HELGOLÄNDER MEERESUNTERSUCHUNGEN
Helgoländer Meeresunters. 43, 263–273 (1989)

The price of patchiness*

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ABSTRACT: Patchy distribution of animals, on a large or small scale, is a common phenomenon. Various explanations have been given for this spatial and temporal heterogeneity, but in many cases the causes are obscure. Patchy distribution of zooplankton is not understood and was not even expected in the fast turbulent currents of the well mixed tidal channels of the Wadden Sea. This patchiness is shown here for a number of plankton species. Methods commonly used for monitoring plankton usually neglect the fact of patchy distribution, and thus results suffer. Interpretation of such data can be highly misleading, particularly when used to assess the environmental status of an area: an overestimate or underestimate of population density may be the result. Sound quantitative data can only be obtained by making great efforts in terms of work and money. The costs entailed by such studies must be valued accordingly.

INTRODUCTION

Many animals show patchy distribution. This property is so well known that languages have many words for it: a flock of sheep, a gaggle of geese, a school of fish, a pack of wolves, a swarm of locusts, and it has even been used as the title for a novel: A flight of curlews ('t Hart, 1986). The reasons for this spatial and temporal heterogeneity in numbers are clear for many species, but are unclear for others. Patchiness occurs on different scales: on a large scale it means the geographical distribution, and, more generally, the suitability of living spaces, which may display a patchy distribution. On a smaller scale, other factors play a role (as illustrated above), and on a very small scale even space itself may be the limiting factor (e.g. in adult barnacles; Crisp, 1961).

Patchiness of species has one advantage for man in that it is easily discernible by sight: a farmer can easily count his sheep and an ornithologist the geese, and fishermen tell (or rather do not tell!) one another where the schools of herring are. Difficulties arise when the patches, as such, cannot be seen or recognised.

Although plankton is usually defined as "wandering" (Hensen, 1887), the real translation is "that which is made to wander or drift", i.e. drifting beyond its own control, hovering with the currents (Hardy, 1956). Therefore, it was usually tacitly assumed that

* Presented at the VI International Wadden Sea Symposium (Biologische Anstalt Helgoland, Wattenmeerstation Sylt, D-2282 List, FRG, 1–4 November 1988)

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plankton organisms in the sea were distributed randomly, and certainly so in the very well mixed Wadden Sea. Later in this paper it will become clear that in this respect the early naturalists (Vaughan Thompson [1828] and Müller [1844], both cited by Hardy [1956]) did not do us a good service by inventing the tow net, as this is an excellent instrument with which to obscure any departure from randomness; tow nets can be used for measuring abundance, provided very long hauls are made!

Since then, a general awareness has been growing, very slowly, that plankton is patchily distributed in the sea, on any scale from hundreds of kms, to sub-dm; a great leap forward in this respect was made by a series of papers by Cassie (1957, 1959a, b, 1960, 1962, 1963), and Clutter (1969). A review has been given by Steele (1976).

Patchiness of organisms has been described as aggregated, contagious, or gregarious distributions; it means that in some places (or in some samples) there are more individuals, and in other places fewer than would be expected in case of a random distribution. Sampling in a patchy population easily leads to an over- or underestimate of density. Methods have been developed in two fields to overcome these difficulties: sampling technology and statistics. By selecting a suitable sampling method, an attempt can be made to eliminate at least some of the patchiness e.g. by long plankton hauls, or anchoring the ship and letting the stream flow through the net, or by double-oblique hauls or continuous plankton recorder.

Patchy distribution is, statistically, usually described by a negative binomial distribution (Southwood, 1966; van der Aart, 1985). Earlier, patchiness in the Wadden Sea channels had been shown for the medusae *Rhizostoma pulmo* and *Chrysaora hysoscella* (Verwey, 1966), but these data are semi-quantitative at best. Creutzberg et al. (1978) found patchiness for larvae of *Pleuronectes platessa,* and it has been shown (de Wolf, 1973) that cypris larvae of *Balanus improvisus* in the fast tidal currents of the well mixed tidal channel Texelstroom are also patchily distributed, and a mechanism responsible for this patchiness was proposed.

