Distribution, patchiness, and population densities of *Pleurobrachia pileus* explained

P. de Wolf

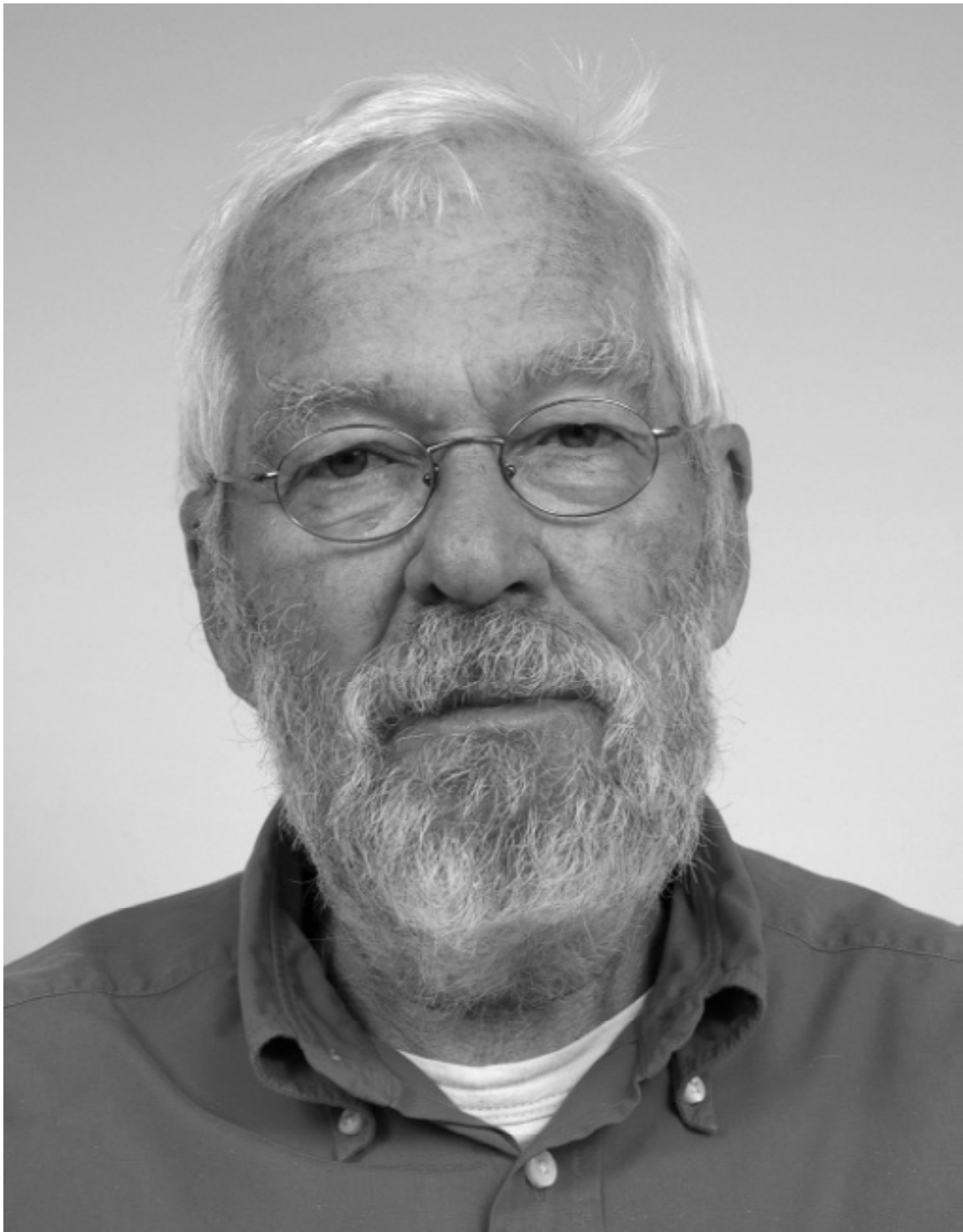(1995)

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Among his many interests, transport mechanisms of organisms has been a special leitmotiv during Piet de Wolf his entire career: one of his master studies supervised by prof. Gerard Baerends en Jenne Zijlstra at the fishery institute in IJmuiden dealt with the impact of vertical migrations on the catch rate of herring and his thesis focusses on dispersal mechanism of barnacle larvae in the Wadden Sea during planktonic life and settling. After his thesis defence, Piet started at TNO and became involved in antifouling research and other applied research projects.

His interest in transport mechanisms renewed when he jointed research cruises on RV Navicula to study the transport of especially ctenophores and medusa in the main gullies of the Wadden Sea in 1982. These cruises were based on the philosophy behind his thesis on dispersal of barnacle larvae: in estuarine systems sediment is transported passively by tidal currents and this signal can be used as a baseline for comparison with transport of various organisms. The experimental set-up was based on high frequent sampling (every 5 min) at a fixed depth during a complete tidal cycle of the abundance of organisms together with abiotic parameters such as current velocity, sediment load and water temperature and salinity. Among various other species, the ctenophore *Pleurobrachia pileus* was the most abundant one during these cruises.

Piet became intrigued by *Pleurobrachia*, especially its patchy distribution and he started to analyse the data. Originally, the idea was to prepare a manuscript dealing with patchiness. The results were presented at the 6th International Wadden Sea Symposium, held at Sylt in November 1988 and subsequently published in the proceedings (De Wolf, 1989).

However, this was not the end but the beginning of the story. Piet became more and more intrigued by *Pleurobrachia* and its life cycle: the unexpected and unexplained population explosions especially in spring, distribution patterns and especially patchiness despite the continuous dispersal in high energy coastal and estuarine areas. Piet started to dig through all the existing literature on *Pleurobrachia* dating back to the beginning of the 19th century. The result was an almost complete compilation of known information on *Pleurobrachia*, followed by an analysis of the data and finally an overall hypothesis about the life cycle of *Pleurobrachia*, thereby explaining various until then unexplained observed phenomena.

It was submitted for publication to the Journal of Sea Research in 1995. At that time, the editorial board of the journal recognised the importance of the manuscript but considered it as too long to be published in its present form and suggested to reconsider and shorten the paper. Piet was disappointed and in his opinion shortening the paper would mean losing essential information. As a consequence nothing happened and the manuscript was not reconsidered and never resubmitted and became part of his legacy.

We consider this manuscript on *Pleurobrachia* as a very valuable document and therefore decided to publish it as tribute to Piet de Wolf as internal report in its original form.

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Abstract

The distribution of *Pleurobrachia pileus* in space and time has been enigmatic despite the efforts of many authors during the last hundred years. The papers of a number of these authors are being reviewed in the present paper. The reason was an attempt to determine the biomass of the species in the Dutch Wadden Sea, where a very patchy distribution was encountered. *Pleurobrachia* species have generally: a very patchy distribution, highly variable population densities, sudden population density increases of up to 4 orders of magnitude, while it is assumed that *Pleurobrachia* has a neritic distribution. It will be shown here, that these properties have a common cause and a simple explanation. The following observations, nearly all made by earlier authors, are relevant: *Pleurobrachia* is not a plankton organism per se, but disappears from the water column during the turn of the tides, like silt; this sinking results in concentration near the bottom. The patchiness of *Pleurobrachia* in the water column is generated by the tidal currents, by resuspension through turbulence. Swimming of *Pleurobrachia* is temperature dependent, and at low temperatures not sufficiently strong to keep the animal at the level where the tidal resuspension brought it. At intermediate temperatures the animals are in suspension for a longer time, and at temperatures over 20°C can form "rafts" at the surface. Than downward mixing can forms patches. The behaviour of *Pleurobrachia* like silt results in concentration by a tidal mechanism in areas of the bottom where also silt is concentrated, resulting in high densities in sedimentation areas. Also therefore *Pleurobrachia* is a coastal, and not a neritic species. In areas away from the coasts, where stratification occurs, *Pleurobrachia* cannot return to the surface, because of weak tidal currents, and low temperatures below the thermocline. In coastal water the temperature increase causes the sudden population explosions, as seen in the plankton catches. The increases are a function of the number of *Pleurobrachia* present on the bottom, the resuspension by the tidal current, and the temperature dependent periods of swimming. This idea is at variance with earlier explanations of the increases on the basis of reproduction and growth; it is argued why these are wrong. It is thought that the results obtained are more generally valid, for a number of other estuarine and coastal species.

Keywords; *Pleurobrachia pileus*, distribution, patchiness, population density, coastal, neritic, review.

1. Introduction

Results on the patchiness of *Pleurobrachia pileus*, obtained in the Dutch Wadden Sea in 1982 (De Wolf, 1989) were the reason for the present paper; it will be shown that patchiness, tidal differences in densities and the well-known population explosions of Ctenophores have a common cause and a simple explanation.

The distribution and transport of plankton species in estuaries and coastal seas, and the supposed retention of species in a restricted area, has been a favoured study object for a long time. Scoresby (1820) noted already for *Pleurobrachia* that there is a problem and proposed a solution: "But how is it, it might be asked, when a current in the waters, inhabited by the minor medusae, is constantly setting to the southward, that these animals are not carried away into a southern region altogether? This question, if we may be allowed to argue hypothetically, admits to an easy solution. Animals, we find, when possessing any power of moving, though they be of the most imperfect kind of organisation, generally employ that power by a sort of instinctive faculty, as may best serve the purpose for which they were called into existence. Now, it would be no stretch of commonly received principles, to suppose, that whenever the minor medusae are carried to a certain extent southward, they may sink in the water of the undercurrent, and by it be conveyed back into their proper element.".

It has been thought (Verwey, 1966) that organisms succeeded to choose their place by swimming, and to maintain their place or reach a different place; in other words they migrate, and thus must have a mechanism for orientation. Many authors have devised complicated systems of behaviour of organisms (adult or larval plankton species, or larvae of benthic species) to explain their sustained presence. Such systems usually comprise extraordinary powers on the part of the animals as to their swimming ability, and their sensory perception possibilities, for orientation (see review by Creutzberg, 1975). It has been argued (De Wolf, 1973) that at least parts of such behaviour are unlikely, if not impossible. For example, Bousfield (1955) supposed that nauplii and cyprid larvae of barnacles maintain their position in the vertical to some degree, throughout the tidal cycle, by swimming to an average depth in response to light intensity; I fail to see how this behaviour could evolve (see 5), and there is a surprise in the very last lines of this paper. Verwey (1966) also thought that light kept mussel larvae at depth; he also supposed that Scyphozoa do migrate long distances. Carriker (1967) believed to have shown that shellfish larvae control their position by swimming under the influence of turbulence, and Wood and Hargis (1969) think that salinity and pressure changes control swimming in the larvae of *Crassostrea virginica*. All this swimming should keep larvae at such a depth in the tidal current that they are transported to the desired place, despite Scoresby's notion that they just sink. Contrarily, Korringa (1941, 1952) noted for larvae of *Ostrea edulis* that currents nor light, nor any other factor tested, influenced the vertical distribution. Further it has been shown, that passive cyprid larvae of barnacles are retained in the western Wadden Sea through tidal currents and sinking (De Wolf, 1973, 1974) like particles of silt in an estuarine accumulation mechanism (Postma, 1954, 1967).

More recently an increasing number of authors have shown that the distribution of invertebrates is physically determined. Tyler and Banner (1977) showed that coastal hydrodynamics do influence the distribution of adult echinoderms, as echinoderm larvae do settle in the same way as fine sediment in Oxwich Bay, Bristol Channel, UK. Steele (1978) remarked that "zooplankton have little directed movement at horizontal scales above a few meters", as they are behaviourally rather passive (Harnner and Hauri, 1981). Hannan (1984) showed that larvae of the polychaete *Mediomastus ambiseta* sink like passive particles in turbulent near bottom flows, and although Cronin (1982) comes to the conclusion, for larvae of the crab *Rhithropanopeus harrisii,* that swimming on the part of the larvae is decisive for their retention, I am not sure that his results cannot be explained using physical factors alone. The conclusion of Butman et al. (1992) is final: "The capability of organisms to select settlement sites by horizontal swimming is limited to essentially still water, since water velocities occurring within millimetres of the sea bed exceed measured swim speeds for most realistic field flows". So far, the examples given were for planktonic stages of benthic animals. For macroplankton, although in not exactly an estuarine or coastal environment, it has been observed that even strong swimmers such as the scyphozoans *Aurelia aurita*, *Chrysaora melanaster* and *Cyanea capillata* are retained in Langmuir cells (Hamner and Schneider, 1986). Hamner and Hauri (1981) have shown, in a marine lake virtually without current, that *Mastigias* (Scyphomedusae) can migrate over long distances, covering approximately 1 km.day^{-1}; and Shanks and Graham 1987) found indications that *Stomolopus* (Scyphozoa: Rhizostomida) can actively orientate its swimming direction using a directional cue in the water column.

Pleurobrachia has been studied since 1965 by Greve, but the first sentence in Greve and Reiners (1980) is a citation from Krumbach (1926), who concluded: "so our impression is further supported that *Pleurobrachia* comes and goes without respect to season, temperature or depth", implying that *Pleurobrachia* is more or less randomly distributed. Despite many papers since Krumbach reached this

conclusion, the distribution of *Pleurobrachia* in space and time is still poorly understood. Authors, from Agassiz (1849) till Williams and Collins (1985a,b), do generally agree on two principles:

1. *Pleurobrachia* is a neritic planktont, and
2. *Pleurobrachia* has a very patchy distribution, in space and time, in all seas.

In my opinion, a further principle must be added:

3. *Pleurobrachia* occurs in the plankton in low densities, but all populations show a sudden increase in population density by a factor of 100 to 10,000 in a short period.

Here I shall comment and elaborate on these principles, and although most of the published work has been done with *P. pileus*, there are limited data on *P. bachei, P. globosa, P. pigmentata*, that show the same principles.

1.1. Neritic occurrence

The original definition of "neritic" (by Haeckel, see Baretta-Becker et al., 1992) was: the aquatic environment overlying the sublittoral zone (0-200 m). Thus, all of the North Sea is neritic, and in accordance with Haeckel's definition *Pleurobrachia* can be found everywhere in the North Sea; but densities do vary to a great extent. However, there are in the literature observations of *Pleurobrachia* from the ocean; Moser (1910) recorded *P. pileus* from the open ocean, near the Seychelles, Ascencion, and between Ascencion and the Cape Verde Islands, as well as Antarctica. Moser (1903) found *P. globosa* and *P. pigmentata* over deep water in East-Indonesia, and Fraser (1970) remarked that specimens of *P. pileus* found over deep water are often in poor condition. He thinks that they have been transported there from a neritic source, and thus considers *Pleurobrachia* to be a neritic species. But, using data from Kuipers (1982), Tungate (1975), Greve and Reiners (1980) and Williams and Collins (1985a,b), there are reasons to doubt this. Part of the problem is probably semantic, as during the years it has become customary to use "neritic" for "coastal", and the results of the authors mentioned show that *P. pileus* has in fact a coastal distribution. For example Kuipers (1982, 1983; unpublished results in Figs. 24 and 25 of the present paper) found that along the west coast of the Netherlands high densities did occur at all stations within 10 miles of the coast, in May and June, while stations at a distance of 20 and 40 miles had 100 to 1000 times lower densities. In July and August no *Pleurobrachia* at all were found, and in October the density distribution is approximately the same as in May and June, be it at a 100 times lower level at all stations.

My tentative conclusion is therefore that, although *Pleurobrachia* may occasionally be found over deep waters, highest densities are found close to the shores; therefore *Pleurobrachia* is a coastal species, rather than neritic. Later it will be shown that the difference between a coastal and a neritic distribution of *Pleurobrachia* is not a semantic triviality, but results from a physical cause. Once this has been recognised also many other papers show indications for a coastal distribution (e.g. Bigelow, 1924; Fraser, 1970). The data of these authors will be discussed, and it will be shown that *Pleurobrachia* can only be a coastal species.

1.2. Patchiness

Patchiness of *Pleurobrachia* is well known and was mentioned by Agassiz (1849) and Mayer (1912). Bigelow (1924) wondered that "when it abounded at one station, only a few were taken at another close at hand", and "is locally abundant beyond all computation". Earlier (De Wolf, 1989) it was noted that the towed plankton net is an excellent instrument to obscure patchiness, and that tow nets can only be used for measuring abundance, under the stipulation that very long hauls are made. Now, I am not even sure any more of that restriction.

A number of authors working on *Pleurobrachia* have ignored patchiness (Russell, 1933), or did not recognise it as such (Klein Breteler, 1971), or tried to smooth it away by using means over large numbers of hauls (Van der Veer and Sadée, 1984), used very long hauls (Van der Baan, 1980), or tried to smooth it using an Isaacs Kitt net with a net opening of 7.29 m^2 (Kuipers, 1982, 1983). It is remarkable that despite all these efforts the data of these authors do still show patchiness.

One would expect that in the fast, turbulent tidal currents along coasts and in the Wadden Sea no patchiness would be possible; nevertheless patchiness is encountered repeatedly (Verwey, 1966; De Wolf, 1973, 1974, 1989; Van der Veer and Sadée, 1984). Thus, there must be a process that counteracts the dispersing effect of turbulent currents, and one of my aims is to explain the formation and breakdown of patches of *Pleurobrachia* in time, as Hammer remarked (1988) that "patches in the sea are ephemeral." This an apt observation, but "ephemeral" has a time scale, and it will be shown that the time scale is given by the tides.

1.3. The population "explosions"

The sudden increases in population densities have been reported by, or can be derived from the data from many authors. Here a few examples will be given. *Pleurobrachia*, in the Channel near Plymouth (Russell, 1933), in the southern North Sea (Tungate, 1975), in the Wadden Sea (Van der Veer and Sadée, 1984), and in the German Bight (Greve, 1969, 1971; Greve and Reiners, 1980) is usually caught in low numbers in the period from January till April. In the beginning of May numbers increase rapidly, by 2.5 orders of magnitude in the Channel, and by 2 orders of magnitude in the Southern Bight. In the Wadden Sea the increase starts in the last week of April, and amounts to 3.5 orders of magnitude in the first week of May. In the German Bight, on the Reede of Helgoland, the increase varies between years from 2.5 to 3.5 orders of magnitude (Greve, 1969, 1971), while between Helgoland and the German mainland coast, in 1979, the increase varied between stations (in June) from 2.5 to 4 orders of magnitude.

Similar population explosions have been observed at a number of other places, and for different species of *Pleurobrachia*, e.g. for *P. bachei* in the coastal waters of California (Hirota, 1974), off Bombay, India for an unnamed species (Chopra, 1960), and for *P. globosa* in coastal waters near Madras, India (Rajagopal, 1963).

A few authors mention a second population increase in September or October, but only in the case of Russell (1933) this increase is larger than in the spring. Van der Veer and Sadée (1984) report a small increase in the autumn of 1982, and Greve (1971, 1988) shows a similar small increase in the autumn of some years, but not in all.

Generally these observations are consistent, but the data of Fraser (1970) taken along the Northeast coast of Scotland from 1925-1939, and 1946-1964 are at variance: no sudden population increases at any time of the year, but a slow increase from 2 *Pleurobrachia*.haul[-1] in February to 14.haul[-1] in November. The hauls of Fraser will be discussed later.

There are two lines of thought as to the cause of these sudden increases in population densities. Greve and Reiners (1980) suppose that *Pleurobrachia pileus* reproduces in the outer part of the estuaries, and that the population increases are due to reproduction and to the increase in size of individuals, growing into the catch. Although this may be part of an explanation, Hirota (1974) showed for *P. bachei*, on the basis of a demographic model, that the doubling time of this population was approximately 32 days, and thus much to slow to explain the local population increases. Further, it seems unlikely that the population increases in the German Bight could be much faster than in the optimal model of Hirota.

The "explanation" for the sudden population increase, suggested by Hirota, is advection but in my opinion this shifts the problem to a different geographical area, and such an area has until now not been found. Thus a different explanation is needed, and I shall give one in this paper.

2. Material and methods

2.1. The tidal occurrence of Pleurobrachia

Pleurobrachia was sampled at 3 stations in the western Wadden Sea (Fig. 1): Texelstroom (station 4, depth 20 m), Scheurrak, (station 5, depth 15 m), and Doove Balg: (station 6, depth 11 m), each for a tidal period, on 24-26 May 1982. Samples were taken at 3 meters below the surface and at 3 meters over the bottom, from ship at anchor, tidal currents running through the nets. All particulars about nets, net-efficiency, mesh size, current meters, and further methodology were as described by Van der Veer and Sadée (1984). Depending upon current velocity (up to ~2 m.s^{-1}) haul duration varied between 5 and 15 minutes, water volumes varied from 81 to 986 m^3. Number of hauls per station varied from 41 to 46 at each depth. Tidal curves were obtained, for each of the stations, from the Tidal Waters Division of the Ministry for Transport and Public Works. Numbers of *Pleurobrachia* per haul were converted into numbers m^{-3}.

2.2. Patchiness methods.

Patchiness is described as in De Wolf (1989) where it has been indicated that a patchy distribution can usually be described by a negative binomial distribution (Southwood, 1966; Van der Aart, 1985). This distribution is described by two parameters, the mean, and the exponent *k*, which is a measure of the amount of clumping, and is often referred to as the dispersion parameter. Generally values of *k* are in the region of 2; if they are larger the distribution approaches and becomes eventually identical with that of a Poisson distribution, whilst fractional values of *k* lead to a logarithmic distribution. The value of *k* is not constant for a population, but often increases as the mean increases. The value of *k* may be computed by several methods (Southwood, 1966). Here I shall use only the quick and easy one:

$$k = \overline{x}^2/(s^2 - \overline{x})$$

Further, analysis of the data uses abundance-frequency distributions; sampling in patchy distributions yields usually high numbers of samples with no or low numbers (Pennington, 1983).

The difficulty of patchiness is that patches in the sea can usually not be seen, and most methods to sample plankton, whether nets or torpedoes, are excellent means to obscure at least part of the smaller scale patchiness. For this reason patchiness can only be observed relative to the scale of sampling (length of haul; volume taken): in a certain haul there may be only locally one very dense patch, or a number of smaller patches, whilst both amount to the same density for this haul. And what is called patchiness is the large variation over a large number of hauls, either taken at the same place over a longer period of time, or taken at a number of different stations (and then usually with no or a small number of replicas), but again taken during a longer period of time. Thus, patchiness already has three dimensions: two in the horizontal plane, and one for time. The fourth is of course depth, although vertical hauls suffer from the same defects as indicated above, and oblique and double-oblique hauls have only the pretension to sample a population. But nets and torpedoes are usually kept very carefully away from the neighbourhood of the bottom, for obvious reasons.

Cushing (1962) has listed meanings of the word "patchiness":

1. Variability due to the gear, which has to be eliminated before the real patchiness can be estimated.
2. The variability of a single haul.
3. The causes of the variability of a single haul.
4. The horizontal extent of a population: a population delineated in terms of its density, and he followed the idea of plankton patchiness for each of these in history. I add a fifth item:
5. The vertical extent of a population, in time.

Steele and Henderson (1992) have recently published a simple model for patchiness, wherein is shown that the fine structure of the patchiness is much more apparent in the herbivores than in their predators, and this is the numerical explanation for the difference in spectral slopes. There are various explanations for this difference, and it is associated with variability in vertical migration, related to the phytoplankton food. Whether such an explanation can hold for *Pleurobrachia*, feeding upon herbivores, remains to be seen. Recently, Levin et al. (1993) published a very valuable review on patchiness.

All authors cited so far have tacitly assumed that their samples were representative for the population of *Pleurobrachia* in the sea, in space and time. For my purpose I shall assume that their hauls are representative for themselves only.

