

Ophiuroid growth within deep-sea sediment traps: A problem for carbon flux measurements at continental margins

Abstract—Large numbers of postlarvae of the bathyal ophiuroid *Ophiocten gracilis* were collected by two time-series sediment traps moored on the continental slope of the NE Atlantic for 102 d at 1,000 and 1,400 m deep (469 and 69 mab), respectively. With time, the organisms collected were progressively larger, suggesting that a single cohort was growing within the collection funnel of the traps but above the preservative solution. We believe that specimens from this cohort occasionally lost their grip on the funnel surface and fell into the preservative. This conclusion is supported by (1) the presence of food within the stomachs of postlarvae (these do not feed in their planktonic phase) and (2) the size of specimens (much larger than those previously found in the plankton). The upper trap was well above the benthic nepheloid layer, and suspension of these organisms by ambient currents is highly unlikely. Ophiuroids contributed up to 7% of the total daily flux of particulate organic carbon (POC) in the top trap and almost 30% in the bottom trap, and although they are not normally considered components of downward particle flux, these specimens had been growing on the material entering the traps and so should be included in this portion. Not all of the epifaunal population will have fallen into the collecting cups, but those that fell had requirements for growth and respiration that were a considerable proportion of the daily flux of POC into the traps (up to 16%). If this epifaunal community (a minimum estimate) was distributed evenly within the cone, a high proportion of the settling material would have come into contact with ophiuroids as it slid down the inside walls of the cone. This problem with the sediment trap technique is probably restricted to the continental slope and shelf and will not occur over abyssal depths.

Sediment traps have often been used to measure downward flux of particulate organic carbon, and there is a considerable body of complementary data to indicate that they function in a quantitative way (e.g., Gardner et al. 1997 and references cited therein). A picture is now emerging of the global trends and the relationship between deep water particle flux and primary production in the euphotic zone (Lampitt and Antia 1997). However, there are a number of features of the trapping technique, both physical and biological, that suggest a degree of caution is required.

Several aspects of the sediment trap technique cast doubt on some of the data derived using them (Yu et al. 2001). The most important physical problem is that the effects of ambient currents are poorly understood, but almost certainly have a significant effect on trapping efficiency (Hargraves and Burns 1979; Gardner 1980; Butman 1986; Baker et al. 1988). Other problems include solubilization of carbon (Knauer et al. 1984), bacterial degradation (Iturriaga 1979; Gardner et al. 1983), resuspension (Gardner and Richardson 1992), and the presence of swimmers (Coale 1990; Michaels et al. 1990; Hansell and Newton 1994).

An aspect that has not been considered to date is the pres-

ence of benthic organisms in trap samples that might have been living on the internal surfaces of the traps (e.g., cone and baffle). These animals might live in the traps, consuming the settled material before it enters the preservative fluid in the cups below. Furthermore, the bodies of these animals could represent a considerable proportion of the particulate organic carbon (POC) flux, despite being normally classified as “swimmers” and, hence, discarded in subsequent analyses.

In the present paper, we report on what we consider to be a large settlement event of *Ophiocten gracilis* (brittle stars) postlarvae into two deep-sea sediment traps and discuss the possible consequences of such a settlement for the assessment of carbon flux in the oceans.

Samples were obtained using two PARFLUX Mark 7G-21 time-series sediment traps moored in 1,469 m of water in the Hebridean slope (56°43'N, 09°25'W) to the west of Scotland. The trap has an opening of 0.5 m² and is covered by a honeycomb baffle of cells 2.5 cm diameter by 6.5 cm deep with 0.5-mm-thick walls. The traps were placed 1,000 and 1,400 m deep (469 and 69 m above the bottom, respectively). The mooring was deployed on 21 April 1996 and recovered on 2 August 1996, with a sampling interval of 7 d. Sampling cups were filled prior to deployment with preservative fluid of 2% borax-buffered formaldehyde and 5‰ excess NaCl. We assume that the animals entering the cups were killed immediately. On recovery, 1 ml of concentrated aristar-grade formalin was added prior to storage at 4°C. Total particulate carbon content was determined on subsamples using a LECO® CHN-900 elemental analyzer. Other subsamples were fumed overnight with concentrated HCl before analysis to determine, by difference, the POC content (Hedges and Stern 1984; Pérez-Castillo et al. pers. comm.).

