

The quantitative estimation of the deep-sea megabenthos; a new approach to an old problem

Megabenthos Quantitative-sampling Bottom photographs Odometer

Mégabenthos Échantillonnage quantitatif Photographie du fond Odomètre

A. L. Rice, R. G. Aldred, E. Darlington, R. A. Wild. Institute of Oceanographic Sciences, Wormley, Godalming, Surrey GU8 5UB, UK.

Received 9/4/81, in revised form 15/6/81, accepted 29/6/81.

ABSTRACT

The abundance of the benthic megafauna in the deep sea is difficult to measure. Manned submersibles probably offer the best means of obtaining such information at present, but because of their limited range and availability most quantitative estimates will continue to be based on data from towed gears. Such gears have in the past been notoriously unreliable, both because they tend to fish inconsistently and because the distance covered is difficult to measure accurately. This paper presents results obtained using an epibenthic sledge fitted with an odometer wheel which is acoustically monitored on the ship during the progress of the haul. The resulting density estimates for several taxa show an encouraging degree of agreement with those based on simultaneously obtained bottom photographs. Some organisms, particularly amongst the sessile forms, are not sampled adequately by the sledge and there is evidence that the odometer may under-estimate the distance fished. Nevertheless, the system seems to be capable of providing more reliable quantitative samples than those hitherto available.

Oceanol. Acta, 1982, 5, 1, 63-72.

RÉSUMÉ

L'estimation quantitative du benthos profond : une nouvelle approche d'un vieux problème.

Dans les zones abyssales, l'estimation de l'abondance de la mégafaune benthique est difficile à réaliser. La solution idéale semble reposer sur l'observation directe à partir d'un submersible habité. Cependant, cette technique est lourde et limitée dans l'espace. Aussi, pendant de nombreuses années encore, ces mesures continueront à être effectuées par des prélèvements réalisés par des engins tractés à partir de navires de surface. Précédemment ces appareils ont apporté des résultats inexacts du fait de leur comportement aberrant sur le fond, et de la difficulté à mesurer précisément la longueur du trait. Le présent travail expose les résultats obtenus en couplant une roue odométrique dont le fonctionnement est contrôlé par acoustique depuis le navire de surface, à une drague épibenthique. Les estimations de densités qui résultent de cette étude pour plusieurs taxons concordent assez bien avec les données obtenues par observations photographiques. Cependant, certains organismes, spécialement pour les formes sessiles, ne sont pas prélevés régulièrement par la drague. Il semble aussi que la roue odométrique sous-estime la surface échantillonnée. Malgré tout, on peut dire que ce système permet un échantillonnage quantitatif plus fiable que les autres techniques jusqu'alors employées.

Oceanol. Acta, 1982, 5, 1, 63-72.

INTRODUCTION

One of the most pressing problems in deep-sea benthic ecology is the quantitative estimation of those organisms which are too large and too sparsely distribution to be collected adequately by corers and grabs. Prior to the last decade or so, this problem did not seem to be particularly important, for the conventional view of the deep-sea ecosystem as one supplied by a fine rain of small food particles falling from the overlying water masses carried the implication that such a food source would primarily support the small creatures of the meiofauna and macrofauna. In comparison with these constituents, the biomass of the megafauna, loosely defined as those organisms which are visible on *in situ* photographs, was expected to be relatively insignificant (see, for instance, Grassle, Sanders, 1973). However, recent work with baited deep-sea cameras (Isaacs, 1969; Hessler et al., 1972; Isaacs, Schwartzlose, 1975a and b) and traps (Paul, 1973; Shulenberger, Hessler, 1974; Shulenberger, Barnard, 1976; Hessler et al., 1978; and Thurston, 1979) has demonstrated the existence of a previously unsuspected large and mobile element in the near bottom fauna, while estimates of the megafaunal biomass at slope depths based on photographs taken from a submersible suggest that it is comparable with that of the macrofauna (Haedrich, Rowe, 1977). Submersibles capable of providing this type of information are restricted both in their availability and range, and most work on the deepsea megabenthos will continue to be based on data and samples obtained with towed gear such as photosleds, sledges and trawls.

Aldred et al. (1976) stressed the difficulties associated with obtaining uncontaminated quantitative samples with towed gear and described an acoustically monitored opening and closing epibenthic sledge which seemed to overcome at least some of them. The initial trials with this sledge, and considerable subsequent experience, confirmed that it collects benthic samples almost completely uncontaminated by mid-water organisms, while the use of an acoustic pinger to monitor its behaviour provides more information about its performance during a haul than is usually available with similar towed gear. Nevertheless, photographs obtained from a 35 mm time lapse camera mounted on the sledge frame emphasized the non-quantitative nature of the samples obtained, the photographs almost always indicating higher densities of megabenthic organisms than those deduced from the net catches (Rice et al., 1979 and Aldred et al., 1979). The main problem seems to be the accurate determination of the length of tow accomplished with the gear in contact with the sea-bed and fishing effectively. Estimates based on the distance travelled by the ship during a haul must at best be very rough approximations of the distance fished even when variations in the amount of wire out and the bottom topography are taken into account. A significant improvement has been the rather sophisticated use by French scientists of direct and reflected signals received from an acoustic beacon mounted on or close to the gear to determine accurately its position when it reaches and leaves the sea-bed (see Laubier et al., 1971). However, no matter how accurate such determinations are, the population densities calculated from them must be minimal since any towed gear fished at great depth is unlikely to sample consistently and remain in contact with the bottom throughout a haul (see Dahl *et al.*, 1976). Our early attempts to overcome these problems were based on the use of a measuring wheel attached to the sledge and fitted with a mechanical counting device to record revolutions as the wheel rolled across the sea-bed. Such wheels have been used on various dredges and trawls in the past, but they have usually suffered from two main drawbacks; first the problem of separating revolutions occurring in mid-water from the total count, and second, the fact that the information about distance fished is obtained only after the gear returns to the surface.