The present paper stems from the wish to determine the numbers of *Pleurobrachia pileus, Aurelia aurita* and *Sarsia tubulosa* in the Wadden Sea, as part of a study on the predation by these coelenterates on larval plaice in the Western Wadden Sea (van der Veer & Sadée, 1984; van der Veer, 1985; van der Veer & Oosthuysen, 1985), and as a database for mathemathical models of the Ems Dollard estuary (Baretta & Ruardij, 1988) and the Western Wadden Sea (EON, 1988).

In addition to the species mentioned, other species that were caught in sufficient numbers such as plaice larvae *(Pleuronectes platessa), Cyanea* sp. (Scyphomedusae), *Eutonina indicans* (Leptomedusae) and *Syngnathus rostellatus* (Nilsson's pipefish) were also analysed. It was found that all but one (*Pleurobrachia* at 16 m depth, Fig. 3) of these were patchily distributed. In this paper, part of the data is presented, and the consequences of the low accuracy, inherent in the negative binomial distribution, are discussed as well as the size of the effort necessary to obtain higher accuracy.

MATERIAL AND METHODS

Cypris larvae of *Balanus improvisus* were collected on 5 July 1968 at station 7 (Fig. 1) by pumping 200 dm^3 water from depths of 2, 4, 6, 8 and 9.5 m below the surface through a

hand-held plankton net into a 200 dm^3 drum; in this way, equal volumes were obtained (de Wolf, 1973).

Sampling of the other species was done at each of 6 stations, 3 in the Ems Dollard estuary, 3 in the Western Wadden Sea (Fig. 1), each for a full tidal period (12.5 h), on 25–27 April 1982 and 24–26 May 1982, respectively. At each station, fishing was carried out at a fixed depth, in the Ems-Dollard at 3 m below the surface, in the Western Wadden Sea at 3 m below the surface and at 4 to 5 m over the bottom.

All hauls were made from a ship at anchor with nets of polyamid plankton gauze (Monodur 2000, 2 mm aperture) with a net opening of 0.7 m^2 and a net length of 5 m. The porosity (0.59) and the mesh area (12 m^2) of the net (definitions according to Smith et al., 1968) proved to be sufficiently large to prevent overflow of the net (van der Veer & Sadée, 1984). The amount of water filtered was measured with a flow meter, attached in the mouth of the net. In general, the reduction of the water flow through the net amounted to 10 %. Depending upon current velocity (up to 2 $m \cdot s^{-1}$) haul duration varied between 5 and 15 min, providing samples of between 100 and 500 m^3 water filtered. About 40–60 hauls could be made at each depth during a tidal cycle.

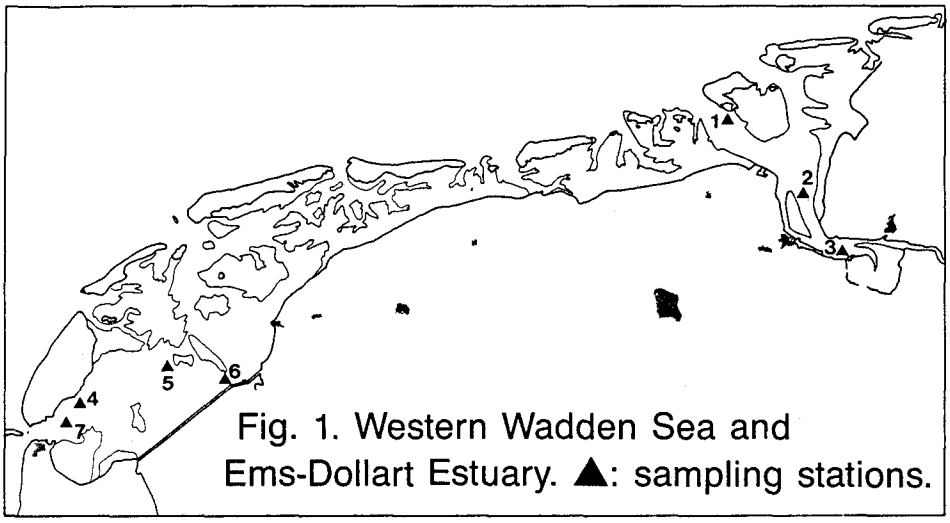

Fig. 1. The Western Wadden Sea and Ems Dollard estuary with sampling stations. (1) Borkum, 26 April 82, depth 10 m; (2) Oostereems, 27 April 82, depth 9 m; (3) Termunten, 28 April 82, depth 6 m; (4) Texelstroom, 24 May 82, depth 20 m; (5) Scheurrak, 25 May 82, depth 15 m; (6) Doove Balg, 26 May 82, depth 11 m; (7) Ankerboei, 5 July 68, depth 11 m