During the analysis of particulate material, it was noticed that a large number of postlarval ophiuroids were present; these were later identified as *Ophiocten gracilis*. The animals were picked out under stereomicroscope, and the disk diameter (DD) and arm length were measured using a digitizing tablet driven by a microcomputer. The stomach contents were examined visually under stereomicroscope, food items being observed through the mouth and skin prior to removal for analysis.

Dry weight (DW) of postlarvae was measured using 50 intact animals of a wide variety of sizes. Each was individually measured and dried at 60°C for 24 h. The animals were weighed and then burned in a muffle furnace for 18 h to estimate the ash-free dry weight (AFDW).

The proportion of material sliding down the inside surface of the cone that is intercepted by ophiuroids can be calculated. We assumed that the downward flux enters the upward-facing opening of the cone in a spatially uniform manner. We also assumed that the ophiuroids were distributed

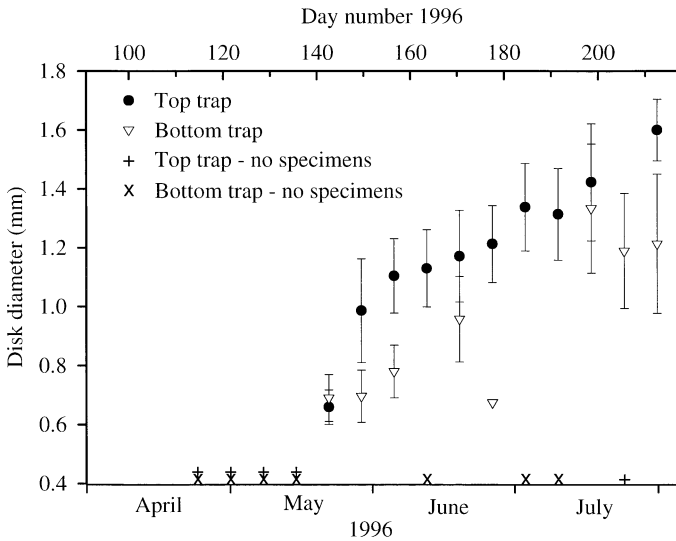


Fig. 1. Size distribution of postlarval *Ophiosten gracilis* collected in sediment traps during the sampling period. Error bars are standard deviations.

evenly over the walls of the cone but that they distribute themselves so as not to be in the “shadow” of a specimen higher up the cone wall. In this way, the proportion of material being intercepted by a specimen depends only on the number and diameter of the specimens. For this calculation, we assumed that all specimens collected during a particular sampling interval had the mean diameter of those collected during that interval. We assumed that all specimens were eventually collected and, therefore, that the number present on the walls during any particular sampling interval was that total number minus those that had already fallen into the sampling cup. Integrating down the sides of the funnel provides the following relationship. At any one time, the proportion of material intercepted by ophiuroids: $P = ND/4\pi R$, where N is the population number half way through the respective sampling interval, D is the mean diameter of the collected specimens, and R is the radius of the top of the funnel.

Results—No ophiuroids were collected by either trap during the first four sampling periods (21 April–19 May), but after that date, 453 specimens were collected in the top and 1,607 in the bottom trap. In the bottom trap, >98% of the specimens were collected during the first three sampling periods after first appearance. In both traps, the mean disk diameter of the individuals showed a progressive increase with time (Fig. 1). Although the size distribution at first appearance was very similar in the two traps, subsequently those in the bottom trap were consistently smaller.

Particulate organic carbon (POC) flux varied between 2.4 and 10.8 $\text{mg m}^{-2} \text{d}^{-1}$ in the top trap and between 1.6 and 13.6 $\text{mg m}^{-2} \text{d}^{-1}$ in the bottom (Fig. 2). Ophiuroids represented up to 7% of the measured daily flux (excluding ophiuroids) in the top trap and up to almost 30% in the bottom (Table 1).

