig. 1B).

3
4 ***Quantifying percentage cover, jelly detritus thickness, and carbon flux***
5

6 Using data on 1) percentage area cover of jelly detritus from the photographic surveys
7 and 2) estimates of the thickness of the detritus, the standing stock of jellyfish, in terms of g
8 C m⁻² of seabed was calculated for the three continental rise areas. Photographic surveys
9 were carried out in the mode of straight line transects covering distances of between 0.3 to 3
10 km at each station. From these transects the percentage cover of jelly detritus was estimated
11 from every fifth photograph. An average altitude of 2.5 m was maintained during the photo-
12 transects, apart from short periods when the camera was taken to within 1 m of the seabed in
13 order to determine the nature of the jelly detritus. By allowing the suspended weight to
14 impact the seabed, and reveal a section through the detritus, or disappear into it, we were able
15 to estimate the thickness of the jelly layer by reference to the known dimensions of the
16 weight. The smallest dimensions of the weight were used to estimate the thickness of the
17 jelly detritus and so our estimates err on the side of caution. From percentage cover and the
18 thickness, the volume and the wet weight (assuming a specific gravity of 1) of jelly detritus
19 were calculated per square metre. Wet weight data per unit area were converted to dry
20 weight and then grams carbon using standard conversions for Scyphomedusae. Conversions
21 of 5.2% for wet weight to dry weight and 12.9% for dry weight to carbon were used (Larson
22 1986).

23
24 ***Sampling of the seafloor***
25

26 Sediment samples were taken with an hydraulically damped Bowers and Connelly
27 "Megacorer" (Gage and Bett 2005). The sediment surface was retrieved intact with
28 essentially no disturbance. One sample was taken on the continental rise (Table 1) in an area

1 in which jelly detritus had been seen in the video transects (Jacobs 2003). An Agassiz trawl
2 was also used in close proximity to the SHRIMP photographic surveys in Area B (Fig. 1B) to
3 collect voucher specimens for the identification of megafauna seen in photographs.

4 5 **Results**

6 7 *Continental slope*

8
9 On the continental slope many individual, dead jellyfish were seen rolling along the
10 seabed in the prevailing current (Fig. 3A). On the upper slope, within the Oxygen Minimum
11 Zone, individuals tended to still be in very good condition although in many cases the
12 swimming bell had become detached from the tentacles (Fig. 3A). There was little evidence
13 that the larger benthic fauna fed upon the medusae. There was little evidence of bacterial
14 breakdown of the jellyfish on the upper slope (shallower than 1000 m).

15 16 *Canyon systems*

17
18 Within the upper reaches of the canyons many dead jellyfish were seen tumbling
19 downslope. At mid-slope depths in some canyons, where large boulders and rocks
20 interrupted the down-canyon flow of jellyfish, large aggregations occurred (Fig. 3B).
21 However, in the lower reaches of the canyons fewer individuals were seen and generally they
22 occurred in small aggregations covered by a white bacterial mat (Fig. 3C).

23 24 *Continental rise*

25
26 The greatest concentrations of decaying jellyfish were found at three locations on the
27 continental rise. For ease of identification, these are referred to Areas A, B, and C (Fig. 1).
28 All stations were surveyed within a few days of each other (Table 1). The appearance of the
29 degrading jellyfish varied from single specimens covered by a white layer of presumed mat-
30 forming bacteria (Fig. 3D), to patches of thick, coalesced jelly detritus (Fig. 3E). In the latter

1 case “fresh” jellyfish often occurred mixed in with the jelly patches (Fig. 3F). There was no
2 evidence that the jelly detritus was being fed upon by larger animals.