After the net washdown, all large coelenterates were counted and the remainder of the sample was preserved in a 4 % formalin-seawater solution and sorted in the laboratory. All flatfish larvae and *Syngnathus rostellatus* were counted and the coelenterates were put in a flat basin and photographed on slides. From these slides, numbers of the various species were counted. For all species, numbers per haul were converted into densities per 1000 m^3.

RESULTS

The results presented here are a random selection of stations from 52 combinations of 6 stations, 2 depths, 8 species and, for *Aurelia* 2 size classes. For 2 species (plaice larvae and *Syngnathus*), all available data are given. The 1968 data for cypris larvae of *Balanus improvisus* are given in Figure 2. Data for the other species are in Figures 3–10.

Great variations in the number of animals per sample are to be seen, for all species, in Figures 3–11, supporting the view of untrustworthiness of single plankton samples.

These data were analysed in two ways: as abundance-frequency distributions of numbers of animals in a sample against the number of samples (Fig. 11), and, in Table 1, as the dispersion parameter K for the negative binomial distribution (Southwood, 1966). Figure 11 shows that nearly all frequency distributions have high numbers of samples with no, or a low number of, animals (on the left of each figure), and all frequency distributions have a long tail stretching to the right with low numbers of samples with higher numbers of organisms, typical for the negative binomial distribution. There are two exceptions: Figure 11C for *Pleurobrachia*, and Figure 11A for cypris larvae. *Pleurobrachia* shows a figure that approaches a Poisson distribution, and hence a random (non patchy) dispersion in the sea, but only at a depth of 3 m, and not at a depth of 16 m (Fig. 11D). The frequency distribution of the cypris larvae is complicated (Fig. 11A), although it is not significantly different from a negative binomial distribution.

Table 1 presents for all species a reduced version of Figures 2–10; it contains the number of samples (n), the mean number of organisms ($\bar{x}$), the standard deviation (SD), the dispersion parameter K of the negative binomial distribution, and D: the accuracy. A D of 0.1 indicates that the estimated mean has a probability of 95 % of being within 10 % of the true mean in the field. D is calculated (Rojas, 1964) from

$$D^2 = \frac{\frac{1}{\bar{x}} + \frac{1}{K}}{n} \qquad (1)$$

wherein

$$K = \frac{\bar{x}^2}{SD^2 - \bar{x}} \qquad (2)$$

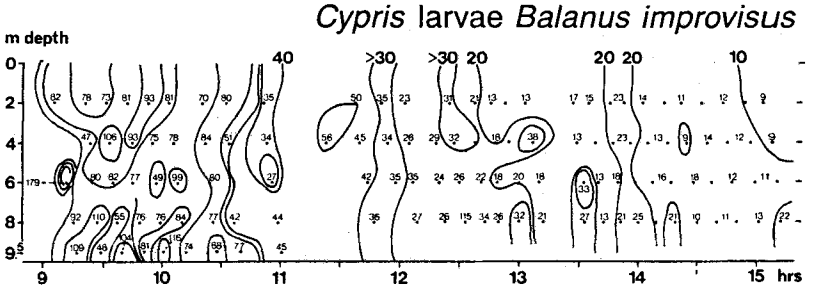

Fig. 2. Numbers of cypris larvae of *Balanus improvisus* per 200 dm^3 at station 7, 5 July 68, at depths of 2, 4, 6, 8 and 9.5 m

From the table, it follows that K varies from 0.34–10.6. For K values larger than 8 the negative binominal distribution approaches the Poisson distribution, as has been shown above for *Pleurobrachia* in Figure 11C, with K = 10.6. Smaller values of K indicate patchiness. The accuracy of the mean for N samples (D) has been calculated; it is seen that most of them are much higher than 0.1. If 0.1 is a reasonable standard for D (Southwood, 1966), the number of samples N necessary to obtain this accuracy can be calculated from (1). It shows that for such accuracy a much higher number of samples than has been collected, is generally needed.

