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Vertical distribution and seasonal abundance of *Aglantha digitale* (O.F. Müller) (Coelenterata: Trachymedusae) and other planktonic coelenterates in the northeast Atlantic Ocean.

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Abstract. The vertical distribution and seasonal variability in abundance of the hydromedusa *Aglantha digitale* (O.F. Müller) and other coelenterates from the north-east Atlantic Ocean are described. The coelenterates were abundant from May to September and reached peak numbers in June, July and September when concentration of 40 individuals m^{-3} were recorded. *A. digitale* numerically dominated the coelenterate population and accounted for over 80% of the dry weight biomass in hauls taken from 1971 to 1974. The data suggests a 2½ month development period for this medusa from egg to mature adult (8 mm) which supports previous published data. During the growth of the medusa there were considerable changes in the ratios of wet to dry weights. At a bell-height of 1 mm the mean dry weight was 22% of mean wet weight and at 8 mm the mean dry weight was 5% of mean wet weight; the percentage decreased further in the largest specimens to 2% at 25 mm. The majority of *A. digitale* occurred in the upper 100 m but in late July the larger specimens extended their distribution to the limit of sampling (500 m). The two most abundant siphonophores , *Dimophyes arctica* (Chun) and *Nanomia cara* A. Agassiz, were found deeper than the main population of *A. digitale*. It is suggested that coelenterates could be an important source of nitrogen for the development of the late bloom of phytoplankton in the north-east Atlantic Ocean.

Introduction

It has long been realised that high concentrations of small coelenterates can drastically reduce the numbers of other zooplankton and may also discourage the presence of adult fish (Lucas and Henderson, 1936; Fraser, 1961; Möller, 1979). Coelenterates are useful indicators of hydrographic conditions; the oceanic species can be used as labels of the incursion of oceanic waters into the mixed waters of the shelf seas (Fraser, 1972). The distribution of medusae in the north-eastern Atlantic Ocean and shelf seas around the UK has been documented by Kramp (1959, 1961) Russell (1953, 1970) and Fraser (1972). There is however a paucity of information on seasonal variability in abundance and vertical distribution of the smaller coelenterates and especially the role that they play in the planktonic ecosystem of the open seas.

The Hydromedusa (Trachymedusae) *Aglantha digitale* (O.F. Müller) is one of the commonest coelenterates in the North Atlantic Ocean and is widely distributed from about 35°N northwards into Arctic waters (Kramp, 1959). This description of the vertical distribution and seasonal variability in abundance of *A. digitale* and other coelenterates is derived from data from two time series of plankton sampling in the north-east Atlantic Ocean spanning a 23 year period.

Materials and Methods

Two sources of coelenterates from Ocean Weather Station (OWS) "India" (59°00′N, 19°00′W) in the north-east Atlantic, were used in this study: (a) vertical hauls with Hensen nets from 100 m to the surface and (b) oblique hauls from 500 m to the surface using the Longhurst Hardy Plankton Recorder (LHPR; see Longhurst *et al.*, 1966, and Longhurst and Williams, 1976).

Hensen net hauls (½ m net mouth diameter, 300 μm net mesh diameter) were taken at approximately weekly intervals from 1952 to 1974 whenever station "India" was manned by British Weather Ships. The sampling was carried out by the ship's companies for the Ministry of Agriculture, Fisheries and Food (MAFF), Fisheries Laboratory, Lowestoft from 1952 to 1969 and for the Institute for Marine Environment Research from 1970 to 1974; the samples from 1952-1963 have been analysed by MAFF and, subsequently selected samples have been analysed by IMER.