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

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

11 To the North of Ra’s al Hadd (Area B, Fig. 1B), single decaying jellyfish and
12 bacterial mats occurred, but close-up views of the seabed showed that most of the sediment
13 surface was covered in a thin layer of slime (Fig. 3G). One deployment of a Megacorer was
14 made in the vicinity. Eleven cores were retrieved from the deployment, all with a layer of
15 jelly detritus about 10 mm thick. At a local scale at least, this corroborates the photographic
16 and video evidence that the vast majority of the sediment was covered in thin layer of jelly
17 detritus. In some cores, lumps of gelatinous detritus were noted. At the base of the jelly
18 detritus there was a thin black layer overlying the sediment surface. On average, the
19 photographs indicated that the jelly detritus thickness was less than 10mm, so a conservative
20 estimate of 5mm has been used. The jelly detritus covered an average 93.4% of the seabed
21 producing a mean standing stock of 31.3 g C m^{-2} (Table 2). An Agassiz trawl deployed in the
22 area retrieved a small sample containing several decomposing carcasses of *Crambionella*
23 *orsini*. The sample and the net had a powerful odour of what was assumed to be rotting
24 jellyfish.

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

9

10 **Discussion**

11

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

20 Robison et al. (2005) highlighted the importance of the mucous feeding nets of
21 larvaceans in transporting carbon rapidly to the deep-sea floor. From a 10-year time series of
22 ROV observations off California they calculated an average carbon flux of $7.6 \text{ g C m}^{-2} \text{ yr}^{-1}$
23 via abandoned larvacean “houses”, roughly equivalent to the seafloor carbon flux at mid-
24 slope depths in the same area ($7.2 \text{ g C m}^{-2} \text{ yr}^{-1}$; Pilskaln et al. 1996). Wiebe et al. (1979)
25 estimated a flux of $3.5 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the dead bodies of the salps in addition to 12 mg C m^{-2}
26 d^{-1} of fast sinking faecal material from a salp bloom during a mid-summer period. This was

1 corroborated by the observations of Cacchione et al. (1978) of dead salps rolling along the
2 nearby outer Hudson Canyon during the same period. The longevity of the salp bloom was
3 unknown, but taking the data of Wiebe et al. (1979) and estimating that the salp bloom lasted
4 2 months, the flux of salp faeces/carcasses could have provided a carbon input of c. 1 g C m^{-2}
5 over the two months. This is equivalent to about half the mean annual downward organic
6 carbon flux in the area, as measured by near-bottom sediment traps (Biscaye et al. 1988).

7 In the mid 1990s Arabian Sea surface waters were notable for large numbers of the
8 swimming crab *Charybdis smithii* (van Couwelaar et al. 1997). The carcasses of many of
9 these crabs were deposited on the abyssal seabed. Seafloor photographic surveys estimated a
10 standing stock of carbon in crab carcasses of about 1 g C m^{-2} (Christiansen and Boetius
11 2000), similar to the lower values of carbon flux noted here in jelly detritus (Table 2).

12 Total annual organic carbon fluxes, as measured by sediment traps at 3100 m off the
13 coast southeast of Oman in the mid 1990s, ranged between $4.3 \text{ to } 4.8 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Honjo et
14 al. 1999). While the jelly detritus standing stock at Area A (Fig. 1B) was about one third of
15 annual downward organic carbon flux, the standing stock of jelly detritus closer to the base of
16 the continental slope (areas B and C, Fig. 1B) was *an order of magnitude greater*, indicating
17 a mass deposition event in the deep sea far greater than anything witnessed before.

18 The causes of the spatial variation in jelly detritus, from high levels of jelly detritus in
19 thick patches on the Oman continental rise just south of Muscat to intermediate levels as a
20 “skin” of jelly over the sediment off Ra’s al Hadd, to (comparatively) low levels of individual
21 jellyfish carcasses more distant from the continental margin are not clear. All the
22 photographic observations were made within a few days of each other, so the differences in
23 the nature of the jelly detritus were probably not related to regional-scale temporal variation.
24 The occurrence of many jellyfish carcasses in canyon systems (Fig. 3B) might indicate the
25 importance of canyon systems in the transport of jelly detritus, particularly since the greatest

1 concentrations of jelly detritus were observed on the continental rise in close proximity to
2 canyons. However, as large jellyfish aggregations were not seen in the deeper canyon areas,
3 down-canyon flows of jelly detritus might be episodic in nature.