The importance of obtaining information on the behaviour of gear during the progress of a haul was appreciated by Holme and Barrett (1977), who fitted their television and photographic sledge, for use in shallow water, with a measuring wheel producing an audible electronic bleep via the towing cable with each completed revolution. A similar system has been developed to solve the peculiar problems of deep-water work, transmitting the measuring wheel signals back to the ship via the acoustic beacon already used to monitor other aspects of the behaviour of the gear. This paper describes this system and provides evidence from simultaneously obtained bottom photographs which indicate that the sledge does, indeed, collect quantitative samples of at least some elements of the benthic fauna.

The sledge (Fig. 1)

The original IOS (Institute of Oceanographic Sciences) epibenthic sledge was described in detail by Aldred et al. (1976). It consisted of a steel frame, provided with two broad skids, to the back of which was attached a single net with a rectangular mouth opening about 2.3 m wide by 0.6 m high. A 35 mm IOS camera (see Collins, in press), taking photographs every 15 or 30 seconds, was mounted within the net frame directed forwards and downwards at an angle of 14° so that its optical axis impinged upon a flat sea-bed at about 1.5 m ahead of the sledge. Because of the acute camera angle, only about 3/4of each frame was considered usable for assessing megafaunal densities, this portion covering about 2.6 m² of sea-bed (see Rice et al., 1979 and Aldred et al., 1979). Apart from the addition of the odometer (see below), the results reported here were obtained from two successive modifications of this basic gear. First, the single net with a graded mesh was replaced by three separate nets, a central one with a 1.0 mm mesh throughout, flanked on either side by a coarse net with a 4.5 mm mesh. Second, since 1978 a suprabenthic net has been added above the original nets to collect near-bottom plankton. This second modification is described in the appendix, but its main relevance to this paper is that it involved increasing the height of the sledge frame to 1.22 m, enabling the camera to be raised and orientated more nearly vertical (at an angle of about 30° to the horizontal). This camera orientation has considerably improved the resolution of the photographs and has therefore reduced the minimum

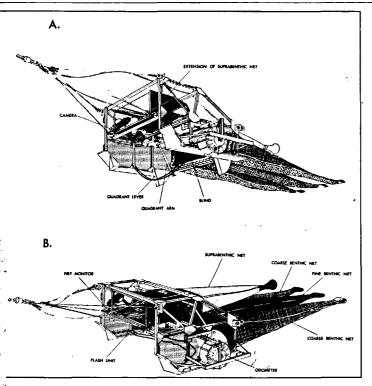


Figure 1

The current version of the IOS epibenthic sledge: (A) attitude adopted in mid-water with the quadrant levers lowered and the net mouths occluded; (B) attitude adopted on the sea-floor with the quadrant levers raised and the nets open.

size of organism which can be counted on them with confidence. Nevertheless, the distal one quarter of the frame is still not sufficiently well illuminated and counts are therefore restricted to the proximal three quarters, covering an area of about 1.0 m^2 (see Fig. 4 c).

The odometer

きょう どう

1

S. States

Ð

12-14-1

- Aller

The rim of the wheel is made from a 150×60 mm strip of "natural" polythene formed into a circle with a circumference of 1.5 m and with the grip increased by 12 equally spaced 25 mm high treads of aluminium angle. The rim is supported by 25 mm diameter polypropylene spokes connecting it to a free-flooding hub of 12.5 mm thick rigid PVC with an internal diameter of 150 mm. The hub revolves on a stainless steel spindle which acts as a pressure housing for a wire wound potentiometer driven via a magnetic coupling and gear box so that 200 revolutions of the wheel (300 m over the ground) result in one complete sweep of the potentiometer. The

potentiometer output is fed into the acoustic beacon to produce a signal with a variable delay relative to the reference signal. One complete potentiometer sweep results in a corresponding sweep on the facsimile recorder, so that revolutions of the wheel can be counted directly from the record during the haul itself. Since the other monitoring signals indicate when the net is horizontal and the blind is open, that is on the sea-bed and capable of fishing (see Aldred *et al.*, 1976), any revolutions of the wheel recorded in the absence of these other signals are readily identified as occurring in midwater and can therefore be disregarded in calculations of distance fished on the bottom.

The ends of the spindle are suspended by rigid side-arms from a bracket protruding to one side of the sledge frame. The side arms are pivoted on the bracket so that they can swing backwards from the vertical, thus raising the wheel assembly, but not forwards. When the side-arms are vertical the lower margin of the wheel extends about 10 cm beneath the sledge frame skids.

RESULTS

The odometer has now been used during three cruises, in conjunction with the old sledge on Discovery cruise 92 in April 1978, and with the new two-tier sledge on Challenger cruise 506 in July 1979 and Discovery cruise 105 in September 1979. However, because of malfunctions either of the wheel or the camera system, only 14 hauls have so far been made with both systems functioning correctly. Moreover, in 5 of these the photographs contain insufficient megafaunal animals to provide reliable density estimates. In each of the remaining cases (Table 1), the identifiable megabenthic organisms visible on each frame were counted, and mean densities were calculated. Similarly, from the calculated area sampled based on the odometer reading and the width of the nets, a second mean density estimate was obtained from the catch using the samples from either the fine net alone or from all three nets, depending upon the size of organisms concerned. The comparison of these two sets of density estimates forms the basis for assessing the sampling efficiency of the gear.

Since the sizes, numbers and life-styles of the organisms used in these computations varied so much from station to station, the hauls are dealt with individually or in small related groups.