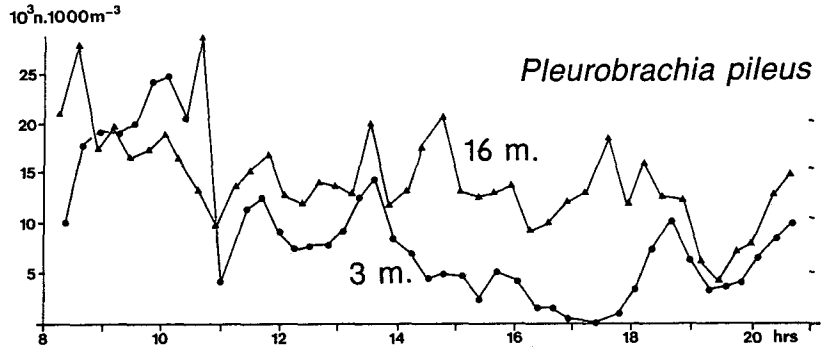

Fig. 3. Numbers of *Pleurobrachia pileus* (Ctenophora) at station 4, 25 May 82, at depths of 3 m (•) and 16 m (△)

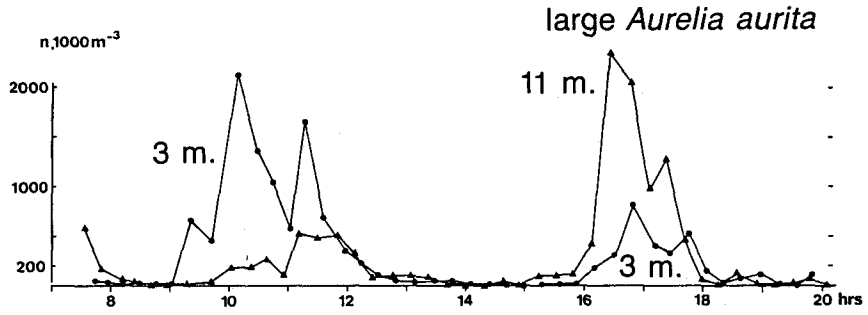

Fig. 4. Numbers of large *Aurelia aurita* (Scyphozoa) at station 5, 25 May 82, at depths of 3 m (•) and 11 m (△)

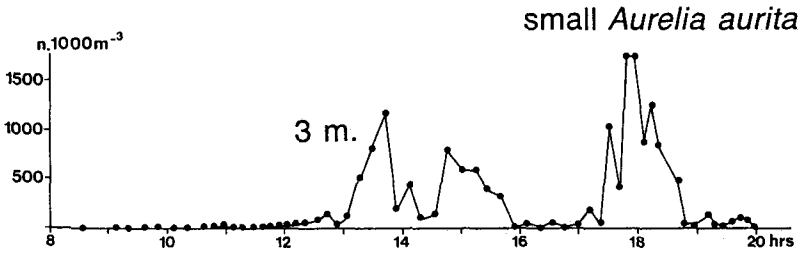

Fig. 5. Numbers of small *Aurelia aurita* (Scyphozoa) at station 2, 27 April 82, at a depth of 3 m

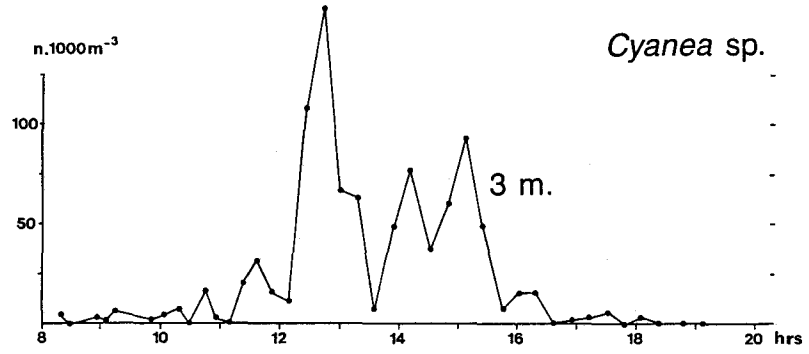

Fig. 6. Numbers of *Cyanea* sp. (Scyphozoa) at station 1, 26 April 82, at a depth of 3 m