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

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

1 **References**

- 2 Arai, M.N. 1997. A functional biology of Scyphozoa. Chapman Hall.
- 3 Axiak, V., and F.S. Civili, 1991. Jellyfish blooms in the Mediterranean: causes, mechanisms,
4 impact on man and the environment. A programme review. UNEP MAP Tech. Rep.
5 Ser. **47**: 1-21.
- 6 Beaulieu, S.E. 2002. Accumulation and fate of phytodetritus on the sea floor. Oceanog. Mar.
7 Biol. Annu. Rev. **40**: 171-232.
- 8 Biscaye, P.E., R.F. Anderson, and B.L. Deck, 1988. Fluxes of particles and constituents to
9 the eastern United States continental slope and rise: SEEP-1. Cont. Shelf Res. **8**: 855-
10 904.
- 11 Brodeur, R.D., H. Sugisaki, and G.L. Hunt, 2002. Increases in jellyfish biomass in the Bering
12 Sea: Implications for the ecosystem. Mar. Ecol. Prog. Ser. 233: 89-103.
- 13 Cacchione, D.A., G.T. Rowe, and A. Malahoff, 1978. Submersible investigation of the outer
14 Hudson submarine canyon, p. 42-50. In D.J. Stanley and G. Kelling [eds.],
15 Sedimentation in submarine canyons, fans and trenches. Dowden, Hutchinson &
16 Ross.
- 17 Christiansen, B., and A. Boetius, 2000. Mass sedimentation of the swimming crab *Charybdis*
18 *smithii* (Crustacea: Decapoda) in the deep Arabian Sea. Deep-Sea Res. II **47**: 2673-
19 2685.
- 20 Creasey, S.S., A.D. Rogers, P.A. Tyler, C. Young, C., and J.D. Gage, 1997. The population
21 biology and genetics of the deep-sea spider crab *Encephaloides armstrongi*
22 Woodmason 1891 (Decapoda: Majidae). Phil. Trans. R. Soc. Lond. Ser. B **352**: 265-
23 379.

- 1 Demopoulos, A.W.J., C.R. Smith, and P.A. Tyler, 2003. The deep Indian Ocean floor, p. 219-
2 237. *In* P.A. Tyler [ed.], *Ecosystems of the world* **28**. Ecosystems of the deep oceans.
3 Elsevier.
- 4 Gage, J.D., and B.J. Bett, 2005. Deep-sea benthic sampling, p. 273-325. *In* A. Eleftheriou,
5 and A. MacIntyre [eds.]. *Methods for the study of marine benthos* (3rd ed). Blackwell.
- 6 Grassle, J.F., and N.K. Maciolek, 1992. Deep-sea species richness: regional and local
7 diversity estimates from quantitative bottom samples. *Am. Nat.* **130**: 313-341.
- 8 Honjo, S., J. Dymond, W. Prell, and V. Ittekkot, 1999. Monsoon-controlled export fluxes to
9 the interior of the Arabian Sea. *Deep-Sea Res. II* **46**: 1859-1902.
- 10 Jacobs, C.L. 2003. RRS *Charles Darwin* cruise 143, 22 Nov – 21 Dec 2002, Scheherezade II:
11 Geological and biological surveys of the Arabian Sea and the continental slope of
12 Oman. SOC Cruise Rep. **42**.
- 13 Jumars, P.A. 1976. Deep-sea species diversity: does it have a characteristic scale? *J. Mar.*
14 *Res.* **34**: 217-246.
- 15 Kingsford, M.J., K.A. Pitt, and B.M. Gillanders, 2000. Management of jellyfish fisheries with
16 special reference to the Order Rhizostomeae. *Oceanogr. Mar. Biol. Annu. Rev.* **38**:
17 85-156.
- 18 Kramp, P.L. 1961. Synopsis of the medusae of the world. *J. Mar. Biol. Ass. UK* **40**: 7-469.
- 19 Larson, R.J. 1986. Water content, organic content, and carbon and nitrogen composition of
20 medusae from the northeast Pacific. *J. Exp. Mar. Biol. Ecol.* **99**: 107-120.
- 21 Mills, C.E. 1995. Medusae, siphonophores and ctenophores as planktivorous predators in
22 changing ocean ecosystems. *ICES J. Mar. Sci.* **52**: 575-581.
- 23 Mills, C.E. 2001. Jellyfish blooms: are populations increasing globally in response to
24 changing ocean conditions? *Hydrobiologia* **451**: 55-68.