There is one practical problem in reporting data on *Pleurobrachia*, and that is the large variation in numbers in sample sizes that are more or less equal. When making figures with a linear scale for the number of animals the impression of the high numbers of animals is correct, but the variability in the lower numbers is lost. In figures on a logarithmic scale this variability can be seen clearly, but then the impression of the large increase and decrease in numbers does not get proper attention. Clearly, authors have been wrestling with this problem in the past, resulting in figures on linear scales (Greve and Reiners, 1988), log-scales (Williams and Collins, 1985a,b), ^{3}log scales (Tungate, 1975) and variable linear scales, and scales that vary from cruise to cruise (Greve and Reiners, 1980). In the present paper I shall illustrate the problem once, on the basis of data of Russell (1933), and I shall keep nagging about the problem without being able to solve it.

2.3. Methods of earlier authors.

Results from a number of authors have been reviewed on the basis of published data; other authors allowed me to use unpublished material. The publications and material reviewed are: Van der Baan (1980), Bigelow (1910, 1914a,b, 1915, 1917, 1920, 1921, 1922, 1924a,b), Fraser (1963, 1966, 1970), Greve (1968, 1970, 1971, 1972, 1984-1988), Greve and Reiners, (1980, 1988), Hirota (1972, 1974), Klein Breteler (1971), Kuipers (1982, 1983, 1985), Russell (1925, 1926, 1927, 1933), Tungate (1975), Van der Veer and Sadée (1984) and Williams and Collins (1985a, b).

Van der Baan (1980) sorted, counted and published on the macroplankton taken by the crew of the Lightship Texel (at 53°01'30" N and 4°22' E, depth 28 m) from the period of 17 January 1961 till 31 December 1966. A net with a mesh size of 2 mm, a round net opening of 1 m^2, and a length of 10 m was fished passively, by tidal currents running through. Samples were originally taken at every flood and ebb, weather permitting, at 0-5 m below the surface (De Kock, 1966). During the autumn of 1962 sampling was reduced to 12 samples per week, and in 1966 to 6 samples per week. Van der Baan published the data in an abridged table. For my purpose counts of *Pleurobrachia* were collected from Van der Baan's original note books. The volumes of the hauls were not known: but counts were converted to numbers.1000 m^{-3} using vertical log data as published by KNMI (1964-1968). Flood and ebb displacements, and the duration of the hauls, were used to calculate the volume of the hauls. This procedure is not without error; the recorded time period is a part of the tidal period (e.g. 5 hours out of the 6 hours 15 minutes of the flood), and begins when the current is sufficiently strong to allows the net to fish. Thus, the pro rata part of the tidal displacement is the part with the fastest currents, and thus

leads to an overestimate of the volume fished and underestimates the density of *Pleurobrachia*. Moreover, the vertical log was read once every hour, and it is not unlikely that the current strength and the current direction varied during the time between readings, and thus the log underestimates the tidal excursion. This, in its turn, leads to an overestimate of the number of *Pleurobrachia*. It is assumed that the overall error is small, as the fishing time was usually a large part of the tidal period (Fig. 3). The calculated volumes varied from 237 to 26,315 m^3, with a median of 8000 m^3 for ebb periods, and 9500 m^3 for floods (Fig. 2). The volume fished has a much wider spread than the time fished (Fig. 3); the last varied from 30 minutes to 8 hours, with a median of 350 minutes for ebbs as well as floods. The difference in variation between fished time and fished volume is undoubtedly partly due to tidal variation, and probably to a large extent due to wind effects on tidal currents. Not all catches could be standardized due to missing vertical log readings, but a total of 3,708 samples could; of these 1,742 did contain *Pleurobrachia*.

Bigelow (1924, printed in 1928) studied the plankton and physical oceanography of the Gulf of Maine and Georges Bank in the period 1912-1920; his data on *Pleurobrachia* are summarized in the 1924 paper. He used about 10 different nets, and only for some of the later cruises it can be found which net was used for a particular catch (Bigelow, 1921). Usually it is not clear which net caught what. Furthermore, his data on *Pleurobrachia* are semi-quantitative only, in terms as "few", "many", "swarm", "three litres". However as a pioneering effort, carried out from the sailing schooner Grampus, his data are still worthwhile, and for the present purpose his table (1924, p. 370) is used, and a few other data.

Fraser (1963, 1966, 1970) fished, over the period 1925-1968, with 1-meter diameter non-closing tow nets for 15 minutes per haul at a speed of 2 knots to the north and east of Scotland. It eludes me how he calculated the volumes fished, but in his 1963 paper he gives a value of 250 m^3 per haul, and in 1970 450 m^3; I think it is ~ 730 m^3. Fraser mentioned no depth at which the samples were taken, but supposedly surface hauls were taken. Quantities caught were not counted, but are given on an arbitrary scale, to which at a later time numbers were attributed by calibration of the arbitrary scale against conserved samples.

The data of Greve on *Pleurobrachia* can be divided in 5 sets. The first (Greve 1969, 1971) concerns the abundance of *Pleurobrachia* on the 10 m deep Helgoländer Reede from May 1966 till August 1968. These data were collected by horizontal tows of 5 - 10 minutes at 1.5 knots, with a net-opening of 0,5 m^2; largest samples were therefore ~ 810 m^3; about 180 samples were taken. The Helgoländer Reede has a high turbulence due to strong tidal currents. Greve assumes that the horizontal tows give a fair representation of the *Pleurobrachia* in the whole water mass. Numbers caught were converted to numbers.m^{-3}. The second data set (Greve, 1971) was collected in the Nordhafen to the North of Helgoland; this is not a harbour, as the name would suggest, but an open sea area of 23 m deep. The data were collected to study the depth-distribution; horizontal tows were made at the surface, at 10 m deep, and very near the bottom with a Helgoländer Knüppel netz (Mielck and Klinne, 1935; Blickman, 1929), in the period 4 March - 19 July 1968. Samples were taken on 12 days, at a fixed time (9.00 o'clock) to exclude the possibility of diurnal changes in the depth distribution. The data for each date are given as percentages at each depth of the total at three depths, and for one day absolute numbers are given. The third dataset is the Helgoland Time Series with data on *Pleurobrachia* since 1974 (Greve and Reiners, 1988; Greve et al., 1990). Although samples have been taken weekly during the period 1974-1982 the figure contains 2 data points per month; further it gives the impression that the usual great variation of numbers of *Pleurobrachia* has been smoothed away. The fourth data set (Greve and Reiners, 1980) covered the German Bight to the south and east of Helgoland by means of 30 stations in 5 sequential, quasi-synoptic cruises, in the period from 23 April - 25 July 1979. *Pleurobrachia* was fished by oblique hauls with a CalCOFI net of 1 m front diameter, 500 µm mesh, fitted with a current meter; mean sample size was 68 m^3; time necessary for the hauls has not been published, but must have been short in view of the volume. Five size-classes were distinguished: 0-3 mm, 3-5 mm, 5-10 mm, 10-15 mm, and >15 mm; the original dataset was used. There is also a fifth dataset covering a much larger part of the German Bight (Stocks, 1961) to the south of 55° N, and east of 6°30' E, and consisting of 5 bi-weekly cruises of 73 stations; however, this one has been only summarily published (Greve 1985, 1986, 1987, 1988, 1989, 1990, 1992; Greve and Reiners, 1988). The area covered is contiguous with the area covered by Tungate (1975).

Hirota (1974) sampled *Pleurobrachia bachei* in La Jolla Bight, California. For the study of the vertical distribution (3-6 November 1969, and 22 May - 1 June 1970) 0.7 m diameter paired opening-closing bongo nets, with mesh-sizes of 53 respectively 153 µm were used. In each vertical 4 to 6 depths were sampled in 10 to 20 m intervals for shallow depths, and at greater intervals in deeper water. A preliminary survey of the horizontal offshore distribution was made on 28 August 1969; 10 stations were sampled to a distance of 11 km from the shore. In the study of November 1969 the offshore sampling consisted of six transects perpendicular to the shore, transects being 3-8 km apart, with 3 or more stations on each, located between 1 and 13 km from the shore. In the second study of the offshore distribution the sampling was done on 2 transects of 7 and 9 stations to a distance of 50 km from shore.

In all offshore distribution studies replicate samples were taken. Seasonal variations were studied from 8 March to 1 May 1970 at 6 stations 1-3 km from shore. As current measurements showed an along shore advection of tens of km per week, the programme was changed to 5 stations at 1.6 km from shore, and about 8 km apart, and 1 station at 8 km from shore; for the period March 1970 - June 1971 about 30 samples were taken at each station. Not all samples have been counted, for a full account see the original paper.

Klein Breteler (1971) made horizontal hauls of 90 minutes duration at 3 stations near the Dutch coast, on 9-10 March 1970, at 1.3, 11, and 13 km to the west of Callantsoog in water depths of respectively 9, 18 and 22 m. These stations were fished from a ship at anchor; tidal currents running through the net. Volumes fished are not known, but can be estimated at about 5,000 m^3. A few observations were made at a distance of 20-28 km from the coast, on 14-15 May 1970, with a towed net at depths of 0, 10, and 20 m. The estimated sample volumes at this station are between 5,000 and 7,000 m^3. The nets used had a mouth opening of 1 m^2, and a mesh of 1 mm^2.

Kuipers (unpublished data of 1982 and 1983) made oblique hauls (from approximately half depth to the surface) with an Isaacs Kitt net, mouth opening 7.29 m^2; mesh size 1.4 mm, in the coastal waters of the Netherlands. His 6 transects are perpendicular to the coast, with stations at 2, 4, 10, 20, and 40 miles from the shore, and were fished 5 times in the period from May to October 1982. Oblique hauls were made from approximately half depth to the surface; volumes taken varied from 487 to 9,352 m^3. In 1983 a transect with 24 stations, beginning in the Wadden Sea, going westward to 4° E, then first north-north-east, and later north to 55° N, crossing the Frisian Front (Creutzberg, 1986; Creutzberg et al. 1984), was made 6 times between February and October. The net was now equipped with a net-probe, and oblique hauls were made from about 2 meters over the bottom to the surface; volumes of the hauls varied between 42,505 m^3 and 421 m^3. Incidental observations by Kuipers (1985) using a mysid net were most interesting. The mysid net has a rectangular opening of about 39 x 15 cm^2; length of the net is ~ 4 m. The net can be mounted under the beam of a small beam-trawl, at variable small distances above the bottom, and is fitted with a current meter.

Russell (1925, 1926, 1927, 1928) caught *Pleurobrachia* with a 2 m diameter ring trawl of stramin, with 16 meshes to the inch, as a by-catch in his studies on the eggs and larvae of fish, on a number of stations to the SSW of Plymouth, Great Britain (Fig. 7) in water depths of 50-75 m; data of horizontal tows of 10 minutes duration, at 2 knots, estimated as ~1,700 m^3 at each of 5-6 depths are given. Depths of the tows were registered by means of a depth recorder. The data of a 15 months-long weekly series of oblique hauls at station A, at 2 miles to the east of Eddystone, in ~50 m deep water are in Russell (1933). Here he fished hauls of 30 minutes; Southward (1970) estimated the volume filtered at ~ 4,000 to 6,000 m^3.

A survey of the southern North Sea by Tungate (1975) between December 1967 and June 1968 covered the area between the Channel Islands and latitude 55°37' N; longitude boundaries of the programme were 0°45' W and 7°45' E. As the programme followed the migrating stock of plaice larvae, to study the predation on those by chaetognaths and *Pleurobrachia*, the area sampled shifted during time. Altogether 967 samples, of which 509 did contain *Pleurobrachia*, were taken with a multiple Lowestoft plankton torpedo (Beverton and Tungate, 1967) fitted with 275 μm filter, in double oblique hauls to 2 m over the bottom, ships speed a constant 5 knots. A distance of up to 1 nautical mile would be covered on each haul, and thus a haul would last 12 minutes and take ~ 240 m^3. The report contains the data of a limited part only of the total area; viz. the area fished in all 10 cruises; this area is called the "ecological box", and is located between 2° E and 4°30' E, 51°45' N and 53°45' N. The data are given in the form of 10 small maps of the ecological box, with shadings representing the density of *Pleurobrachia*.m^{-2}. However, there is no legend to the shadings used (it is: blank means no *Pleurobrachia*, and increasingly dense shadings are used for densities of 1-3, 3-9, 9-27, 27-81, 81-243, 243-729 and >729 *Pleurobrachia*.m^{-2}). For the present paper original data-sheets were made available. The counts as numbers.m^{-3} will be used, as the depth values of the stations, used by Tungate to calculate the numbers.m^{-2}, have rather large variations for single stations between cruises, and thus add to the total variation. This extra variation could falsely be attributed to patchiness (cf. Cushing, 1962). In the present paper data of all stations will be used.

Pleurobrachia was studied by Van der Veer and Sadée (1984) in 2 tidal gullies in the western part of the Wadden Sea, at stations 5 - 10 m deep (stations 1, 2 3 in Fig. 1), during February – August 1981 and February - December 1982. Usually one to four ebb and flood periods were sampled every week, and on each tide at least 5 hauls were made; in 1982 391 hauls were made. The duration of the double oblique hauls varied from 10 to 45 minutes, depending on current velocity, providing samples from 300 to 2,000 m^3. Haul volumes were measured by means of a current meter in the net opening; a second net-independent current meter allowed for the determination of net efficiency. Numbers counted were corrected for net efficiency and converted into numbers.1,000 m^{-3}. Mesh size of nets was 2.0 mm. Subsamples were taken to determine a size distributions in mm. The original dataset for 1982 has been used for figs. 26, 27 and 28 of the present paper.

Williams and Collins (1985a) studied *Pleurobrachia* in the Severn Estuary and the Bristol Channel from November 1973 to February 1975. They made 11 cruises on a grid of 58 stations, with a between-station distance of about 5 miles, and made at each station a double oblique haul with a 20″ diameter Lowestoft high-speed plankton sampler (Beverton and Tungate, 1967) fitted with a 280 μm mesh nylon net (see also Williams and Collins, 1985b, and Collins and Williams, 1981), to "provide a zooplankton sample integrated over the whole water column". Hauls had a length of approximately 1.85 km, at a ship speed of 3 knots. The theoretical volume of water filtered was therefore $\sim$ 190 m^3. Estimates of the volumes of water filtered were corrected for sampler efficiency (Harding and Arnold, 1971). The positions of the stations have been corrected for tidal excursions (up to 25 km at spring tide), using a computer program based on Admiralty tidal data. Data on numbers of *Pleurobrachia* are given in Williams and Collins (1985a) as density contours, and in Williams and Collins (1985b) in five logarithmic density-classes (from 0 to 100.m^{-3} for individual stations. The first paper gives separate results for juvenile *Pleurobrachia* <5 mm) during 6 surveys, and data for adults (>5 mm) for 11 surveys.

This compilation of the methods used by these authors, is a clear illustration of the saying "so many men, so many opinions"; all authors were convinced that their own method was the most suitable to sample the population of *Pleurobrachia*. Whether or not they were right in that belief remains to be seen!

3. Results

The data, obtained in the western part of the Wadden Sea in 1982 (see 3.1) led to a review of the results of authors cited; to do them their due it is necessary to sum up their results fully, as a large part of the data had not been published before (Van der Baan, 1980; Tungate, 1975; Kuipers, 1982, 1983; Klein Breteler, 1971). Furthermore my conclusions are often at variance with theirs. Keywords in this exercise are: patchiness, (maximum) population density, the sudden fast increases in density and neritic distribution. Authors will be treated in chronological order.

3.1. Pleurobrachia in the large channels of the Dutch Wadden Sea.

The data collected at three stations in the main channels of the Western Wadden Sea in 1982 have been used to study the changes in density and patchiness. Table 1 gives dispersion parameters *k* for stations and depths. The dispersion parameters show that the distribution of *Pleurobrachia* was usually logarithmic; only the deep sample in Texelstroom had a more or less Normal distribution.

The numbers of *Pleurobrachia* near the surface were systematically lower than those near the bottom (Figs. 4-6) and the numbers change with the tide. The mean values over the tidal period, for stations and depths, are in Table 8.

On Texelstroom (Fig. 4), between 8 and 11 h, on the last part of the flood (upper graph) the numbers near the surface increased from 10 to 30.m^{-3}. In the same period the numbers near the bottom (lower graph) diminished from over 25 to about 4.m^{-3}. At the turn of the tide, just before 11 h., the numbers at the surface decreased to 5.m^{-3}, and the numbers near the bottom start to increase. During the increase of the ebb current the number caught near the surface increased to about 10.m^{-3} and subsequently diminished to 0.m^{-3} at about low tide. During the following flood period, beginning at 17.15 h., the catches near the surface increase, from zero to about 10.m^{-3}, more or less parallel with the increase of the current velocity from 20 cm.sec^{-1} to 200 cm.sec^{-1}, while at the same time the numbers at 3 meters over the bottom decrease.

At the station Scheurrak-Omdraai, the numbers caught (Fig. 5) were generally lower than those on Texelstroom. However, at the surface on the flood between 7 and 10 h, the numbers increase, and subsequently, during the last part of the flood and the beginning of the ebb period, from 10 to 15 h, the numbers gradually decrease, and at 15 h no *Pleurobrachia* are caught in the surface waters. On the last part of the ebb, from 15 to 17 h, the numbers at the surface increase, in a smooth curve; and thereafter decrease again until nearly none are present at low tide at 18 to 19 h. Series of observations like this one are never long enough; but the beginning of the flood does show just one sample, at 20 h, with an increased number of *Pleurobrachia*, as was also found in Fig. 4. The numbers of *Pleurobrachia* in the samples taken at 2 meters above the bottom are generally higher than those at the surface.

The numbers of *Pleurobrachia* in the Doove Balg (Fig. 6) are lower than at the two other stations, with at the surface and near the bottom a mean number of about 2.m^{-3}. There are two remarks to be made. The first is a sudden increase of the density in the bottom samples, to 8.m^{-3}, at 11.45 h, and about one hour later this density is also found in the near-surface sample. Secondly, about 2 hours after high water the numbers of *Pleurobrachia* in the near-surface samples are very low, but with increasing current strengths of the ebb the numbers increase again in a curve very similar to the ones in Figs. 4 and 5.

At all stations there is thus a tidal variation in numbers; there is also a variation on a smaller scale, despite the sample size of 300 to 1,000 m^3.

Comparing the numbers of *Pleurobrachia*.m^{-3} at the three stations shows a diminishing of the density from the tidal inlet to the coast. The numbers on Texelstroom (highest value: 30.m^{-3}) do agree with the values found by Van der Veer and Sadée (1984; see 3.11) in the western Wadden Sea, and are somewhat lower than those found by Kuipers (1982; see 3.10) in the coastal waters of the North Sea in the same period. Going inward into the Wadden Sea the numbers of *Pleurobrachia* in the catches decrease. This cannot be explained by changes in temperature or salinity. From the North Sea inward the temperatures at the three stations increase, from respectively. 12-14°C, to 15-16°C and 15-17°C, and the salinities decrease from 29-31 S via 25-29 S to 25-27 S. The salinity differences are too small to explain the differences in population density, and higher temperatures should give higher densities instead of lower (cf. Greve, 1970; Bigelow, 1924).

3.2. Mayer

Mayer (1912) was one of the first to note the patchiness of *Pleurobrachia*. His paper contains two relevant remarks: "it has been my custom to go out upon the ocean during periods of tropical calm, when the surface is unrippled", and "at Newport, Rhode Island, the surface of the sea is sometime covered with thousands of square yards with great submerged rafts of *Mnemiopsis leidyi*, the individuals touching one the other, and the same phenomenon occurs with *Pleurobrachia pileus* or *Bolinopsis infundibulum* off the coast of northern Maine". From these remarks I conclude that he never went far out to sea (tropical calm!), and hence *Pleurobrachia* was found in large numbers close to the shore, and can be very patchy.

3.3. Bigelow

Bigelow studied the plankton and the physical oceanography of the Gulf of Maine, U.S.A, in the period 1912-1925, and more occasionally a few adjacent areas (Georges Bank and New York Bight); plankton was sampled at 360 stations (Bigelow 1914a,b; 1915; 1917; 1921; 1922; 1924a,b (printed in 1928).

I hesitate to criticise the great volume of work of Bigelow, but the sheer size of the publications (~ 2200 pages) has led to contradictions, that cannot now be solved anymore. He usually notes which nets were used at a certain station, but not which net caught what. However, in Bigelow (1924a) is noted that it was known for a long time that *Pleurobrachia* occurs in the Gulf of Maine during the summer and the early autumn, but that nothing was known about the other seasons. He found them "in March, April and May very generally all around the periphery of the Gulf of Maine, but so closely confined to shoal water, that we took it only twice outside the 100 m depth contour, and there (on the shoals) it is locally abundant beyond all computation". In the following months *Pleurobrachia* extends its range offshore in the Gulf until "in midsummer and early autumn it is to be expected anywhere north of a line from Cape Cod to Cape Sable both near land and over the deep basin". *Pleurobrachia* was not found, at any season, over the southern deeps of the Gulf, in the eastern channels or over the eastern half of Georges Bank. However, in July 1912, no *Pleurobrachia* were found on 20 stations near the coast, in depths <50 fathoms, while in August 1912, 10 stations out of 26 in the same area were positive (Bigelow, 1914a). Of these, 8 were near the coast, and 2 over deep water (> 100 fathoms).

At three near-coast stations swarms were encountered; and although at station 40 a dense swarm was found, a few miles to the east there were no *Pleurobrachia* at all.

In the period from November 1912 - May 1913 (Bigelow, 1914b) 10 stations were worked 8 miles south of Gloucester in 35-40 fathoms. On November 20th many *Pleurobrachia* were found at a temperature of 9.2°C, and on December 4th a few in water of 7.9°C. During the rest of the period none were caught, at temperatures <7°C. During the period the water at all stations was well mixed, is clear from temperature and salinity profiles.

Bigelow (1915) sampled in July 1913 the area between New York Bight and Chesapeake Bay, and in August the Gulf of Maine again: "Although *Pleurobrachia* was widely distributed it was by no means uniformly abundant." Swarms were found off New York to Cape May: the 30 fathoms deep waters were "filled with it". The patches extended 25-30 miles seaward, in July and early August. South of Cape May they were much less common. In the Gulf of Maine *Pleurobrachia* was taken at half of the stations, generally along the coasts, and less in the deeper water in the centre of the Gulf. A swarm was encountered at the station on the German Bank, to the SW of Nova Scotia, in water of 31 fathoms. The swarms in the south, in July, reached the surface only once; at the other stations swarms were limited to depths below 5 fathoms, the water being 15-30 fathoms deep at stations of abundance. This happened during day as well as night. Also in the Gulf of Maine (and on the German Bank) the catches were usually made in deeper hauls.

From July-October 1915 Bigelow (1917) sampled 126 stations in the Gulf; *Pleurobrachia* was found at 17 stations, and of these 6 were on the German Bank and off the coast of Nova Scotia. In the 1916 cruises (Bigelow 1922) *Pleurobrachia* was found at 5 stations only, in August, in the New York area, in very small numbers. Bigelow (1924) then concludes: "that although *Pleurobrachia* does not depend on the bottom at any stage of its development, it is more neritic than oceanic in the Gulf of Maine", and that his records do not suggest that any definite ebb and flow takes place in the numbers of *Pleurobrachia* from season to season. Numbers may be smaller in autumn and winter, due to "the contraction of its area of distribution to the coastal zone as the winter advances".

Bigelow's papers show that *Pleurobrachia* is a neritic species; with a tendency of being close to the coast, showing a patchy distribution, and a fast increase in numbers in spring, and an indication for being missing in July and a second increase in numbers in August, just as in the North Sea. However, although he notes that the absence of positive catches of plankton may be just as well a valuable contribution, he does not give an explanation of the total absence of *Pleurobrachia* in his 24 stations in coastal water between 9 July and 7 August 1912, although the usual array of nets has been fished. And his remark on "*Pleurobrachia* being not dependent on the bottom at any stage of its development" makes no sense; this he did not show.

