THE ECOLOGY OF THE CTENOPHORE *PLEUROBRACHIA PILEUS* IN SCOTTISH WATERS

By

J. H. FRASER

Marine Laboratory, Aberdeen, Scotland

A short review of the literature on the distribution and ecology of *Pleurobrachia* is given and supplemented by data taken between 1925 and 1968 in the Scottish area. It is a neritic species in the northern North Sea and reaches its greatest abundance in October and November following a possible minor peak of abundance in early summer, but in some years (e.g. 1965) the summer peak can exceed that of the autumn.

Pleurobrachia is a non-selective carnivore, feeding on what is available in the plankton, and swarms can greatly reduce the amount of zooplankton in large areas of water. Spawning is continuous while conditions are suitable, but changing conditions can sometimes give the effect of two separate spawnings in a year.

Although there are reports in the literature of *Pleurobrachia* eating eggs and larvae to the extent of reducing the recruitment potential of the fish and shellfish, this has not been found in the Scottish area where crustaceans form 80% of the diet, and reaching 97%. Because of the reduction in zooplankton, however, swarms of *Pleurobrachia* could be responsible for larval fish mortalities, even if the fish themselves are only rarely eaten, and they could affect also adult herring and other plankton feeders.

There is a rapid increase in the numbers of cercarian parasites of *Pleurobrachia* from August to September.

INTRODUCTION

Pleurobrachia is an important carnivore in the plankton and records have been maintained of its abundance in the plankton collections taken by Scottish research vessels for a number of years, and of its food contents since 1965.

Whilst acting as a student assistant in 1957, Mr. R. LILEY extracted information for me with the object of reviewing the literature on ctenophores, emphasis being placed on distribution, feeding, and their influence on the fisheries. References in this paper to literature before 1957 are largely taken from his notes and this I acknowledge with thanks to him.

Only one certain species of the genus, *P. pileus* (O. F. MÜLLER), is found in the North Atlantic region, as others described are doubtfully synonymous.

DISTRIBUTION IN THE ATLANTIC AREA

MORTENSEN (1912) and KRAMP (1913) discuss the general distribution of this species. The genus *Pleurobrachia* is certainly cosmopolitan. MORTENSEN (1912) believes that *P. pileus* itself is cosmopolitan, but there is some disagreement as to

J. Cons. int. Explor. Mer	33	No. 2	149–68	Copenhague, Août 1970

its limitations. The German South Polar Expedition found it in great abundance in the Antarctic Sea (MOSER, 1909), and MOSER records it also as occurring at the Seychelles, at Ascension and between Ascension and the Cape Verde Islands. *P. pileus* is probably distributed throughout the whole of the eastern Atlantic, though it is possible that it is less common in the tropical than in the northern and southern regions. These authors agree that this species is abundant on both sides of the North Atlantic. In the temperate boreal waters of Europe it is numerous round the British Isles, English Channel, North Sea, Skagerak, all the Danish Seas and in the Baltic, off the coast of Norway and in the southern Norwegian Sea. In the Arctic Sea it is known only from Spitzbergen. It occurs at Faroe but doubtfully in Icelandic waters (KRAMP, 1939). According to MORTENSEN (1912) and KRAMP (1943) it does not occur in Greenland waters but BIGELOW (1910) and HANSEN (1949) believe otherwise. BIGELOW (1915) states that *P. pileus* occurs along the NE American coast from Labrador to at least as far south as Pamlico Sound. Although *Pleurobrachia* may occur in small quantities in the open ocean it is primarily a neritic animal. KRUMBACH (1927) suggests that the reason for the few records of this species on the high seas is that for them to be near the surface a perfectly calm sea is necessary, a comparatively rare occasion in the open ocean. He recalls that in the literature of FOL and HAEKEL there is a record of *Pleurobrachia* in the open sea off the Canary Isles. BIGELOW (1924) discusses this problem after having made several cruises in the coastal waters of NE America. He finds that *P. pileus* remains confined to shoal water of the Gulf of Maine until well into May, and after this time the animal extends its range offshore. He concludes that, although *P. pileus* does not depend upon the bottom at any stage in its life history, it is more neritic than oceanic and that this appears to be equally true of it in other areas. Although it ranges from the Antarctic to Spitzbergen it is confined in general to the neighbourhood of the land or coastal banks and is seldom taken from high seas far from land.

DISTRIBUTION IN SCOTTISH WATERS

P. pileus, being essentially a neritic species, occurs round all the Scottish coasts, including the whole of the North Sea, and over the shelf-waters west of Scotland. Specimens found over deep water are often in poor condition and in areas to which they could have been transported from some neritic source, for example over deep water east of Rockall Bank. When they occur over deep water they are usually found singly or in very small numbers but in November 1965 fairly high numbers (up to 300 per haul in a 1m tow net) were taken at the western entrance to the Faroe Shetland Channel. These, too, could have been brought there with the north-easterly drift of oceanic water along the edge of the continental shelf west of Scotland and so mixing with the neritic water at the interface (FRASER, 1961).

The greatest abundance of *P. pileus* in Scottish waters is normally off the north coast, in the Moray Firth and off the east of the Firth of Forth (Fig. 1). As shown below, however, the numbers of *Pleurobrachia* found prior to 1965 were much lower than in 1965–66, and the sparse data from 1967 and 1968 indicate higher than average numbers, though not so high as 1965–66.

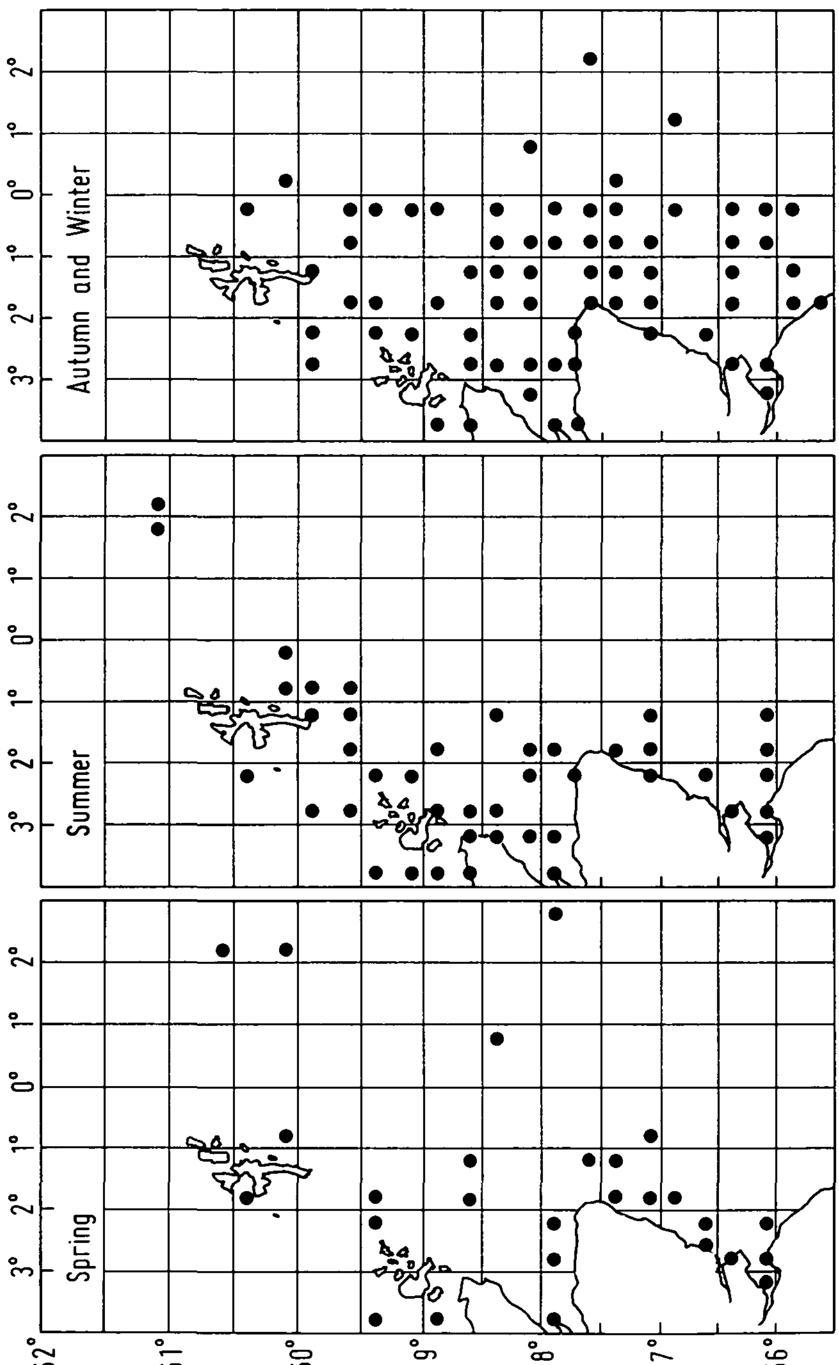

Figure 1. Areas in which *Pleurobrachia pileus* was common (over 40 per haul) 1925–39, 1946–60.