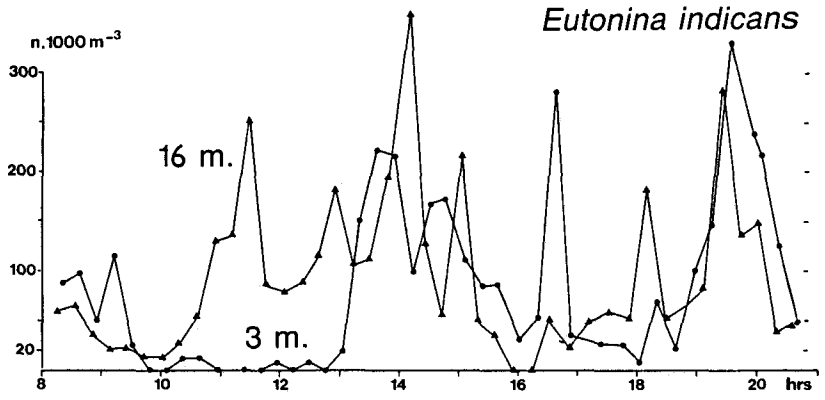

Fig. 7. Numbers of *Eutonina indicans* (Leptomedusae) at station 4, 24 May 82, at depths of 3 m (•) and 16 m (△)

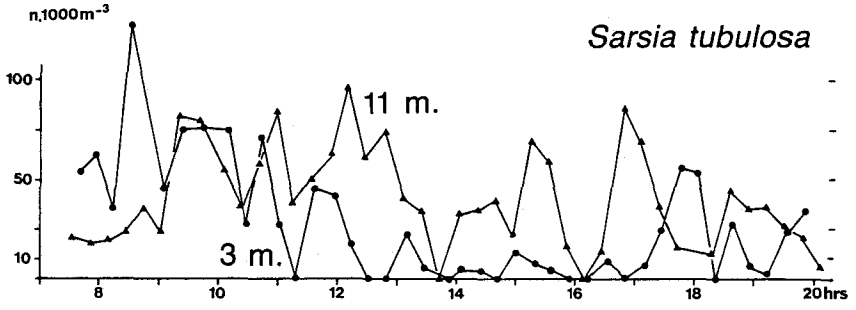

Fig. 8. Numbers of *Sarsia tubulosa* (Anthomedusae) at station 5, on 25 May 82, at depths of 3 m (•) and 11 m (△)