Earlier I noted that mostly no records have been kept as to which net caught how many *Pleurobrachia*, but there are useful data for the spring of 1920 (see Table 2). First of all it must be noted that of a total of 86 stations 30 only did contain *Pleurobrachia*, either at the surface, or in a vertical haul. The table shows that *Pleurobrachia* in this period was caught in surface hauls at 8 out of 27 stations, in numbers varying from "few" to "many". It is striking, however, that the numbers of *Pleurobrachia* in the vertical hauls are nearly always higher, and often much higher, than in the surface hauls. Further it must be noted that the largest catch in a vertical haul was made in a half depth haul at the shallowest station (28 m); and, further, that all large catches were made in relatively shallow water. All stations with depths > 100 m show very small catches. Thus, in addition to the earlier mentioned neritic and patchy distribution *Pleurobrachia* has also a depth distribution, and it is difficult to understand how a weak swimmer can maintain a depth distribution as indicated above in a very well mixed water column (cf. the temperature and salinity profiles in Bigelow, 1924b); an explanation follows later.

3.4. Russell (1925)

Russell (1925) fished on 15-16 July 1924, in the English Channel at station L 4 (Fig. 7) 5 series of hauls, each at 5 depths, and found no *Pleurobrachia*; this is to be taken that none were present, as a few *Beroe* were recorded. A similar observation was made on 17-18 July 1925 (Russell, 1928), when very few *Pleurobrachia* were found, and those mainly deep in the water. In 1926 Russell (1927) fished *Pleurobrachia* mainly at stations A and E (Fig. 7), and remarked: "This Ctenophore, when present, appeared rather inconsistent in its vertical distribution, being more or less irregularly distributed from the surface downwards". When they were numerous (July 1st) the depth of maximum abundance lay apparently between the surface and 15 m. And as to seasonal distribution: "While being very scarce up till May 19th, from June 4th onwards *Pleurobrachia* was relatively abundant".

The sudden increase in population density can also be observed in the approximately weekly catches in the period 4 February 1930 till 16 April 1931 (Russell, 1933) (Fig. 8); within a few weeks the numbers per haul increased by a factor 1,000.

All Russell's stations are close to the shore. As to the density it is remarkable that even the largest catch, 1370 *Pleurobrachia* per $\sim$ 5000 m^3 (0.27.m^{-3}), on 24 September 1930, is very low compared with values found by later authors in the coastal waters of the North Sea, and elsewhere. The lowest density observed is 0.000,2.m^{-3}. Moreover, there is twice a sudden increase of population density, in May and in September, while also, in contrast to the observations by other authors, the increase in September is the highest. Russell's data are too scarce to comment on patchiness, but the figure (Fig. 8) is suggestive.

3.5. Fraser (1963, 1966, 1970)

Fraser (1963, 1966, 1970) summed up the data on *Pleurobrachia* collected to the north and east of Scotland in the years 1925-1939 and 1946-1968. The data of the period 1925-1964 have only limited quantitative value. Regrettably, the omission to note the numbers of negative hauls makes the data less useful, as patchiness indices cannot be calculated. It is noted, however, that *Pleurobrachia* is patchily distributed (by observation of "top" hauls; in 1925-1964 of 1,000, in 1965 of 2,000, and of >3,000 in 1967, so there must have been quite a number of zero-hauls, in view of the low mean values).

His figure (Fig. 9) shows that the mean density *Pleurobrachia* over the period 1925-1964 has a minimum in February and increases to a small early summer peak in June, and, after a small drop in numbers, increases to a maximum abundance of 14 *Pleurobrachia* per haul in the late autumn ($\sim$ 0.02.

m^{-3}). In the years 1965-1968 accurate counts have been made, but again with omission of negative hauls, resulting in Fig. 10; maximum mean abundance in 1965 rises to nearly 0.7.m^{-3} in July, and in 1966 to 0.4.m^{-3} in October. Maximum abundance in single hauls are ~3.m^{-3} in 1965, and ~ 4.m^{-3} in 1967. Thus 1965 and 1966 have higher densities than earlier years; Fraser (1970) suggests that "it is clearly possible that the conditions of the previous winter may have an important effect upon the abundance of ctenophores during the summer months", and he cites Delap and Delap (1905) and Kramp (1913) who made similar observations. Of course, this suggestion of Fraser may be true in the sense Fraser gives to it, but I expect that it may be even more true in a different sense (see 4.2).

Thus, compared to other areas of the North Sea, densities are very low, patchiness is present, and the sudden increase in population density is variable: by about one order of magnitude for the mean over the years 1925 - 1964, by 2.5 orders of magnitude in 1965, but then over a period of a month, and of about the same order in 1966, but over a period of four months. Fraser is the first author with a long series of observations, but whether his remarks on the long term changes in population density holds will be seen in the discussion.

3.6. Van der Baan (1980)

The *Pleurobrachia* data from the catches of macroplankton at the light ship Texel in the period 1961-1966 were published by Van der Baan (1980) in a Table, reproduced here as Table 3. She concluded that *Pleurobrachia* density increases slowly from the beginning of the year, followed by a sudden peak of thousands per haul in Mayor June; after that peak *Pleurobrachia* disappeared from the catches. In 1963 and 1965, however, a few hundreds per haul were caught in September and/or October (although none were caught in the other years), and after that *Pleurobrachia* disappeared practically, to reappear again in low numbers in the catches in the second half of December.

An example of the standardised data of Van der Baan, in numbers.1,000^{-3} is given in Fig. 11, for 1961. The density varies from zero to a highest value of 1,846.m^{-3} (on June, 6, 1963). The data do show a high degree of patchiness, as is clear from Fig. 11, and from the frequency distribution of density versus number of samples for the period 1961-1966 Fig. 12). Also the values of the dispersion parameter *k*, calculated for every year and for every month indicate patchiness: of the 78 values calculated 76 had a value <1, indicating a logarithmic distribution, and hence patchiness (Southwood, 1966); January 1961 had *k* = 1,27, also indicating patchiness, and, for reasons not understood, January 1964 a value *k* = 8.25. Patchiness is thus outspoken even on a very large scale, as haul-lengths varied from 0.2 to 26 km, with a median of ~ 9 km. On the other hand, changes in density can be very abrupt. There are observations were a flood does carry a density of the order of 100 - 1,000 m^{-3}, while on the returning ebb the density is 0, but the reverse occurs just as often. Furthermore, patchiness occurs at all times of the year, and the degree of patchiness is fairly constant over the year; this is an indication that the process that generates patchiness is independent of population density.

The data do not allow for a conclusion to what extent *Pleurobrachia* is a neritic species, as all data were collected at the same station in 28 m of water; the highest density found, however, fits well in the range of data of other authors working in the open North Sea (Tungate, 1975; Kuipers, 1982, 1983; Greve, 1984) but is very low (1.8.m^{-3}) compared to the values found closer to the coast (Greve, 1984; Greve and Reiners, 1980, 1988; Kuipers, 1982, 1983; Van der Veer and Sadée, 1984; De Wolf, 1989, this paper).

The sudden increase of the population density in May shows differences between the years, as is clear from the weekly means (Fig. 13); in 1961 the increase is about 2 orders of magnitude in 3 weeks' time. The year 1962 is a very poor year altogether, with a maximum catch of ~ 100 to 1000 m^{-3}, and consequently also the sudden increase is only one order of magnitude, in one week. In 1963 the increase is large: 2.5 orders of magnitude in the first week of June. In 1964 the maximum population density is reached in the second week of June, with an increase of 2 orders of magnitude over a period of 3 weeks. The timing is the same in 1965, but here the increase is 2.5 orders of magnitude, and -surprise- 1966 is altogether different. In that year there is a slow but steady logarithmic increase from January, and there is an order 1 increase already in April, and a similar increase again in May (Fig. 14).

Two further observations must be noted here. After the sudden population increase the density drops to practically zero, which means that no *Pleurobrachia* >2 mm are present, although it cannot be excluded that smaller ones are. In the year 1963 and 1965 there are a few small catches in September and October. In all years *Pleurobrachia* appears again in the catches in the last weeks of December; however it is striking that in most years they disappear again from the catch in the second half of January till mid-February, the coldest part of the year, although also in this respect 1966 is possibly anomalous. This could, however, also be due to the changed sampling-regime of 1966.

3.7. Tungate's report (1975)

Tungate's report (1975) contains the data for his "ecological box". The isoplethes in the figures on the distribution of *Pleurobrachia,* as numbers.m^{-2} (Fig. 15), suggest that more data are available than are used the report. Also, as patchiness cannot be calculated from the data read from the figures, copies of original data-sheets were made available by the MAFF -Laboratory, Lowestoft.

For our present purpose all data were used, and the area sampled was divided in three parts:
-Tungate's "ecological box", sampled in all cruises, and in some cruises with more than the standard set of stations.
-the area south of the "box", with a maximal extension to 49°37' N and 0°45' W, in cruise 2.
-the area north of the box, to 54°37' N and 6°45' E, in cruises 5 and 7.
A compilation of the data is given in Table 4; in this table a few exceptionally large values have been omitted. Two of these were in the southern area, both for the same station among the Flemish Banks, with 27.m^{-3} (cruise 1) and 129.m^{-3} (cruise 4), the station being at a distance of 17 miles from the Belgian coast in 27 m of water (Tungate's datasheets give a depth of 27 m, but the sea chart indicates 9 fathoms). The third high value was at 8 miles from the Dutch coast (cruise 10), in 9 m deep water; with a catch of 97.m^{-3}, and the fourth (also during cruise 10), with 24.m^{-3}, was at 40 miles from the coast, west of Texel.

Inspection of Table 4 shows that there is a considerable difference between cruises in mean numbers of *Pleurobrachia*, during the first 8 cruises, even when the four hauls mentioned above are omitted; and the densities vary also between areas. The mean density in the southern area is 0.5.m^{-3}; in the ecological box 0.3.m^{-3}, and in the northern area 0.022.m^{-3}. Comparison of the ecological box and the northern area for the last 2 cruises shows that the box has a mean density of 2.2.m^{-3}, and the northern area 0.3S.m^{-3}. It must be kept in mind that even the mean value found by Tungate for the "ecological box" is higher than the highest density caught by Van der Baan (1980) at the L. V. Texel (in the area of the "box"!). The table shows further that in all three areas, and during all cruises, *Pleurobrachia* is patchy distributed; *k* values being usually <1.

The distribution of *Pleurobrachia* in the three areas does not give any information as to the question of it being neritic or not, all three areas being in the neritic domain. But it is remarkable that the 4 stations with a density larger than 20 *Pleurobrachia*.m^{-3} were all close to the coast, even in the period when the density over the whole area was very low.

The sudden increase of the population density in May - June could not be observed in the southern area as only a few stations were worked during the later cruises, and these few stations were furthermore immediately adjacent to the "ecological box". In the box the population density (Figs. 15 and 16) increased by 2.5 orders of magnitude between 30 April and 5 June, while in the northern area the increase commenced after 20 May; due to the lack of later data a conclusion about the size of the increase in the northern area is not possible.

Tungate noted that "the rapid increase (in the ecological box) was limited approximately by the 11°C isotherm". In the southern area the effect cannot be observed (Fig. 17), as there are no samples in the desired temperature range. In the ecological box the increase begins around 9°C, in the northern area it begins at 11.5°C. However also at higher temperatures there are many samples with low densities.

Summarising: Tungate's report and data show that *Pleurobrachia* is patchy all over the area. Whether or not *Pleurobrachia* is a neritic species cannot be judged, but a few high densities are found close to the coast. Further densities are lower in deeper water, although the mean density given for the northern area might be an underestimate, as the sudden increase in that area lies largely outside the sampling period. Lastly, there is an indication that the sudden increase in density has a relation to the increase of temperature. However, the results of later authors are needed to fully appreciate this remark.

3.8. The German Bight.

Greve has published extensively on *Pleurobrachia* in the German Bight in the period 1968-1992. A review of all data collected in the German Bight is given in Greve (1992).

3.8.1. Population densities.

The results from the Reede of Helgoland in 1966-1968 (Greve 1969, 1971) show small differences in maximum densities between the years: in 1966 >20 *Pleurobrachia*.m^{-3}, in 1967 about 12.m^{-3}, and in 1968 ~ 18.m^{-3} (Fig. 18). However, Greve and Reiners (1988) show that the differences between years can be much larger, from a few to 70.m^{-3}. The data obtained at a number of depths in Nordhafen (Greve, 1971) are given in percentages of the total number of *Pleurobrachia* (Table 5). Absolute numbers were given for 27 May.

Usually the bottom haul has by far the highest percentage. Samples were taken at 9.00 o'clock, to exclude possible effects of diurnal vertical migrations. Greve looked for wind and temperature effects

as causes for this distribution, but did not reach a clear conclusion. Absolute densities on 27 May were: at the surface $0.14.m^{-3}$, at 10 m depth $0.65.m^{-3}$, and at 23 m $15.2.m^{-3}$.

The densities obtained with oblique hauls (Greve and Reiners, 1980) at stations in the open water of the German Bight, are higher than either at the Reede or in the Nordhafen, and are among the highest ever and anywhere, with a maximum of 753 *Pleurobrachia*.m^{-3}, nearly all in the size classes of 3-10 mm, at the station at a few miles from Helgoland.

The dataset on the larger part of the German Bight (Greve and Reiners, 1988) has been published as a three-dimensional figure only, without indication of the numbers caught.

3.8.2. Patchiness.

Fig. 18 illustrates the population development on the Helgolander Reede in 1966-1968 and suggests 1.5 - 2 orders of magnitude difference between successive samples, indicating patchiness; the dispersion parameter k was calculated for values taken from the figure in Greve (1969), k= 0.71. The Nordhafen data cannot be used to study patchiness in a horizontal dimension, but there is an indication of vertical patchiness, with a dense population near the bottom, although not on all occasions when sampled.

The original data Greve and Reiners (1980) do allow for calculation of the dispersion parameter for each of the cruises and for the size classes, see Table 6. Also here, over a large area with spacing between stations varying from 6-20 km, the distribution of numbers of *Pleurobrachia* is clearly logarithmic, indicating patchiness.

The figure that reports the distribution of *Pleurobrachia* in the German Bight in 1984 shows patchiness (Greve, 1985; Greve and Reiners, 1988). However, the lack of numbers and a legend makes it impossible to judge the result properly; the same, regrettably, holds also for the data of the Helgolander Time Series (Greve and Reiners, 1988, Fig. 10).

3.8.3. The increase of the population density.

Greve (1971) noted that in the years 1966-1968 a more or less identical development of the population density was observed: from March till the end of May there was a steady increase of the density. The figures shows that the increase is logarithmic, and the maximum densities are reached in mid-June 1966, in the end of May 1967, and in the beginning of June 1968. Also the figure for the period 1974-1982 (Greve and Reiners, 1988) from the Helgolander Time Series shows that maximum densities are usually to be found in June, and sometimes in July.

The same figure shows that the sudden increase can be very different from year to year, the maximum varying from a few to $70.m^{-3}$. In the fitted curve the patchiness has been smoothed away to a high degree, as is evident if the smoothed $70-m^{-3}$ is compared with the $753.m^{-3}$ individuals in a single sample, in 1979 (Greve and Reiners, 1980; see 3.8.1).

Examples of the population densities in Greve and Reiners (1980) are given in Fig. 19. The increase in population density is clear; it occurs between cruise 2 (14 May) and cruise 3 (5 June), amounts to a factor 100 to 1000, and, in the period between 5 June and 25 June, has a further increase by a factor 2 to 3. It must be noted that while at some stations cruise 4 has the highest population density, the majority of stations have the highest values in cruise 3, and a few do show hardly any difference between cruises 3 and 4. However, the differences in the population density between the stations in cruise 3 and 4 is never more than a factor 2 to 3.

It is most remarkable, in Fig. 19 that all size classes do increase simultaneously. This make it hard to believe Greve's suggestion that the reproduction and growth are responsible for the density increase, for than a population wave in time would be expected starting from the low numbers for all size-classes (as in cruise 2). First there would be an increase in the small sizes and gradually the larger size classes would grow into the catch. This is not seen in any of the stations.

3.8.4. Neritic or coastal.

Whether *Pleurobrachia* is a neritic or a coastal species cannot be derived from the data of Greve and Reiners (1980), as the greatest depth in the area is 45m, and the stations were taken in depths from 3 to 23 m. At all stations high densities of *Pleurobrachia* were encountered, even to a distance of 40 miles offshore.

The data of Greve and Reiners (1988), taken in a much larger area than those of 1979 and although published in a summarily manner, do hold an indication of a coastal distribution: on the northerly and westerly edge of the area, where depths are generally over 40 m, always low densities are found. From the figure cannot be judged how low the values are.

3.9. The Californian coast (La Jolla Bight)

Hirota (1974) is probably the first author writing on *Pleurobrachia* without using the word patchiness; the nearest he comes to it is "variability" or "swarm" (but then for different, although allied, species; and in other areas). Secondly, Hirota discusses whether or not *Pleurobrachia bachei* is the same species as *P. pileus*, and is of the opinion that it is separate species. Nevertheless, its properties as to patchiness, distribution, and sudden increase of the population density do show hardly any differences from those of *P. pileus*, in other areas. There is one difference: in the vertical distribution; there is an indication, according to Hirota, that *P. bachei* has a diurnal vertical migration, but I consider this doubtful. Hirota further published a graph, relevant for tidal influence on the numbers of *Pleurobrachia* caught.

3.9.1. Neritic occurrence

The neritic area along the Californian coast is very small; the 250 fathoms isobath is located at about 10 km from the shore at most, and in La Jolla Canyon even less. Hirota remarks that the coastal water stretches from the shore to a distance of about 8 km, and that coastal is equivalent to neritic. Highest abundance's of *Pleurobrachia* are found, however, in a zone of 3 km adjacent to the shore, as follows from 7 transects perpendicular to the shore. Six of these consisted of 3-5 stations, and lengths of the transects varied from 7 to 13 km; the transects were about 3-8 km apart. At transects taken in places where the shelf is small, numbers of *Pleurobrachia* at the station nearest to the shore were 600-700.100 m^{-3}, and diminished seaward to 20.100 m^{-3}. In transects where the shelf is (a bit) wider, the numbers are an order of magnitude lower, and maxima are usually further away from the shore, but also here the numbers diminish over deeper water.

The transects to a distance of 50 km from the shore consist each of about 16 stations, and show values between 500-2000.m^{-3} near the shore, diminishing to zero at 50 km from the shore. There is a difference between these 2 transects, the transect near Scripps Institute showing a logarithmic decrease seaward, and the other transect has a logarithmic decrease near the coast, and at 30 km from the coast a 10 fold increase, probably due to advection by the coastal gyre. From these observations follows clearly that *Pleurobrachia bachei* has a coastal distribution.

3.9.2. Patchiness

Notwithstanding the replicate samples of the bongo nets used, the sample sizes of 5-50 m^3, and the remark: "Present field sampling techniques in plankton studies are often such that it is not possible to obtain sequential samples from the same target population", Hirota appears not to have bothered about the patchiness encountered. Patchiness is evident, in the first place from the use of log scales for the numbers of *Pleurobrachia* in all figures, and secondly from the wide ranges between replicate hauls. This is illustrated in his figure on the seasonal variation in numbers, for the period 8 March 1970-2 June 1971, from 6, 5 or 3 stations at 1.6 km from the shore. There is in these data a wide range around the median abundance, of the order of one-fifth to five times the overall median. Or, on 8 March 1970 at one station, the numbers caught were 7, 10, 60, 100, 102, 104 and 140 under 1 m^2, and at the same station, on 1 April 1970 the numbers varied between 0 and 80. Actually, the "values from different stations were in several instances closer to each other than they were to their respective replicate sample". For this reason the sampling program was during the year reduced to 3 stations; this could very well have had an effect not bargained for by Hirota: the low median value in the second year may well be owing to the small number of stations.

3.9.3. The variation of the population density during the year

The variation of the population density during the year does not show the several orders of magnitude increases reported by other authors, nor do the smaller increases occur in very short periods. Using the median densities for all stations there are increases of one order of magnitude in April-May and in the second half of August, and there is a slightly larger increase in January - February. Maximum population densities encountered can be derived from the data of the transects made for the offshore distribution: 1 sample with 900 - 1000 *Pleurobrachia*.100 m^{-3}, and 2 samples from the seasonal variation study, with 1000.m^{-2} at a depth of about 10 fathoms, to be taken as 50.m^{-3}. These three samples were taken at the same station.

3.9.4. Vertical distribution

Hirota found *Pleurobrachia* mainly in the upper 50 meters at all stations, and from a limited number of data concludes that there are indications for a vertical migration, from a median depth of 15 m during day time to a median depth of 30 m at night. However, although these data were collected while following a drogue, there are in my view sufficient reasons to reject this.

The first is given by Hirota himself, in his remark on the impossibility of sampling the same water mass in sequential samples (see 3.9.2). The second is to be found in the magnitude of the difference of the densities at the depths sampled: these density differences are small in comparison with the patchiness differences. Thirdly, the diurnal vertical migration alleged would be a reverse vertical migration, with high densities in the surface layer at night (Ohman, 1990; Hutchinson, 1967) and last but not least, Hirota gives a much larger set of data in his figure on the relation between abundance and tidal height (see 3.9.5.); if this last relation is true, the supposed vertical migration can be a tidal effect. Also, the times spent in collecting the samples makes a distinction between time and tide impossible. Furthermore, lines illustrating the thermoclines suggest that different water masses have been sampled.

3.9.5. Tidal influence on density of Pleurobrachia

The figure from Hirota (1974) (Fig. 21) illustrates the density data collected during the year in their relation to predicted tidal height; these data are taken at stations in shallow depths, at 1.6 km from the shore. The slope of the line is significantly different from zero, and Hirota considers that result unexpected, as tidal currents are probably not the same at different locations along the coast. Nevertheless he makes a most significant remark: "the results suggests that over an annual average, abundance at any one time and place of sampling could be affected by as much as a factor four due to tidal variations alone at locations 1.6 km from shore", and "the average range due to tidal effects is about the same magnitude as the annual average difference between mean abundance's of stations 5 and 6". I shall return to each of these remarks in the discussion.

3.10. The Dutch coast

Just as in Hirota's data do the data collected by Klein Breteler (1971) contain an indication of a tidal effect on the numbers caught. Data are given for ship at anchor, on the transect perpendicular to the coast near Callantsoog in Fig. 22, and those with a towed net in the coastal water of the North Sea in Fig. 23. It is remarkable that only once (Fig. 22) several thousands of *Pleurobrachia* have been caught; in all other hauls the catch was at least an order of magnitude smaller. This large catch was made at 2 hours after low water, and thus during the fast currents of the flood. The data, collected with a towed net equipped with a current meter, show generally the highest numbers of *Pleurobrachia* in the deepest samples; only during the flood, at 22.30 h., the numbers in the samples taken near the surface and at a depth of 10 m increase, while the number in the catch at 20 m are lower. Temperatures at the time of sampling were below 11°C. Further Klein Breteler saved for the future a note on *Pleurobrachia* catches made by a student course in 1962: "during ebb and flood many more *Pleurobrachia* were caught than during slack tides".

Kuipers unpublished data for 1982 are in Fig. 24. On 10-13 May 1982 *Pleurobrachia* was found at all stations; the 2, 4 and 10 mile stations do have densities between 3 and 126 *Pleurobrachia*.m^{-3}. The stations at 20 and 40 miles have densities that are 2 orders of magnitude lower, thus with densities between 0.01 and 1.m^{-3}; exceptions are one station with less than 0.01.m^{-3} and one with more than 10.m^{-3}.

On 7-9 June 1982, this picture has changed. Over the whole area densities between 0.01 and 100 are encountered, and even in the coastal zone there are a number of stations with low densities, or no *Pleurobrachia* at all. In July and August no *Pleurobrachia* were caught, again with one exception, in July 1982, of 0.01-0.1.m-3; in October 1982, the situation is the same as in May and June, be it at a 2 orders of magnitude lower level: at the near shore stations between 0.01 and 1 *Pleurobrachia*.m^{-3} were caught, and further from the coast none, which means that a density < 0.001.m^{-3}.