TAPLE 1. Size range of *Pleurebrachia*. Numbers are average per

Height in mm	2	3	4	5	6	7	8	9	10
1965									
March	–	–	–	–	–	–	–	–	–
April	–	+	2	1	1	+	+	+	+
May	–	+	5	18	17	6	3	2	2
June	–	–	2	3	11	7	3	7	4
July	–	65	182	173	126	89	64	41	25
August	–	175	119	161	57	58	17	7	7
September	14	16	23	26	21	23	15	12	13
October	–	1	5	20	16	20	22	17	23
November	–	–	–	6	12	27	22	23	35
December	–	–	–	–	+	+	1	1	1
Totals	14	257	338	408	261	230	147	110	110
1966									
February	–	–	–	–	+	1	1	+	–
March	–	–	–	–	–	–	–	–	–
April	–	–	+	–	+	–	–	+	+
May	–	2	6	12	7	5	4	2	2
June	1	4	5	10	10	11	11	5	4
July	–	2	3	9	6	9	8	7	7
August	3	48	98	56	9	17	9	–	17
September	6	38	46	62	35	35	46	27	28
October	–	–	15	45	50	32	102	102	33
November	3	1	3	+	5	5	11	13	12
Totals	13	95	176	194	122	115	192	156	103
1967									
January	–	–	–	–	–	–	–	–	+
March	–	–	–	–	–	–	–	–	–
April	–	–	–	–	–	1	–	–	–
May	+	1	3	5	8	2	3	4	2
June	+	4	8	9	5	5	4	5	5
July	260	12	155	155	34	12	16	27	59
September	–	–	2	4	11	8	7	3	1
Totals	260	17	164	173	58	28	30	39	67
1968									
May	5	4	2	–	–	–	–	–	–
June	–	–	5	1	–	2	2	4	2
July	6	5	6	3	4	3	2	2	+
September	+	2	5	5	3	5	+	1	1
October	–	1	1	4	4	4	1	–	–
November	–	1	1	2	1	+	+	+	–
Totals	11	13	20	15	12	14	5	7	3

SEASONAL ABUNDANCE IN THE NORTHERN NORTH SEA AND ADJACENT AREAS

Data collected by the Scottish research vessels during the periods 1925–1939 and 1946–64 have been used to give an average annual picture of the abundance of *P. pileus*. The data are based on numbers taken by 1m non-closing nets towed at 2 knots for 15 minutes. In many of the collections, including almost all the early collections, the abundance of *Pleurobrachia* was given by the use of symbols, r(are), f(ew), sev(eral), c(ommon) etc.To enable these to be averaged and presented in graphical form a series of arbitrary numbers has been given, based partly on discussion with colleagues and partly by going back month from positive hauls. The total T2 is based on all hauls.

11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	Total	T2
–	–	–	–	–	–	–	–	–	–	–	–	–	1	–	+	+	+	1+	+
+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5	4
1	1	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	55+	21
4	1	1	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	45	7
21	9	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	795	546
4	3	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	609	517
7	2	1	+	1	–	+	–	–	–	–	–	–	–	–	–	–	–	174+	68
10	8	3	4	1	1	1	+	+	–	+	–	–	–	–	–	–	–	152+	87
62	74	39	19	32	9	2	–	–	–	–	–	–	–	–	–	–	–	362	108
1	2	1	1	1	+	+	+	–	–	–	–	–	–	–	–	–	–	9+	5
110	100	45	25	36	10	4	+	+	–	+	–	–	1	–	+	+	+	–	–
–	+	–	+	–	+	+	–	–	–	–	–	–	–	–	–	–	–	3	2
–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	+
+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	2	+
2	1	1	1	+	+	–	–	–	–	+	+	–	–	–	–	–	–	47	10
3	2	1	1	1	–	–	–	+	–	–	–	–	–	–	–	–	–	73	32
4	5	3	2	–	+	1	–	–	–	–	–	–	–	–	–	–	–	66	18
–	4	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	261	167
18	19	7	4	3	+	–	–	–	–	–	–	–	–	–	–	–	–	374	258
51	31	18	4	4	2	–	–	–	–	–	–	–	–	–	–	–	–	498	329
9	11	5	4	2	1	+	–	–	–	–	–	–	–	–	–	–	–	85	71
87	74	35	16	10	3	1	–	+	–	+	+	–	–	–	–	–	–	–	–
–	+	–	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	2	+
–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	2	+
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	+
1	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	30	18
5	5	1	2	1	–	+	–	–	–	–	–	–	–	–	–	–	–	59	25
17	17	18	5	–	–	–	–	–	–	+	–	–	–	–	–	–	–	783	528
2	4	1	+	+	–	–	–	+	–	–	–	–	–	–	–	–	–	44	21
25	27	20	7	1	1	+	–	+	–	+	–	–	–	–	–	–	–	–	–
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11	3
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16	4
+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	31	1
+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	22	17
–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	15	15
+	+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	6	5
1	+	+	+	+	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–

over a selected series of stored samples. The figures chosen for this purpose (for *Pleurobrachia*) are, $rr = 1$, $r = 3$, $r - f = 5$, $f = 8$, $f - sev = 10$, $sev = 15$, $sev - c = 20$, $c = 40$, $c - cc = 70$, $cc = 100$, $ccc = 300$.

No claim for precision can be made for these figures, nor is the precise volume of water filtered taken into account. Nevertheless they should be of about the right order and roughly comparable on this general basis. An average figure was obtained for each month of each year and these then averaged to give a single figure for each month covering the 34 years. By this method most of the major discrepancies due either to errors in assessment or to abnormally large or small local populations will be smoothed out. The results are given in Figure 2.

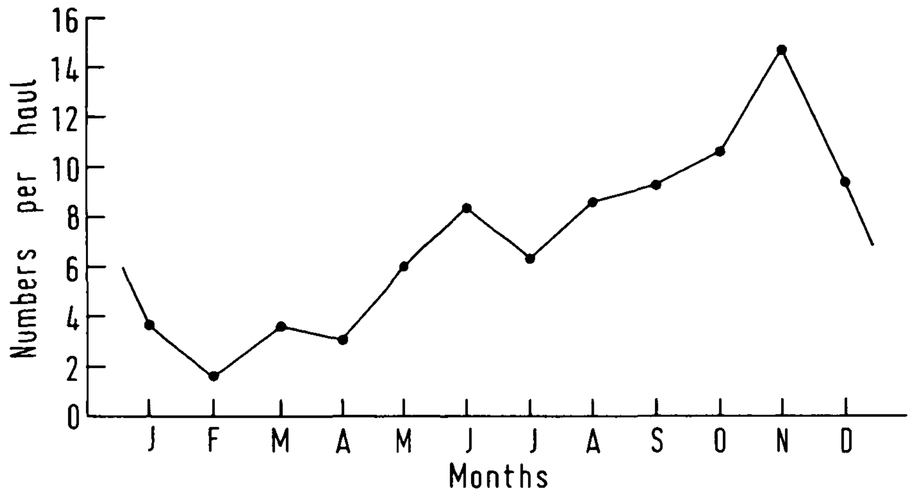

Figure 2. Seasonal abundance of *P. pileus* in Scottish North Sea waters over a long term period, 1925–39, 1946–64.