A detailed sampling programme was carried out at OWS "India" from March 1971 to September 1974 (Williams *et al.*, 1973, 1974, 1975 and 1976); 73 oblique hauls were taken with the LHPR fitted with a net and filtering gauze of 280 μm nylon net. The combined hauling and towing speed was 3.7 to 4.6 km h^{-1} on double oblique hauls between the surface and 500 m; only the ascent samples were used in this study. Plankton samples were collected at one-minute intervals, giving samples at approximately 10 m depth intervals. An average of 500 m^3 of water was filtered during each ascent haul and the plankton was preserved in neutral formalin. There was regular sampling over an extended period during 1973 (2 April to 18 October) and this year was chosen for a study of coelenterates; 12 LHPR hauls taken during the hours of daylight were selected for a detailed taxonomic analysis. All coelenterates were extracted, identified as far as possible, and counted; of the 8827 *Aglantha digitale* in the samples, 2385 were measured and wet and dry weights taken of 400 specimens. Measurements (± 0.08 mm) of bell height included the gelatinous apical projection. Specimens were also identified and measured from Hensen net hauls taken between 11 September and December 27, 1972 (8 hauls), 5 January to February 20, 1973 (7 hauls), 31 October to December 6, 1973 (4 hauls) and 7 January to April 1, 1974 (5 hauls).

Results

Seasonal distribution and abundance

The mean seasonal abundances of *Aglantha digitale*, siphonophores and other medusae in the upper 100 m at OWS "India" for the period 1952 to 1963 are shown in Figure 1. *A. digitale* has been separated into two sub-species *A. digitale digitale* (O.F.Müller) and *A. digitale rosea* (Forbes) on the basis of size and of the number of marginal sensory clubs. Medusae identified from OWS "India" were *A. digitale rosea*, although there were problems in observing and counting the marginal sensory clubs in the preserved material. Some authors (see Russell, 1953) consider that the differences may only be varietal and that they have arisen because of the wide distribution of this species over a great range of environmental conditions.

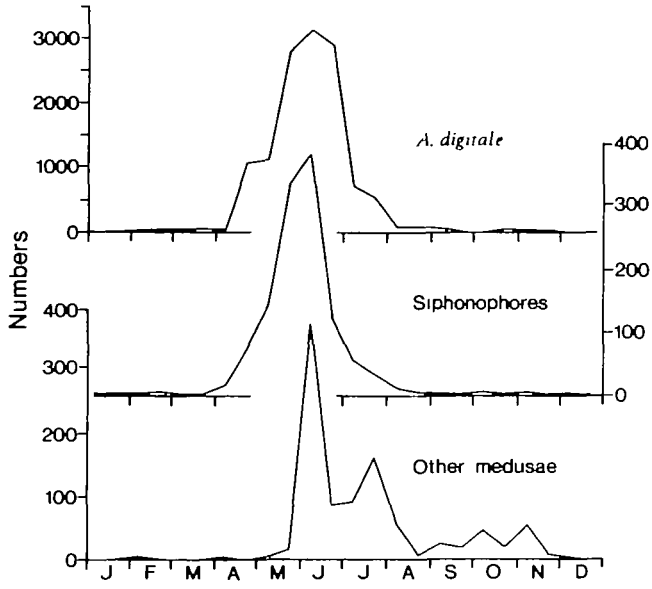

Fig. 1. Seasonal distribution and mean abundance of coelenterates from 100 m Hensen net hauls at OWS "India", 1952 to 1963, in the north-east Atlantic Ocean.

Siphonophores accounted for less than 10% of the coelenterates present; seventeen species were recorded together with large numbers of unidentified eudoxid stages. The three most abundant siphonophores occurring in the 12 year period were *Dimophyes arctica* (Chun), *Nanomia cara* A. Agassiz and *Lensia conoidea* (Keferstein and Ehlers). Other siphonophores were:

Agalma elegans (Sars)
Bassia bassensis (Quoy and Gaimard)
Ceratocymba sagittata (Quoy and Gaimard)
Chelophyes appendiculata (Eschscholtz)
Euodoxoides spiralis (Bigelow)
Halistemma rubrum (Vogt)
Hippopodius hippopus (Forskål)
Lensia achilles Totton
Lensia fowleri (Bigelow)
Lensia multicristata (Moser)
Lensia subtilis (Chun)
Physophora hydrostatica Forskål
Sulculeolaria biloba (Sars)
Vogtia glabra Bigelow

Other Hydromedusae present were *Sarsia* sp., *Bougainvillia* sp., *Bougainvillia brittanica* Forbes, *Leuckartiara nobilis* Hartlaub, *Halopsis ocellata* A. Agassiz and *Solmaris corona* (Keferstein and Ehlers).