On the northward transect in 1983 (Fig. 25) there are in February no *Pleurobrachia* in the Wadden Sea, and low densities in the North Sea. April has low densities in the Wadden Sea, and an increase in density near the coastal zone in the North Sea. Further from the coast, and going northward, no *Pleurobrachia* were caught, but near the Frisian Front and on the Oyster Grounds low densities are encountered; here the densities increase in May, and still further in June. In the part of the transect in the Wadden Sea there is equally a two orders of magnitude increase in May, but in the end of June most *Pleurobrachia* have disappeared from the Wadden Sea, while they still increase in numbers in the area of the Frisian Front. No *Pleurobrachia* are found in the Wadden Sea in September (but see Van der Veer and Sadée (1984), and par. 3.11), and in October small densities reappear in the Wadden Sea, while there are no *Pleurobrachia* in the North Sea.

The 1985 data of Kuipers and Witte are most interesting, although limited in number. They made comparisons of catches at a number of stations around the Meetpost Noordwijk, 7 miles from the West coast of the Netherlands, by using an Isaacs Kitt net, a vertical net and a mysid net; data are in Table 7. The data show that, in 5 out of a total of 7 cases where catches can be compared, the mysid net caught the highest density just above the bottom. Thus, Kuipers and Witte showed that *Pleurobrachia* is a coastal species, as the real high densities are found in the coastal zone and the Western Wadden Sea; in April, May and June there is also on the Oyster Grounds a population, in 30-40 m of water, that is about a 100 times denser than in the area around, but this population is still 100 times less dense than the coastal population. From calculation of the patchiness index follows that the data collected for the whole area, in 1982 as well as 1983, can be described by a logarithmic distribution, and this is also true for separate areas containing the coastal stations (2, 4, and 10 miles from the coast) and for off-shore stations (20 and 40 miles from the coast), as well as for the population on the Oyster Grounds. Furthermore this holds for every single cruise.

The sudden increases of population density are ample demonstrated by the data, in the coastal area, the Wadden Sea and on the Oyster Grounds; for the dense April-June populations in the coastal area and the Wadden Sea, and for the less dense autumn population in the Wadden Sea. The maximum population density encountered by Kuipers was 126.m^{-3} at a station 4 miles from the Dutch coast, in May.

3.11. *Small channels in the Western Wadden Sea.*

The data of Van der Veer and Sadée (1984) have been published as means of the catches over a week, and although the figure gives an excellent impression of the sudden increase of the population in the second half of April and the beginning of May in 1981 and 1982, the great variation between catches has been lost, due to the use of a linear scale. Therefore the data for 1982 have been plotted in Fig. 26 on a logarithmic scale; it shows that the means over a tidal period, either flood or ebb, have a variation of 1-1.5 order of magnitude, at all population densities.

The dispersion parameter k for days, stations, and tides with 5 or more hauls varies from 0.71 to 6.74, indicating patchiness during the tide.

Maximum population densities, as means over a period of a week, were 17,000.1,000.m^{-3} in 1981 and 14,000.1,000 m^{-3} in 1982; the maximum density in a single haul, on 5 May, was 49,500.1 000.m^{-3}.

As no temperature data have been collected during the fishing, a ten years mean value for the Marsdiep area for the period 1983-1992 has been used in Fig. 27 to show the effect of the 11°C. isotherm on the sudden increase of the population in the first half of May. Van der Veer and Sadée (1984) have published data on the size distribution of *Pleurobrachia;* for the present purpose their original data for 1982 have been used in Fig. 28 a(ebb) and b(flood), giving the percentage for each size class, for station 1 (Fig. 1).

It is striking that there are during the year hardly any *Pleurobrachia* in the size classes 6-11 mm. From the beginning of the year till May nearly all *Pleurobrachia* are around 4 mm, and only in the second half of April there are a few animals of 6-10 mm. Larger animals (>11 mm) are only occasionally seen during March and the first half of April, and then mainly in the ebb samples (Fig. 28a). From mid-April the small sizes disappear, and the impression is obtained that they grow in a very short period to sizes >11 mm. In the period from April till September there are hardly any animals in the small size classes; only a few animals of 12 mm and larger are caught. From September till November again a group of small animals is present, and as earlier there is no indication of growth of this group into the size classes of 9-11 mm. This group of small animals disappears from the catches in November, and the group of large animals (>12 mm) is present till the end of the year, and has the same slow growth as noted above for the small animals in the second half of April.

This pattern of growth during the year cannot be understood if all samples are taken from the same population; in the discussion it will be shown that there are reasons to believe that different parts of the population are caught. Summarising the work of Van der Veer and Sadée: there is a sudden increase of the population by 1.5 orders of magnitude in the second half of April, and this is clearly related to the temperature. The patchiness in the area is less outspoken than in the open North Sea. Maximum population densities found are lower than those in the coastal area of the North Sea. The growth pattern of *Pleurobrachia* in the Wadden Sea suggests that several different populations have been sampled during the year.

3.12. *Bristol Channel and Severn Estuary.*

The results obtained by Williams and Collins in 1973 and 1974 can be discussed on the basis of their published papers only (Collins and Williams, 1981; 1982) and Williams and Collins (1985a,b), as

their database has been lost. They note, that "the high tidal energy, combined with topography, produce a thoroughly mixed water column under all but exceptional circumstances, with extreme high turbidity and wide variations in salinity". Their samples have been taken at all stages of the tide, and in view of the large tidal excursions (up to 25 km at springtide), sampling positions have been corrected to the location where they would have been at the nearest high water. However, these values are not the same as the values that would have been obtained if the fishing had been done at high tide, as will become clear later (cf par. 3.12). There is no marked vertical stratification in the area sampled; further west, in the Celtic Sea, vertical mixing times are larger than 6 hours (Uncles, 1983; Uncles and Joint, 1983), leading to stratification.

The data on *Pleurobrachia* are confusing: in Williams and Collins (1985a) the geographical distribution and seasonal variations for small <5 mm) and large (>5 mm) *Pleurobrachia* are given separately, and in (1985b) the distribution and variations are given without indication of size of the animals. Further, in the first paper the data are given as computer drawn contour maps, and these maps do show, in a number of places, differences with the maps in (1985b). However, the maps in Williams and Collins (1985b) do not contain the small animals, and thus for the present purpose the data on large animals in (1985b) will be used, while the data on small animals will be taken from (1985a).

The data on the large *Pleurobrachia* (>5 mm) (Williams and Collins, 1985b) (Fig. 29a) do not allow for conclusions as to whether *Pleurobrachia* has a neritic or an oceanic distribution, but none were found when they fished in water deeper than 50 m (April, July, August, September, and February 1975); this indicates a coastal distribution. Further, in January the higher numbers are found in shallow water, and with a few exceptions the same tendency holds for the other months, except May and June, again indicating a coastal distribution. In May and June *Pleurobrachia* is distributed all over the area but in May the higher densities are in the area between the Northern shore and the 10.5°C. isotherm (Fig. 29b) and in June they are numerous everywhere in the area, with temperatures >12°C. at all stations.

The data from the figures do not allow for calculations of patchiness; however, in all months all five categories of density are present, and often numbers at adjacent stations differ in one or more orders of magnitude; this too can be taken as an indication of patchiness.

In June the whole area fished has a temperature of over 12°C, and the numbers caught are the highest of the year, although there is still a considerable patchiness. Thus, also in the Bristol Channel and the Severn Estuary the sudden population explosion is present in May, and again this has, as was found by Tungate (1975), a relation to temperatures at a level around 11°C. However, the highest population densities encountered (Williams and Collins, 1985a) are an order of magnitude lower than found by other authors in coastal waters: in June the maximum number of juveniles and adults was 10-12.m^{-3}.

Pleurobrachia <5 mm were recorded for 6 cruises between February and September 1974; in February the area sampled has a nearly even distribution with 0.1-1.0 animals per m^3; only along the coast in Carmarthen Bay, to about 10 km from the shore, numbers of 1.00-10.0 were caught. In April numbers of small animals are lower over a large part of the area, but those that are present appear to concentrate toward the Northern coast of the Channel, and toward the Severn estuary. This tendency can also be observed in May, while also the density of the small *Pleurobrachia* increases. In June, over large parts of the area, small animals are present either in high densities (1-10.m^{-3}), or are not found at all; it appears likely that they have grown larger than 5 mm. In August and September there are only a few localities with similar densities, all adjacent to the shores, and at all other stations there are no small *Pleurobrachia*. Thus, summarising, *Pleurobrachia* in the Bristol Channel and the Severn Estuary are not in any respect different from those in the North Sea, but the numbers are generally smaller .

4.   A discussion, combining the available data.

This chapter brings together the results into an unifying concept of the behaviour of *Pleurobrachia pileus*, as to patchiness, the mean population density, the sudden increases in population density and the neritic (or coastal) distribution. It will be shown that these four are related, and originate from one single mechanism.

4.1. Patchiness.

In the introduction it has been remarked that *Pleurobrachia* is patchy distributed, and in the review of the papers this has repeatedly been confirmed, either qualitatively (Mayer, 1912; Bigelow, 1924a), or quantitatively; either in a vertical direction (Mayer, 1912; Russell, 1927), or at the surface only (Fraser, 1963, 1966, 1970; Van der Baan, 1980). Later also in oblique hauls, with plankton-torpedoes (Tungate, 1975; Greve and Reiners, 1980; Williams and Collins, 1985a, b), or nets, (Kuipers, unpublished. results, 1982), and these authors believed that these attempts were sufficient for adequate sampling, although their data still do show patchiness. Hirota (1974) did not bother about patchiness in

his data, although he complains about the difficulties to obtain adequate samples, and Van der Veer and Sadée (1985) and De Wolf (1988, this paper) tried to reach adequate sampling by large numbers of samples and they still found patches.

All authors have been sampling waters that are generally well mixed, and it is not understood how a weak swimmer like *Pleurobrachia* succeeds in maintaining patches, against the dispersing effect of mixing. On the basis of the tidal stirring in western Wadden Sea (Ridderinkhof and Zimmerman, 1992) it has been calculated that *Pleurobrachia* at a density of $8.m^{-3}$, and thus with a mean distance between animals of 0.5 m, would have a mean between-animal distance of tens of meters, after one tidal period. This degree of mixing would destroy patchiness, and it appears unlikely that patches can be maintained by swimming, as this would necessitate a staying power of hundreds of meters per tide, as well as very accurate direction keeping possibility, and means of observation and orientation.

Therefore, it is thought that patches are formed passively, and that a concentration mechanism is necessary. Such a concentration mechanism has been shown earlier to exist for the cypris larvae of barnacles, by sinking to the bottom. Franks (1992) has shown that animals tend to concentrate at fronts, and after all, what is the bottom (or the surface) but the ultimate front. The sinking rate of the cyprids could be measured, and patches were thought to be formed by resuspension (De Wolf 1973, 1974); There are no data on the sinking rate of *Pleurobrachia,* but Klein Breteler (1971) noted that students courses (around 1962) had observed that *Pleurobrachia* disappeared (or at least was not caught) from the upper water layers during slack tides, and the supposition was made that they sank to the bottom. If this assumption is right, it must be possible to find *Pleurobrachia* on, or near, the bottom. Anderson (1974) tried to study the swimming behaviour of *Pleurobrachia,* as to depth, in an aquarium (depth 10.7 m, diameter 3.7 m), but his results are not consistent, and do show a large variation between repeated experiments.

Many cases of high densities of *Pleurobrachia* in deeper water layers have been mentioned (Bigelow, 1924; Greve, 1971; Klein Breteler, 1971; Tungate, 1974; Kuipers and Witte, 1985; De Wolf, this paper). However, all authors viewed *Pleurobrachia* as plankton in the sense given originally by Hensen (1887), and consequently there are in the literature only limited data of *Pleurobrachia* found on or near the bottom, just because hardly anybody looked for them there! However, the oldest observation is by Runnstrom (1931), who mentioned small *Pleurobrachia* from the "Fjordtiefe" in the Herdla and Hjeltefjord (Norway). Verwey (1942) mentioned that "Nicht nur die Medusen selbst sind (diese) Anhäufungen (near the bottom) unterworfen, auch die Rippenqualle *Pleurobrachia pileus* (O.F.Müller) wird bisweilen in so grossen Zahl mit den engmaschigen Schleppnetz gefischt, dass man wohl eine passiven Anhäufung am Boden annehmen muss. Fang or 117* vom 27 Juni 1939 enthielt ungefähr 30.000 Stuck dieser Art. Dabei mussen durch die grossen Maschen in vorderen teil des Netzes grossen Quantitäten hindurch gegangen sein". (Two remarks must be made. In the first place Verwey makes a mistake, as the number 117 carries a *, which means that a net with small meshes throughout was used at that station, and secondly station 117* is nearly the same as station 2 of Van der Veer and Sadée (1984), see Fig. 1). Duineveld (1990) reports large *Pleurobrachia* (~3 cm) from the bottom in the Outer Silverpit, south of the Dogger Bank, caught with a box corer at a depth of 44 m. The data of Kuipers and Witte for the coastal area of the Netherlands, obtained with a small mysid net fishing just over the bottom have been mentioned; they caught a maximum of 410 *Pleurobrachia*.m^{-3}, that is about 5 animals.m^{-2}. Many authors complained of large numbers of *Pleurobrachia* when fishing for other animals; among them Bergman (personal. comm.) who fished with a small beam trawl for plaice larvae in the western Wadden Sea. Beukema (unpublished data), when sampling with a van Veen grab to the north of Terschelling (Fig. 30) on 22 and 23 May 1973 found at 20 stations numbers varying from 0 to 400 *Pleurobrachia*.m^{-2} on the bottom. (And, incidentally, also patchiness in the numbers of *Pleurobrachia* on the bottom, as is clear from Fig. 30).

On the Dutch coast *Pleurobrachia* do wash ashore, mainly in periods with prolonged easterly winds. I observed the behaviour of *Pleurobrachia* in small tidal pools and tidal channels on the sandy beach and during bright weather the animals could be seen lying on the bottom. (It is rather difficult to see the animals in the water, from above, but the shadows of the animals on the sand bottom can be seen easily). I also observed that *Pleurobrachia* were transported in the small channels by currents of up to 10 cm.sec^{-1}; generally over distance of a few cm, just above the bottom, and every now and then bouncing on the bottom. Anderson (1974) tried to study the swimming behaviour of *Pleurobrachia*, as to depth, in an aquarium (depth 10.7 m, diameter 3.7 m), but his results are not consistent, and do show a large variation between repeated experiments. Anderson (1974) tried to study the swimming behaviour of *Pleurobrachia*, in relation to depth, in an aquarium (depth 10.7 m, diameter 3.7 m), but his results are not consistent, and do show a large variation between repeated experiments. Also the data of Tungate (1975) contain information on very dense populations on or near the bottom. At one station on the Flemish Banks (station 27) exceptionally high numbers of *Pleurobrachia* for the time of the year were caught with the plankton torpedo on two occasions (cruises 1 and 4). Tungate notes for this station a water depth of 27 m, while the sea chart gives a depth of 8 fathoms (=14.4 m). As the plankton torpedo

was towed with a speed of 5 knots, to within 2 m of the bottom, and although scientists are generally very careful with plankton nets and torpedoes in the neighbourhood of the bottom, it is not impossible that in these 2 cases the plankton torpedo touched the bottom, and picked up a number of animals out of a very dense patch of *Pleurobrachia* on or just above the bottom. Also for 2 other stations exceptionally high values were recorded, at an odd time of the year.

Thus, once being aware of the fact that *Pleurobrachia* might be on the bottom, the results of Jago et al. (1993) on seston, are applicable to *Pleurobrachia* as well; they also found that under conditions of suitable weather, the bed erosion rate was limited by the availability of suitable bed material. Read *Pleurobrachia* for "suitable bed material", and there is a further factor explaining the patchiness of *Pleurobrachia*, in the same way as has been used to explain the patchiness of barnacle cyprids (De Wolf, 1973).

The presence of *Pleurobrachia* on the bottom can further explain a number of observations that cannot otherwise be explained. An example is found in Bigelow (1924a): he concluded that *Pleurobrachia* "is a creature of the upper strata of water", while his data show (Table 2 of the present paper) that this at least is not true in March and the first half of April. Of course it is possible that he was impressed by the large numbers of *Pleurobrachia* caught in the surface waters, but he did not show that waters, deeper than those in which he fished, did not contain *Pleurobrachia*. Another example is given by Greve (1971). He noted (Table 5) that the part of the *Pleurobrachia* population in the water column caught with a bottom-net, is often, but not always, very large. Here, again, the observation does not fit the general opinion that *Pleurobrachia* is a plankton species, and Greve clearly did not appreciate the importance of the observation.

The observations in the Wadden Sea (Figs. 4-6) show that the numbers of *Pleurobrachia* in the water column (here represented by a series of samples taken at 3 m below the surface) do change in relation to the current speed. The numbers increase during the flood and it is taken that this is the result from the resuspension and mixing into the water column from animals that have been lying upon the bottom. A similar observation can be seen in Fig. 23, where Klein Breteler (1971) found a sudden increase, at a few meters over the bottom only, during the flood.

Earlier (De Wolf, 1973) the patchy distribution of barnacle larvae has been explained using a model for the non-stationary vertical distribution of a suspension during a tidal cycle (Joseph, 1954). More recently, however, Uncles and Joint (1983) estimated vertical mixing time-scales for the Bristol Channel, UK, and showed that chlorophyll a concentrations are well mixed throughout the year, and that this is a consequence of the short vertical mixing time-scales in comparison with phytoplankton generation times. As they considered phytoplankton production to be a tracer released at the surface, to be mixed downward and resulting in complete mixing, their results are applicable to *Pleurobrachia* as a tracer to be mixed away from the bottom into the water column. Uncles and Joint give a calculation for the time necessary for complete mixing. If "complete mixing" is understood to be the appearance of *Pleurobrachia* at the surface, their calculation describes the time necessary for the increase of *Pleurobrachia* numbers at 3 m under the surface in Figs. 4-6. Thus, the applicability of this equation is a further argument for the mixing of *Pleurobrachia* into the water column. Now, for continuity reasons, it is thought that the vertical mixing and sinking are cause for the generation of patchiness of *Pleurobrachia*. If *Pleurobrachia* rises from the bottom to the surface with a certain water mass in one place, than an equal water mass from the surface, without *Pleurobrachia*, must sink resulting in two neighbouring water masses with different amounts of *Pleurobrachia*: the result is patchiness.

During the tide the original patches are dispersed by ever smaller eddies (Rothschild and Osbom, 1988) and, also, the number of *Pleurobrachia* in the water column diminishes through sinking. Variability in currents owing to wind and tide further add to the changes of the patches.

Comparison of the densities of *Pleurobrachia* in the data-sets of Van der Baan, and Tungate gives a further indication and this time for the Southern Bight of the North Sea, that *Pleurobrachia* is generally more numerous in the deeper part of the water column. Also Hirota's figure (1974) on the relation between the stage of the tide and population density of *P. bachei* is an indication for the vertical mixing of *Pleurobrachia* into the water column.

Concluding, there is ample evidence that *Pleurobrachia*, although until now considered to be plankton, sinks and lives on or very close to the bottom in shallow seas during part of the year. The sinking to the bottom is a concentration mechanism, and tidal mixing produces patchiness of *Pleurobrachia*, a patchiness that later on is broken down, either partly or possibly wholly. A further argument for this mechanism can be derived from the density distribution of *Pleurobrachia*.

4.2. Population densities of Pleurobrachia.

The data on the density of *Pleurobrachia* in the North Sea do show a striking variability between areas, and certainly not a simple neritic distribution. As noted earlier the distribution is rather coastal than neritic. However, even along the eastern coast the differences between areas are large, as is shown

in Table 8. These data must be used with caution; the mean values are unreliable because of patchiness.

The differences between areas follow from the mean densities in the periods of low densities (July - September, and November - mid-April), as well as during the population explosions from mid-April till July. The differences can also be seen in the values of the highest density found, during the population explosions.

The mean values for population densities, during the period when the animals are numerous, increase from $0.05.m^{-3}$ (western Channel) to $1.1.m^{-3}$ (Southern Bight), to $35.9.m^{-3}$ along the Dutch coast, and $96.5.m^{-3}$ in the German Bight. A similar result is seen in the maximum values, encountered at any time, with $0.27.m^{-3}$ in the western part of the Channel, $24.0.m^{-3}$ in the Southern Bight (but $1.8.m^{-3}$ at LV Texel), $126.m^{-3}$ close to the Dutch coast and $753.m^{-3}$ in the German Bight. The low values at L V Texel might be explained from a mesh size of 1 mm, and might explain the difference in the data of Tungate (1975) and Van der Baan (1980). It is however plausible that horizontal surface tows taken are the cause, as all other values are from oblique hauls (Kuipers, 1982; Tungate, 1975; Greve and Reiners, 1980), and thus the difference is a further argument for a *Pleurobrachia* population staying longer periods near the bottom.

The mean values obtained when *Pleurobrachia* is less numerous give similar results. Areas further from the coast do have, even when *Pleurobrachia* is numerous, relatively low densities, *e.g.* the North Sea north of 53°45' has a mean of $0.35.m^{-3}$, and a maximum of $11.0.m^{-3}$; the area to the Northeast of Scotland has a mean of about $0.7.m^{-3}$ Fraser, 1970). Also the values at the stations at a greater distance from the Dutch coast are lower, with a mean of $10.1.m^{-3}$, and a maximum of $78.8.m^{-3}$.

The distribution of *Pleurobrachia* as found in the Dutch coastal zone imitates the distribution of suspended matter in the same area (Visser et al., 1991). This is a further argument for the sinking of *Pleurobrachia,* and once this has been accepted, several other phenomena become clear, as will be shown in the following. In front of the Belgian Coast a complex system of mud banks are situated. These Flemish Banks are built up through sedimentation in calm weather, while they are eroded during winter storms (Gosse, 1977; Eisma, 1981). This may explain the high numbers of *Pleurobrachia* found there by Tungate (1975), and also the large variations found by the same author between stations and in time, on the Flemish Banks. Other sinks of suspended matter in the southern North Sea are the Wadden Sea, estuaries, German Bight, Oyster Grounds and the coastal zone during periods of calm weather (Postma, 1981). In the small coastal zone of Scotland only a limited number of *Pleurobrachia* sinks during the winter, and during storms a large proportion of the population is washed away, to sink in deep water and never to return to the surface.

Thus, *Pleurobrachia* behaves as a large particle that sinks to the bottom during periods of quiet weather. Owing to tidal asymmetry, a cycle of sedimentation, resuspension, and subsequent tidal displacement exists (Postma, 1967; Dronkers, 1986), which leads in the long run to displacement to the sinks, as is furthermore demonstrated by the very high densities of *Pleurobrachia* in the German Bight.

Also the Wadden Sea is a sink for suspended matter, but contrary to expectation the population densities found for *Pleurobrachia* in the water of the Wadden Sea are not higher than, and not even as high as, those found in the coastal water of the North Sea. This follows also from Table 8: the coastal zone of the North Sea has 35.9 *Pleurobrachia*.m^{-3}, and the large channels of the Wadden Sea near the tidal inlet 14.4 *Pleurobrachia*.m^{-3}. Van der Veer and Sadée (1984) found in small gullies near the tidal inlet 6.8 *Pleurobrachia*.m^{-3}. In the same period and area, De Wolf (this paper) caught in surface as well as near bottom hauls, numbers that diminished from the tidal inlet in the direction of the mainland coast. The tidal gullies diminish in size in the same direction. The decrease of the population densities of *Pleurobrachia,* from the coastal water of the North Sea to the mainland coast of the Wadden Sea, is ascribed to mortality of *Pleurobrachia,* either by desiccation on the tidal flats at low tide, or by the high amounts of suspended matter in the inner parts of the Wadden Sea. This idea is in line with the observation of moribund *Pleurobrachia* found on the bottom in the sediment-rich mouth of the Dollard, a part of the Wadden Sea on the frontier between the Netherlands and Germany (De Wolf, unpublished observation).