These show that *Pleurobrachia* has its minimum in February rising to a small early summer peak in June, possibly followed by a drop but then increasing to its main maximum abundance in late autumn, particularly in November. The average numbers taken, as shown in Figure 2, are small, ranging from 0 to 15, but there is a great deal of patchiness and the numbers in a single haul can reach about 1 000. In the recent peak years one haul in 1965 contained about 2 000 and one in 1967 over 3 000. The amount of water filtered in a haul will be variable but in the order of 450 m^3 so that the number of *Pleurobrachia* even in peak hauls is only 2 to 7 per m^3 which is low compared to *Bolinopsis* which can reach 400 per m^3 in the Arctic (KAMSHILOV, 1960).

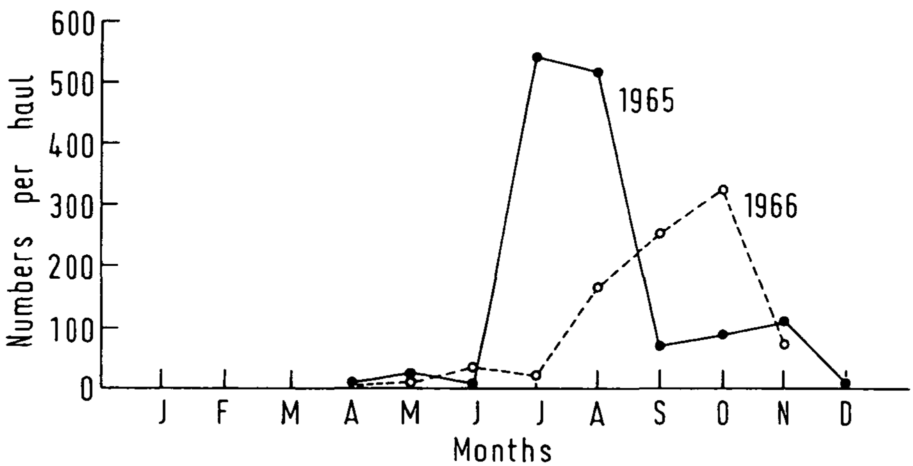

Figure 3. Seasonal abundance of *P. pileus* in the peak years 1965 and 1966.

Conditions in 1965 were abnormal in that the summer abundance of *Pleurobrachia* in the northern North Sea occurred in July and August instead of June, and that in this year the summer peak greatly exceeded the autumn peak although the actual numbers in November (Fig. 3) were very much higher than in the long period average. The year 1965 was, in fact, a peak year for *Pleurobrachia* in Scottish waters. In 1966 although numbers were still very high the seasonal proportions were much more normal with only a small peak in June.

Although no size data are available from the earlier collections, details of the distance from the oral to the aboral pole were recorded from 1965 onwards and are given in Table 1. Data from 1967 and 1968 are sparse both in the numbers of samples taken and the seasonal coverage.

The difference between the abnormal year, 1965, and the more typical 1966 is seen in the table. In March 1965 only large specimens were found, all over 22 mm, but in April specimens of 3 mm were taken with the greatest number at 4 mm. By May these had grown to 5–6 mm and by June to 6–9 mm. In July, August and September young specimens, 2–4 mm, were again found and these had grown to 6–10 mm by October and 7–15 mm by November. This suggests two spawnings in that year, one in spring and one in late summer.

The analysis of the 1966 samples is not so clear as very young specimens were taken from April to November. From these data and evidence in the literature it would therefore seem that spawning may be more or less continuous and that when conditions, not yet specified, are suitable, spawning is vigorous. Whilst this usually occurs towards the end of the summer it can often occur to a lesser degree also in spring and occasionally, as in 1965, this can be the dominant period, possibly connected with a better survival over the previous winter. An indication of this possibility is seen in that from November 1964 to May 1965 there was a positive temperature anomaly of at least 0·2°C in an area in the north-western North Sea, area F, according to SMED (1965, 1966), and the size frequencies in March 1965 (Table 1) showed the presence of unusually large specimens.

The 1967 and 1968 sampling was inadequate, and the July 1967 figures in particular may be very biased in that one haul, out of only five in that month, contained 3 104 specimens.

As KRAMP (1913) says, it is difficult to set any rule to the periodical appearance of the different species of ctenophores in different areas. Each species appears to be very independent of hydrographical conditions and may appear and disappear quite fortuitously without regard to season, temperature or depth. BIGELOW finds a very similar situation regarding the occurrence of ctenophores in the coastal waters of the north-east coast of North America. A feature of the ctenophores of cold or Arctic waters not present in tropical water populations, is the common appearance of great swarms of one or two species. MAYER (1912) writes of records of "great rafts thousands of square yards" in area of one of the ctenophores, *Mnemiopsis*, *Bolinopsis* or *Pleurobrachia*. These three, especially *Pleurobrachia*, do appear in very large quantities at different times of the year and at different places. The greatest quantities of ctenophores appear mainly during late summer and autumn and represent the accumulation from the summer spawning. Large quantities may appear earlier in the year as in May 1929 (RUSSELL, 1935), or in December (SCOTT, 1919). MCINTOSH (1927) finds that ctenophores are so abundant throughout the year at St. Andrews (E. Scotland) that it is difficult to decide when their annual maximum occurs. *P. pileus* appears to be the most abundant ctenophore of British waters and it is only this species which regularly appears there in vast quantities, and often to the exclusion of other zooplankton.

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. The observations of DELAP and DELAP (1905) on the plankton of Valencia Harbour over the period 1899 to 1905, give evidence to support the suggestion. They record that after the severe winter of 1902–3 *P. pileus* was scarce throughout the summer of 1903, though more numerous from August to October, and they believe the stormy winter of 1902–3 to be responsible. KRAMP (1913) records a similar sequence of events in the abundance of *Pleurobrachia* in the English Channel and Belgian area of the southern North Sea. It appears that the same conditions which caused *Pleurobrachia* to be scarce in Valencia may have been responsible for a similar situation in the Channel, and it seems likely that it was the severe winter of 1902–3.

TIME OF REPRODUCTION

Pleurobrachia, like other ctenophores, is hermaphrodite, and the sexual products are discharged into the sea through the mouth. They spawn in patches near the surface, the eggs being released singly together with masses of slime, and fertilisation probably occurs in the sea. Nothing appears to be known about the time it takes an individual to shed all its reproductive products.

Most of the records which give any information regarding the life history of this species indicate that those ctenophores which appear at the surface during April, May and June are the product of the previous year's spawning. The data show that immature *Pleurobrachia* increase in size and the gonads mature within a few weeks and spawning then takes place from late June until early autumn. MCINTOSH (1927) records a pear-shaped embryo within its capsule on 2. July of one year, and later in November observed many small (about 1·75 to 2·5 mm) specimens. In the Plymouth Marine Fauna (1931), it is recorded that the adults are not seen after June and that minute specimens appear in August and September. There appear to be two peaks in abundance of *P. pileus* at Plymouth, a small peak in May and a larger one of young forms in September and October, with comparatively few recorded in August (RUSSELL, 1933). On the other hand KRAMP (1913) states that *Pleurobrachia* is common in the English Channel during August. RUNNSTRÖM (1931) states that in Herdlafjord and Hjeltefjord the reproduction of *Pleurobrachia* takes place chiefly in late summer and into autumn, after which the grown individuals disappear. KRAMP remarks that the adults die off in autumn.