Table 1

Details of the epibenthic sledge hauls used in this paper to compare the densities of megabenthic organisms calculated from the photographs and from the catches.

Ship	Haul No.	Date	Position	Depth	Distance fished
Discovery	9756 # 9	13/4/1978	49°47.1N:14°1.5W	4 039-4 069 m	546 m
Discovery	9756 # 14	15/4/1978	50°4.0N:13°55.6W	3 680-3 697 m	631 m
Discovery	9779 #1	24/4/1978	49°22.3N:12°49.1W	1 398-1 404 m	837 m
Challenger	50609 # 1	8/7/1979	51°39.7N:14°16.5W	400 m	300 m
Challenger	50610 # 1	8/7/1979	51°26.5N:13°24.1W	980 m	331 m
Discovery	10111 # 8	9/9/1979	49°32.6N : 13°7.1W	1 630-1 640 m	665 m
Discovery	10112 # 2	9/9/1979	50°25.2N:13°20.3W	2 640-2 650 m	310 m
Discovery	10112 # 3	10/9/1979	50°19.1N:13°25.8W	2 740-2 755 m	570 m
Discovery	10113 # 1	10/9/1979	50°16.1N:13°31.6W	2 755-2 760 m	550 m

Table 2

Density data for the megabenthic organisms taken in haul 9779 #1 at 1400 m in the Porcupine Sea-Bight.

		Photograph data $(94 \text{ frames} = 244 \text{ m}^2)$			Catch data (area fished 1917 m ²)						
	Species	A	Maga dansita	Animals collected				Mean – density			
Species			Mean density (m ⁻²)	LHS	Centre	RHS	Total	(m^{-2})	6		
Benthogone	rosea	24	0.098 ± 0.46 (*)	78	55	85	218	0.114			
Phormosom		17	0.070 ± 0.034 (*)	52	38	51	141	0.074			
Laetmogone		4	0.016	12	6	27	45	0.023			
Bathyplotes	natans	2	0.008	17	4	5	26	0.014			
Zoroaster f		1	0.004	4	1	12	17	0.009			
Coryphaeno		1	0.004		-	44 S	13	0.007			
Lepidion eq		3	0.012	25	722	121	3	0.002			
Hoplosteth		2	0.008		-	70	5	0.003			
Coelorinchu		1	0.004		-		2	0.001			

(*) where sufficient data are available the photograph densities are given together with twice the standard error of the means.

Haul 9779 #1

The photographs obtained during this haul contained a variety of megabenthic animals including holothurians, echinoids, asteroids and fishes (see Table 2 and Fig. 2).

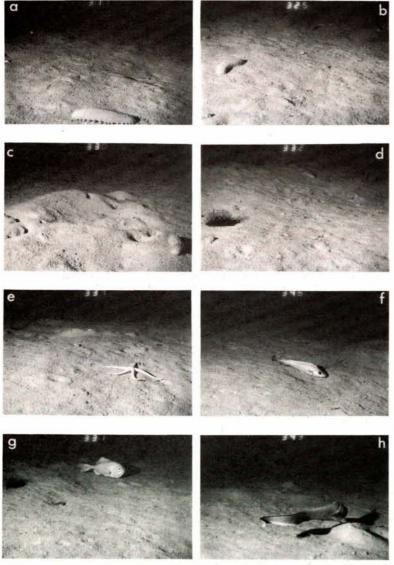


Figure 2

Examples of photographs obtained during haul 9779 #1 (see Table 1): (ac) Benthogone rosea; (d) Phormosoma placenta; (e) Zoroaster fulgens; (f) Lepidion eques; (g) Hoplostethus atlanticus and Phormosoma; (h) Coryphaenoides sp. According to the odometer the sledge sampled an area about eight times greater than that covered by the usable photographs so that if the megabenthic animals had been both uniformly distributed and efficiently collected the catches should have contained about eight specimens for each one photographed. However, most of the species were uncommon both in the photographs and in the catches, and while the central net caught consistently fewer animals than the outer ones the numbers contained in the coarse nets were both unequal and inconsistent, indicating that the animals were by no means evenly distributed. Understandably, therefore, there seems to be no consistent relationship between the densities based on the photographs and those based on the catches in these cases, the photographs indicating the higher density for the fishes Lepidion eques (Gunther), Coelorinchus occa (Goode and Bean) and Hoplostethus atlanticus Collett, while the reverse is true for Coryphaenoides spp., the holothurians Laetmogone violacea Theel and Bathyplotes natans (M. Sars) and asteroid Zoroaster fulgens Wyville Thomson. Moreover, as in many other hauls, a number of megabenthic species were represented by small numbers in the catches but were absent from the photographs. In particular, 25 specimens of the eel Synaphobranchus kaupi Johnson and seven specimens of the asteroid Plutonaster bifrons (Wyville Thomson) were captured but neither species was photographed.

Two species, however, the holothurian Benthogone rosea Koehler and the echinothurian Phormosoma placenta Wyville Thomson, were common in both the photographs and the catches. The distribution of the catch between the three nets suggests that for both species the fine net had fished only about 75-80% as efficiently as the coarse nets, but while the density estimates based on the catches were somewhat higher than those based on the photographs, they fall well within the 95% confidence limits of the latter (Table 2).