The Wadden Sea is thus a trap for *Pleurobrachia,* and Fig. 24 (Kuipers: 7-9 June 1982) gives an indication that the coastal water losses an appreciable amount of *Pleurobrachia* to the Wadden Sea: the stations on both sides of the tidal inlet, in coastal water, do not contain any *Pleurobrachia,* whereas the stations at a greater distance from the tidal inlet do contain large numbers, as earlier.

The German Bight is also a pre-eminent sink of suspended matter, and has the highest densities of *Pleurobrachia.* Greve and Reiners (1980) explain this from hibernating *Pleurobrachia* in the estuaries along the German Bight, which are supposed to be transported in spring as a population-"wave" through the German Bight in a northward direction. However, the estuary-like Wadden Sea does not have young *Pleurobrachia* in winter (see Fig. 28), and the population-"wave" can be explained in a different manner (par. 4.3).

The population densities to the Northeast of Scotland (Fraser, 1963, 1966, 1970), on the Oyster Grounds (Kuipers, 1983), in the Central North Sea (Tungate, unpublished. data; Greve, 1985, 1988), as

well as in the Western part of the Channel (Russell, 1933) are much lower than the densities near the coast (see Table 8). (Kuipers found on the Oyster Grounds mean values that are much higher than those of Tungate, but then Kuipers did not sample early in the year, when *Pleurobrachia* is really scarce, and thus Kuipers means are artificially high.) The low densities in the more open seas will be explained in par. 4.3.

4.3. Population explosions.

The rapid increase of population density is known for nearly all places where *Pleurobrachia* has been observed but only Greve (1980) and Hirota (1974) have tried to give an explanation. Greve uses population dynamics (reproduction) and Hirota's solution is trivial: he supposes that the increase is due to advection (see 3.9).

In an effort to understand the population dynamics of *Pleurobrachia* at Greve's stations a simple growth model has been made by P. Ruardy (NIOZ). This model calculates numbers of *Pleurobrachia* in the five size classes (n1-n5), as observed by Greve and Reiners (1980). For each size class the number present on 1 May (in the model) is taken to be the mean of the data of the 1st and 2nd cruise. The modelled number of animals in each size class increases through growth and reproduction. The model has no mortality, this is left out for lack of data; the model is, in all respects a "worst case" model, and "worst case" is in favour of Greve's notion. Growth indices for an increasing temperature during time have been derived from Greve's laboratory studies on growth (Greve, 1972: Fig. 7), and temperature development during time from Greve's database. The time necessary for growth of animals from the egg stage to 3 mm has been extrapolated from Greve's figure, and is taken as 8 days at 20°C, 11 days at 15°C, 18 days at 10°C, and 22 days at 6°C. Reproduction has been taken as equivalent with egg production (which means that the time necessary for embryonic development is supposed to be zero; the animals start to grow immediately as given above). The number of eggs produced is known of two experiments only (Greve, 1972) to be 7,075, respectively 3,900 over a period of 17 days, for animals of animals of egg producing size (>5,5 mm) are supposed to produce the 5,500 eggs.17 days^{-1}. It is further assumed that all eggs develop until maturity. From this worst case model follows a doubling time of the population of $\sim$ 15 days, and this, of course, is insufficient to explain a population explosion of >2 orders of magnitude in 3 weeks' time. (There is a population explosion in the model, and but after >3 months; and, for reasons not understood, in the size class 5-10 mm.

The model makes it unlikely that the population increases can be explained from growth and reproduction, in Greve's case as well as in all others. A further argument against reproduction and growth as the cause for the sudden population increases is the simultaneous increase in all size classes (Fig. 19).

There is a different explanation for the sudden population increases, as follows. Tungate (1975) noted a relation between the higher densities of *Pleurobrachia* and the 11°C isotherm. Also Greve (1972) noted a temperature influence on the increase of numbers but this increase is not fast enough. Hirota supposed that the increase is a result from advection; this I have rejected in par 1.3. I postulate that the increase is a result from vertical mixing by the tide, followed by swimming. If a period of sustained swimming at a certain level in the water column is followed by a period of sinking [hop and sink behaviour (Hauri and Weihs, 1976] and the lengths of the periods of swimming are temperature-dependent a mechanism has been obtained which prevents the necessity for the animal to swim long distances, while at the same time the sudden density increases can be explained.

To test this theory the data of Van der Baan (Fig. 11), Tungate (Fig. 17), Greve and Reiners (Fig. 19) and Van der Veer and Sadée (Fig. 27) have been used. The horizontal surface-tows of Van der Baan (see 3.6) have a median duration of 5 h.50 min (Fig. 3), a large part of the tide. From mid-January till mid-February, the coldest time of the year, they do contain only very small numbers of *Pleurobrachia*. Earlier it has been shown that *Pleurobrachia* is staying on or near the bottom, and is resuspended by the tidal currents. This also happens in the present case but because of the low temperatures *Pleurobrachia* sinks rapidly to the bottom again, and even the long hauls do collect low numbers. Later in the spring, with slowly rising temperatures, *Pleurobrachia* is equally transported into the water column by the tidal currents, but now swims for periods that increase with temperature. As the reaction of invertebrates to temperature-rise usually follows a sigmoid curve, the numbers of *Pleurobrachia* in the catches increase faster with rising temperature until, at $\sim$ 11°C in the end of April or the beginning of May high numbers are present in the surface waters for a sufficiently long period to be caught.

The results of Tungate do not, at first sight, prove his idea that "the rapid increase of the population density is limited (in the ecological box) by the 11°C isotherm". In Tungate's figure (Fig. 15) there is an indication that the higher densities and the higher temperatures, in the middle of May, are in the southern part of the box, but in Fig. 17b there are hardly indications that the 11°C isotherm is relevant. In the ecological box the increase in density is rather at 9°C, and in the northern area there are no observations around 11°C, but the increases clearly at a temperature over 12°C.

Further remarks are related to the results of Van der Baan. Firstly, the densities in the "ecological box" do not increase gradually over the period December - mid-May, but are rather constant at a low density, and then increase suddenly in mid-May. The densities found by Van der Baan are generally much lower, but increase gradually from February onward. This can be explained by the difference in fishing methods of Van der Baan and Tungate: Van der Baan's horizontal surface tow of long duration, and Tungate's double-oblique haul of 12 min. duration, in combination with the proposed behaviour of *Pleurobrachia*. If *Pleurobrachia* is resuspended in a certain period of strong tidal currents, and thereafter sinks or swims during a certain period of the tide, a (nearly) tide-long horizontal tow will catch *Pleurobrachia* during that certain period, even if it does not catch *Pleurobrachia* during the rest of the haul; the mean density in this haul will therefore be low. A series of 12 min. long horizontal hauls, in the same situation, would often catch nothing at all, but sometimes would catch a high density. A double-oblique haul of 12 min. would catch an even higher density, as during part of the 12 min. it fishes in a higher density, as present in deeper water.

For the differences between Van der Baan and Tungate as to the densities in the coldest period of mid-winter, and as to the differences in the increase of the catches during the spring, a similar way of reasoning can be applied. The density in mid-winter, in Van der Baan's data, is 0.1-1.0.1000 m^{-3}, and the mean found by Tungate is - 30.1000 m^{-3} (from ~ 1.m^{-2}). The resuspension brings *Pleurobrachia* during a short period near the surface, before they sink again, and the double oblique haul fishes a longer time in a higher density. The differences in the increase during the spring are more difficult to explain, but follow the same line. Here the important moment is, that the resuspension of *Pleurobrachia* by the tide follows a pattern: the tidal wave, and the nets making the long surface hauls of Van der Baan are always present when the tidal wave of *Pleurobrachia* passed by. On the other hand, Tungate's short lasting hauls have only a limited chance of hitting the *Pleurobrachia*-wave, and although the catches are larger when they hit (see above), the chance of a hit is low, as *Pleurobrachia* does hardly swim in water of low temperature, and thus is suspended for a short period only.

Also the data of Greve and Reiners (1980) on population densities have been plotted against temperature (Fig. 20); these data have the advantage that during each cruise there were considerable temperature differences over the part of the German Bight studied, of up to 8°C.; during cruise 1 e.g. the highest temperature near the coast was 11.7°C, and the temperature near Helgoland was 3.6°C. It has been noted earlier that in the German Bight the sudden increase in population densities occurs at a later date than e.g. the Western Wadden Sea (Van der Veer and Sadée, 1984), in Dutch coastal water (Kuipers, 1982), at LV Texel (Van der Baan, 1980) and in the Southern Bight of the North Sea (Tungate's data, this paper Fig. 16). The timing found in the data of Greve and Reiners is however in agreement with Tungate's results for the area north of 54°37' N. Also in the German Bight it is clear that the sudden increases in population densities are a response to the temperature increase to 11°C.; the more so as the increases in population density follow the temperature wave, as it moves out from the coast to the open sea, as is clear from the figures in Greve and Reiners (1980). In this respect the stations in front of the Elbe estuary during the second cruise attract attention (Greve's Fig. 13, 1980); here a few stations have relatively high numbers of *Pleurobrachia* in an area where the other stations have low densities, and the stations with high numbers have temperatures over 11°C, and adjacent stations to the west, have low numbers of *Pleurobrachia*, at t <11°C. Fig. 20 shows that the size classes of 0-10 mm the sudden increase is indeed found at just over 11°C. It is clear that this does not hold throughout; in quite a few combinations of stations and cruises there is either a smaller increase or no increase at all.

Here again the same arguments are valid: the chance of hitting the *Pleurobrachia* wave is even smaller in Greve's case, as he made very short hauls. Further, there are indications that at temperatures >11°C. a higher proportion of combinations of stations and cruises shows the sudden increase for the smallest size class, and this proportion diminishes with size class; also, in the smallest size class, at temperatures over 11°C there are less low densities. This effect diminishes the larger the animals are, and for the 10-15 mm animals it cannot be observed. Such differences in effects of temperature on different size classes have not been noted before. Greve explained the population explosion in the German Bight by a population wave. moving or transported from the estuaries. where they hibernated, outward in a northerly direction. Of course. *Pleurobrachia* are transported by currents while they are suspended in the water column. but to prove a behaviour of *Pleurobrachia* as proposed by Greve would need more data, such as showing the presence of *Pleurobrachia* in estuaries during the winter.

The data of Van der Veer en Sadée (Fig. 27) also show the effect of the 11°C isotherm, but in mid-April (Fig. 26). The effect is not as clear as in the North Sea. but then the stations of Van der Veer and Sadée were in shallow water, and it is possible that they, at lower temperatures (7-8°C), caught many *Pleurobrachia* that were brought sufficiently high into the water column by tidal currents, while swimming on the part of the animals played a smaller role. In Fig. 28 the curious distribution of *Pleurobrachia* over the size-classes can only be explained by sorting by tidal currents, but the increase of density of the larger size-classes suggests a larger contribution of swimming at higher temperatures.

Further evidence for the influence of temperature on *Pleurobrachia* is found in the data of

Williams and Collins, and Russell. Fig. 29a (of Williams and Collins, 1985a,b) shows a large difference in population density between the northern and southern parts of the Bristol Channel in May; comparison with the temperature map (Fig. 29b) suggests an effect of the 10.5°C isotherm. In the case of Russell (1933) the sudden increase occurred between 29th of April and 7th of May, and temperature data for station E1 give values for mid-monthly means for April of 9.92°C and May of 11.51°C; also here the increase fits the 10.5°C isotherm. Of all datasets there is only in Russell's case (Fig. 8) a strong population increase in September, although it is possible that the increase is not as strong as it seems, as the maximum value is based on one single sample only. In the data of other authors increases of the catches at this time of the year are not so strong. Possibly this is due to the growing of the summer generation to a sufficiently great size (see 5).

Thus there is ample evidence, for the Central and Southern North Sea, as well as for the Channel and the Bristol Channel, that the sudden increase of the population density of *Pleurobrachia* has a relation to the temperature, and that swimming keeps the animals suspended in the water column.

4.4. Coastal, neritic or oceanic distribution ?

The coastal, neritic and oceanic distributions can also be explained from the principles given above. *Pleurobrachia* sinks like silt in coastal areas during periods when tidal and wind generated currents are weak are absent (De Wolf, 1973, 1988, this paper), and is resuspended by strong currents. Swimming by *Pleurobrachia* is temperature dependent; at low temperatures *Pleurobrachia* swims only for short periods, does not succeed to keep a certain depth, and slowly sinks. At higher temperatures *Pleurobrachia* swims for longer periods, and once brought to a given depth by tidal or wind currents succeeds to stay there for a longer period. At still higher temperatures *Pleurobrachia* swims still better, and now swimming prevents sinking, and in areas with relatively high temperatures *Pleurobrachia* even may reach the surface and form "rafts" (Mayer, 1912; Bigelow, 1915; cf. Franks, 1992).

In coastal areas and estuaries *Pleurobrachia* accumulates like silt during winter, in low temperatures, and every now and then is resuspended in strong currents (Greve, 1969; Klein Breteler, 1971; De Wolf, 1988); if a net is around at that moment they can be caught. The accumulation leads to high densities in areas rich in silt, not only on the bottom, but also by resuspension in the water. It may be difficult for *Pleurobrachia* to survive on a sandy bottom (Greve, personal communication; but see also Greve, 1969), but a silt bottom is different. Further, there is an example of the Trachymedusa, *Tesserogastria musculosa* living in the silt of the soft bottom of the Oslo fjord (Beyer, 1958). During winter; *Pleurobrachia* are transported with strong turbulence and storms from the coast to deeper water, where they sink, as e.g. at the Frisian Front. When the temperature rises sufficiently in spring, also at the Frisian Front *Pleurobrachia* is transported to the surface by tidal and wind induced mixing, and stays there some time by swimming.

Part of the dense concentrations near the coast are after resuspension advected away from the coast to sink in deeper water. Those that sink under the thermocline do never return to the surface, and those that did not yet sink are the neritic animals. The part of the *Pleurobrachia* population that sinks in an area with stratification, sinks into cold water. As stratification develops only in areas where the tides are not sufficiently strong (cf. Tett et al., 1992) *Pleurobrachia* cannot reach the surface anymore, as they cannot be resuspended, and they cannot swim strong enough because the deep water is too cold. Thus part of the population disappears from the surface to the bottom, and the part of the population that remains above the thermocline is low in numbers, as can be seen in the results of Fraser (1970), Kuipers and Witte (1983), Tungate (1975), and Greve (1988). Williams and Collins (1985a,b) sampled not far enough to the West of the Bristol Channel to be able to observe this (cf. Uncles and Joint, 1983).

Oceanic catches of *Pleurobrachia* are rare, as most of the population advected there will have sunk. However, a few stay long enough in the surface waters to be caught near Ascension, between Ascension and the Cape Verde Islands, or near the Seychelles (Moser, 1910), or Rockall (Fraser, 1970). Relevant is the remark of Fraser that oceanic *Pleurobrachia* are usually in poor condition, suggesting a long period of swimming. There are also observations, by Fraser (1963, 1966, 1970), Moser (1910), and Scoresby (1820), that contradict this hypothesis.

The data of Fraser (see 3.5) are remarkable for the aberrant behaviour of *Pleurobrachia*, but it can be shown that this is only apparent, and can be understood in terms of dispersal, as given above. Fraser's data show a low peak in the population density in June, and the maximum abundance is found in late autumn, and then this abundance is also not impressive; the mean population density is always very low, even in years with relative high densities. And where other authors find sudden large increases in population density, in the case of Fraser these are small, and not sudden either. It must be admitted that the increase in density in June coincides with the passage of the 11°C isotherm (Becker et al., 1986), but then this increase is also slight. Fraser (1970) notes that the previous winters may have an important effect on the numbers of *Pleurobrachia* during the following summers, and this could be true; for if *Pleurobrachia* has a behaviour as has been sketched above, sinking and maintaining position in the water

column by swimming to a sufficient extent only when the temperature rises to or above 11°C, than *Pleurobrachia* sinks to the bottom during each winter, and in stormy winters may well be transported to deep water, and be lost (cf. Tett et al., 1992). Furthermore, the Northeast coast of Scotland is rather steep, and the thermocline comes close to the coast. Thus there is only a small area where *Pleurobrachia* can hibernate and return to the surface, and a very large sink from which *Pleurobrachia* cannot return. This may explain the influence of stormy winters, resulting in low population densities. Close to the coast there may be a sudden increase of the population in June, but this cannot be seen in Fraser's data, as the many stations further from the coast, where no increase can occur, influence the mean values (see Fraser's Fig. 1, 1970).

There are observations from the polar regions that cannot be explained. Scoresby (1820) observed *Pleurobrachia* on the west coast of Spitsbergen. This observation was later confirmed by Rőmer (1903); in 1898, in ice free water to the west and north of Spitsbergen he observed *Pleurobrachia* on 19 out of 82 stations. *Pleurobrachia* was caught at a lowest temperature of 1,6°C (probably from near bottom (cf. Moser, 1910), but Römer published no methods). Moser (1910) reported *Pleurobrachia* at the winter station of Drygalsky's Gauss expedition, from March 1902 to March 1903, at approximately 65°S, 90°E. She considers *Pleurobrachia* numerous ("eine grosze Anzahl") but the actual number recorded is 18 individuals; this may be not so numerous, the point remains that these 18 *Pleurobrachia* survived (or reproduced ?) at near zero temperatures. Another example of *Pleurobrachia* living (or surviving ?) at low temperatures is given by Siferd and Conover (1992); they reported 1 single *Pleurobrachia* in ca. 250 hauls totalling ~50,000 m^3, in Resolute Passage (Canadian High Arctic) under 2 m of ice (from a statistical point of view this is single-individual patchiness (k=-0.005 !). It is to be regretted that Siferd and Conover did not keep track of this *Pleurobrachia*, as they noted considerable tidal currents under the ice. However, it is not known anymore at which depth this *Pleurobrachia* was caught. Altogether the numbers of *Pleurobrachia* in polar regions are very low, but it can hardly be assumed that they were advected from more temperate climates, and on the other hand it is difficult to see how they manage to survive.

There are further observations that are not understood but the data cannot be properly judged either. All authors cited so far have been working in waters with strong tides; attempts to falsify these result using data on *Pleurobrachia* in seas without tides, as the Mediterranean Sea and Black Sea were not successful. Quantitative data on *Pleurobrachia* for the Mediterranean have not been found, but there are -limited- data on the Black Sea. The papers by Nikitin (1924, 1929) contain data on the distribution of *Pleurobrachia* and show that the depth distribution is not uniform but do not allow any conclusion as to patchiness. However, they are suggestive for a vertical migration of *Pleurobrachia* during the year, in a tideless sea, in response to temperature. Nikitin (1924) published some data for August 1923, on the influence of temperature on *Pleurobrachia* and other species, and noted that *Pleurobrachia* was not found at the surface with a temperature of 22°C, did occur at a depth of 25 m, with a temperature of 14°C, and was more abundant at 50 m and 8.4°C. Nikitin (1929) illustrates the distribution of *Pleurobrachia* in a time-depth graph, and shows that *Pleurobrachia* is from mid-December till the end of April present in the whole water column from the surface to a depth of 125-150 m; in May they are no longer present in surface waters and in June they are present only below 25 m. In November they reappear in the surface waters. During the year *Pleurobrachia* thus occurs only at temperatures under 12°C.

The data of Vinogradov et al. (1985) for the Black Sea, do show considerable differences in depth distribution in the stations sampled, but *Pleurobrachia* generally is found at depths of 60-120 m. The data are insufficient for conclusions as to patchiness. It must be kept in mind that the data are limited, and that patchiness has not been taken into account, nor the fact that the limited amount of catches do not represent a process but a state.

5.   Seasonal distribution and life history of *Pleurobrachia* pileus.

Before summarising the results in the form of a life history, it must be noted that in my opinion *Pleurobrachia* is, for long periods of the year, not a plankton organism. In the literature there are ample indications that *Pleurobrachia* lives on or just above the bottom for long periods (see 4.1), and it is remarkable that earlier authors never came to this conclusion. As a result of this behaviour there are no *Pleurobrachia* catches that "provide an integrated sample over the whole water column" (Williams and Collins, 1985a), and that holds also for all samples on which the following life history is based. Some results that have been mentioned earlier will be repeated and there are a number of new points of view. The life history begins in the coldest time of the year.

In February there are only very low numbers of *Pleurobrachia*, but there are some, in the surface waters near the L V. Texel (Figs. 11 and 13); these cannot have been very small animals, as Van der Baan used a mesh size of 2 mm. Low numbers are also found in oblique hauls in the Channel, the Southern Bight and the central North Sea (Figs. 15 and 16). To the Northeast of Scotland the mean number of *Pleurobrachia* in February is the lowest of the year (Fig. 10), and also on the Helgoländer

Reede (Fig. 18) the density is low. No *Pleurobrachia* are caught in the Dutch Wadden Sea (Fig. 25), but at a few stations in the coastal waters of the North Sea very low numbers are found (Fig. 25). Very low numbers are caught in the smaller gullies of the Dutch Wadden Sea (Fig. 26), and these are animals of 3-5 mm (Fig. 28a). At most stations in the Bristol Channel no *Pleurobrachia* are found, but a few are caught in Carmarthen Bay (Fig. 29a). In the Gulf of Maine, *Pleurobrachia* was caught at a few stations only, and at temperatures < 7°C no *Pleurobrachia* were found at all. The data from the western part of the Channel (Fig. 8) are ambiguous; in 1930 there are a few *Pleurobrachia*, but in 1931 there are none. This is not because of a difference in temperature; as the *Pleurobrachia* does hardly swim at low temperatures, the chance that the net hits the tidal wave of *Pleurobrachia* is very small. From the limited data available it follows that in the winter by far the largest part of the population consists of small animals. In the western Wadden Sea they are 3-5 mm (Fig. 28a), and in the Bristol Channel the density of animals < 5 mm is an order of magnitude higher than of animals > 5 mm (Fig. 3a resp. 3b in Williams and Collins, 1985a).

   In March *Pleurobrachia*, in the western Wadden Sea, have not grown (Fig. 28a and b), in most areas the numbers increase. The western part of the Channel is an exception, Russell caught none in March 1930 nor in 1931. But to the Northeast of Scotland the long term mean doubles relative to February (Fig. 10). At the L V. Texel there is a small increase (Fig. 13), but this varies strongly between years. In the eastern part of the Channel, the Southern Bight and the central North Sea there is no increase in density (Fig. 16), at Helgoland there is a 2.3 fold increase in 1967 (but the only sample in March 1968 does not have a single *Pleurobrachia* !) (Fig. 18). In the western Wadden Sea the density increases, and the variation between samples also (Fig. 26); in the Bristol Channel there are less stations without and more stations with higher densities than in February (Fig. 29a). As there is no growth, it is unlikely that the increase in density is due to reproduction, and therefore the increase is thought to be due to an increased advection of *Pleurobrachia* from the bottom, and a higher proportion of the population swimming for short periods in the water column.