From the reference given above it would seem that there is normally only one generation in a year. BROWNE (1905) believes that there are two generations a year, but he does not discuss this in detail. Presumably he regards the *Pleurobrachia* which appear in spring as the young of a late winter spawning by the previous summer's brood. He records that on 5. June, 1901, the largest specimen he obtained in the Firth of Clyde was 12 mm, which is much less than many specimens taken in winter. SCOTT (1919) records that during the presence of a large swarm in the Barrow Channel (Irish Sea) during December 1919, many of the specimens measured 22 mm or more. These larger animals may well give rise to a spring brood which matures in time to spawn in autumn. SCHODDNYN (1926) states that he observed the eggs of *Pleurobrachia* in May and in August, in the Bay of Ambleteuse (Straits of Dover, between Boulogne and Cap Gris Nez). He also remarks that the young forms appeared in May, June and September. BIGELOW and LESLIE (1928), in their notes on the plankton of Monterey Bay, California, record that it seemed that one generation of *P. pileus* grew nearly or quite to maturity in the Bay during the first three weeks of July. From these data it appears that spawning takes place to a greater or lesser extent throughout a great deal of the year. McINTOSH (1890) records that *Pleurobrachia* exhibits a great irregularity in size during January, and he believes this to be due to the length of time that spawning is carried on. He found that free ova were not uncommon in February, and that many minute specimens appeared at the end of March. Throughout the summer *Pleurobrachia* of all stages were common. In a plankton sample from the North Sea taken by the Scottish research vessel in the middle of August 1957, were *Pleurobrachia* ranging in size from about 3 mm to 15 mm which seems to indicate that spawning had taken place throughout the warmer months of the year.

Spawning is not then restricted to a particular season and occurs as the animals mature. In British waters this usually takes place from late spring until autumn. Individuals which mature early and spawn in spring give rise to individuals which could mature and spawn in early autumn, so that in this case there would be two generations in a year. It is of interest that in the warmer water of the Mediterranean reproduction of ctenophores may take place throughout the year (KOWALEVSKY, 1866; HEIDER *in* KORSCHALT and HEIDER, 1895), and it may be that maturity is temperature correlated.

It is generally believed that after reproduction most of the spent adults die and disintegrate. McINTOSH (1890) remarks that there is little evidence of a general destruction of adult forms at a given period, but certainly the adults gradually disappear after shedding their ova. Both young and remaining old individuals lie deep during winter. RUNNSTRÖM (1931) found them below 100 m in Norwegian fjords.

McINTOSH (1888) states that at St. Andrews (east coast of Scotland), *Pleurobrachia* is observed at all seasons of the year. He remarks that ctenophores appear to be less common at Plymouth (English Channel) than at St. Andrews, noting that at Plymouth there may be no trace of ctenophores when at St. Andrews they are common. In the southern North Sea they become common in May and June, and less numerous in July and August. A second peak, mainly of young individuals, occurs in late August, September and early October.

In the Irish Sea they are not frequently observed in the first four months of the year but are common from May to November. SCOTT (1913) records the occurrence of a vast swarm in the north Lancashire coastal waters from mid-June until the second week in September, and in 1919 he recorded a similar invasion during December. In the Mersey estuary at Liverpool in 1931, *Pleurobrachia* eggs were found as early as 4. March but the young stages were not really abundant until August although adults occurred throughout the summer.

KRAMP (1913) states that *Pleurobrachia* occurs constantly in all Danish waters, having a maximum abundance in the Skagerak in May and in November. In the Kattegat the maximum occurs in February and in the Belt

Sea in May. LINDQUIST (1958) sums up the situation in the Baltic. RUNNSTRÖM (1931) reports it fairly common in the upper water layer of the Norwegian fjords from May to September, especially in May and June.

VERTICAL DISTRIBUTION

It is difficult to make a general statement regarding the vertical distribution of ctenophores. They are generally regarded as creatures of the upper strata, being recorded from the surface down to a depth of 200 m or more. Within this vertical range they are often distributed apparently inconsistently with regard to time of day or season of the year. It seems generally believed that ctenophores occur at or near the surface of the sea during summer, especially on calm sunny days. When the sea is at all disturbed at the surface then the ctenophores sink downwards. On the other hand, BIGELOW (1924) records that *Pleurobrachia* may lie deep throughout the day in mid summer even in bright and calm conditions. BIGELOW (1924) states that *Beroë* under stormy conditions sinks down to 40–100 m in summer or in winter, and this is also the opinion of MAYER (1912). MCINTOSH (1888) remarks that ctenophores are not always near the surface but are often for long periods, in the changeable British climate, in deeper waters. It is difficult to come to any conclusion as ctenophore behaviour is not yet throroughly understood. AGASSIZ (1874) remarks that *Pleurobrachia* is sometimes common near the surface even in rough weather, but *Beroë* and *Bolinopsis* sink deeper the greater the disturbance.

There does not appear to be a diurnal change in vertical distribution in response to light. SAVAGE (1926) in a plankton cruise in the North Sea noted that, while most plankton species underwent diurnal vertical changes in distribution, *Beroë cucumis* did not. BIGELOW (1915) also states that ctenophores do not respond to sunlight. This appears to contradict the findings of ROSE (1913).

The vertical distribution of ctenophores does then appear to be controlled in part by the state of the surface waters. In general the various species appear at the surface more often during the late spring, summer and autumn when the sea is more often calm than in winter, when the creatures sink into the depths and, as a result, are less frequently observed. RUNNSTRÖM (1931) found them below 100 m during winter in Norwegian fjords. BIGELOW (1915) on the other hand seldom found *Pleurobrachia* deeper than 50 m. At most times of the year they were more regularly at between 20 and 30 m depth.

FEEDING BEHAVIOUR

All ctenophores are voracious feeders. LEBOUR (1922, 1923) investigated the feeding habits of the three species of ctenophore taken at Plymouth and she states that *Pleurobrachia* is apparently a miscellaneous feeder and its food is probably determined by what is abundant at the time. She carried out her investigations upon specimens immediately they had been taken from the sea, and specimens maintained in the laboratory aquaria.

The observations of other workers tend to confirm those of LEBOUR. References are: MAYER (1912), BIGELOW (1910, 1924), THORSON (1946), RALPH and KABERRY (1950), RUSSELL (1935), NELSON (1925), CHUN (1880), MAIN (1928), KINCAID (1915), KRUMBACH (1927), BISHOP (1968).

KUHL (1932) describes the food catching behaviour of *Pleurobrachia* as observed in an aquarium. The most usual prey-catching attitude is a stationary position with mouth upwards and the tentacles up to 20 cm long, with their lateral filaments extended like nets. The tentacle may not hang vertically down but may extend out to the side in practically any position. When a catch is made the tentacle contracts, wiping the prey off on the rim of the mouth as it does so. The animal increases its prey territory by extending its tentacles as it swims spirally through the water. As it swims to a certain extent away from its delicate tentacles the tentacles reflect the swimming movements like a vapour trail. The tentacles are said to trap the prey by means of the colloblasts. HARDY (1956) states that the prey "are continually being caught on the adhesive cells which jerk out and spring back again as their victims try to escape".

WEILL (1935) states that the generally accepted beliefs regarding the sticky colloblast granules and the elasticity and contractility of the collopode or spiral filament, are assumptions based upon the structure rather than the observed functioning of the colloblasts. In his observations upon the colloblasts of four species of ctenophore, he was not able to verify these various assumptions. In fact, he is of the opinion that any mobile animal attached to the colloblast would immediately detach the colloblast from the tentacle. He concludes that the colloblasts do not represent an organ of prehension. However, the fact remains that the tentacle catch the prey. Judging by the observation of RALPH and KABERRY (1950), that the prey sometimes appears to die immediately, it is possible that a poisonous substance is involved as is suggested by HYMAN (1940). Weill remarks that it is possible that the granules rapidly disappear or dissolve when prey comes into contact with the colloblast and he compares this rapid liberation of granules with the emission of mucus elsewhere in the animal kingdom. LEBOUR (1922) records that a *Pleurobrachia* played a pipe-fish for half an hour before the fish escaped. This hardly indicates the existence of a poison.