Hauls 50609 #1 and 50610 #1

The photographs from both of these hauls were dominated by the pennatulid *Kophobelemnon stelliferum* (O. F. Muller) (Fig. 3 *a-e*), with those from station 50609 indicating a mean density of more than 2.0 m^{-2} . The catches, however, contained very few pennatulids

b

indicating mean densities ten to one hundred times lower (see Tables 3 and 4). Smaller numbers of the cerianthid anemone Cerianthus multiplicatus Carlgren were also obtained in each haul (Fig. 3g, h), but the catches again indicated much lower densities; indeed, not a single Cerianthus was taken in haul 50610#1 whereas the photographs indicate an expected catch of about sixty. Taken alone these results suggest that the sledge had fished very inefficiently during its passage across the seabed. However, the photographs from station 50610 also contain a variety of additional megafaunal organisms, including other coelenterates, molluscs, echinoderms and fishes (Fig. 3 b-f, 5 e-h and Table 4) for all of which there is a rather close agreement between the photograph and catch densities. With the possible exception of Phormosoma placenta these results individually are not particularly convincing since the organisms concerned are uncommon in both the photographs and the catches. In combination, however, they strongly suggest that the sledge sampled these species efficiently and that the dearth of pennatulids and cerianthids in the catches must therefore have resulted from its inability to collect these fairly deeply "rooted" organisms.

Haul 10111 #8

The 161 frames obtained during this haul, each covering a usable area of 1.0 m^2 , were dominated by the elasipod holothurians *Elpidia* sp., ranging from 5 to 10 mm in total length (Fig. 4g, h), and *Benthogone rosea* Koehler, ranging from 150 to 200 mm in total length.

The photographs contained a total of 280 *Elpidia*, with individual frames containing a maximum of eight,

Table 3

Density data for two coelenterates taken in haul 50609 # 1 at 400 m in the Porcupine Sea-Bight.

		graphic data s each of 1 m ²)	Catch data (area fished 687 m ²)			
×	Animals photo- graphed	Mean density (m ⁻²)	Animals	Mean density (m ⁻²)		
Kophobelemnon stelliferum	129	2.26 ± 0.13	9	0.013		
Cerianthus multiplicatus	10	0.17 ± 0.08	2	0.003		

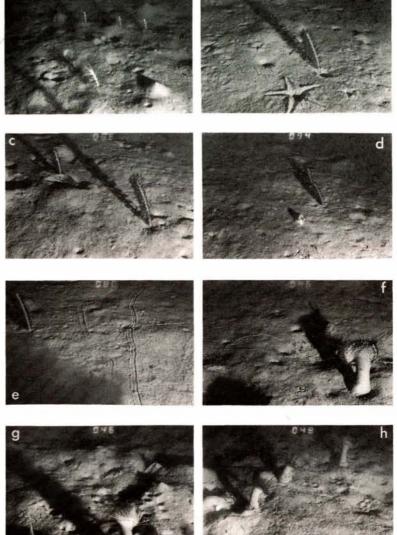


Figure 3

a

Examples of photographs obtained during hauls 50609 # 1 (a, g and h) and 50610 # 1 (b-f) (see Table 1): (a) juvenile Kophobelemnon stelliferum; (b) K. stelliferum and an asteroid feeding depression; (c) K. stelliferum and Lepidion eques; (d) K. stelliferum and Galeodea rugosa; (e) K. stelliferum and Galeodea trails; (f) Phelliactis hertwigi and Galeodea trails; (g and h) Cerianthus multiplicatus.

Table 4

Density data for the megabenthic organisms taken in haul 50610#1 at 980m in the Porcupine Sea-Bight.

	Photographic data (53 frames each of 1 m ²)			Catch data (area fished 751 m ²)					
		Mean		Animals	Mean				
100 04	Animals of photographed (density (m ⁻²)	LHS	Centre	RHS	Total	- density (m ⁻²)		
Kophobelemnon stelliferum	27	0.51 ± 0.11	4	8	3	15	0.020		
Cerianthus multiplicatus	4	0.08 ± 0.036	-	-	-	0	-		
Phelliactis hertwigi	1	0.02	8	4	4	16	0.021		
Galeodea rugosa	1	0.02	5	3	5	13	0.017		
Phormosoma placenta	8	0.15 ± 0.06	32	36	43	111	0.148		
Echinus affinis	4	0.08 ± 0.045	24	24	36	84	0.112		
Laetmogone violacea	4	0.08 ± 0.036	22	17	22	61	0.081		
Lepidion eques	1	0.02	-		100	10	0.013		
Synaphobranchus kaupi	1	0.02	-	-	-	21	0.028		

Table 5

Density data for the holothurians Elpidia sp. and Benthogone rosea taken in haul 10111 #8 in Porcupine Sea-Bight.

		ograph data les each of 1 m ²)	Catch data (area fished by all nets 1 52			m ⁻²)	
	A	Mean		Animals	Mean		
	Animals photograph	density ed (m ⁻²)	LHS	Centre	RHS	Total	density (m ⁻²)
Elpidia sp.	278	1.74 ± 0.26	568	1 009	284	1851	1.996 (*)
Benthogone (rosea 10	0.06 ± 0.38	60	25	62	147	0.096

(*) Because the Elpidia were too small to be retained efficiently by the coarse outer nets this figure is based on the catch of the centre net only and on one third of the estimated total area fished.