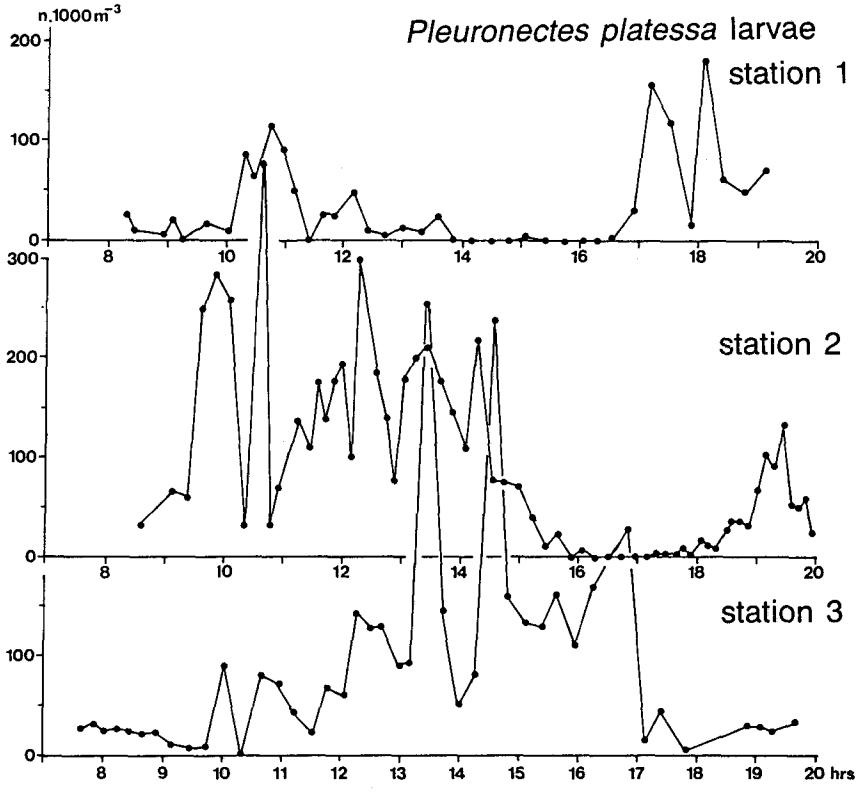

Fig. 9. Numbers of larvae of *Pleuronectes platessa* at stations 1 (upper line), 2 (middle) and 3 (lower) on 26, 27, 28 April 82, at a depth of 3 m

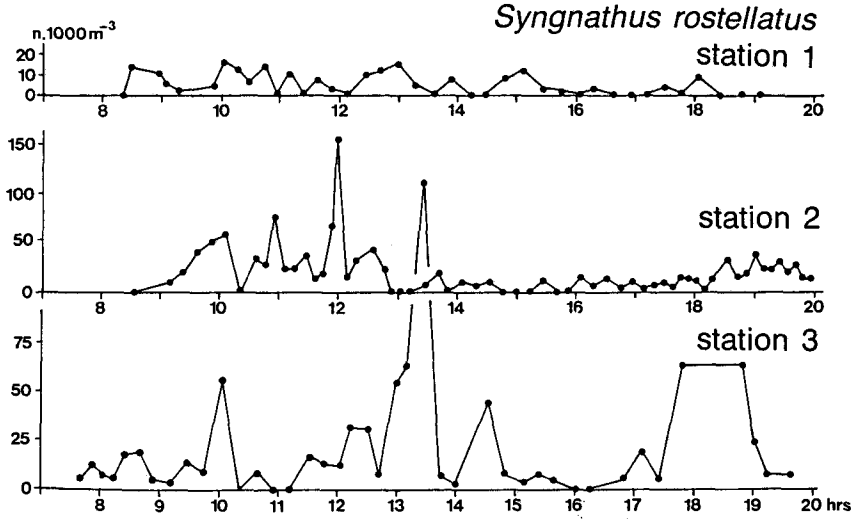

Fig. 10. Numbers of *Syngnathus rostellatus* at stations 1 (upper), 2 (middle), 3 (lower line) on 26, 27, 28 April 82, at a depth of 3 m