FOOD

During 1965 over 47 000 *Pleurobrachia* were taken in 367 hauls in the northern North Sea. Where the total number in a haul was less than 100 all specimens were examined for food content; where the number exceeded 100 a sub-sample of at least 50 was examined. The total number of specimens actually examined was 6 162. The monthly averages of those containing food varied from 4 to 60% and the average for the year was 26%. A similar method was adopted for subsequent years. In 1966 2 307 specimens were individually examined out of a total of 14 657 and the corresponding figures for 1966 were 4–40% with the yearly average of 21·5%. For 1967 the figures are 836 out of 5 314, 0–58% and 19%. For 1968 they are 404 out of 515, 0–100% and 27%, but as the North Sea sampling was so very sparse the north-west Scottish coastal areas are also included in the small sampling for 1968. Details of the percentages containing food in the various months of the year are tabulated in Table 2.

Details of the analyses of the food in the stomachs are given in Table 3 and these confirm the findings of LEBOUR (1922, 1923) that *Pleurobrachia* are carnivores but miscellaneous feeders. BISHOP (1968) says that *P. bachei* (accord-

TABLE 2. Percentage of *Pleurobrachia* containing visible food in various months.

	1965	1966	1967	1968		1965	1966	1967	1968
January	–	–	0	–	July	22	38	17	20
February	–	6	–	–	August	11	13	–	–
March	60	6	0	–	September	27	38	58	59
April	24	4	0	–	October	30	18	–	4
May	19	40	31	35	November	31	22	–	31
June	4	13	28	50	December	28	–	–	–

TABLE 3. Food of *Pleurobrachia* in Scottish waters from 1965 to 1968, given in number of organisms per 1000 stomachs

	February March April May*			June July August September				October November December**			Average
	1965	1966	1967	1965	1966	1967	1968	1965	1966	1968	
Calanus spp	270	100	233	72	73	22	53	41	35	67	97
Pseudo- and *Paracalanus*	8	13	12	14	4	13	21	16	3	19	12
Metridia lucens	3	6	–	3	2	5	5	2	–	–	3
Centropages spp	+	22	12	3	16	3	11	4	16	5	9
Temora longicornis	4	52	28	43	42	19	227	20	3	5	44
Acartia spp	63	870	–	45	61	161	174	26	22	19	144
Oithona spp	21	164	113	13	38	8	42	6	11	–	42
Other copepods	–	3	–	4	8	2	11	8	11	10	6
Unidentified copepod remains	9	27	44	19	65	2	32	40	30	–	27
Copepod eggs	12	–	–	1	–	–	–	–	–	–	1
Copepod nauplii	2	19	–	2	5	1	115	+	–	5	15
Total Copepoda	392	1276	442	219	314	236	691	163	131	130	399
Evadne	4	410	–	16	12	2	132	+	–	24	60
Podon	+	157	–	1	27	2	32	–	–	5	22
Ostracods	–	–	–	–	1	–	–	–	–	–	+
Cirripede larvae	39	150	–	2	20	5	16	1	3	–	27
Cumacea	–	–	–	–	–	–	–	3	–	–	+
Amphipoda	–	–	–	1	2	1	–	25	14	–	4
Euphausid calyptopis	7	33	–	–	1	–	–	–	–	–	4
Euphausid furcillia	5	7	–	1	2	2	–	–	–	5	2
Mysids	–	–	–	–	–	–	5	–	–	–	1
Decapod larvae	11	9	–	2	6	21	26	3	3	–	8
Total Crustacea	458	2042	442	242	385	269	902	195	151	164	525
Phytoplankton	+	–	12	–	–	–	–	–	–	–	1
Invertebrate eggs	–	138	4	273	50	1	–	8	–	–	47
Coelenterates	–	–	24	–	–	–	–	+	–	–	2
Cyphonautes	–	1	–	–	–	–	–	–	–	–	+
Annelids and larvae	–	1	92	1	–	–	–	+	–	–	9
Lamellibranch larvae	–	1	4	1	–	–	–	2	–	–	1
Spiratella	3	27	–	20	76	8	53	61	19	5	27
Echinoderm larvae	–	–	–	+	–	–	–	–	–	–	+
Oikopleura	1	13	80	1	–	–	–	–	–	–	10
Thaliacea	–	–	–	+	–	–	–	3	–	–	+
Fish eggs	5	6	4	–	–	1	–	–	–	–	2
Fish larvae	+	–	–	–	–	–	–	–	–	–	+
Unidentifiable	9	36	153	37	63	75	32	59	125	19	61
Totals	476	2265	815	575	574	354	987	328	295	188	686

* No adequate data for 1968. ** No adequate data for 1967.

TABLE 4. Seasonal percentage of food types by numbers (excluding unidentifiable remains) in *Pleurobrachia* from Scottish waters

	January to May			June to September				October to December			Average
	1965	1966	1967	1965	1966	1967	1968	1965	1966	1968	
Calanus	57	4·5	35	12·5	14	8	5·5	12·5	21	40	21
Total Copepoda	82	57	67	38	61	85	73	50	77	77	68
Total Crustacea	96	91	67	42	75	97	96	60	89	97	81
Fish eggs	1	0·3	0·6	0	0	0·3	0	0	0	0	0·2
Fish larvae..........	+	0	0	0	0	0	0	0	0	0	+

ing to MAYER (1912) *P. bachei* is a synonym of *P. pileus*) selected smaller rather than larger prey yet selected older rather than younger stages of the copepod *Pseudocalanus minutus*. NAGABUSHANAM (1959) feeding *Bolinopsis* in an aquarium said this species was unable to catch larger copepods, such as *Calanus*, or decapod larvae, though KAMSHILOV (1959) considered *Calanus* to be its dominant food. In her 1922 paper LEBOUR says that *Calanus* is the dominant food of *Pleurobrachia*, but in 1923 she says "*Pleurobrachia pileus* will eat fishes eagerly" and gives an illustration of a *Pleurobrachia* of 18 mm height full of young herring.

Examination of the food of *Pleurobrachia* from the Scottish collections shows fish to be of comparatively little importance. Except for one egg in September 1967, fish eggs were found only in the spring period and in small numbers, 5 eggs in 1 000 stomachs in 1965, 6 in 1966 and 4 in 1957. Fish larvae were recorded only in 1965 and then less than one larva in 1 000 stomachs.

From Table 4 it can be seen that Crustacea are the dominant food, making up about 80% of the total food by number and reaching 97%. By volume the crustaceous food would be even more emphasized. In the summer of 1965 there were large numbers of invertebrate eggs and, although the volume of 273 eggs would be approximately equal to one *Calanus*, they reduce the crustaceous content by number to 42%. Amphipods in the autumn would, because of their size, be of more importance than their numbers suggest.

Differences between the food taken by *Pleurobrachia* in the two years of good sampling, 1965 and 1966, can be noted. For example, in the early season of 1966 the figures for *Acartia* are about 14 times those for 1965 and the larger number of small copepods in 1966 is associated with a smaller number of *Calanus*, 100 instead of 270. The invertebrate eggs occurred earlier in the diet in 1966 than in 1965. *Podon* and *Evadne* were more abundant in 1966, and *Spiratella* was earlier in 1966. These differences will reflect the composition of the plankton and not any differences between the appetites of the *Pleurobrachia*. The apparent big difference between the spring crustaceous figures – 458 and 2 042 – becomes approximately 700 and 500 mg when reduced to wet weights, 1965 with its greater number of *Calanus* being greater than 1966.

The maximum amount of food seen in any one individual can be quite large; for example, a *Pleurobrachia* of 13 mm contained 1 *Calanus*, 1 *Centropages*, 44 *Acartia*, 4 *Evadne*, 2 *Podon* and 1 cyprid larva of *Balanus*. Another of 12 mm contained 12 *Calanus* and 4 *Acartia*.