   In April the density in the western part of the Channel has increased from 0 to 10-20 *Pleurobrachia*.5,000 m^{-3} (Fig. 8); the long term mean value to the Northeast of Scotland declines a bit, but this is thought to be due to between-sample variation (Fig. 10). At L V. Texel there is again some increase in the weekly-mean densities, but the differences between years are larger than in March; and especially in April 1966 there is a large increase in the weekly-mean (Fig. 13). In the Southern Bight of the North Sea and in the central North Sea there is hardly any change in the mean density (Fig. 16), due to the very large number of samples with hardly any *Pleurobrachia*, and only a small number of samples with large catches (again, for the differences in the data of Tungate and Van der Baan see 4.3). Fig. 18 shows a small increase in the Helgoland samples. In April there are also *Pleurobrachia* in the deeper channels of the Wadden Sea (Fig. 25) (transported to the Wadden Sea by tidal currents, and originating from the coastal waters of the North Sea). There are low numbers at the Frisian Front, where on the silt bottom *Pleurobrachia* have been aggregated during the foregoing months, possibly even since the summer. In the smaller gullies of the Wadden Sea it is apparent that the numbers increase faster than at other places; because of the small depths the animals are suspended in the water column during a longer period of each tide. In the Bristol Channel there is a clear indication of transport of the animals towards the estuary (Fig. 29a), as is suggested for the Wadden Sea in Fig. 25. (This process can also be recognised for the < 5 mm individuals in Fig. 3 of Williams and Collins, 1985a). In April the small gullies of the Wadden Sea show a population of two size-classes: 2-5 mm and >12 mm. The lack of animals of intermediate sizes suggests that the larger animals are now transported to the Wadden Sea, originating from the coastal water of the North Sea, as mentioned above. The almost absence of intermediate size classes indicate that there are two different populations. Furthermore, laboratory experiments by Greve (1972) show that at the prevailing temperature (4 - 8.6°C) growth is too slow to explain the appearance of the >12 mm *Pleurobrachia*. Nevertheless is remarkable that the smaller size classes disappear altogether in the beginning of May. It cannot be excluded that a sorting mechanism separates different size-classes.

   In May there is nearly everywhere a large increase, of orders of magnitude, of the populations. This holds for the Channel (Fig. 8), for L V Texel (Figs. 11, 13) (but not in 1962, when a small increase occurred in June), for the Southern Bight of the North Sea (Fig. 16) in the beginning of May, and in the end of May also in the central North Sea (Fig. 16), and for the German Bight, but mainly in June (Fig. 19). In May a high density of *Pleurobrachia* in the waters along the Dutch coast (Fig. 24), and a considerable increase of the number of stations with *Pleurobrachia* on the northward transect (Fig. 25), albeit in low numbers. In the northern half of the Bristol Channel the numbers increase equally in May (Fig. 29a). For all these stations it can be shown that there is a relation with temperature, as has been suggested originally by Tungate (1975), although there are in some cases deviations from the 11°C. In fact values vary from 8 to 12°C; Russell's data fit to 10.5°C (see 4.3); the full data of Tungate result in 9.5 - 12°C (Fig. 17b), or 12°C (Fig. 17c); from the data of Greve (1980): 11.5°C (Fig. 20). In the small gullies of the Wadden Sea it is difficult to choose (Fig. 27) between 8 and 11°C, and the Bristol Channel

data (Fig. 29a) fit the 10.5°C isotherm. The explanation of these data does not follow from a direct influence of a temperature of 11°C on swimming or non-swimming, but follows from the interaction of sinking of *Pleurobrachia*, the tidal mixing into the water column and the water depth and the temperature-dependent swimming effort of *Pleurobrachia*. The size of the catch depends also on the place of the net in the water column. In deeper water the tidal wave does not resuspend the *Pleurobrachia* easily from the bottom, and the water-temperature is lower, and therefore the stations in deeper water (central North Sea) and in colder water (German Bight) have a sudden increase of numbers only at a higher (12°C) surface-temperature. At shallow Wadden Sea stations (Fig. 27) the tide mixes the animals over the whole water column, and even at lower temperatures (8°C), with a smaller swimming effort, they remain sufficiently long in the water column to ensure a large catch.

In the beginning of May the small size class (2-5 mm) in the small gullies of the Wadden Sea disappears (Fig. 28a,b), and there is during May no clear indication of growth of the larger (12-15 mm size) class. Both phenomena can only be understood if sampling from different populations is supposed. Greve (1971) supposed that small *Pleurobrachia* are transported to the open sea, to explain the sudden population increase; as has been argued earlier this is unlikely for two reasons. Firstly, it is difficult to think of a mechanism that imports a certain size-class at one moment and exports the same size-class 2 months later. Secondly, this needs a highly unrealistic mechanism by which - at the same time - small *Pleurobrachia* are imported and large ones are exported from the estuary. In view of the nearly complete lack of the size-classes of 6-11 mm, and keeping in mind the Wadden Sea serves as a sink for silt, it is thought that *Pleurobrachia* is imported by the tides into the Wadden Sea like silt, and the two size-class groups are two different populations imported at different moments from the coastal waters from the North Sea. In Fig. 28 a and b there are a few animals in the intermediate size-classes (6-11 mm), and it appears likely that these represent the growth of *Pleurobrachia* in the Wadden Sea; this would mean that there is only very little growth of *Pleurobrachia* in the small channels of the Wadden Sea. These data are in urgent need of confirmation, as they contradict the suggestion that *Pleurobrachia* is an important predator in the Wadden Sea (Van der Veer and Sadée, 1984). The data of Williams and Collins (1985a,b) are not suitable to test this. A further remark is that the small size-class does not reproduce in the Wadden Sea as Greve (1971) has shown that the smallest size for reproduction is 5.5 mm. Therefore the increase in population density (Fig. 26) results from the import from the coastal water of the North Sea, and further the population increase in Fig. 26 is not an indication for the size of the import, as there is a considerable mortality, by predation of *Beroe* (Greve, 1971) and desiccation on the tidal flats at low tide (Fig. 4-6; Van der Veer, pers. comm.).

In June there are still a considerable number of *Pleurobrachia* in the water column, but in the Channel the density decreases by a factor 10, and after mid-July no *Pleurobrachia* are caught (Fig. 8); at the L V Texel even before mid-June numbers are decreasing; however year-to-year variation is considerable (Fig. 13), but usually in the beginning of July they are down to < 0.1.1,000 m^{-3}. At Helgoland numbers in July are low (Fig. 18), although at the Helgoländer Reede not as low as elsewhere. At the stations in the German Bight the largest values are in the end of June, but in the last week of July none or hardly any are caught (Fig. 19). In the Dutch coastal waters none are caught on 13-14 July 1982 (Fig. 24), and in the end of June 1983 there are still a small number present at the Frisian Front (Fig. 25). In the Wadden Sea there are hardly any after mid-June (Fig. 26), and these are animals of 12-15 mm (Fig. 28a). In the Bristol Channel high numbers are present all over the area in June (Fig. 29a), and in July only a few catches of low numbers, and at most stations none were caught. It is generally believed that the population decrease is caused by predation by *Beroe* (Greve 1969, 1971). This was also observed in the Wadden Sea (station 4, Fig. 1), in the last week of June 1994, when the density of *Beroe* was > 1.m^{-3}.

In the literature there are no ideas on the whereabouts of *Pleurobrachia* in the period when none are caught; I think that small animals, resulting from reproduction of the June population, are on or close to the bottom, and so escape predation by *Beroe*, and cannot be caught by any net. These small animals will be transported by tidal processes close to the bottom, but their swimming effort is too small, even at the prevailing temperatures, to remain dispersed in the water column. They grow slowly, and the fastest growing animals form the small "population explosion" in September - October, as they are larger they develop a greater swimming capacity. The "population explosion" in the early autumn results generally in densities a factor 100 smaller than during the spring increase, with the exception of the Channel, where the catches in September till mid-October are the largest of the year (Fig. 8). The data of the L V Texel show that there are considerable differences between years: only two of the six years have a small population increase in the period of September until mid-October (Fig. 13). In the Dutch coastal waters there is, close to the coast, a small increase in end October (Fig. 24), comparable to the large channels of the Wadden Sea (Fig. 25). The small gullies of the Wadden Sea also have an increase, again a factor 100 lower compared with the spring increase, but at these shallow stations the catches remain at the September level till the end of the year (Fig. 26). It is thought that in the shallow water the animals are resuspended to a relatively higher level over the bottom and the oblique hauls have a

larger chance to obtain the catch. In the Bristol Channel the autumn increase is in August and September (Fig. 29a). There is no clear, separate, increase in numbers on the Helgoländer Reede (Fig. 18), but as in the small shallow gullies of the Wadden Sea (Fig. 26), the numbers remain high till the end of the year. The depth at the Reede is 6 m, and the tidal current carries *Pleurobrachia* from deeper water to the Reede (Greve, 1971), thereby mixing them into the water column, just as on the shallow stations of the Wadden Sea. During the period of relatively high densities in September and October in the western Wadden Sea there are mainly small animals in September (3 - 7 mm) and from the end September till the end of the year also large (>12 mm) animals. Thus, as in spring, there are two size classes, while the intermediate sizes are lacking (Fig. 29a,b).

The pattern that has been sketched can be explained as follows. The small animals that are present at all stations early in the year do grow slowly, and growth rates increase with increasing temperatures. The animals of the 2 size groups start to reproduce in March, that is to say: those >5.5 mm of the small size classes (1st cohort) and all of the >12 mm size group (2nd cohort). Of these, the egg production of the 1st cohort is low (small animals), and therefore this cohorts adds in the beginning only small numbers of young animals to the population. The 2nd cohort (large animals) produces many eggs, but the animals arrive later in the Wadden Sea; it cannot be estimated what part each of the cohorts contributes to the population. The first cohort grows during the spring to adult size, and falls prey to *Beroe* in June, but they must have reproduced already in April and May when there are hardly any *Beroe*. The second cohort also reproduces, and in July both cohorts consist of small animals that, for lack of swimming power, settle to and stay on the bottom. The first cohort consists of the largest animals, being born earlier, and these have therefore the best chance during the summer to grow; they grow to such an extent that they form the population increase in September and October.

The offspring of the second cohort develops slower, being smaller, and for a large part stays near the bottom; they are, during the period between September and March, transported like silt particles and therefore collected near the coasts, in the estuaries and in the German Bight. As this period is much longer than the summer period the concentration near the coasts is much more efficient than during the few summer months, and therefore the spring population increase is generally much larger than the autumn increase. Thus, *Pleurobrachia* can have 1 or 2 generations per year.

The explanations given above do not explain the results of Russell (Fig. 8) and Fraser (Fig. 10). Russell (1933) found a population increase in September higher than the one in spring; however, the densities caught in the Channel are nearly the lowest found (see Table 8), and each of the data points in Fig. 8 represents a single haul only. In view of the patchiness of *Pleurobrachia* it is assumed that this result of Russell is due to chance. The aberrant distribution in time of Fraser has be explained (see 4.4) as a result of a limited number of *Pleurobrachia* in the small area of shallow water near the coast, and the proximity of deep water which, because of stratification in summer, is a sink for *Pleurobrachia*. Fraser's stations are nearly all over deep water, and the *Pleurobrachia* caught are animals in the process of being advected away from the coast. The ratio between the deep area and the coastal area is large, and because of this the numbers of *Pleurobrachia* are low, and furthermore the number diminishes further as gradually more and more *Pleurobrachia* sink below the thermocline.

Concluding: whether or not *Pleurobrachia* is a plankton organism is a matter of choice. The argument pro is that at a high temperature they are in the water column (nekton); but the argument contra is that at lower temperatures they sink gradually to the bottom, and must be regarded as seston, or as epibenthos after arrival at the bottom. But on the other hand, if swimming is necessary to remain in the water column, this is an indication that they are nekton; and if they do not swim, they sink to the bottom, and then they can be described, following Drebes (1974) as "inverse tychoplankton", or are they tychoplankton? (Drebes defined this as bottom-living phytoplankton that live temporary as neritic plankton!). However, the original definition of plankton (Hensen, 1887) covers all these possibilities: "Ich verstehe darunter Alles was im Wasser treibt, einerlei ob hoch oder tief, ob todt oder lebendig." It is likely that the mechanisms described here do have a more general validity in well mixed waters, especially for other species of Ctenophores, but also for Scyphozoa, and possibly also for other plankton. Indications for this can be found in the distribution in time of *Mnemiopsis leidyi*; this species is the most common Ctenophore in Narragansett Bay, and shows sudden increases in numbers, in July or August, of 2 to 4 orders of magnitude (Kremer, 1976). Kremer made a simulation model following the same lines as Greve, and explained the increases from reproduction: "in the early summer, when the smaller zooplankton are abundant, the ctenophore growth and reproductive rates seem to be sufficient to account for the tremendous observed biomass increase". Kremer's model, however, supposes that the conversion rate from small zooplankton to ctenophore is 75 %, and this is rather high. Further, intensive sampling did reveal an overwintering population (in the plankton !) of $0.000,1.m^{-3}$. Although the model of Kremer is more complicated than the models of Greve and Ruardij (this paper), a lower conversion rate in Kremers model would give the same result as the Ruardij's model: a population explosion, but too late in the season. Therefore I suppose that also *Mnemiopsis* is living on the bottom during the winter, and in higher numbers than found by Kremer in the plankton.

Another example for a Ctenophore is given by Kamshilov (1960) off the Murmansk Coast in the White Sea. He observed *Bolinopsis infundibulum* in densities up to 400.m^{-3}, and also *Beroe cucumis* in large numbers. Both species were particularly abundant in shallow waters and in inlets, and there are indications that both species are more numerous near the surface in spring and summer, and the bottom in winter. And, as has been argued in the present paper, patchiness in well mixed waters requires a concentration mechanism.

There is also a well-documented example for patchiness and sinking for the Scyphozoa. Verwey (1942) trawled (1933-1939) in the western part of the Wadden Sea and in Dutch coastal water (hauls of 15 minutes) and found occasionally large numbers of *Aurelia aurita* and *Rhizostoma pulmo* (up to 400 respectively. 80.10,000 m^{-2}) on the bottom. Later (in 1964) he fished at three different depths during a number of tides, and found periodic changes in numbers of *Chrysaora hysoscella* and *Rhizostoma pulmo* (Verwey, 1966), with numbers varying from 1.haul^{-1} at the turn of the tide to 560.haul^{-1} at full flood for *Rhizostoma*, respectively 2.haul^{-1} and 91.haul^{-1} for *Chrysaora*. The figures of Verwey do show, moreover, that the maximum density of *Rhizostoma* during flood is near the surface, during the ebb current the maximum is only about halfway between surface and bottom. Verwey explained these results by swimming of the animals, induced or released by tidal currents with orientation on gravity and/or light, while arguing that the distribution of the animals in the water was not a distribution by turbulence, but he never realised the difference between the process and the result of turbulence. His data illustrate random stages of the process of turbulence in time, and Verwey expected the final result of turbulence after a long time: complete mixing of the animals.

A further example from the Scyphozoa is *Chrysaora hysoscella*, a coastal species in the south-eastern North Sea (Hay et al., 1990); this species, like all other coastal species, would be transported northward because of the residual tidal current, unless there is a mechanism to prevent this. And sinking like silt is sufficient to keep the species near the coast.

It is also possible that retention in estuaries is an apparent problem only. In well mixed estuaries silt is deposited and the same holds for barnacle cyprids (De Wolf, 1973), and for *Pleurobrachia* (this paper), and sinking is generally sufficient to ensure retention by tidal mechanisms. All swimming by plankton animals to ensure retention is useless as they are nearly constantly swimming against the dispersing effects of the turbulence of tidal currents.

Furthermore, it is difficult to see how such behaviour can have evolved, as in well-mixed waters there is a continuous exchange of surface and bottom waters by turbulence of tidal and/or wind currents. For continuity reasons an organism swimming upward, orienting on light or gravity has thus a 50% chance of being transported downward, and a 50 % chance of being transported upward. If light or gravity is the stimulus there is a discrepancy between the stimulus and the effect: if the animal swims to the light, or away from gravity, for 50% of the time the swimming in the desired direction results in being transport in the wrong direction. It cannot be understood how an organism could use a certain stimulus, if the result of the effort evoked is random because of turbulence. Even an Olympic swimmer like *Calanus finmarchicus* cannot cope with the mixing in the Southern Bight of the North Sea, and does not occur there (cf. Tett et al., 1993). In more general terms, the species in well mixed coastal seas, where no seasonal stratification develops during the year, are by necessity opportunists that can cope with the mixing process without spending energy on swimming.

6. Literature

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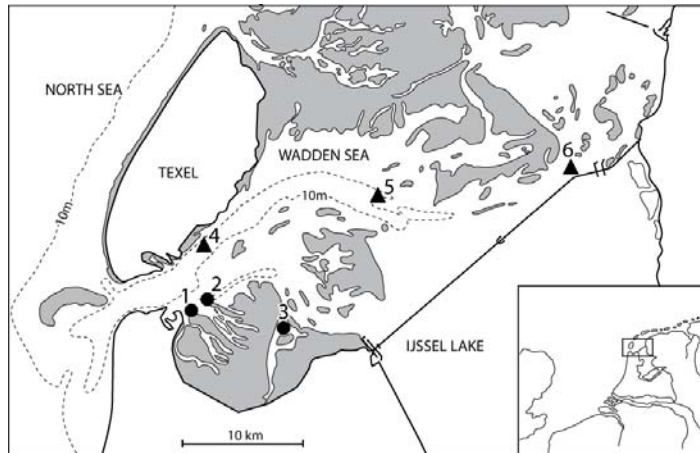
Figure 1.   Stations 1, 2, 3 of Van der Veer and Sadée fished in the western part of the Wadden Sea during 1982 (Van der Veer and Sadée, 1984) and Stations 4, 5 and 6 fished between 24 -26 May 1982 (De Wolf, this paper).
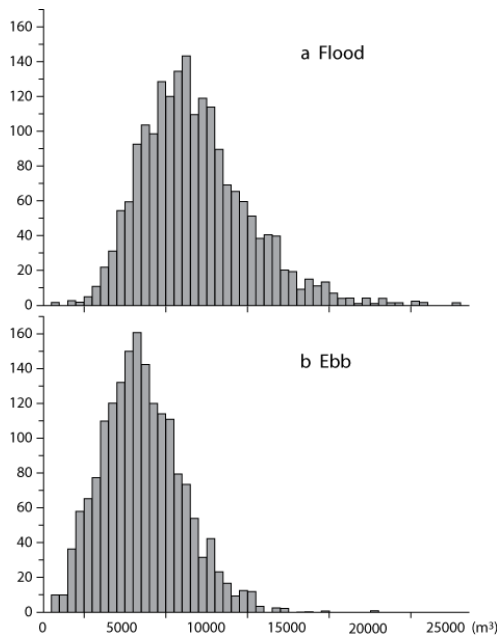

Figure 2.   Frequency distribution of volumes of catches, fished from the Lightship Texel, 17 January 1961- 31 December 1966, calculated from the original data of Van der Baan (Van der Baan, 1980) and data obtained by vertical log on tidal excursions for the same period (KNMI, 1964-1968); a. flood periods, b. ebb periods. X-axis: volume fished, y -axis: number of hauls.