- 1 Miyake, H., D.L. Lindsay, J.C. Hunt, and T. Hamatsu, 2002. Scyphomedusa *Aurelia limbata*
2 (Brandt, 1838) found in deep waters off Kushiro, Hokkaido, Northern Japan. *Plankton*
3 *Biol. Ecol.* **49**: 44-46.
- 4 Miyake, H., D.L. Lindsay, M. Kitamura, and S. Nishida, 2005. Occurrence of the
5 scyphomedusa *Parumbrosa polylobata* Kishinouye, 1910 in Suruga Bay, Japan.
6 *Plankton Biol. Ecol* **52**: 58-66.
- 7 Moseley, H.N. 1880. Deep-sea dredging and life in the deep sea III. *Nature* **21**: 591-593.
- 8 Pfannkuche, O., and K. Lochte, 2000. The biogeochemistry of the deep Arabian Sea:
9 overview. *Deep-Sea Res. II* **47**: 2615-2628.
- 10 Pilskaln, C.H., J.B. Paduan, F.P. Chavez, R.Y. Anderson, and W.M. Berelson, 1996. Carbon
11 export and regeneration in the coastal upwelling system of Monterey Bay, central
12 California. *J. Mar. Res.* **54**: 1149-1178.
- 13 Purcell, J.E., W.M. Graham, and H.J. Dumont, 2001. Jellyfish blooms: ecological and
14 societal importance. *Dev. Hydrobiol.* **155**: Kluwer Academic Publishers.
- 15 Robison, B.H., K.R. Reisenbichler, and R.E. Sherlock, 2005. Giant larvacean houses: rapid
16 carbon transport to the deep sea floor. *Science* **308**: 1609-1611.
- 17 Roe, H.S.J., D.S.M. Billett, and R.S. Lampitt, 1990. Benthic/midwater interactions on the
18 Madeira Abyssal Plain; evidence for biological transport pathways. *Prog. Oceanogr.*
19 **24**: 127-140.
- 20 Smith, C.R., and A.R. Baco, 2003. Ecology of whale falls at the deep-sea floor. *Oceanogr.*
21 *Mar. Biol. Annu. Rev.* **41**: 311-354.
- 22 van Couwelaar, M., M.V. Angel, and L.P. Madin, 1997. The distribution and biology of the
23 swimming crab *Charybdis smithii* McLeay, 1838 (Crustacea; Brachyura; Portunidae)
24 in the NW Indian Ocean. *Deep-Sea Res. II* **44**: 1251-1280.

- 1 Wiebe, P.H., L.P. Madin, L.R. Haury, G.R. Harbison, and L.M. Philbin, 1979. Diel vertical
2 migration by *Salpa aspersa* and its potential for large-scale particulate organic matter
3 transport to the deep sea. *Mar. Biol.* **53**: 249-255.
- 4 Wiggert, J.D., R.R. Hood, K. Banse, and J.C. Kindle, 2005. Monsoon-driven biogeochemical
5 processes in the Arabian Sea. *Prog. Oceanogr.* **65**: 176-213.

Table 1. Station data for deployments referred to in the text (for the complete cruise listing see Jacobs 2003).
 (Area: physiographic setting; Station: unique deployment identifier; Gear: AgT-Agassiz trawl, MgC-Megacorer, SHR-SHRIMP; CTD- Conductivity, temperature and depth probe with O₂ sensor).