PREDATION ON CTENOPHORES

Although ctenophores can hardly provide a nutritious food supply it is known that several species of fish will feed upon them occasionally. MORTENSEN (1912) notes that sometimes specimens of *Acanthias vulgaris* have their stomachs full of *Pleurobrachia*, and also records *Pleurobrachia* in the stomach of *Cyclopterus lumpus* from the North Sea. MORTENSEN states that *Cyclopterus* feeds upon *Mertensia ovum* in Greenland waters. BIGELOW (1924) observes that *Mola mola*, which is an occasional visitor to the Gulf of Maine, subsists chiefly upon these watery organisms. He had no knowledge at that time of any of the herring tribe or gadoids feeding upon ctenophores. However, JENSEN and HANSEN (1931) and HANSEN (1949) observed that cod off West Greenland often fed upon the ctenophores *Beroë*, *Bolinopsis*, *Mertensia* and *Pleurobrachia*, even to gorging. HANSEN believes that this is due to the fact that they are easy prey owing to their abundance and slow movements. KAMSHILOV (1960b) stated that under experimental conditions cod preyed vigorously on *Beroë*, hardly ever attacking *Bolinopsis*. RAE (1967, 1968) found that in the North Sea and Icelandic waters cod sometimes took *Beroë* but he does not include *Pleurobrachia* in cod food. GRAHAM *et al.* (1954) make similar observations from the Bear Island area.

In the Irish Sea during summer 1913 it was observed that the extremely abundant mackerel were feeding almost entirely upon vast swarms of *Pleurobrachia* which visited the area that year. For fully three weeks almost every mackerel stomach examined was filled with *Pleurobrachia* along with a variety of pelagic organisms (SCOTT, 1913, 1924).

The only other animals which feed upon ctenophores are a few medusoid coelenterates and other ctenophores. LEBOUR (1923) observed *Cosmetira pilosella*, *Aequorea* spp. and *Chrysaora isosceles* take *Pleurobrachia pileus* as food. As these observations were made upon specimens in captivity, it is difficult to estimate how important a source of food *Pleurobrachia* provides. LEBOUR is of the opinion that medusae and *Pleurobrachia* are the favourite food of *Chrysaora*. *Beroë* feeds almost entirely if not entirely on lobate ctenophores.

Although *Pleurobrachia* and other ctenophores are not popular food for predators, their metabolism during life and the products of their disintegration after death will play an important part in re-cycling nutrients for use by the phytoplankton.

EFFECT OF CTENOPHORES ON THE PLANKTON

Judging by the description of the feeding behaviour and the food species preyed upon, it is clear that lobate ctenophores are not very selective and will feed upon most organisms which come within their range and that they can manage to trap. Probably when ctenophores are present in small numbers they do not have any significant effect upon the zooplankton, but when they appear in abundance, especially in large and dense swarms, then they may have a drastic effect. There are numerous records of the presence of ctenophores monopolising the water over large areas. Thus BIGELOW and LESLIE (1928) write of the plankton of Monterey Bay, that while copepods were important at one station or another in combination with various other organisms, "without exception they were relatively scarce wherever *Pleurobrachia* were notably plentiful. This scarcity no doubt results from the efficiency with which *Pleurobrachia* fish with their trailing tentacles". Earlier BIGELOW (1915) observed the great impoverishment of the plankton on the German Bank due to *Pleurobrachia pileus*, which "when it swarms, seems to obliterate or devour everything else in the water". Later (1924) he also noted that wherever *Pleurobrachia* swarm they sweep the water clean of zooplankton and that copepods in particular are exterminated locally though they may swarm nearby. Similar observations have been made by FRASER (1961) and for the ctenophore *Bolinopsis* by KAMSHILOV (1959) and *Mnemiopsis* by BISHOP (1967).

INFLUENCE ON THE FISHERIES

Ctenophores apparently affect the fisheries in three direct ways as well as playing their part in the nutrient cycle:

(1) as food of fish
(2) in competition with fish for their food
(3) destroying fish eggs and larvae and shellfish larvae.

CTENOPHORES AS FOOD OF FISH

Mention has already been made of the various fish which are known to feed upon ctenophores. It is clear that in general ctenophores do not provide an important food but are eaten merely when little else is readily available. *Beroë* seems to be more important as fish food than the others but there is one recorded instance in which *Pleurobrachia* is reported to have been important as a food supply for fish. SCOTT (1913) writes on the extreme abundance of mackerel in the Irish Sea resulting in good fishing off Walney during summer 1913, and he suggests that in all probability this abundance was due to a remarkably extensive invasion of *Pleurobrachia* which appeared early in July and remained for almost a month. During that time almost every mackerel stomach was filled with *Pleurobrachia*. It is interesting that SCOTT noted that although the mackerel of the Irish Sea have usually finished spawning by July, on this occasion only three spent females and one mature male were observed in July, and the fish in September appeared no more advanced than many at the end of June. Is it possible, he asks, that the poorly nutritious, though abundant, food of *Pleurobrachia* delayed the maturing of the gonads?

CTENOPHORES IN COMPETITION WITH FISH

There are numerous suggestions but little concrete evidence that ctenophores compete seriously with fish for a common food supply. Previous work, and the details given in this paper, show the importance of copepods in particular as food for *Pleurobrachia* and it seems reasonable to believe that in such a situation the fish feeding upon the plankton will be affected by this competition for food. RUSSELL (1931), discussing the part played by the crustacea in the economy of the seas, states that the immense swarms of plankton predators "especially the ctenophores, must play havoc among the copepod population and serve as serious competitors to the fish themselves, at times even depleting the supply. This is especially noticeable at times when ctenophores predominate in the catches, as on such occasions the remaining animal plankton appears exceptionally poor." BISHOP (1967), dealing with *Mnemiopsis leidyi*, says that this ctenophore eats about 22 000 copepods per m^3 daily in the Patuxent River, (Chesapeake, U.S.A.) and is responsible for 52% of the daily summer mortality of *Acartia tonsa*.

It might reasonably be expected that herring would be involved in competition with ctenophores, as their principal food organisms are crustacea and chief of these is *Calanus finmarchicus*. LUCAS and HENDERSON (1936) in their paper on the association of jelly fish and other organisms with catches of herring found that "Small berrylike jellies", possibly *Pleurobrachia*, were recorded once with a catch of nine crans which is less than the corresponding port average. Evidence for the existence of competition lies in the report of MANTEUFEL (1941) on the observations in the Barents Sea during the period 1931 to 1939. During June the *Calanus* and Euphausiacea achieve their annual maximum abundance providing the 'red feed', largely *Calanus*, which the herring consume eagerly. During the abundance of crustacean food the fat content of the herring rises from 3 to 23% of the body weight. This store of fat is drawn upon in the winter when the fish lie deep and almost cease feeding. In the spring of 1938 the zooplankton was scarce, apparently related to the occurrence of unusual numbers of the ctenophore *Bolinopsis*. The scarcity in the plankton resulted in delayed summer fattening of the fish, a lower average level of fatness and a reduced rate of growth.

Beroë feeds on *Bolinopsis* (which is more abundant than *Pleurobrachia* in Arctic waters) and KAMSHILOV (1960, 1961) has shown that when cod feed on the *Beroë* the numbers of *Bolinopsis* increase and *Calanus* becomes reduced. This could be of importance in the brood survival rates of the larval cod and other fish in the area as during their early stages they feed on copepods.

THE DESTRUCTION OF FISH EGGS AND THE LARVAE OF FISH AND SHELLFISH

That ctenophores (excluding *Beroë*) can seriously affect the fisheries by predation on their planktonic stages has often been suggested in the literature, but there is little concrete supporting evidence. Some examples are given. MAYER (1912) remarked that in the northern seas where ctenophores occur in vast swarms they constitute a serious menace to cod fisheries by devouring the pelagic eggs and young fish. BIGELOW (1924) was convinced of their economic importance and states, p. 368, that, "There is reason to believe, too, that *Pleurobrachia* is a serious enemy to the successful reproduction of sundry fishes (e.g. cod and haddock) by feeding on their buoyant eggs, few of which can escape destruction in localities where ctenophores are numerous. Indeed it is doubtful if more than a trifling proportion of the fish eggs of any sort that are spawned on German Bank can survive there with *Pleurobrachia* so plentiful in that neighbourhood all the year round. In short, the local abundance of the latter may well determine the productivity or otherwise of any particular area in the Gulf (of Maine) as a nursery for gadoids or flat fish. Hence it is fortunate for the inhabitants of New England that the spawning ground for haddock on the eastern part of Georges Bank seems practically free from *Pleurobrachia*."