37   Distribution, patchiness and population density in *Pleurobrachia*   P. de Wolf
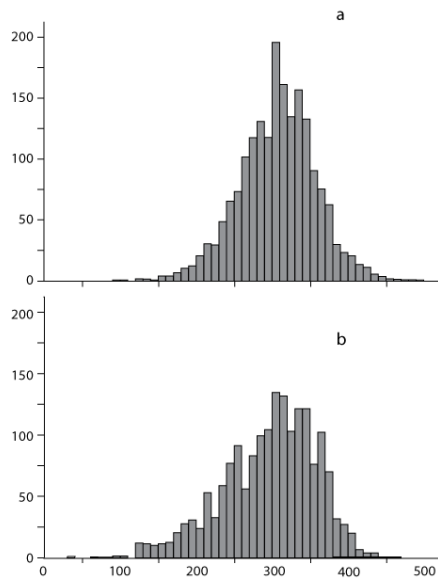
Figure 3. Frequency distributions of the duration of the hauls of Figure 2; a: flood periods, b: ebb periods. X-axis: time in minutes, y -axis: number of hauls.
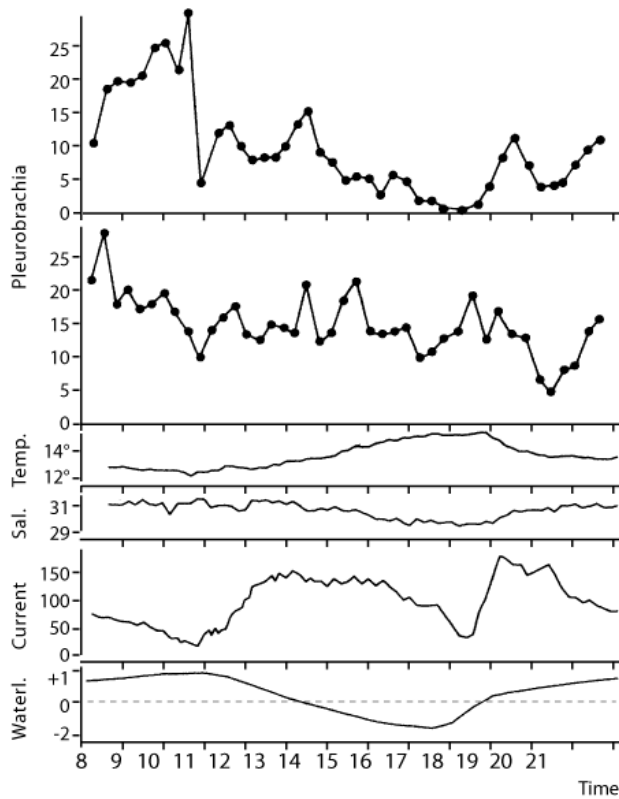
Figure 4. Numbers of *Pleurobrachia* pileus.m^{-3}, at 3 m under the surface (upper graph) and at 2-3 m, over the bottom (lower graph), fished on 24 May 1982 on Texelstroom (Station 4 in Fig. 1), between 8 and 21 h. Other graphs contain, from top to bottom, data on temperature, salinity, current strength and water level height.
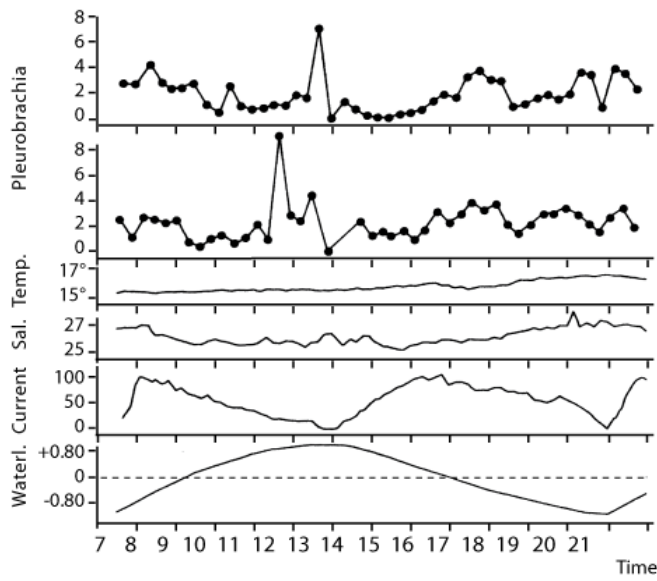
Figure 5.   Legend as for Figure 4, but for 25 May 1982 on Scheurrak-Omdraai (station 5 in Fig. 1) between 7.30 and 20 h.
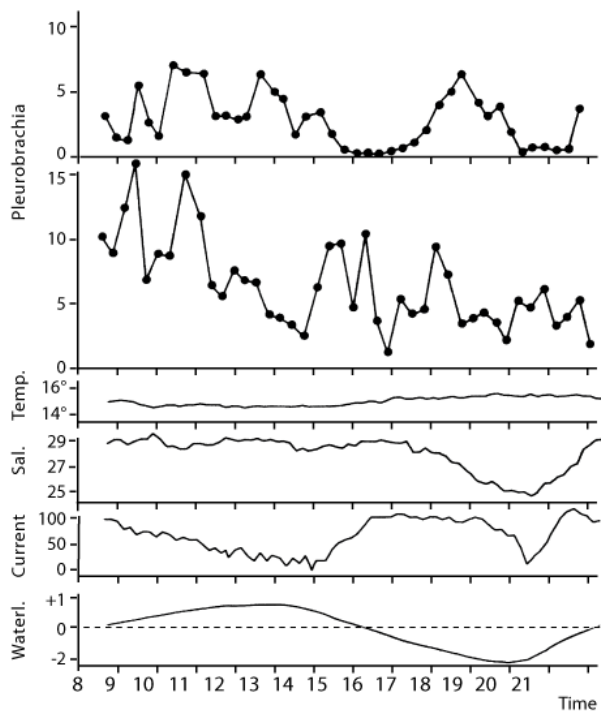
Figure 6.   Legend as for Fig. 4, but for 26 May 1982, on the Doove Balg (station 6 in fig.1) between 7.30 and 21 h.
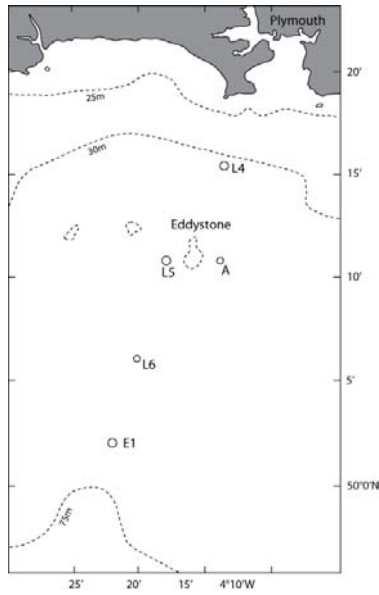
Figure 7.   Chart of sampling stations used by Russell (1925,1927,1928, 1933), off Plymouth.
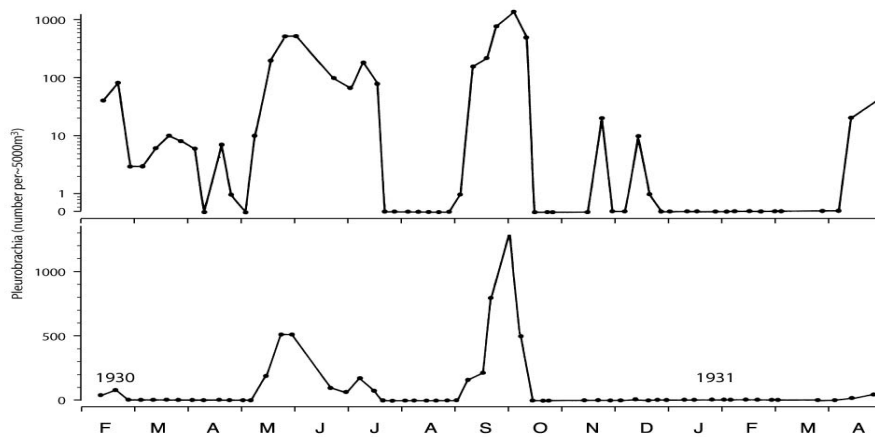
Figure 8.   Population densities in the English Channel between 4 February 1930 and 16 April 1931 (Russell, 1933). Data on a ^{10}log scale and on a linear scale to illustrate the difference; on the log scale the eye underestimates the size of the population increases in May and September, and on the linear scale the smaller variations between February and May, and in November-December, cannot be shown.
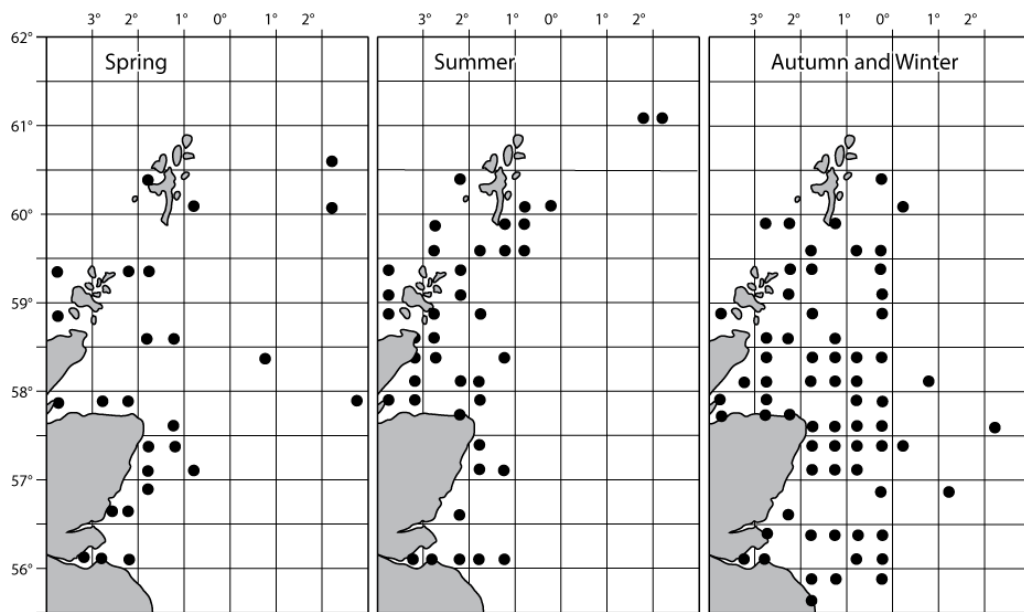
Figure 9.   Stations to the Northeast of Scotland, where "*Pleurobrachia* was common" i.e. > 40.haul^{-1} (Fraser, 1970).
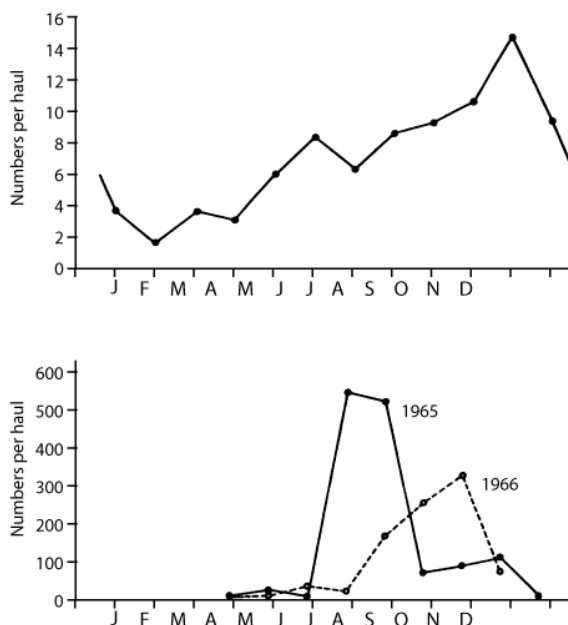
Figure 10.   Seasonal variations in abundance of *Pleurobrachia* pileus; mean values over all samples, for the period 1925-1939, 1946-1964 (a), and 1965, 1966 (b) (Fraser, 1970).
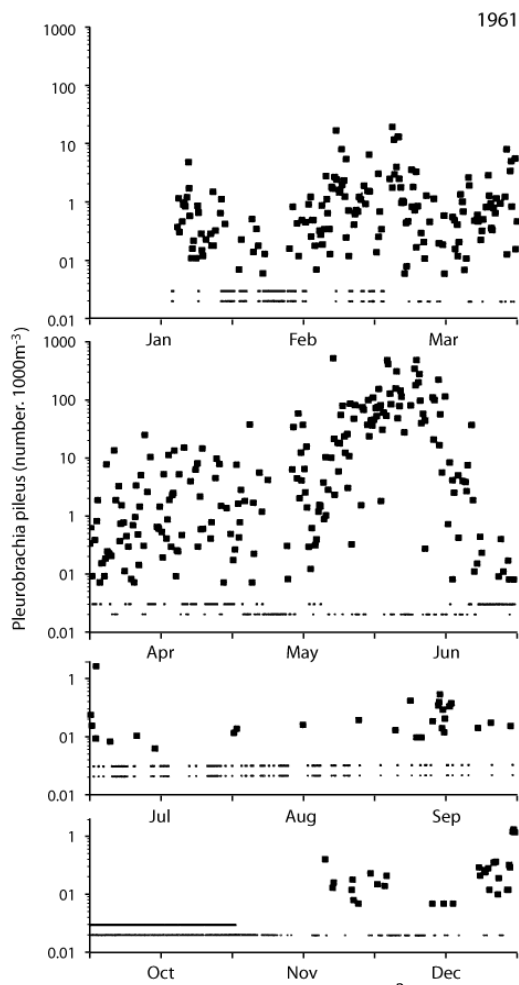
Figure 11.   *Pleurobrachia* (number.1,000 m^{-3}) in horizontal surface hauls at L V. Texel during 1961 (Van der Baan, unpublished data).
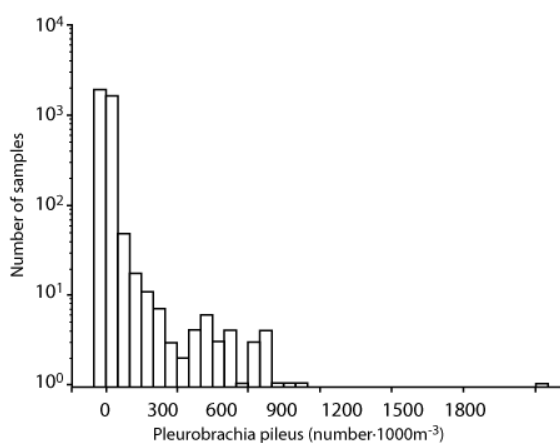
Figure 12.   The relation between the number of samples and number of *Pleurobrachia* pileus.1,000 m^{-3}, for 1961-1966 in horizontal surface hauls, (Van der Baan, unpublished data).
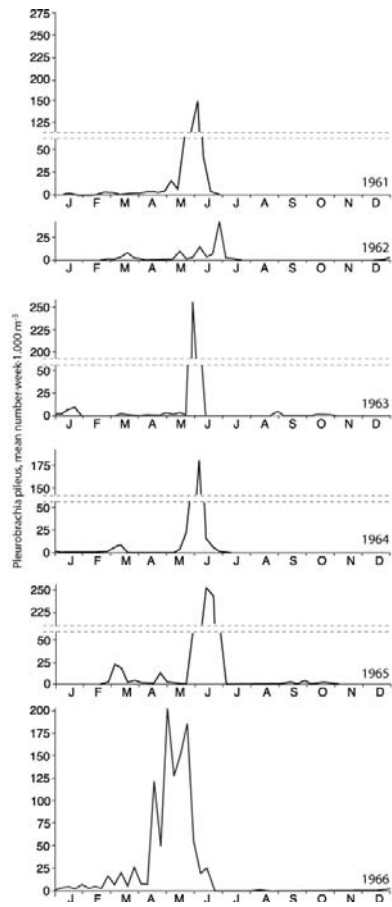
Figure 13. Mean number of *Pleurobrachia*.1,000 m^{-3}, per week, at L V Texel for 1961-1966 (Van der Baan, unpublished data).
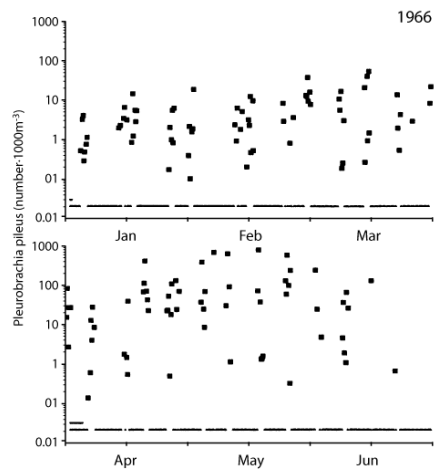

Figure 14. Number of *Pleurobrachia*.1,000 m^{-3} in the first half year 1966 (Van der Baan, unpublished data).
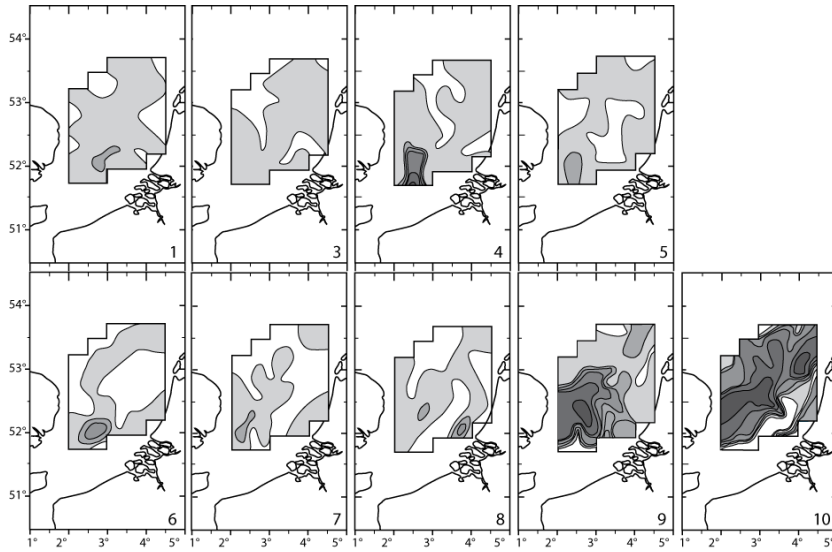
Figure 15.   Distribution of *Pleurobrachia* in the "ecological box" in the Southern Bight of the North Sea, December 1967- June 1968. Shadings represent [3]log values (Tungate,1975).
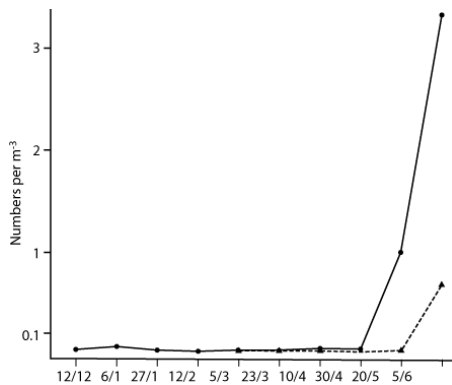

Figure 16.   The sudden increase of the density of *Pleurobrachia*, in number.m^{-2}, for the "ecological box" and for the area north of the "ecological box" (in the area south of the "box" the sudden increase cannot be observed as in the period when it should occur no samples were taken) (Tungate, 1975). Solid line: area 2; dashed line: area 3.
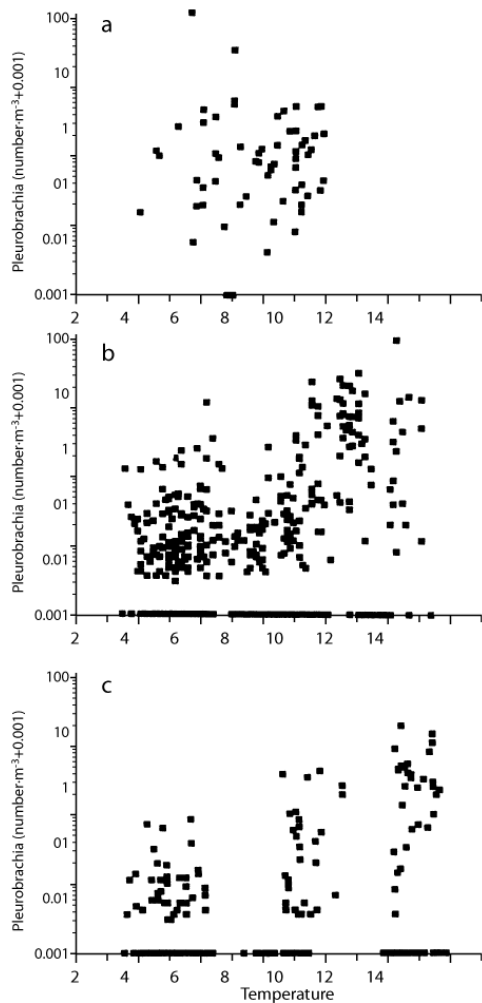
Figure 17.   Numbers of *Pleurobrachia*.m^{-3}, for 3 areas sampled by Tungate; a. south of the "ecological box"; the influence of the temperature cannot be seen as the temperature was too low. b. In the area of the "ecological box" the numbers increase at about 9,5°C. c. In the area north of the "ecological box"; in the temperature range 10,5-12,0°C. no samples have been taken, but at t> 12°C the numbers increase.
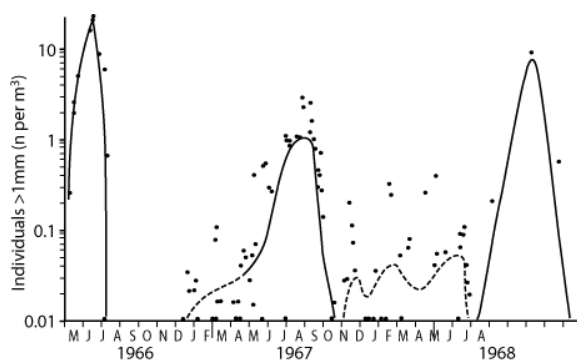

Figure 18.   Density of *Pleurobrachia* pileus on the Reede at Helgoland ; points represent results, and curves have been fitted by eye (Fig. from Greve (1971).
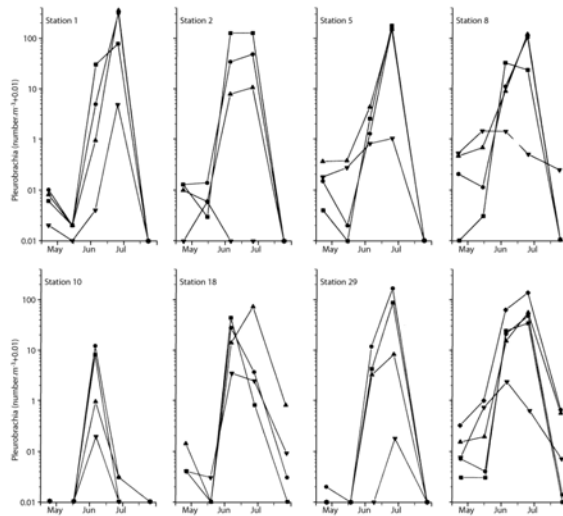
Figure 19.   Population density for each of 4 size-classes for 7 randomly chosen stations, and mean population densities of 30 stations, also for each of 4 size-classes, and for the sum of these classes, of *Pleurobrachia pileus* in the German Bight (Greve and Reiners, 1980). The data for the largest size class (15-20 mm) have been omitted, as only a few specimens in this class were caught in cruises 1 and 2, and then at 3 stations only. Legend: Closed square: 0-3 mm; closed circle: 3-5 mm; closed triangle: 5-10 mm; closed diamond: sum of all size classes.
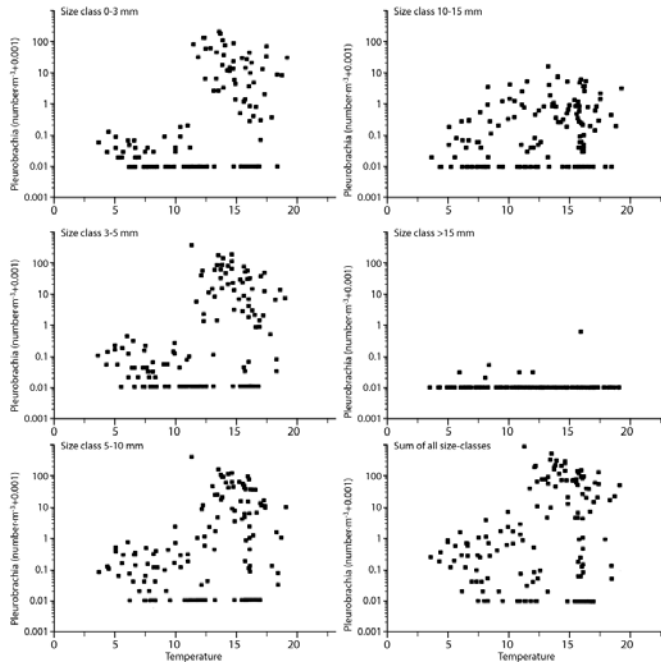

Figure 20.   Relation between temperature and population density of *Pleurobrachia pileus* in the German Bight (data from Greve and Reiners, 1980).
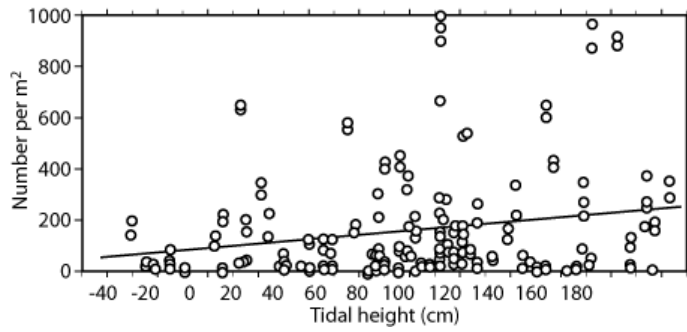
Figure 21. The relationship between density *Pleurobrachia* and tidal height. The densities are in numbers.m^{-2} sea surface (Y-axes), and the tidal heights are in cm (X-axes), for samples at all stations at 1.6 km from shore (Hirota, 1974).
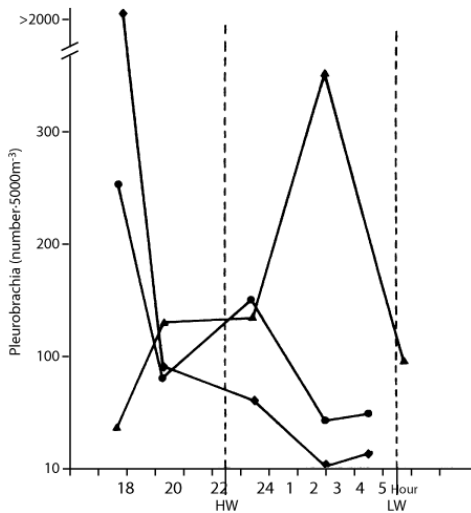
Figure 22. *Pleurobrachia* on a transect perpendicular to the Dutch coast near Callantsoog, on 9-10 March 1970. There is only one sample with a fair number of *Pleurobrachia* in the 1.5 h. long haul, taken just above the bottom, a few hours after the beginning of the flood (data from Klein Breteler, 1971). Legend: closed diamond: surface samples; closed circles: 10 m below the surface; closed triangles: near bottom.