The stomach content analysis of the collected specimens (Fig. 3) demonstrates that detrital material was usually found

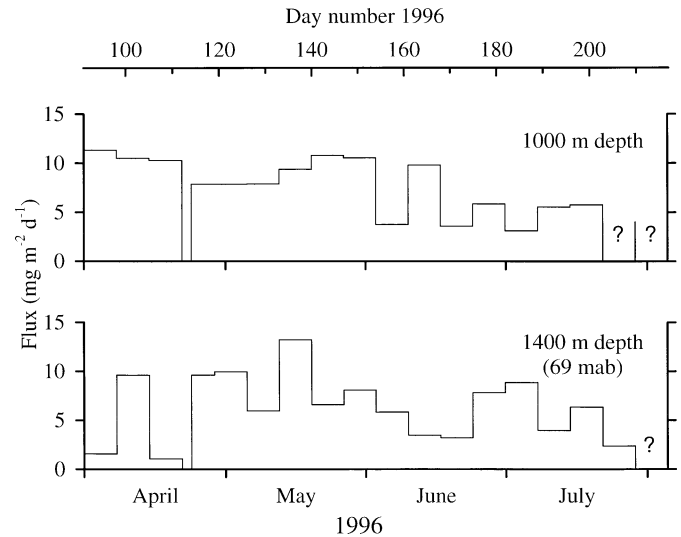


Fig. 2. POC flux into the two traps. During three sampling periods, data were not available because of POC analyzer malfunction.

Table 1. Percentage of the daily POC flux represented by ophiuroids at 1,000 and 1,400 m. DD, disk diameter; ND, no data.

Open date	POC Flux mg m^{-2} day^{-1}	No. specimens collected	Mean DD (mm, \pm SD)	% POC flux of ophiuroids
1,000 m				
23 Apr	7.86	0	0	0
28 Apr	7.85	0	0	0
5 May	7.88	0	0	0
12 May	9.37	0	0	0
19 May	10.78	4	0.66 ± 0.06	0.07
26 May	10.52	195	0.99 ± 0.18	6.59
2 Jun	3.75	64	1.10 ± 0.13	7.32
9 Jun	9.79	35	1.13 ± 0.13	1.61
16 Jun	3.56	22	1.17 ± 0.16	3.02
23 Jun	5.84	57	1.21 ± 0.13	5.09
30 Jun	3.11	6	1.34 ± 0.15	1.26
7 Jul	5.52	48	1.31 ± 0.16	5.51
14 Jul	5.74	11	1.42 ± 0.20	1.50
21 Jul	ND	0	0	ND
28 Jul	ND	11	1.60 ± 0.10	ND
1,400 m				
23 Apr	9.61	0	0	0
28 Apr	9.94	0	0	0
5 May	5.94	0	0	0
12 May	13.22	0	0	0
19 May	6.58	345	0.69 ± 0.08	10.60
26 May	8.07	1,156	0.70 ± 0.09	29.36
2 Jun	5.82	84	0.78 ± 0.09	3.43
9 Jun	3.45	0	0	0
16 Jun	3.21	2	0.96 ± 0.15	0.20
23 Jun	7.8	1	0.68	0.02
30 Jun	8.85	0	0	0
7 Jul	3.94	0	0	0
14 Jul	6.32	4	1.33 ± 0.22	0.42
21 Jul	2.35	5	1.19 ± 0.20	1.08
28 Jul	ND	10	1.21 ± 0.24	ND