LEBOUR (1922) observed that small medusae and ctenophores frequently contained small fish, clupeoids, whiting, wrasse, *Cottus* and many others were taken. RUSSELL (1935) investigating the seasonal abundance of young fish near Plymouth observed that the post larval stages of certain spring spawners were poorly represented in the year 1929, and he says (p. 167) that "one cannot escape the possible conclusion that they (*Pleurobrachia*) may have been responsible for the absence of the peak in the abundance of young fish which should have occurred just at that time".

The work of NELSON (1925), though concerned with an American lobate, *Mnemiopsis leidyi*, illustrates very clearly the effect ctenophores may have on the shell fisheries. NELSON observed that there was close correlation between the abundance of *Mnemiopsis* and the intensity of oyster sets and shipworm infestation. In 1921 and 1922 there were heavy sets of *Ostrea*, *Teredo* and *Bankia*. On 25. June 1921 the average number of oyster larvae in the surface waters was 362 per l, two days later 87 per l, representing the normal mortality. During these two years, *Mnemiopsis* was rare or absent. In 1923 the oyster set was a failure, there being only one or two spat on every third shell compared with 1 000 spat on each shell in previous years. The number of larvae per litre on 23. June, 1923, was 609, two days later it was only 0·54 per l. There was also light infestation by *Teredo* and *Bankia* that year. Apart from the vast swarms of *Mnemiopsis* present at that time, there was no other known factor which could have been responsible. In nearby waters where *Mnemiopsis* did not swarm there was a normal oyster set. This important effect of *Mnemiopsis* upon the oyster larvae population is easily understood when one considers that NELSON found one specimen containing 126 oyster larvae. BURKENROAD (1930) and NELSON (1928) give further evidence as to the importance of *Mnemiopsis* upon the oyster fishery of America. KINCAID (1915) believes that *Pleurobrachia* may be a serious enemy of the oyster in Washington waters through the large numbers of the larvae of the latter which it consumes.

The cruise of the Scottish research ship "Explorer" from 1–18. October, 1951, recorded *Pleurobrachia* as occurring in considerable numbers in the northern Moray Firth, at the same time as herring larvae were virtually absent from the Moray Firth proper but in considerable numbers along its eastern boundary and along the Aberdeen coast.

Whilst these suggestions may very well be true the examination of the food content of *Pleurobrachia* in Scottish waters over a four year period shows predation on fish eggs and larvae to be negligible in this area.

This does not mean *Pleurobrachia* will have no effect on the fisheries, but it will have its most serious effect when an abundance coincides with the critical phase in the early larval planktonic stages. This may be due to direct feeding, or in the Scottish area where this has been shown to be of little significance, to an indirect effect due to shortage of a crustaceous food source for the fish larvae.

PARASITES OF PLEUROBRACHIA

Cercarian parasites are well known from *Pleurobrachia* (see DOLLFUS, 1963 and REBECQ, 1965). LEBOUR (1916) identified the late cercarian stage of *Opechona* (*Pharyngora*) *bacillaris*, a parasite of the mackerel, clinging to the inside of the stomach of *Pleurobrachia pileus*. The cercaria found in the *Pleurobrachia* from the northern North Sea are probably also *Opechona* but the eye-spots and oral suckers are not so prominent as in *O. bacillaris* which indicates *O. retrac-*

TABLE 5. Numbers of cercaria per 1000 *Pleurobrachia*

	March to August	September to February
1966	17	3230
1967	33	450
1968	25	4720

tilis as being more likely. *O. retractilis* is a parasite of whiting (I am indebted to Mr. K. MACKENZIE of this Laboratory for these data).

Opportunity was taken when examining the stomach contents to count these. They occurred both inside and outside the stomachs of the *Pleurobrachia*, those outside being very much more abundant. There was a remarkably higher incidence of parasitism during the winter months (September to February) than in the spring and summer (March to August) – see Table 5 – the change being quite sudden at about the end of August.

Although the month with the highest average – over 4 cercaria to each *Pleurobrachia* – was November, very high individual numbers were also found in September. Particularly high figures were 140 and 120 found in individuals of 12 and 11 mm in September and 104 in one of 14 mm in November.

The sudden increase in parasitism from low figures in August to high figures in September suggests that this was due to infection then and not to a cumulative build up of numbers with the increasing age of the host.

Nematode parasites are much less common and occurred singly in September.

SUMMARY

Pleurobrachia is very widely distributed in neritic waters, often existing in great numbers. In Scottish waters the greatest numbers are found off the north and east coasts. Peak numbers there, over a long time period, are found in late autumn, but sometimes, as in 1965, there is a summer peak.

Spawning occurs from late spring until autumn in Scottish waters, but maturity may be temperature controlled as it can occur throughout the year in warm water. Vertical migration seems variable and is not adequately understood.

Pleurobrachia is a carnivore but a miscellaneous feeder, and although previous works have emphasised the importance of fish larvae in the food this has not been found from Scottish waters where crustacea form about 80% of the diet and can reach 97% with copepods usually dominant. Very few fish eggs and larval fish were found.

Pleurobrachia is sometimes eaten by fish (*Acanthias*, *Cyclopterus*, *Mola*, *Scomber*) but *Beroë* is preferred by gadoids. Some medusae eat *Pleurobrachia* and it, with other lobate ctenophores, are the sole food of *Beroë*.

Pleurobrachia can severely reduce the zooplankton content of water in which they swarm and it can reasonably be assumed that they are therefore competitors for food with herring and other pelagic fish, and with the planktonic larvae of most fish in neritic waters. In some areas they are known to be predators of larval fish and the pelagic larvae of shellfish such as oysters.

They become heavily infested by cercarian parasites from August onwards, which later become parasites of fish, particularly whiting.

REFERENCES

AGASSIZ, A., 1874. "Embryology of the Ctenophorae". Mem. Am. Acad. Arts Sci., **10**: 384–87.

BIGELOW, H. B., 1909. "Coelenterates from Labrador and Newfoundland". Proc. U.S. natn. Mus., **37**: 301–20.

BIGELOW, H. B., 1915. "Separation of the coast water between Nova Scotia and Chesapeake Bay, July and August 1913". Bull. Mus. comp. Zool. Harv., **59**: 151–359.

BIGELOW, H. B., 1926. "Plankton of the offshore waters of the Gulf of Marine". Bull. Bur. Fish., Wash., **40**: (2) 1–509.

BIGELOW, H. B., & LESLIE, M., 1930. "Reconnaisance of the waters and plankton of Monterey Bay, July 1928". Bull. Mus. comp. Zool. Harv., **70**: 429–581.

BIGELOW, H. B., & SEARS, M., 1939. "Studies of the waters of the continental shelf, Cape Cod to Chesapeake Bay". Mem. Mus. Comp. Zool. Harv., **54**: 183–378.

BISHOP, J. W., 1967. "Feeding rates of the ctenophore *Mnemiopsis leidyi*". Chesapeake Sci., **8**: 259–61.

BISHOP, J. W., 1968. "A comparative study of feeding rates of tentaculate ctenophores". Ecology, **49**: 996–97.

BROWNE, E. T., 1905. "A report on the medusae found in the Firth of Clyde (1901–1902)". Proc. R. Soc. Edinb., **25**: 738–78.

CHUN, C., 1880. "Die Ctenophores des Golfes von Neapel und der Angrenzenden Meeres-Abschnitte". Fauna Flora Golf Neapel, **1**: 313 pp.

DELAP, M., & DELAP, C., 1906. "Notes on the plankton of Valencia Harbour 1902–1905". Rep. Sea inld. Fish. Ire., 1905 (2) 141–59.