Area	Station	Gear	Date	Position		Depth (m)		Sample
				Start (N)	Start (E)	Min	Max	
Rise A	55785#1	SHR	17 Dec 02	22° 42.20′	060° 39.05′	3189	3196	431 photos
Rise B	55782#1	SHR	16 Dec 02	23° 00.94′	060° 03.13′	3169	3188	837 photos
Rise B	55783#1	AgT	16 Dec 02	23° 00.49′	060° 03.77′	3168	3168	Trawl catch
Rise B	55784#1	SHR	17 Dec 02	22° 58.59′	060° 08.73′	3157	3170	542 photos
Rise B	55788#1	MgC	18 Dec 02	23° 01.00′	060° 02.98′	3185	3185	11 Cores
Rise C	55704#2	CTD	29 Nov 02	23° 29.57′	059° 14.06′	0	3101	T, S and O ₂ profiles
Rise C	55791#1	SHR	19 Dec 02	23° 30.27′	059° 29.91′	3299	3314	867 photos
Slope	55734#1	SHR	06 Dec 02	22° 35.19′	059° 53.30′	307	902	1220 photos
Slope	55740#1	SHR	07 Dec 02	22° 46.54′	059° 57.70′	2005	2020	150 photos
Slope	55741#1	SHR	07 Dec 02	22° 42.21′	059° 56.46′	1495	1521	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′	1288	1492	524 photos
Canyon	55727#1	SHR	04 Dec 02	23° 19.27′	059° 02.51′	2300	2400	665 photos
Canyon	55746#1	SHR	08 Dec 02	22° 49.08′	059° 45.88′	2458	2466	183 photos
Canyon	55747#1	SHR	08 Dec 02	22° 44.62′	059° 45.52′	1869	2014	633 photos
Canyon	55748#1	SHR	08 Dec 02	22° 39.17′	059° 49.11′	1616	1702	384 photos

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 analysed	59	178	117
Data range, jelly detritus cover (%)	0-24	68-100	0-100
Mean area covered by jelly detritus (%)	2.3	93.4	16.6
(95% confidence limits)	(1.8 - 2.9)	(92.3 - 94.7)	(10.7 - 23.4)
Thickness of jelly layer (mm)	10	5	70
Mean standing stock(g C m ⁻²)	1.5	31.3	78.0
(95% confidence limits)	(1.2 - 2.0)	(31.0 - 31.8)	(50.2 - 109.9)

Figure legends

Figure 1.

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

Figure 2.

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

Figure 3.

Seafloor photographs from the Oman margin. Scale bars refer to 50 cm in all cases. (A) Stn. 55734#1. Jellyfish carcasses at c. 350 m depth, within a depth zone occupied by many deep-sea spider crabs, *Encephaloides armstrongi* (Creasey et al., 1997). While 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 1400 m south of Muscat. (C) 55746#1. Decaying jellyfish patch at the base of a rock outcrop and individual decaying jellyfish at 2460 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 3160 m. (H) 55791#1. Jelly detritus patch (RHS) with clear edge and seabed with patches of phytodetritus (LHS).