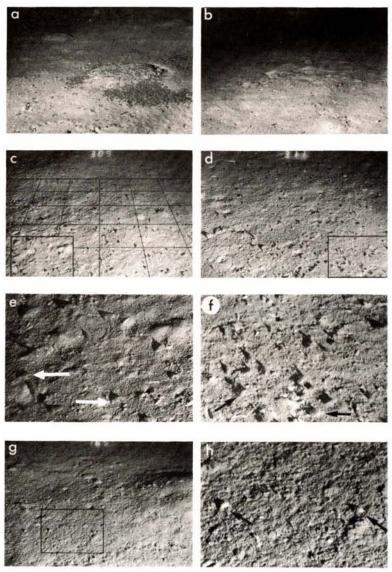


Figure 4

Examples of photographs obtained during hauls 9756 # 14 (a, b), 10113 # 1 (c-f) and 10111 # 8 (g, h) (see Table 1): (a) dense aggregations of jwenile holothurians, Kolga hyalina; (c, d) less concentrated, and therefore less easily visible, K. hyalina, (e, f) enlargements of the outlined areas of (c) and (d) respectively, with some of the holothurians arrowed; (g) photograph including seven Elpidia; (h) enlargement of outlined area of (g) with two Elpidia specimens arrowed. The usable area in photograph (c) is marked out in a grid of 20×20 cm squares.

indicating a mean density of $1.74 \pm 0.26 \text{ m}^{-2}$. Since the animals were too small to have been retained efficiently by the coarse nets the catch data from only the fine central net were used, indicating a mean density of 2.0 m^{-2} , that is just within the 95% confidence limits of the density estimated from the photographs.

However, this comparison is complicated by the results obtained for Benthogone. Only ten individuals of these larger holothurians were photographed, indicating a mean density of $0.062 \pm 0.38 \text{ m}^{-2}$. Since none of the Benthogone entering the nets could have been lost by passing through the meshes the catch data for all three nets were used, indicating a mean density of 0.096 m⁻² (Table 5). Like the Elpidia result, this figure is higher than the photograph density, but is again just within the 95% confidence limits. But as in the hauls dealt with above, the Benthogone were not collected equally by all three nets, the coarse nets containing more than twice as many as the fine net. This suggests that the fine net may not filter efficiently throughout a haul and that some organisms which lay in its path may be pushed aside and enter the coarse nets instead. Assuming that the Benthogone were distributed uniformly with respect to the sledge width, the net catches suggest that the central net fished effectively for only about half of the total path covered during the haul. If this conclusion applies equally to the Elpidia, the true density of these small holothurians should be about twice that estimated from the catch of the central net, that is about $4.0 \,\mathrm{m}^{-2}$, and much higher than the density indicated by the photographs (see also below).

Hauls 9756 #9, 9756 #14 and 10113 #1

The photographs obtained during these hauls, taken in depths ranging from about 2 700 to a little over 4 000 m, contained very few megabenthic animals other than juveniles of the elasipod holothurian Kolga hyalina Danielssen and Koren. In the two hauls obtained at station 9756 the holothurians ranged from about 3.0 to about 7.0 mm in length and were very strongly aggregated (see Billett and Hansen, in prep.), the numbers recognized in single frames ranging from two to more than 700 (Fig. 4a, b). Despite this strong aggregation, however, the density estimates based on the catches and on the photographs were remarkably similar, with both techniques indicating mean densities of between about 35 and 50 m^{-2} (see Table 6). At station 10113, on the other hand, the animals were rather larger, mainly ranging in length from 6 to 9 mm, they were much less abundant than in the earlier hauls and were less strongly aggregated, with individual frames containing a maximum of about 70 holothurians (Fig. 4e, f). Being larger, the holothurians should have been more readily recognizable in the photographs from this haul than in those from station 9756, while the presence of less strong

aggregations might have been expected to result in an even closer agreement between the densities indicated by the photographs and the catch. Nevertheless, the catch data indicated a much higher density than did the photographs, falling outside the 95 % confidence limits of the latter (Table 6). Moreover, all of these catch densities were based on the contents of the central fine net only. and there is no reason to believe that this net fished any more efficiently during these hauls than during those in which the relative effectiveness of the three nets could be checked from the distribution of the catches of the larger megabenthic species. Consequently, the catches of Kolga, and therefore the estimated densities, should probably have been considerably higher than those recorded and, like the Elpidia catch densities from station 10111, significantly higher than those based on the photographs.

Hauls 10112 # 2 and 10112 # 3

The catches from both of these hauls contained large numbers of the asteroid Hymenaster sp., again mainly in the outer nets, though the catches of all three nets were used to estimate the densities since the smallest animals collected were about 15 mm in diameter. In both hauls the densities estimated from the catches were higher than those derived from the photographs and were very close to the 95% confidence limits of the latter (see Table 7). But whereas the smallest Hymenaster visible in the photographs measured about 40 mm across the arm tips, about one third of the animals captured in each of the hauls were smaller than this, suggesting that the true density was underestimated using the photographs because the small individuals were not visible. Indeed, when the densities are calculated using only those animals in the catches greater than 40 mm in diameter the agreement with the photograph densities is remarkably

Figure 5

Examples of photographs obtained during hauls 10112 # 2 (a-d) and 50610 # 1 (e-h) (see Table 1): (a-d) specimens of Hymenaster sp. (arrowed): (e) Laetmogone violacea and Kophobelemnon stelliferum; (f) Phormosoma placenta and L. violacea; (g) Echinus affinis and K. stelliferum; (h) E. affinis, P. placenta and L. violacea trail with faecal casts.

Table 6

Density data for the holothurian Kolga hyalina from three epibenthic sledge hauls in the Porcupine Sea-Bight.

	Haul		Photogra	aph data		Cate	e net)		
		Frames used	Area (m ²)	No. of animals	Mean density (m ⁻²)	Area fished (m ²)	No. of animals	Mean density (m ⁻²)	
	9756 # 9	45	42.75 (*)	1455	34 ± 30	417	14623	35.2	
	9756 # 14	46	43.7 (*)	2186	50 ± 35	481	21522	44.9	
	10113 # 1	66	66	614	9.3 ± 4	419	6419	15.3	

(*) Because of the small size of the holothurians and the low camera-angle used in these hauls, restricted areas of the photographs were used in several cases.

Table 7

Density data for Hymenaster sp. taken in hauls 10112#2 and 10112#3 in the Porcupine Sea-Bight.