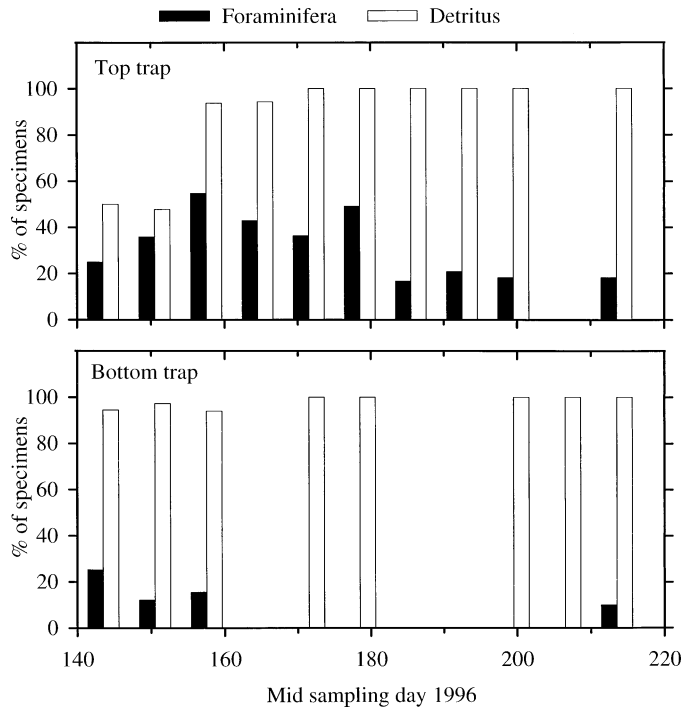


Fig. 3. Percentage of specimens in the top and bottom traps containing either foraminifera or detritus in their stomach.

in the stomachs, but in addition to this, foraminifera were often found and occasionally polychaetes and eggs. This all supports the contention that the specimens were feeding on the inside surfaces of the sediment trap cone.

Discussion—Before discussing the carbon demands of the population of brittle stars or their effect on particles sinking into the traps, we should consider whether there is incontrovertible evidence that growth occurred within the trap. Although specimens were not actually seen growing or dwelling in the trap, the conclusion from a number of lines of evidence must be that this was the case. The first data to support this is a progressive increase in size of individuals collected throughout the study period (Fig. 1). Taken in isolation, the inference from this could be that a nearby planktonic or suspended benthic population contained individuals that were growing as a result of a single reproductive event and that this population was being sampled by the traps. However the second line of evidence concerns the size of planktonic specimens: Postmetamorphic *Ophiocten gracilis* are planktonic until they reach a size of about 0.6 mm DD with up to eight arm segments, at which time they settle to the seabed where they remain as benthic organisms for the rest of their lives (Hendler 1975; Gage and Tyler 1981). As can be seen from Fig. 1, almost all of the specimens collected were larger than this size and some were 1.8 mm DD with >20 arm segments. To our knowledge, postlarval ophiuroids of this size have never been recorded in the plankton, excluding the possibility that we were repeatedly sampling a planktonic population. A visual analysis of the stomach contents of a number of individuals revealed the presence of foraminifera, unidentified detritus, and even a polychaete

worm (Fig. 3). This suggests that organisms were eating the particulate material reaching the trap because there is no evidence to date showing that postlarval ophiuroids are able to feed while in their planktonic phase. Mileikovsky (1968) emphasizes that larvae of ophiuroids are limited in their range of dispersal because they cannot remain afloat for long after metamorphosis and because postlarvae lack suitable food conditions in the plankton. However, Strathmann (1974) points out that metamorphosed ophiuroids collected from the plankton exhibit no signs of starvation and argues that maybe further evidence would show that these animals either can feed or do not spend much energy while in the plankton.

The remaining explanation from the increasing size of collected individuals is that they were suspended from the sediment. As already mentioned, such large individuals have never been recorded from plankton samples, but even if this was due to chance, it is very unlikely that these large specimens could be suspended to a height of nearly 500 m. The benthic nepheloid layer, which is caused by particles <20 μm , is about 100 m thick at this site (Lampitt unpubl.), and it is very unlikely therefore that particles as large as the ophiuroids we collected would be suspended a further 400 m above it. Furthermore, specimens in the bottom trap were smaller than those in the top trap, the reverse of what would be expected if appearance in the traps was simply a result of suspension of benthic organisms. If this was the case, one would expect not only greatly enhanced numbers in the bottom trap but also a higher proportion of larger individuals that presumably would be suspended lower in the water column than smaller specimens.

The increase in disk diameter of collected specimens can only sensibly be explained as a consequence of growth within the sediment traps but above the preservative fluid in the collection cups. Adventitious losses of members of this epifaunal population into the preserving solution could be considered random sampling of the population.