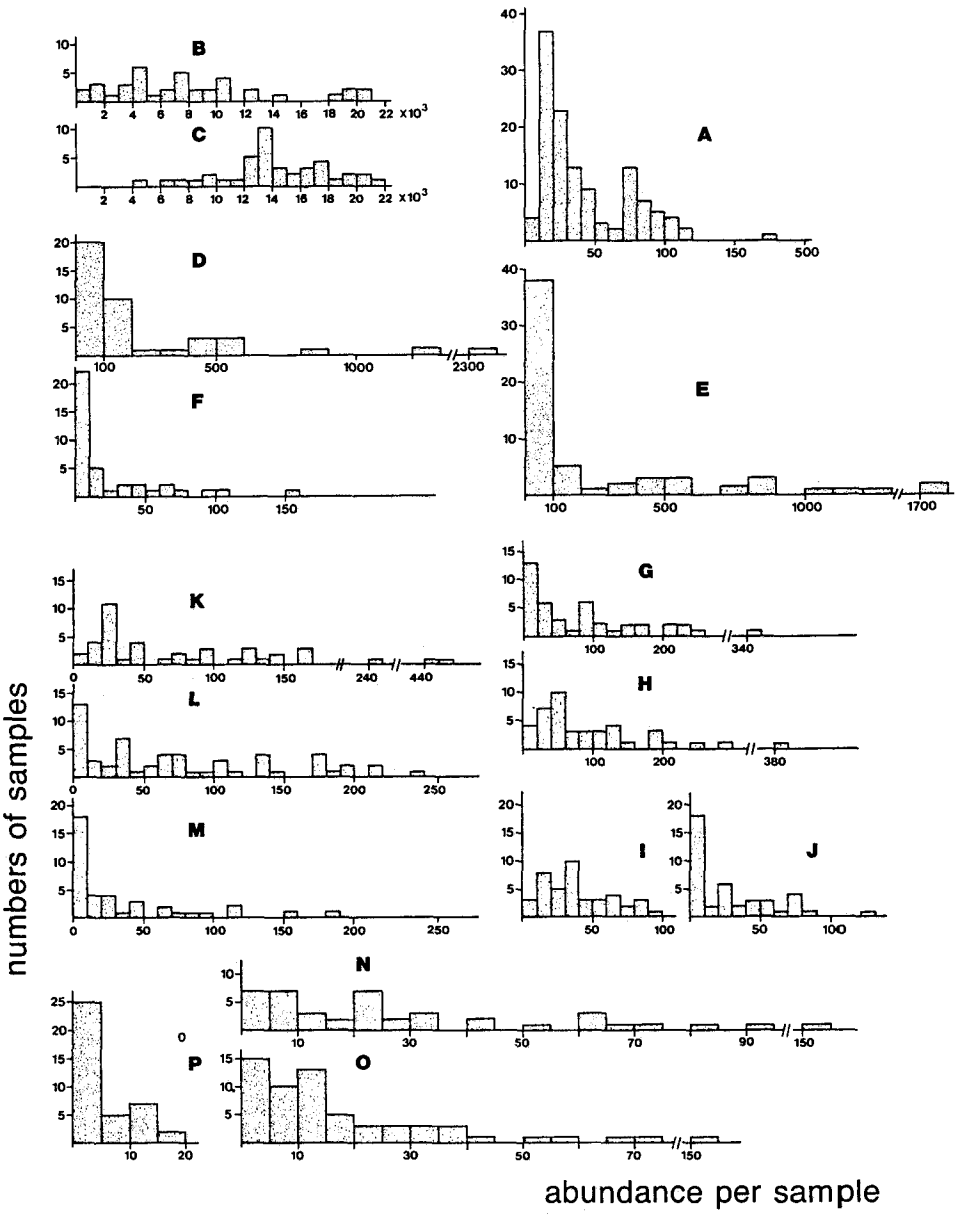

Fig. 11. Frequency distributions of numbers of samples (y-axes) against numbers of organisms (x-axes) for all samples from Figures 2–10. A: Cypris larvae; station 7, 123 samples; B: *Pleurobrachia*, 3 m deep, station 4, 42 samples; C: *Pleurobrachia*, 16 m deep, station 4, 42 samples; D: large *Aurelia aurita*, 11 m deep, station 5, 42 samples; E: small *Aurelia aurita*, 3 m deep, station 2, 61 samples; F: *Cyanea* sp., 3 m deep, station 1, 40 samples; G: *Eutonina indicans*, 3 m deep, station 4, 42 samples; H: *Eutonina indicans*, 16 m deep, station 4, 42 samples; I: *Sarsia tubulosa*, 11 m deep, station 5, 42 samples; J: *Sarsia tubulosa*, 3 m deep, station 5, 41 samples; K: larvae *Pleuronectes platessa*, 3 m deep, station 3, 42 samples; L: larvae *Pleuronectes platessa*, 3 m deep, station 2, 61 samples; M: larvae *Pleuronectes platessa*, 3 m deep, station 1, 39 samples; N: *Syngnathus rostellatus*, 3 m deep, station 2, 61 samples; O: *Syngnathus rostellatus*, 3 m deep, station 3, 42 samples; P: *Syngnathus rostellatus*, 3 m deep, station 1, 39 samples

Table 1. Number of samples (n), mean number of organisms ($\bar{x}$), standard deviation (SD), dispersion parameter of the negative binomial distribution (K) and the accuracy (D), for the samples taken, and the number of samples necessary for D = 0.1