	Photograph data				Catch data						
Haul					Ani	mals colle	ected	Mean density			
	No. of frames (each 1 m ²)	Animals photographed	Mean density (m ⁻²)	Area fished (m ²)	LHS	Centre	RHS	All animals (m ⁻²)	Animals >40 mm diam. (m^{-2})		
10112 # 2 10112 # 3	52 91	12 12	$\begin{array}{c} 0.230 \pm 0.150 \\ 0.132 \pm 0.070 \end{array}$	710 1 305	90 119	64 26	123 114	0.390 0.198	0.28 0.13		

close (see Table 7). The smallest Hymenaster recognized on the photographs are so clearly visible (see Fig. 5 *a*-*d*) that it seems unlikely that smaller animals would have been undetected if they had been present on the surface of the sediment. A more plausible explanation of the discrepancies between the photograph densities and those based on the total catches is that the smallest Hymenaster were buried beneath the sediment surface and were therefore collected but not photographed.

DISCUSSION AND CONCLUSIONS

Towed trawls and dredges have generally been assumed to under-estimate the densities of benthic organisms because of their failure to fish efficiently throughout their presumed passage across the sea-bed. Before the addition of the measuring wheel to the epibenthic sledge used in this study, density estimates based on the catches were consistently lower than those based on the simultaneously obtained photographs (Aldred et al., 1979) thus supporting this premise and suggesting that the area effectively fished was being over-estimated. Now that the fishing distance is measured with the wheel this no longer seems to be consistently true. For while there is often an encouraging degree of agreement between the densities estimated by the two techniques, the hauls examined in this paper include some examples of densities based on the catches which are higher than those based on the photographs and others which are lower.

The photographic technique will produce underestimates of abundance if the organisms concerned are indiscernible on the photographs, either because they are too small, as was probably the case with the holothurians Kolga and Elpidia, or because they are buried within the sediment, as in a proportion of the Hymenaster population. Similarly, density estimates based on the catches are likely to be low if the sledge does not collect the animals effectively, either because it does not penetrate sufficiently deeply into the sediment, as in the case of the pennatulids and the cerianthids, or because the nets become clogged and no longer filter efficiently. The sledge will also, of course, under-estimate the abundance of the very mobile benthopelagic forms such as many of the fishes and some crustaceans because of their ability to take evasive action. The quantitative estimation of this highly mobile element of the nearbottom megafauna remains an unsolved problem, although progress will perhaps be made in the near future using acoustic techniques (see, for instance, Wishner, 1980) and very large nets (K. L. Smith, pers. comm.).

It is more difficult to envisage how either the photographs or the sledge catches could produce over-estimates of abundance, although this would be true of the catch estimates if the odometer failed to operate properly. A major malfunction of the odometer should be detectable from a combination of the Mufax and the photographic records, for if the wheel stops while the sledge continues to fish, the camera will photograph successively different portions of the sea-bed. A less dramatic odometer fault, for instance if it lost traction and skidded slightly and more or less continuously during its passage across the soft sediment, would be more difficult to detect and there is some indication in the results that this may, indeed,

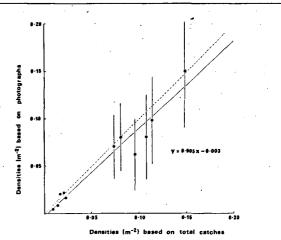
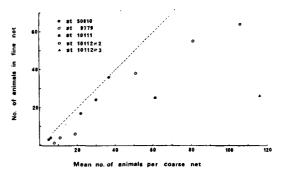


Figure 6

Relationship between the estimated densities based on the catches and the photographs for those organisms thought to have been sampled adequately by both techniques (see text). The vertical lines indicate twice the standard error on either side of the mean for those cases in which the data warrant this. The regression line (solid) and the line of equal value (broken) are included.

have occurred. In Figure 6 the densities based on the total catches are plotted against those based on the photographs for those organisms which appear to have been sampled efficiently by both techniques, that is excluding the cerianthids, the pennatulids, *Hymenaster*, the small holothurians and the fishes. There is a close agreement between the techniques and, in view of the large standard errors, the differences between them are not statistically significant. Nevertheless, the regression line suggests that the catch densities exceed the photographic densities, which are assumed to be the correct ones, by an average of about 10%.

This result would be expected if the odometer underestimates the distance fished by about one tenth, while the sledge captures all of the organisms in its path. But the fine central net, at least, is clearly not perfectly efficient since it catches significantly fewer of the large organisms than the outer nets (see Fig. 7). Similarly, the sledge as a whole is probably not totally efficient but pushes a proportion of the potential catch ahead of itself or to either side. The density estimates based on the catches are therefore subject to two antagonistic errors, neither of which are at present quantifiable. For some of the larger organisms these errors seem to be approximately equal, resulting in density estimates which





Relationship between the fine and coarse net catches of those organisms retained effectively by both. The coarse net catches are the means of those of both outer nets in each haul. Although there is a great deal of variation between hauls, the relative efficiences of the two types of net seem to be fairly consistent within a single haul. are very similar to those calculated from the photographs. But the estimated densities for the smaller organisms, based entirely on the catches of the centre net, are also as high or even higher than those based on the photographs. Unless the centre net is relatively more efficient at capturing these smaller organisms than the larger ones, and there is no evidence to suggest that this is so, then its catches should have been considerably higher and the densities based on the photographs. This suggests that the photographic technique seriously underestimates the density of small organisms, presumably because they are difficult to see.