The results presented above suggest that there was a major settlement event in mid-May, and from the size distribution of the collected specimens, there is no evidence of a second settlement. We believe that this single cohort settled on the internal walls of the sediment trap cone or, somewhat less likely, on the vertical sides of the baffle or mooring rope. Although ophiuroids lack the suckered tube feet present in many asteroids and echinoids, they are very good climbers and may have been able to live on that surface, despite its smoothness and high inclination angle (70° to the horizontal). Cones of sediment traps are designed with smooth internal surfaces to offer the smallest possible resistance to settling particles by allowing the particles to slide down into the collection cup. The presence of epifauna such as ophiuroids will increase surface roughness and prevent detrital material from reaching the sampling cup. This could create a local environment where POC would be consumed by ophiuroids and possibly by other organisms such as swimmers and bacteria present in the water within the cone but above the preservative (Iturriaga 1979; Gardner et al. 1983). Recovery of Parflux traps is carried out without a sampling cup under the cone and any epifauna remaining on the trap walls at the end of the deployment would be washed off and

lost during recovery. On the assumption that all the specimens on the cone wall had been collected during deployment and none were washed off during recovery, we calculate that up to 0.95% of the surface of the cone would have been covered by the ophiuroids. Although this may seem to be a small proportion of the surface area, up to 37% of the material falling onto the sides of the cone and subsequently sliding down its sides would come into contact with an ophiuroid (see below).

Having established without doubt that growth of the ophiuroid cohort occurred within the trap above the preservative, we can now calculate the demands of this population for organic carbon supplied exclusively by the material falling into the trap. Although it is clearly an underestimate, we can assume for this exercise that all of the specimens clinging to the sides of the cone were collected prior to recovery of the traps. The organic carbon demands of this population can be considered, first, on the basis of that required for growth as measured by the increase in size of the collected individuals and, second, from the expected metabolic demands of the population. Growth was estimated simply as the increase in mean size of specimens collected from one sampling interval to the next. Metabolic demand was estimated from published values of weight-specific respiration, R , across the marine animal kingdom (Mahaut et al. 1995).

$$R = 0.0074C^{-0.24}$$

Body carbon $C = 0.5 \times \text{AFDW}$ and respiratory demand R is expressed as the proportion of body organic carbon per day.

Although there will be large uncertainties in this assessment because the taxonomic range was wide (invertebrates to fish), this provides a rudimentary estimate in the absence of data specific to ophiuroids. An alternative way to estimate the effect of the ophiuroid population on the incoming material is to calculate the proportion of the material falling onto the sides of the cone that will come into contact with an ophiuroid. Once again, we assume that all of the epifaunal specimens fell into a collecting cup at some stage. The number of specimens in the cone thus decreases to zero during the deployment, hence reducing the effect of the population on the detrital material. However, their body size increases, thus enhancing the effect of each individual and counterbalancing to a degree the effect of reducing numbers. A model was constructed that demonstrates the very large potential effect of quite a small population of rather small individuals by intercepting sedimenting particles as they slide down the sides of the collecting funnel.

The average ratio Production: Metabolism was found to be 0.43, a value near to the expected ratio of ~ 0.5 (Humphreys 1979), and this was used to calculate total organic carbon demand (respiration + growth) from methods 1 and 2. Figure 4 shows the organic carbon demand as a percentage of the downward flux based on estimated metabolic rate (method 1) and on measured growth (method 2) and the proportion of the downward flux intercepted by an ophiuroid. The estimates of organic demand agree fairly closely, whereas the proportion of intercepted material is much higher and up to 37%. This does not imply that 37% of the flux