DOLLFUS, R. P., 1963. "List of paleartic and Indian Sea Coelenterata where have been found some digenetic Trematoda". Bull. Inst. Pêch. marit. Maroc, (9–10) 33–57.

FRASER, J. H., 1961. "The oceanic and bathypelagic plankton of the North East Atlantic". Mar. Res., (4) 48 pp.

FRASER, J. H., 1962. "The role of ctenophores and salps in zooplankton production and standing crop". Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer, **153**: 121–23.

GRAHAM, M., TROUT, G. C., BEVERTON, R. J. H., CORLETT, J., LEE, A. J. & BLACKER, R. W., 1954. "Report on research from 'Ernest Holt' into the fishery near Bear Island, 1949 and 1950". Fishery Invest., Lond., Ser 2, **18**: (3) 87 pp.

HANSEN, P. M., 1949. "Studies on cod". Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer, **123**: 77 pp.

HARDY, A. C., 1956. *The Open Sea.* Collins, London. 335 pp.

HYMAN, L., 1940. *The Invertebrates, Protozoa through Ctenophora.* McGraw-Hill, N.Y. 726 pp.

JENSEN, A. S., & HANSEN, P. M., 1931. "Investigation on the Greenland Cod (*Gadus callarias* L)". Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer, **72**: (1) 41 pp.

KAMSHILOV, M. M., 1959. "Interrelations between organisms and the part they play in evolution". Zh. obshch. Biol., **20**: 370–78.

KAMSHILOV, M. M., 1960a. "Feeding of Ctenophore, *Beroë cucumis* (Fabr.)". Dokl. Akad. Nauk SSSR, **130**: 1138–40.

KAMSHILOV, M. M., 1960b. "Biology of Ctenophores off Murman". ICES CM 1960 (157) 5 pp. (mimeo).

KINCAID, T. B., 1915. "Oyster culture in Washington". Trans. 2nd A. Mtg Pacif. Fish. San Francisco, p 4.

KORSCHALT, E., & HEIDER, K., 1895. *Text book of the Embryology of Invertebrates*, (1). Swan Sonnenschein, London. 484 pp.

KOWALEVSKY, A., 1867. "Entwickelungsgeschichte der Rippenquallen". Zap. imp. Akad. Nauk., Ser. 7., **10**: (4) 36 pp.

KRAMP, P. L., 1913. "Coelenterata". Bull. trimest. Résult. Crois. période. Cons. perm. int. Explor. Mer, (3) 522–38.

KRAMP, P. L., 1939. "Medusae, Siphonophora and Ctenophora". Zoology Iceland, **11**: (5b) 37 pp.

KRAMP, P. L., 1943. "Medusae, Siphonophora and Ctenophora". Meddr Grønland, **121**: (12) 20 pp.

KRUMBACH, TH., 1928. "Ctenophora". Tierwelt N.-u. Ostsee, Lief. 7, **3**: (f) 50 pp.

KUHL, W., 1932. "Rippenquallen beim Beutefang". Natur Mus., Frankf., **62**: 130–33.

LEBOUR, M. V., 1916. "Medusae as hosts for larval trematodes". J. mar. biol. Ass. U.K., **11**: 57–9.

LEBOUR, M. V., 1922. "Food of Plankton organisms". J. mar. biol. Ass. U.K., **12**: 644–77.

LEBOUR, M. V., 1923. "Food of Plankton organisms". J. mar. biol. Ass. U.K. **13**: 70–92.
LINDQUIST, A., 1958. "Über das Vorkommen von *Pleurobrachia pileus* (O. F. Müller) (Ctenophora) in den nördlichen Teilen der Ostsee". Commentat. biol., **17**: (2) 1–10.
LUCAS, C. E., & HENDERSON, G. T. D., 1937. "Association of jellyfish and other organisms with catches of herring". J. mar. biol. Ass. U.K. **21**: 293–304.
McINTOSH, W. C., 1888. "Notes from the St. Andrews Marine Laboratory". Ann. Mag. nat. Hist., Ser. 6, **2**: 464–72.
McINTOSH, W. C., 1890. "On the occurrence of the ctenophores throughout the year". Ann. Mag. nat. Hist., Ser. 6, **5**: 43–7.
McINTOSH, W. C., 1926. "Additions to the marine fauna of St. Andrews since 1874". Ann. Mag. nat. Hist., Ser. 9, **18**: 241–66.
MAIN, R. J., 1928. "Observations on the feeding mechanism of a Ctenophore, *Mnemiopsis leidyi*". Biol. Bull. mar. biol. Lab., Woods Hole, **55**: 69–78.
MANTEUFEL, B. P., 1941. "Plankton and herring in the Barents Sea". Trudy polyar. nachno-issled. Inst. morsk. ryb. Khoz. Okeanogr., **7**: 125–218.
MAYER, A. G., 1912. "Ctenophores of the Atlantic coast of North America". Pubis Carnegie Instn. (162) 58 pp.
MORTENSEN, TH., 1912. "Ctenophora". Dan. Ingolf-Exped., **5**: (2) 95 pp.
MOSER, F., 1909. "Die Ctenophoren der deutschen Südpolar-Expedition 1901–1903". Dt. Südpol.-Exped., **11**: Ser. Zool. (3) 141 pp.
NAGABUSHANAM, A. K., 1959. "Feeding of a ctenophore, *Bolinopsis infundibulum* (O. F. Müller)". Nature, Lond., **184**: 829.
NELSON, T. C., 1925. "Occurrence and feeding habits of ctenophores in North Jersey coastal waters". Biol. Bull. mar. biol. Lab., Woods Hole, **48**: 92–111.
RAE, B. B., 1967a. "The food of cod in the North Sea and on the west of Scotland grounds". Mar. Res., (1) 68 pp.
RAE, B. B., 1967b. "The food of the dogfish *Squalus acanthias* L.". Mar. Res., (4) 19 pp.
RALPH, P. M., & KABERRY, C., 1950. "New Zealand Coelenterates. Ctenophores from Cook Strait". Zool. Publs Vict. Univ. Coll., (3) 11 pp.
REBECQ, J., 1965. "Considérations sur la place des trématodes dans le zooplancton marin". Annls Fac. Sci. Marseille, **38**: 61–84.
RUNNSTRÖM, S., 1931. "Eine Uebersicht über das Zooplankton des Herdla- und Hjeltefjordes". Bergens Mus. Arb., (7) 67 pp.
RUSSELL, F. S., 1933. "Seasonal distribution of macroplankton as shown by catches in the 2-metre stramin ring-trawl in offshore waters off Plymouth". J. mar. biol. Ass. U.K., **19**: 73–82.
RUSSELL, F. S., 1934. "The study of copepods as a factor in oceanic economy". Fifth Pacif. Sci. Congr., **3**: 1933: 2023–34.
RUSSELL, F. S., 1935. "Seasonal abundance and distribution of the pelagic young of teleostean fishes caught in the ring-trawl in offshore waters in the Plymouth area". J. mar. biol. Ass. U.K., **20**: 147–80.
SCHODDUYN, M., 1926. "Observations faites dans la baie d'Ambleteuse (Pas de Callais)". Bull. Int. océanogr. Monaco, (482) 64 pp.
SCOTT, A., 1913. "The mackerel fishery off Walney in 1913". Rep. Lancs Sea-Fish. Labs, (22) 19–25.
SCOTT, A., 1919. "A mid-winter invasion of *Noctiluca* and *Pleurobrachia*". Rep. Lancs Sea-Fish. Labs, (28) 6–10.
SCOTT, A., 1924. "Food of the Irish Sea Herring in 1923". Proc. Trans. Lpool biol. Soc., **38**: 115–19.
THORSON, G., 1946. "Reproduction and larval development of Danish marine bottom invertebrates". Meddr Kommn Danm. Fisk.- og Havunders, Ser. Plankton, **4**: (1) 523 pp.
WEILL, R. M., 1935. "Le fonctionment des colloblasts". C. r. hebd. Séanc. Acad. Sci., Paris, **201**: 850.