In summary, the system described here still has serious shortcomings as a quantitative sampler of the megabenthos, both because the odometer probably does not measure the distance fished accurately and because the nets do not filter efficiently. Moreover, some groups of organisms are not collected effectively by the sledge because of their ability to evade capture. Nevertheless, despite these problems the catch and photograph densities for several groups are remarkably similar, indicating that the sledge is capable of providing quite reliable quantitative samples. With the continued use of the camera to provide a check on the overall performance of the gear, we hope that the IOS epibenthic sledge will provide better estimates of the abundance of the deep megabenthos than have hitherto been available from any towed sampler.

Acknowledgements

We are grateful to many colleagues at IOS and to the officers and crews of the research vessels *Discovery* and *Challenger* for their assistance at sea. Our thanks are also due to Drs M. Grasshoff, Forschungsinstitut Senckenberg, Frankfurt, K. Riemann-Zürneck, Institut für Meeresforschung, Bremerhaven, and J. D. Taylor, British Museum of Natural History, London, for identifying material for us.

		·	\$
REFERENCES	٠.		

Aldred R. G., Wild R. A., 1979. An improved cod-end system for midwater nets, J. Plankton Res., 1, 187-189.

Aldred R. G., Thurston M. H., Rice A. L., Morley D. R., 1976. An acoustically monitored opening and closing epibenthic sledge, *Deep-Sea Res.*, 23, 167-174.

Aldred R. G., Riemann-Zürneck K., Thiel H., Rice A.L., 1979. Ecological observations on the deep-sea anemone Actinoscyphia aurelia, Oceanol. Acta, 2, 4, 389-395.

Baker A. de C., Clarke M. R., Harris M. J., 1973. The NIO combination net (RMT1+8) and further developments of rectangular midwater trawls, J. Mar. Biol. Assoc. UK, 53, 167-184.

Billett D. S. M., Hansen B. (in press.). Abyssal aggregations of Kolga hyalina Danielssen and Koren (Echinodermata, Holothuroidea) in the North-East Atlantic: a preliminary report, Deep-Sea Res.

Collins E. P. (in press). Recent developments in deep-sea photography at IOS, Proceedings Symposium on the engineering and scientific applications of underwater photography, Woods Hole, April 1980, Mar. Sci. Int., Woods Hole, Massachusetts.

Dahl E., Laubier L., Sibuet M., Stromberg J.-O., 1976. Some quantitative results on benthic communities of the deep Norwegian Sea, *Astarte*, 9, 61-79.

Grassle J. F., Sanders H. L., 1973. Life histories and the role of disturbance, Deep-Sea Res., 20, 643-659.

Haedrich R. L., Rowe G. T., 1977. Megafaunal biomass in the deep-sea, Nature, London, 269, 141-142.

Hessler R. R., Isaacs J. D., Mills E. L., 1972. Giant amphipods from the abyssal Pacific Ocean, *Science*, NY, 175, 636-637.

Hessler R. R., Ingram C. L., Yayanos A. A., Burnett B. R., 1978. Scavenging amphipods from the floor of the Philippine Trench, *Deep-Sea Res.*, 25, 1029-1047.

Holme N. A., Barrett R. L., 1977. A sledge with television and photographic cameras for quantitative investigation of the epifauna on the continental shelf, J. Mar. Biol. Assoc. UK, 57, 391-403.

Isaacs J. D., 1969. The nature of oceanic life, *Sci. Am.*, 221, 146-162. Isaacs J. D., Schwartzlose R. A., 1975 *a*. Active animals of the deep-sea floor, *Sci. Am.*, 233, 84-91.

Isaacs J. D., Schwartzlose R. A., 1975 b. Biological applications of underwater photography, Oceanus, 18, 24-30.

Laubier L., Martinais J., Reyss D., 1971. Opérations des dragages en mer profonde. Optimisation de trait de déterminations des trajectoires grâce aux techniques ultrasoniques, *Rapp. Sci. Tech.*, *CNEXO*, **3**, 1-26. Poul A. Z. 1007.

Paul A. Z., 1973. Trapping and recovery of living deep-sea amphipods from the Arctic Ocean floor, *Deep-Sea Res.*, 20, 289-290.

Rice A. L., Aldred R. G., Billett D. S. M., Thurston M. H., 1979. The combined use of an epibenthic sledge and a deep-sea camera to give quantitative relevance to macro-benthos samples, *Ambio Spec. Rep.*, 6, 59-72.

Shulenberger E., Hessler R. R., 1974. Scavenging abyssal benthic amphipos trapped under oligotrophic central North Pacific Gyre waters, *Mar. Biol.*, 28, 185-187.

Shulenberger E., Barnard J. L., 1976. Amphipods from an abyssal trap set in the north Pacific gyre, Crustaceana, 31, 241-258.

Thurston M. H., 1979. Scavenging abyssal amphipods from the northeast Atlantic Ocean, Mar. Biol., 51, 55-68.

Wishner K. F., 1980. Near-bottom sound scatterers in the Ecuador Trench, Deep-Sea Res., 27 A, 217-223.

Appendix

The modified epibenthic sledge

The sledge used since 1978 is a further development of that described by Aldred et al. (1976). Apart from the addition of the odometer wheel briefly described in the text, the main modifications have been the replacement of the single benthic net with a graded mesh by three separate nets each of a single mesh throughout, and the addition of a suprabenthic net which opens and closes simultaneously with the benthic nets and takes a sample from about 0.6 to 1.2 m above the sea-bed. This second modification has involved increasing the height of the sledge frame, allowing the camera to be raised and set at a steeper angle. Finally, the acoustic telemetering system has been improved to provide more precise information about the behaviour of the gear. The following brief description of the sledge should be readily followed in conjunction with the accompanying illustration (Fig. 1).