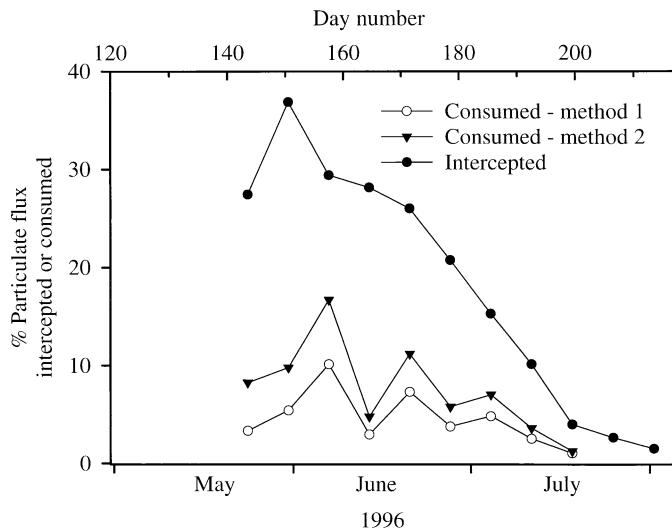


Fig. 4. Potential influence on material entering the top sediment trap in terms of the percentage of the material intercepted or consumed by the population of epifaunal ophiuroids. Consumption is estimated either from the calculated metabolic rate (method 1) or from the increase in weight from one sampling period to the next (method 2) (see text). The percentage of material intercepted by specimens is based on the proportion of material sliding down the sides of the trap funnel that would come in contact with a specimen.

is consumed but that a very large proportion of it comes in contact with ophiuroids and could then be ingested.

We can now consider the implications of these observations for the interpretation of sediment trap data. The specimens living within the cone will have had a demand for organic carbon for both somatic growth and respiration. Consumption for growth should not be considered a direct loss from the settling material because it is retained within the enclosure of the trap. As long as the animals' bodies are included in the flux, and assuming they are all eventually collected in the preservation fluid, the integrated total flux will be unaffected, although some of the flux would be transferred to a subsequent sampling interval. In contrast, metabolic losses would be a direct loss from the material entering the traps as organic carbon is converted into CO_2 . In the present study this amounted to less than 4%.

The serious problem for the sediment trap technique described above will not be experienced in all regions of the ocean. Although ophiuroids are found throughout the marine environment, including shallow and deep water (Piepenburg and von Juterzenka 1994), in the open ocean they are only found in high numbers on the continental slope (Gage and Tyler 1981; Fujita and Ohta 1989, 1990; Shin and Koh 1993). Planktotrophy is a common mode of development for ophiuroids, with growth of the planktonic larvae stimulated by seasonal increases in primary production. Settlement of postlarvae is therefore likely to be an important feature of regions in which brittle stars are abundant (Gage and Tyler 1981; present study). It is therefore in these slope areas that care should be taken in the analysis of sediment trap material.

Postlarval ophiuroids, whenever found in traps, should be considered part of the total downward flux of carbon because

the majority of their body carbon will have been derived from sinking particles normally considered the principal vehicles for POC flux. The losses of organic carbon through remineralization are a direct loss from the primary flux, and in future, results from sediment trap studies on continental slopes should be enhanced by a few percent to take such losses into account. Parflux sediment traps are usually recovered with an open hole at the base of the collection funnel, thus losing epifaunal organisms within the trap. We suggest that in future, this hole should not be left open and that, on recovery of the traps, the water within the cone should be filtered to collect epifaunal organisms that grew inside the trap funnel, the mass of which can then be added to the calculated flux. Furthermore, such sampling would establish the full extent of epifaunal colonization of the internal surfaces of deep-sea sediment traps. We have only gone so far as to demonstrate that the error associated with such colonization is potentially very large.