Species	Station	No.	Depth (m)	n	$\bar{x}$	SD	K	D	n needed for D = 0.1
Cypris larvae	Texelstroom	7	2, 4, 6						
Balanus improvisus			8, 9.5	123	41.9	32.5	1.73	0.07	
Pleurobrachia	Texelstroom	4	16	42	14395	4417	10.6	0.05	
			3	42	9437	7266	1.7	0.12	59
Aurelia (large)	Scheurrak	5	11	42	283	488	0.34	0.26	294
			3	41	308	485	0.40	0.25	250
Aurelia (small)	Oostereems	2	3	61	262	425	0.38	0.21	264
Cyanea	Borkum	1	3	40	23	36	0.42	0.25	242
Eutonina	Texelstroom	4	16	42	93	81	1.34	0.13	76
			3	42	83	87	0.92	0.16	110
Sarsia	Scheurrak	5	11	42	40	25	2.68	0.10	40
			3	41	22.8	30.9	0.56	0.21	182
Pleuronectes larvae	Borkum	1	3	39	34.5	46	0.57	0.21	178
	Oostereems	2	3	61	92	91	1.04	0.13	97
	Termunten	3	3	42	88	98	0.80	0.17	126
Syngnathus	Borkum	1	3	39	4.9	5.5	0.95	0.18	126
	Oostereems	2	3	61	18.8	24.3	0.62	0.17	167
	Termunten	3	3	42	19.8	28.3	0.50	0.22	205

DISCUSSION

The patchy distribution of the cypris larvae of *Balanus improvisus* was confirmed by de Wolf (1973). He sampled these larvae by pumping 200 dm^3 of seawater in 54–66 secs, at a current speed varying between 25 to 150 $cm \cdot s^{-1}$; the scale of this patchiness was therefore 13.5–99 m.

The sampling technique using the tidal currents flowing through the net was designed to avoid patchiness. Tidal currents during sampling at the various stations varied from 10–25 $cm \cdot s^{-1}$ at the turn of the tide (and occasionally 0 $cm \cdot s^{-1}$ for short periods, but then we did not fish), to 1–2 $m \cdot s^{-1}$ (depending upon the station) at full flood or ebb. The period of fishing varied from 15 min (at slack tides) to 5 min (at full currents), and thus the designed sample-lengths were between 200–600 m; and designed sample volumes varied from 100–400 m^3. The actual measured sample volumes varied from 100–520 m^3.

In spite of this design to avoid patchiness, all species studied – even holoplankton such as *Pleurobrachia, Sarsia, Eutonina, Cyanea, Aurelia* – are patchily distributed in the fast turbulent currents in the well mixed tidal channels of the Wadden Sea. Therefore, although at least part of the patchiness on a scale of < 200–600 m has been removed, part of it is clearly still there, while there may be a patchiness on a still larger scale.

Table 1 shows the consequences of this patchiness: our estimate (the mean x for each series of samples) of the mean density of the organisms in the sea is for most species not more than ± 20 %, and in a few cases less. The amount of our effort, in the present study, was large; in the field work, 8 people were involved, besides 1 ship + 3 crew members: sorting and counting took 1.5 person years. In terms of money, the programme from which the data in Figures 3–10 are taken cost just over DM 100 000, which means that each of the graphs costs DM 2000 and that is relatively cheap due to (a) the low costs of sorting large *Aurelia, Syngnathus* and *Cyanea*, and (b) the use of all species caught. The cost of Figure 2 was about DM 12 000 (use of only one species).

There is a second consequence in Table 1: due to the D^2 in the relation between number of samples and accuracy, an accuracy of 0.1 (Southwood, 1966) would demand a 4–5 times larger effort (last column), provided that the same sampling strategy was used.

For monitoring populations, a different approach could possibly be used. However, use of larger nets and much longer hauls would give rise to an additional source of variance due to the – then necessary – subsampling of the catch, apart from the difficulties inherent in the use of large unwieldy nets, and larger ships. Moreover, it is no solution for a study on the formation of patches, their evolution, and how they maintain themselves.

As to the title of this paper: Patchiness is a very common property of organisms. Due to our inability to see the patches in the sea, sampling programmes must be designed especially for this patchiness; for the sake of reasonable accuracy large numbers of samples, or great efforts, are generally needed; hence, patchiness is very costly, whether in terms of money or in lack of accuracy, or both.

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