Frame

The frame length (1.92 m) and width (2.29 m) have remained unaltered, but the height has been increased to 1.22 m. To support the extra weight, the soles of the skids have been extended forwards and the sloping part has consequently been shortened and steepened; a ploughshaped wedge has been added to the front of each skid to prevent the build up of sediment on the leading edge. The benthic nets are attached to the back of the lower part of the frame, as in the original sledge, but the mouth of the suprabenthic net is pivoted on two tubular bearings in the centre of the upper half of the frame. Ideally, the mouth of this net should have been situated at the front of

A. L. RICE et al.

the frame, but the provision of a linkage from the quadrant levers with sufficient mechanical advantage to open the mouth of the net proved to be impractical. As a compromise, a fixed rectangular tunnel of the same mesh as the suprabenthic net has been fitted in front of it. In the open position the mouth of the suprabenthic net encloses the rear of this tunnel; in the closed position the mouth frame pivots backwards and the net is draped over a raised bar producing a baffle effect.

Nets

The original sledge carried a single net with a graded mesh. Such a net obviously selects in a very complex manner and since 1978 it has therefore been replaced by a series of three smaller nets, a central one made throughout of 1.0mm mesh and two outer ones of 4.5mm mesh. Although the resulting three separate catches results in a rather greater use of containers and preservative, there is a considerable saving of effort at sea since the coarse outer nets winnow almost completely during hauling so that only the catch of the fine central net needs extensive sieving. The cod-end of each of the nets consists of a canvas tube which is closed by being flattened out, rolled up from the end and secured under a canvas flap with Dutch lacing. This system can be easily untied even with the weight of a large sample on it.

The suprabenthic net has a mouth $1.0 \,\mathrm{m}$ wide and $0.6 \,\mathrm{m}$ high, and during fishing the bottom bar is approximately $0.6 \,\mathrm{m}$ above the sea-bed. The net is made of $0.33 \,\mathrm{mm}$ mesh throughout and is provided with a scaled-down version of the quick release conical bucket with a fine mesh liner as described by Aldred and Wild (1979) and used with the RMT mid-water system.

Acoustic monitoring system

The net monitor is an updated version of that described by Baker, Clarke and Harris (1973) and is similar to that now used on the RMT system. It differs from the midwater monitor in not having the command system used to open and close the mid-water nets, but it has several additional inputs to monitor the behaviour of the gear. We are now able to monitor directly the depth, temperature, distance run, camera operation and also the points at which the sledge becomes horizontal (i. e. reaches the bottom), the nets open and close and if, for any reason, the sledge turns over. In addition there is an inclinometer which can be attached to the sledge in various positions. So far it has been used to measure the extent to which the supra-benthic net opens and the rollangle adopted by the sledge in mid-water.

Operation

Handling this larger (half-ton) sledge has not proved to be as difficult as was feared, provided the ship has an open stern. In this case the sledge is moved in the horizontal attitude on a four legged sling and positioned with the back of the skids outboard. The lift is now transferred to the towing bridles and the sledge is tipped over the stern.

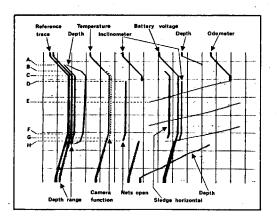


Figure 8

"Mufax" record of a simulated sledge haul from shortly before to shortly after the fishing period. Time proceeds from top to bottom, the dotted horizontal lines marking five-minute intervals. At the beginning of the record the sloping traces indicate that wire is still being paid out and the gear is therefore moving away from the ship. A series of successive changes in the traces monitor events as the sledge approaches the bottom. (A) The sledge enters a new depth range, a second range trace appears and the depth trace begins a new scanning phase. (B) The sledge reaches the bottom indicated by the change in slope of the depth trace. At the same time the "net horizontal" trace appears and the camera begins to operate causing a displacement of the temperature trace as each photograph is taken. At this stage the sledge is stationary on the sea-bed and is standing on the quadrant levers which are still lowered. The traces continue to move diagonally since wire is still being paid out. (C) The winch is stopped and all the traces therefore become more or less vertical. (D) The sledge is pulled forwards off the quadrant levers, indicated by the appearance of the "net open" trace and a sudden change in the inclinometer trace. As the sledge begins to move across the bottom the odometer trace starts a sweep. (E) The odometer reaches the end of its traverse and moves to the right to begin a second sweep. Since each complete sweep represents a horizontal distance of 300 m, this "haul" covered a total of about 790 m. (F) Hauling in begins and the traces therefore all begin to move to the left. (G) The front of the sledge lifts off causing the "net horizontal" trace to disappear and the camera to stop functioning. At this stage the nets are still open since the quadrant levers are still raised and the odometer is still working. (H) The sledge is now clear of the bottom, the "net open" trace is lost and the inclinometer trace moves back to its mid-water position.

Retrieval is equally simple, bringing the sledge high against the stern of the ship and then pulling it onto the deck using a capstan or auxillary winch.

Once the sledge has been shot and the initial panic of sorting out the plethora of traces has passed, it is quite easy and exciting to fish. As bottom contact is made and fishing commences a number of events occur, the monitoring of which gives precise information on the behaviour of the gear (Fig. 8). Two new traces make their appearance, indicating that the sledge is horizontal and the net is open. The camera begins to operate, with the exposure of each successive frame indicated by a temporary displacement of the temperature trace. As the sledge begins to travel along the sea-bed the odometer trace moves across the chart, one complete sweep indicating a traverse of 300 m by the sledge. If the inclinometer is fitted to the mouth of the suprabenthic net its trace indicates the degree to which the net has opened. It is also sensitive enough to detect the front of the sledge tending to lift off the bottom. This usually happens shortly before the sledge leaves the sea-bed altogether and can, if necessary, be quickly countered by paying out more wire.