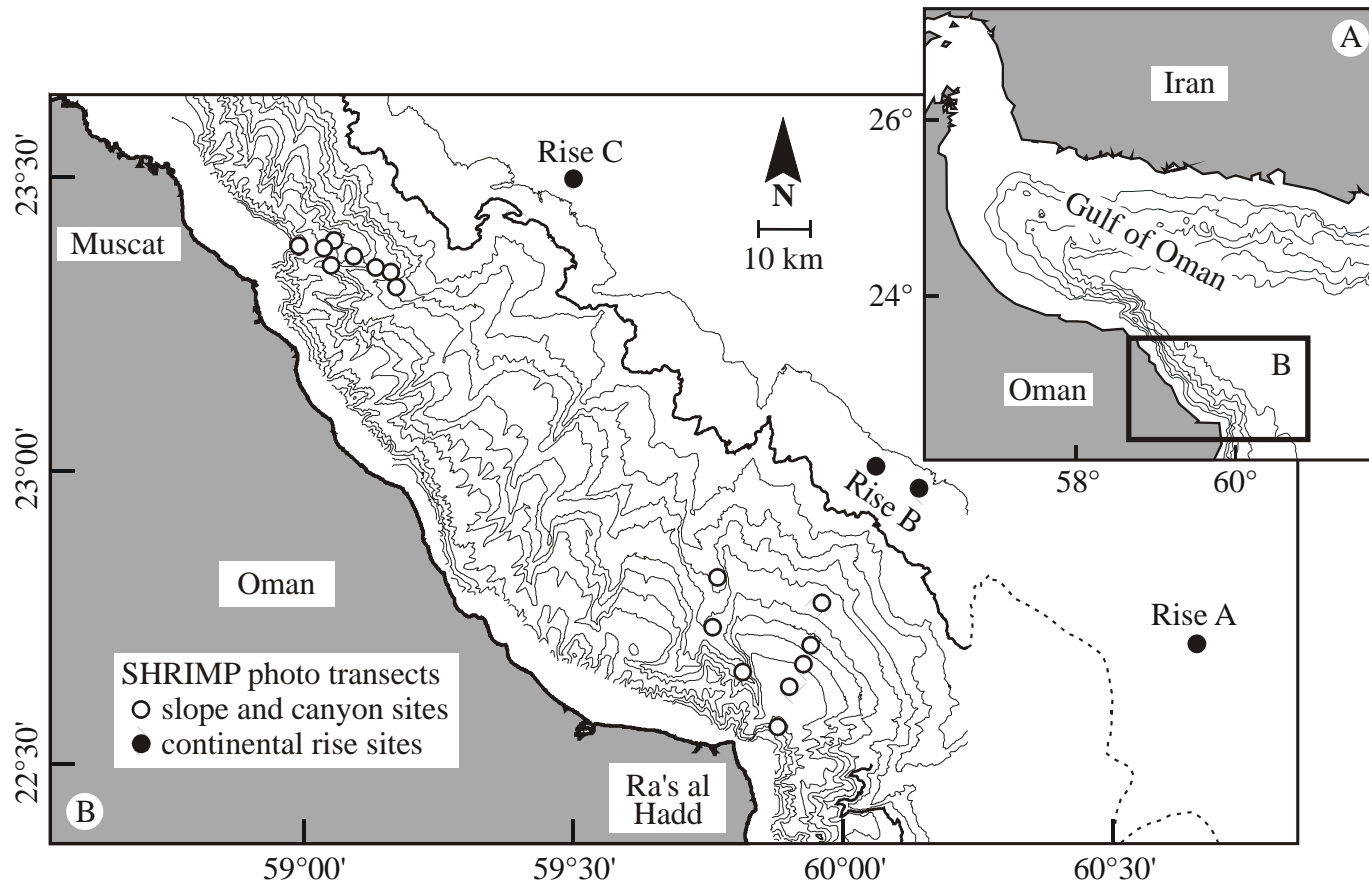


Figure 1. (Billett et al.)

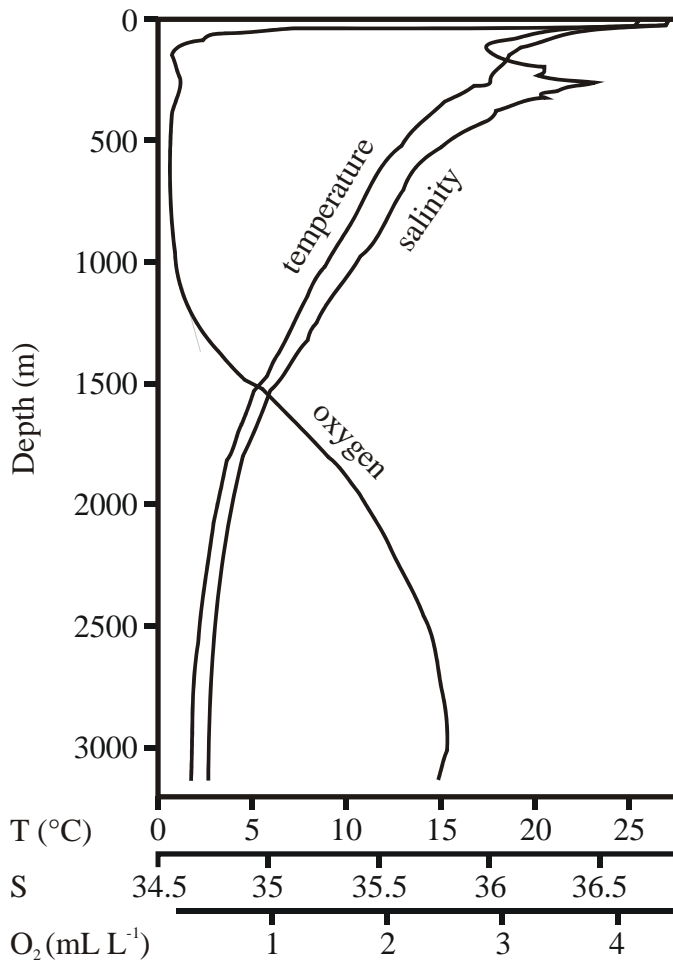


Figure 2 (Billett et al.)