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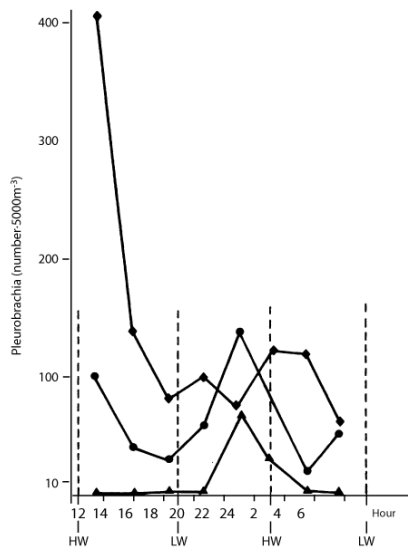
Figure 23. *Pleurobrachia* in the coastal water of the North Sea, at the surface (closed triangles), at 10 m (closed circles), and at 20 m below the surface (closed diamonds), at a distance of 20-28 km from the coast on 14-15 May 1970. The densities are low (cf the data of Kuipers and Witte, 1982, in Fig. 24), but the first sample, taken just at high tide, has a density that is much higher than the other samples (data of Klein Breteler, 1971).
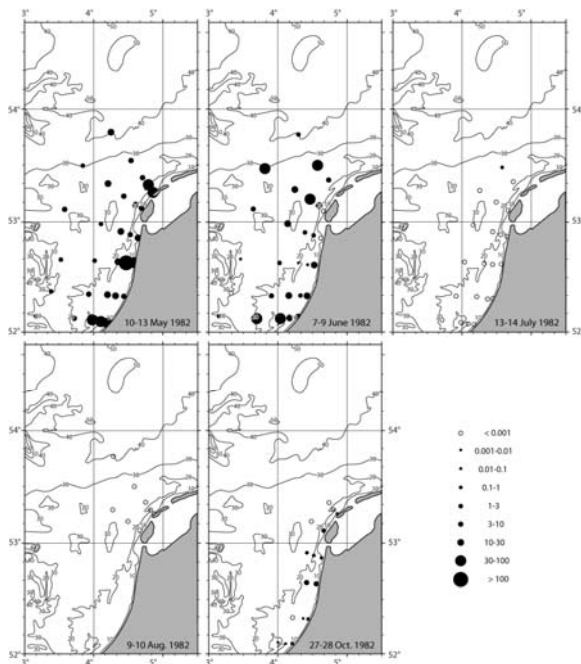
Figure 24. Distribution of *Pleurobrachia* in the coastal waters of the Netherlands; legend indicates numbers.m-3 (unpublished data of Kuipers and Witte, 1982).
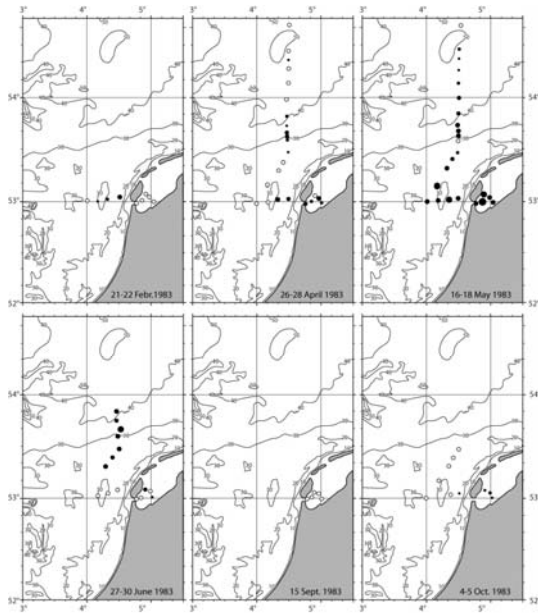
Figure 25.   Distribution of *Pleurobrachia* along a transect in the North Sea; for legend see Fig. 24 (unpublished data of Kuipers and Witte, 1983).
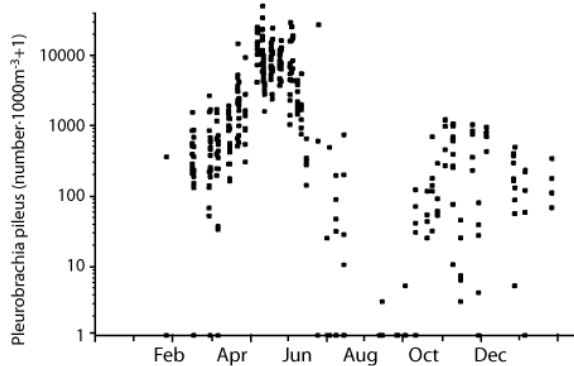
Figure 26.   Density of *Pleurobrachia* on stations of Van der Veer and Sadée, taken in 1982 (for stations see Fig. 1). There is a high density in the beginning of May, and a relatively high density in October. *Pleurobrachia* is nearly absent in the second half of June, in July and in August. Compared with other authors the variation between samples is small; this may be due to the small depths of the stations.

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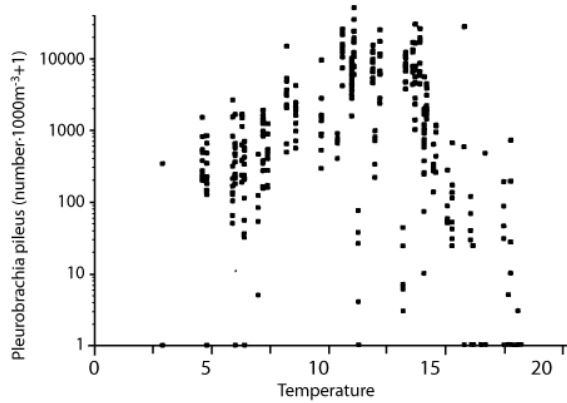
Figure 27.   Relation between numbers of *Pleurobrachia* and temperature for the original data of Van der Veer and Sadée of 1982. As no temperature data were collected during fishing, a 10-year mean temperature file for the Marsdiep has been used. Contrary to the results of other authors the population density increases gradually during the spring; this may be due to the small depth of the stations.
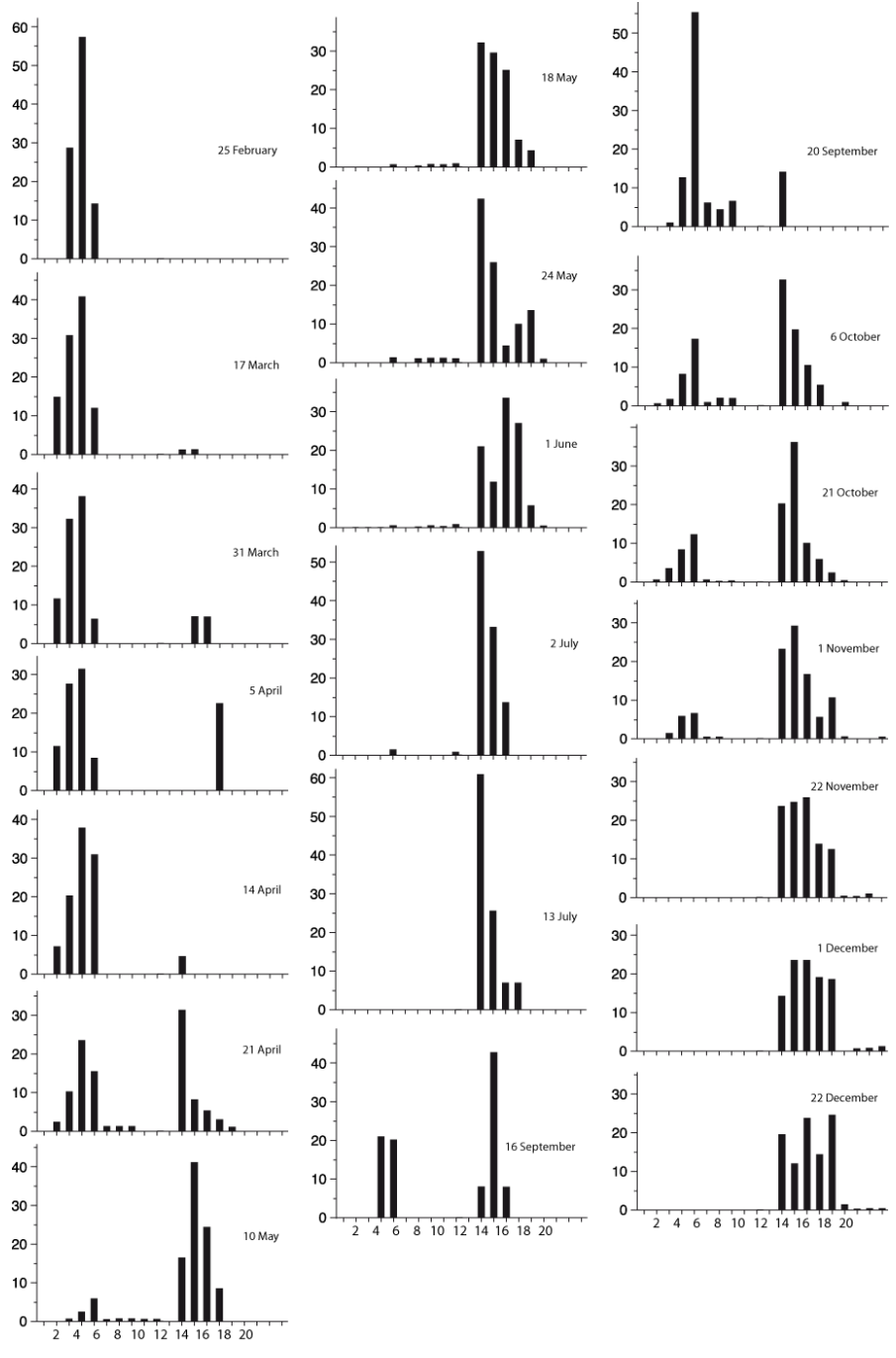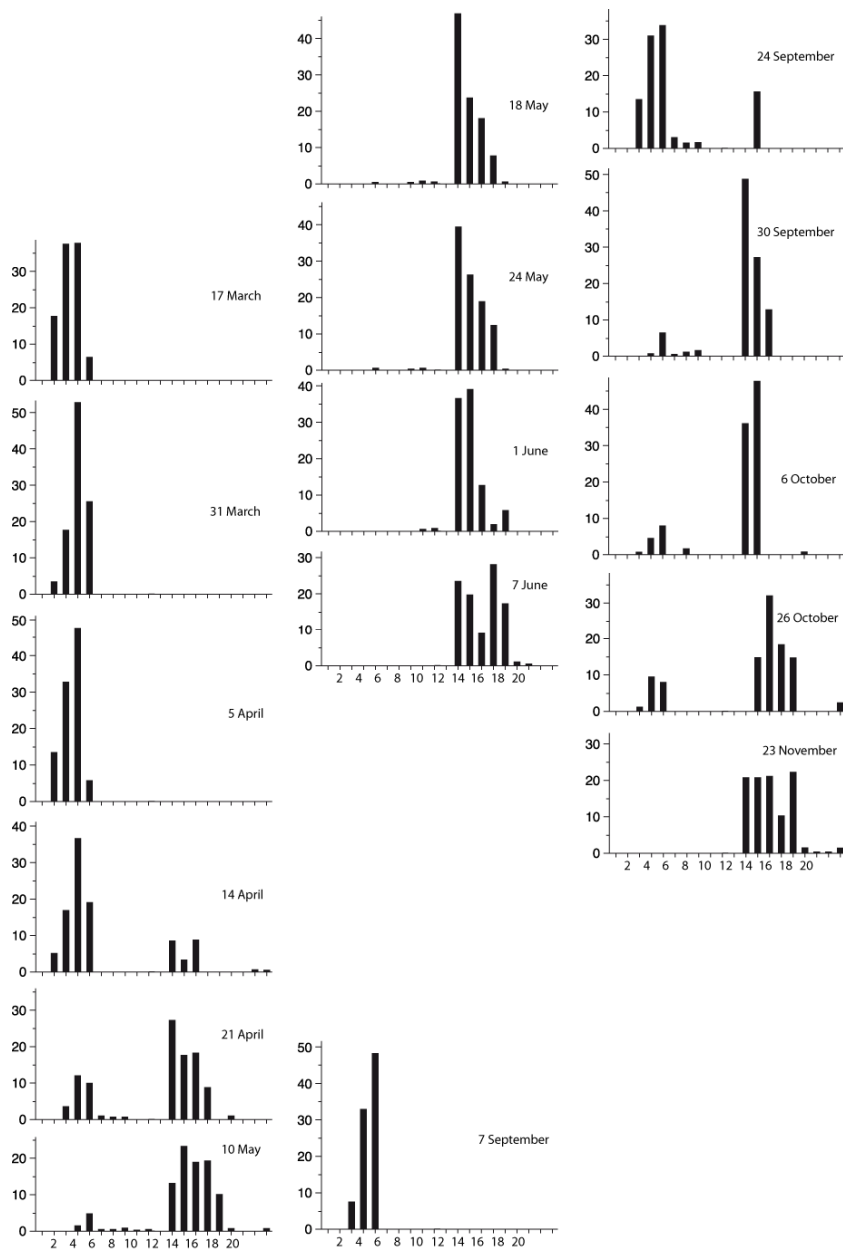
Figure 28   a and b. Size-distributions of *Pleurobrachia* in the western Wadden Sea, in 1982, on Station 1 and 2 (see Fig. 1); catches on the ebb current in Fig. 28a, flood-catches in Fig. 28b. X-axis: size in mm, y-axis: percentage. It is remarkable that *Pleurobrachia* of 6-11 mm are extremely rare. Furthermore, there are considerable differences between ebb and flood on the same day, e.g. 17 March, 31 March, 5 April and 14 April; this is thought to be due to sorting by the currents.
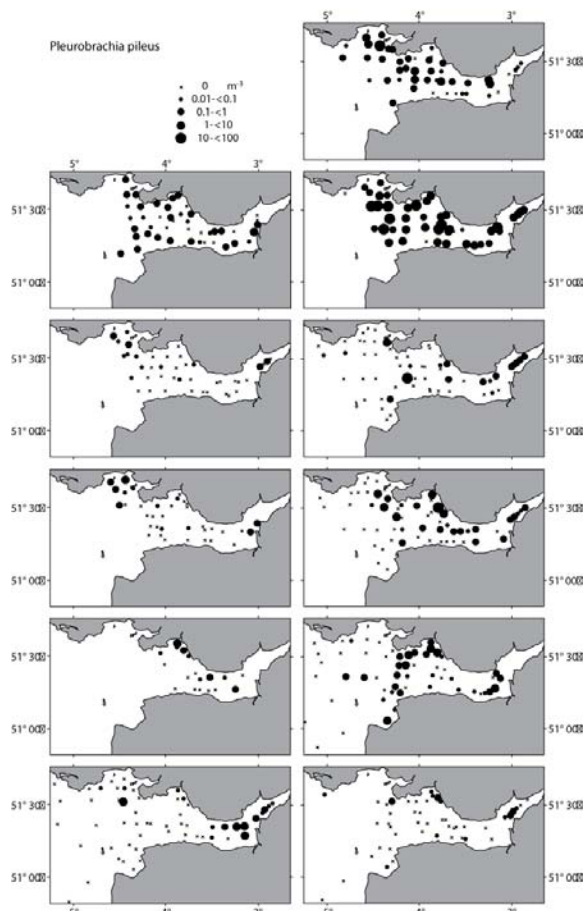
Figure 29a   Distribution and density of *Pleurobrachia* in the Bristol Channel and Severn Estuary
(Williams and Collins 1985b).

Figure 29b. "Temperature isotherms" (sic) of the Bristol Channel and Severn Estuary in May 1974
(Williams and Collins, 1985b; Fig. 8).

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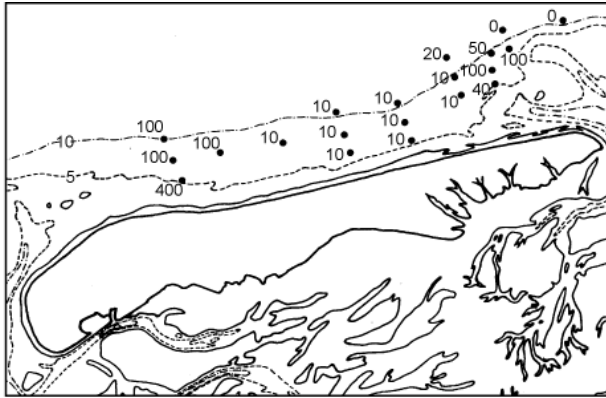
Figure 30.   Numbers of *Pleurobrachia* on the bottom; Van Veen grabs of 0.2 m², to a total of 2 m2, at each of 17 stations, with depths between 5 and 10 m to the north of Terschelling, on 22 and 23 May 1973; unpublished data of J.J. Beukema

Table 1. Dispersion parameters (k) for *Pleurobrachia*. M-3, for stations and depths in the western
          Wadden Sea, 24-26 May 1982

		3 meter under surface	2-3 meter over bottom
Texelstroom	24 May 1982	1.69	10.7
Scheurrak-Omdraai	25 May 1982	1.74	3.43
Doove Balg	26 May 1982	1.97	2.38

Table 2. Catches of *Pleurobrachia* in 1920 (from Bigelow, 1924a), supplemented with depth data from Bigelow (1921)

Station	Depth (m)	Station number	Date	Sample depth	Number *Pleurobrachia*
Off Sequin Island	50	20058	March 4	Surface	None
				30-0 m	Many
Cape Elisabeth	95	20059	March 4	Surface	None
				60-0	Few
Isles of Shoals	98	20060	March 4	Surface	None
				90-0	Few
Off Borton Harbor	50	20062	March 5	Surface	Many
				30-0	Many
Browns Bank	91	20072	March 13	Surface	None
				75-0	Many
Off Shelburne	75	20073	March 17	Surface	None
				70-0	35
Off Shelburne	160	20074	March 19	Surface	None
				125-0	Few
Off Shelburne	95	20075	March 19	Surface	None
				80-0	2 liters
Off Machias	61	20080	March 22	Surface	None
				40-0	1 litre
Off Petit Manan	206	20081	March 23	Surface	None
				140-0	Occasional
Off Yarmouth	68	20083	March 23	Surface	Occasional
				30-0	1 litre
Off Scal Island	55	20084	March 23	Surface	Few
				30-0	Many
German Bank	70	20085	March 23	Surface	100+
				60-0	100+
East side of basin	176	20086	March 23	Surface	None
				150-0	Few
Off northern Cape Cod	180	20088	March 24	Surface	None
				75-0	Few
Off Cape Ann	134	20090	April 9	Surface	None
				60 (cl net)	Few
Platts Bank	98	20094	April 10	Surface	None
				60-0	Few
Off Cape Elisabeth	93	20095	April 10	60-0	2
Off Sequin Island	80	20096	April 10	Surface	Few
				35-0	Few
Off Mount Desert	73	20099	April 12	Surface	None
				35-0	Few
Off Yarmouth	66	20102	April 13	Surface	12
				30-0	Many
German Bank	92	20103	April 15	Surface	None
				60-0	Swarm
Off Seal Island	46	20104	April 15	Surface	Many
				25-0	4 liters
Browns Bank	83	20106	April 16	Surface	Few
				40-0	Many
Off northern Cape Cod	89	20117	April 18	40-0	Few
Cape Cod Bay	28	20118	April 20	15-0	6 liters
Massachusetts Bay	90	20119	April 20	Surface	None
				40-0	Few
Off Merimac River	85	20112	May 8	Surface	None
				65-0	Few
SW Georges Bank	70	20128	May 17	Surface	Many
Continental Edge	170	20129	May 17	Surface	None
				50-0	Many

Table 3. Catches of *Pleurobrachia pileus*, in numbers per haul (Van der Baan, 1989). The figures represent the highest catch per half-month, for the years 1961-1966.

	1961	1962	1963	1964	1965	1966
Jan I		10	40	21	3	64
Jan II	36	11	153	18	49	57
Feb. I	8	14	11	5	14	61
Feb. II	109	14			25	4	142
March I	140	32	4	200	348	233
March II	74	400	28	190	124	450
April I	146	120	11	9	91	200
April II	120	13	49	8	600	2000
May I	450	52	72	3	175	3000
May 2	2000	500	88	800	55	3000
June I	5000	800	8000	>30000	500	1000
June II	250	250	1	300	3000	1
July I	1	>5000	7	25	500	
July II	1	>100	4	6	4	1
August I	1	4	3	8	1	16
August II	1		9	1	3	
Sept I	15	2	200		200	
Sept II	1		9	1	100	
Oct I	1		21		250	
Oct II		5	23	1	55	
Nov I	3		21	2		1
Nov II	2	1	7	1		
Dec I	1	1	5	8	1	1
Dec II	12	5	5	9	5	68

Table 4. Compilations of Tungate's (1975) data. For each cruise and area, the number of samples, the mean number of *Pleurobrachia*.m^{-3} and the dispersion parameter *k* is presented. The high values for 4 stations mentioned in the text have been omitted from the calculations.

Cruise		South			Box			North			
	Number	Mean	*k*	Number	Mean	*k*	Number	Mean	*k*	Period
1	21	0.671	0.95	33	0.028	0.06	5			8-16 Dec 67
2	27	0.551	0.69	16	0.062	0.06				3-10 Jan 68
3	9	0.371	0.91	32	0.019	0.03	24	0.016	0.016	23-31 Jan 68
4	10	1.05	6.93	44	0.021	0.05	42	0.020	0.015	9-15 Feb. 68
5	7	0.098	0.18	50	0.015	0.01	66	0.003	0.002	27 Feb – 9 March 68
6				49	0.030	0.01	6	0.045		19-27 March 68
7				52	0.053	0.02	68	0.007	0.002	5-14 April 68
8	3			57	0.034	0.01	50	0.040	0.008	27 April – 3 May 68
9	2			56	1.056	0.65	34	0.212	0.020	16-23 May 68
10	3			62	3.355	6.62	83	0.863	0.671	1-9 June 68

Table 5. Depth distribution of *Pleurobrachia* in Nordhafen (depth 23 m), Helgoland in 1968 after Greve (1971). The sample of 9 April taken in the Tiefe Rinne (depth 52 m).

Date	Surface		10 m		23 m	
	%	Temperature	%	Temperature	%	Temperature
4 April	14	3	59	3	27	3
8 March	19	3	2	3	79	3
9 April	1		2		97 (52 m)	
29 April	1	7.2	39	6.9	60	6.9
13 May	53	7.9			47	7.8
21 May	4	9.4	32	7.8	64	7.8
27 May	1	9.8	4	9.6	95	9.4
5 June	45	10.6	40	10.6	15	9.3
14 June	18	13.6	62	11.3	20	10.5
24 June	2	11.3		11.3	98	11.3
9 July	6	15.5	29	14.6	65	14.2
19 July	4	15.8	12	14.0	84	14.0

Table 6. Dispersion parameters *k* for *Pleurobrachia*.100 m^{-3} based on 30 stations for different size classes and cruises (Greve and Reiners, 1980).

Size-class	Cruise 1	Cruise 2	Cruise 3	Cruise 4	Cruise 5
0-3 mm	0.53	0.22	0.74	0.37	
3-5 mm	0.45	0.44	0.95	0.44	0.19
5-10 mm	0.62	0.20	0.57	0.59	0.15
10-15 mm	0.32	0.39	0.54	0.44	0.20
15-20 mm	0.09	0.24	0.03		
All sizes	0.66	0.40	1.47	0.67	0.16

Table 7. Unpublished data on *Pleurobrachia pileus* (numbers m^{-3}) fished with an Isaacs Kittnet, a vertical net and a mysid net around Meetpost Noordwijk in 1985 (Kuipers and Witte, unpubl.). Positions are given as a small distance from the Meetpost Noordwijk, in the wind-direction given, or as latitude and longitude.

Date	Time	Position	Isaacs Kidnet	Vertical net	Mysid net
24.4.85	14.20	OZO	0.74	7.2	15.4
	16.50	ZZW		3.3	
	17.15	WNW	0.65	0.43	1.03
	22.00	OZO	17.9		18.7
	23.25	WNW	31.3		1.03
30.5.85	13.00	NNO		52.03	206.2
	14.00	OZO		101.9	410.2
	15.30	52.09N4.11E		186.7	70
	16.35	52.04N4.05E			71.9
	19.40	WNW			43

Table 8. Population density of *Pleurobrachia pileus* (numbers m^{-3}).

Area	Method	Mean Low density	Mean High density	Highest value	Author
Channel, western part	Net, oblique haul	0.003	0.08	0.27	Russell, 1925
Channel, eastern part	Torpedo, oblique haul	0.5			Tungate, 1975
Southern Bight ("Ecol box")	Idem	0.3	2.2	24.0	Idem
North Sea (north of 53^{0}45'	Idem	0.022	0.35	12.0	Idem
North Sea (LV Texel)	Net, surface haul	0.004		1.8	Van der Baan, 1980
North Sea, Dutch coast 2-10 m	Isaac Kittsnet, oblique hauls	0.28	35.9	126.0	Kuipers and Witte, unpubl.
North Sea, Dutch coast 20-40 m	Idem		10.1	78.8	Idem
Wadden Sea	Idem	0.20	14.4	35.6	Idem
North Sea, Frisian front	Idem	0.14	5.9	18.5	Idem
Wadden Sea	Net, horizontal surface hauls	0.31	6.8	21.7	Van der Veer and Sadée, 1984
Wadden Sea, Texelstroom	Surface hauls		9.9	29.3	De Wolf, unpubl.
	Bottom hauls		14.5	28.2	Idem
Wadden Sea, Scheurrak	Surface hauls		2.4	7.1	Idem
	Bottom hauls		5.8	15.8	Idem
Wadden Sea, Doove Balg	Surface hauls		1.9	7.2	Idem
	Bottom hauls		2.2	9.4	Idem
German Bight	Calcofi net, oblique hauls	0.60	96.8	753.0	Greve and Reinders, 1988
North Sea, N and E of Scotland	Net, horizontal hauls	~0.004	~0.7		Fraser, 1963, 1966, 1970

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