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References

- BAKER, E. T., H. B. MILBURN, AND D. A. TENNANT. 1988. Field assessment of sediment trap efficiency under varying flow conditions. *J. Mar. Res.* **46**: 573–592.
- BUTMAN, C. A. 1986. Sediment trap biases in turbulent flows: Results from a laboratory flume study. *J. Mar. Res.* **44**: 601–644.
- COALE, K. H. 1990. Labyrinth of doom: A device to minimize the “swimmer” component in sediment trap collections. *Limnol. Oceanogr.* **35**: 1376–1381.
- FUJITA, T., S. AND OHTA. 1989. Spatial structure within a dense bed of the brittle star *Ophiura sarsi* Ophiuroidea: Echinodermata. in the bathyal zone off Otsuchi, Northeastern Japan. *J. Oceanogr. Soc. Jpn. Nihon Kaiyo Gakkai* **45**: 289–300.
- , AND ———. 1990. Size structure of dense populations of the brittle star *Ophiura sarsi* Ophiuroidea: Echinodermata. in the bathyal zone around Japan. *Mar. Ecol. Prog. Ser.* **64**: 1–2.
- GAGE, J. D. P. A. AND TYLER. 1981. Non-viable seasonal settlement of larvae on upper bathyal brittle star *Ophiocten gracilis* in the Rockall Trough Abyssal. *Mar. Biol.* **64**: 153–161.
- GARDNER, W. D. 1980. Field calibration of sediment traps. *J. Mar. Res.* **38**: 41–52.
- , AND M. J. RICHARDSON. 1992. Particle export and resuspension fluxes in the western North Atlantic, p. 339–364. *In* G. T. Rowe and V. Pariente [eds.], *Deep-sea food chains and the global carbon cycle*. Kluwer.
- GARDNER, W. D., K. R. HINGA, AND J. MARRA. 1983. Observations on the degradation of biogenic material in the deep ocean with implications on the accuracy of sediment trap fluxes. *J. Mar. Res.* **41**: 195–214.
- , P. E. BISCAYE, AND M. J. RICHARDSON. 1997. A sediment trap experiment in the Vema Channel to evaluate the effect of horizontal particle fluxes on measured vertical fluxes. *J. Mar. Res.* **55**: 995–1028.
- HANSELL, D. A., AND J. A. NEWTON. 1994. Design and evaluation of a “swimmer”-segregating particle interceptor trap. *Limnol. Oceanogr.* **39**: 1487–1495.
- HARGRAVE, B. T., AND N. M. BURNS. 1979. Assessment of sediment trap collection efficiency. *Limnol. Oceanogr.* **24**: 1124–1136.
- HEDGES, J. I., AND J. H. STERN. 1984. Carbon and nitrogen determinations of carbonate-containing solids. *Limnol. Oceanogr.* **29**: 657–663.
- HENDLER, G. 1975. Adaptational significance of the patterns of ophiuroid development. *Am. Zool.* **15**: 691–715.
- HUMPHREYS, W. F. 1979. Production and respiration in animal populations. *J. Anim. Ecol.* **48**: 427–453.
- ITURRIAGA, R. 1979. Bacterial activity related to sedimenting particulate matter. *Mar. Biol.* **55**: 157–169.
- KNAUER, G. A., D. M. KARL, J. H. MARTIN, AND C. N. HUNTER. 1984. In situ effects of selected preservatives on total carbon, nitrogen and metals collected in sediment traps. *J. Mar. Res.* **42**: 445–462.
- LAMPITT, R. S., AND A. N. ANTIA. 1997. Particle flux in deep-seas: Regional characteristics and temporal variability. *Deep-Sea Res. I* **44**: 1377–1403.
- MAHAUT, M. L., M. SIBUET, AND Y. SHIRAYAMA. 1995. Weight-dependent respiration rates in deep-sea organisms. *Deep-Sea Res.* **42**: 1575–1582.
- MICHAELS, A. F., M. W. SILVER, M. M. GOWING, AND G. A. KNAUER. 1990. Cryptic zooplankton “swimmers” in the upper ocean sediment traps. *Deep-Sea Res.* **37**: 1285–1296.
- MILEIKOVSKY, S. A. 1968. Some common features in the drift of pelagic larvae and juvenile stages of bottom invertebrates with marine currents in temperate regions. *Sarsia* **34**: 209–216.
- PIEPENBURG, D., AND K. VON JUTERZENKA. 1994. Abundance, biomass and spatial distribution patterns of brittle stars Echinodermata: Ophiuroidea. on the Kolbeinsey Ridge north of Iceland. *Polar Biol.* **14**: 185–194.
- SHIN, H. C., AND C.-H. KOH. 1993. Distribution and abundance of ophiuroids on the continental shelf and slope of the East Sea Southwestern Sea of Japan, Korea. *Mar. Biol.* **115**: 393–399.
- STRATHMANN, R. R. 1974. Introduction to function and adaptation in echinoderm larvae. *Thalassia Jugosl.* **10**: 321–339.
- YU, E.-F., R. FRANCOIS, M. P. BACON, S. HONJO, A. P. FLEER, AND S. J. MANGANINI. 1991. Trapping efficiency of bottom-tethered sediment traps estimated from the intercepted fluxes of ²³⁰Th and ²³¹Pa. *Deep-Sea Res. I* **48**: 865–889.

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