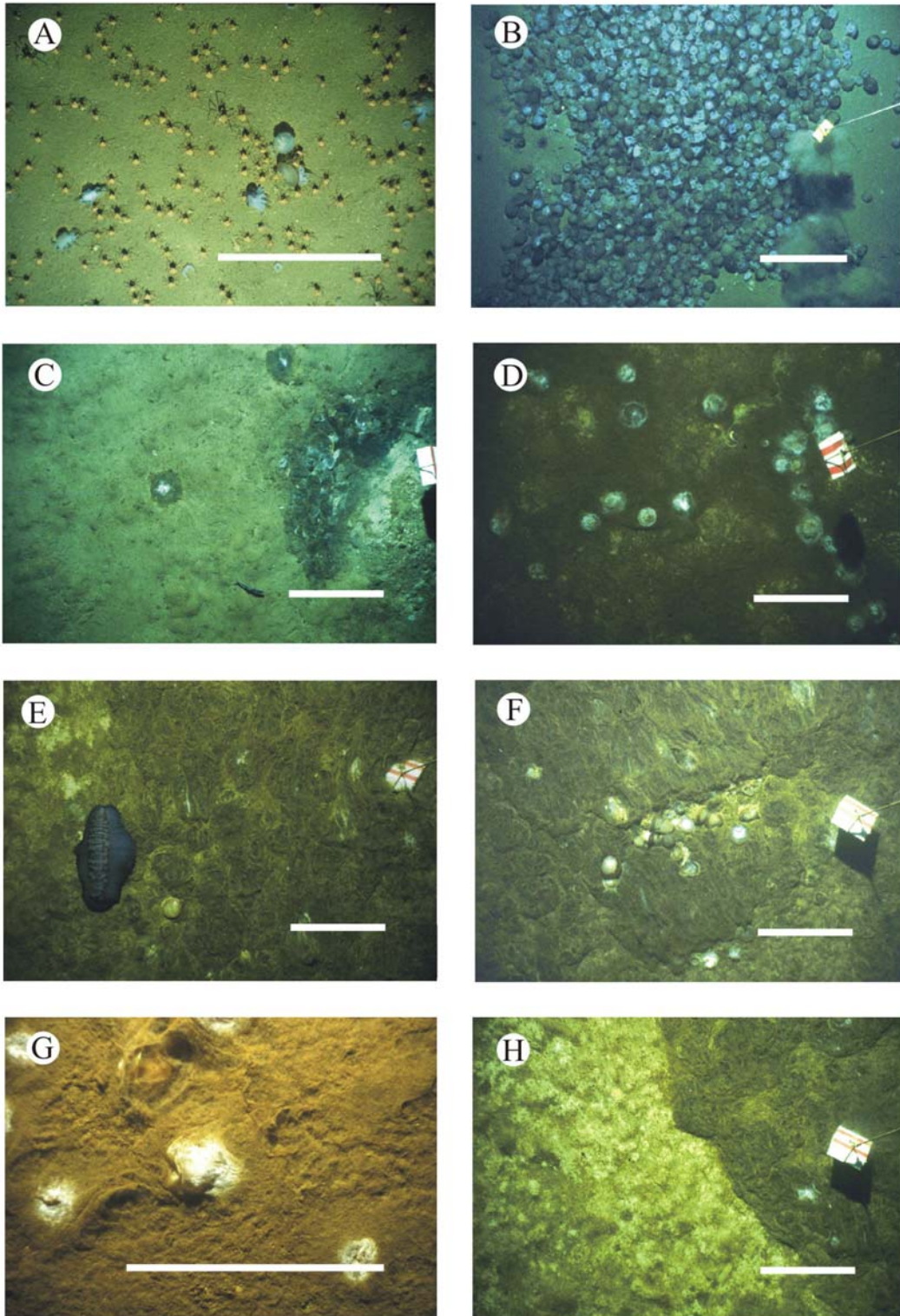


Figure 3 (Billett et al.)