The mean seasonal peak of abundance of *Aglantha digitale* and other coelenterates, from 1952 to 1963, occurred in June (Figure 1); they first appeared in early April and declined by the end of July. Seasonal fluctuations of abundance of coelenterates in the LPHR hauls taken at OWS "India", 1971 to 1974, are shown in Figure 2; and increase in numbers was observed in April and May in all four years, (as in the earlier series shown in Figure 1,), and peak abundance was reached in July (1971) and June (1972-1974) before a decline in August and September. Of the 9710 coelenterates identified from the 12 LPHR hauls, taken

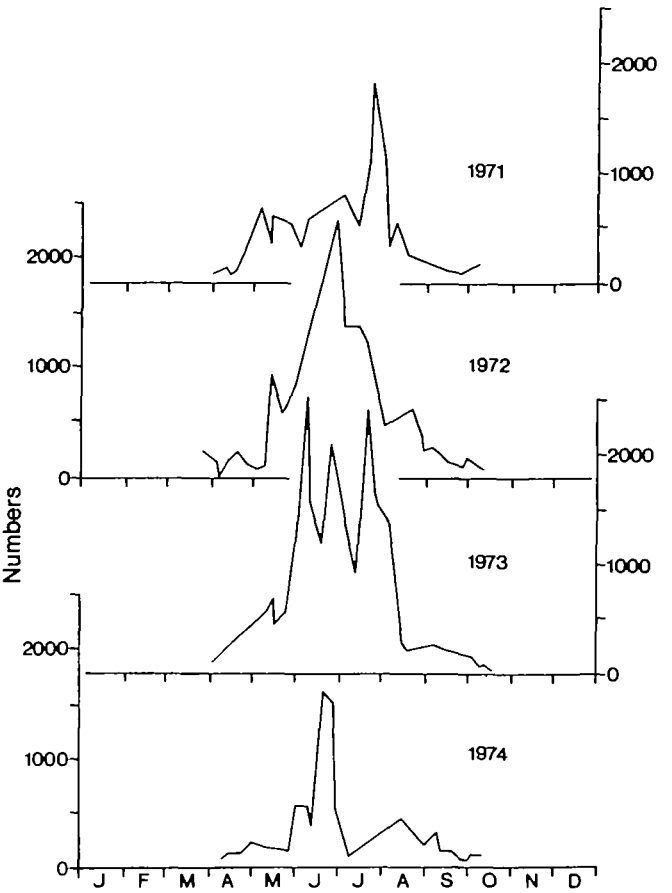

Fig. 2. Seasonal distribution and abundance of coelenterates from 500 m LHPR hauls at OWS "India", 1971 to 1974, in the north-east Atlantic Ocean.

in 1973, 90% were *A. digitale* (Figure 3) and of these 91% were caught in the top 100 m; thus, the numbers taken in the Hensen net (1952 to 1963) may be taken as equivalent estimates of those between the surface and 500 m. The siphonophores in the 12 hauls were primarily *Dimophyes arctica, Nanomia cara, Lensia* spp. and unidentified eudoxids. The remaining medusae consisted of a few Anthomedusae, Trachymedusae and coronate Scyphomedusae species. The seasonal peak of abundance of *A. digitale* occurred in June and July, slightly later than the siphonophores in June (Figure 3).

Vertical distribution and abundance

The vertical distribution and abundance of *Aglantha digitale* from the 12 LHPR hauls taken in 1973 is shown in Figure 4, in which the data are divided into five arbitrary size classes (based on bell-height). The smallest individuals were mostly in the upper 100 m and were present from early May to Mid-August. Most of the larger specimens were also in the upper 100 m but in late July, they extended

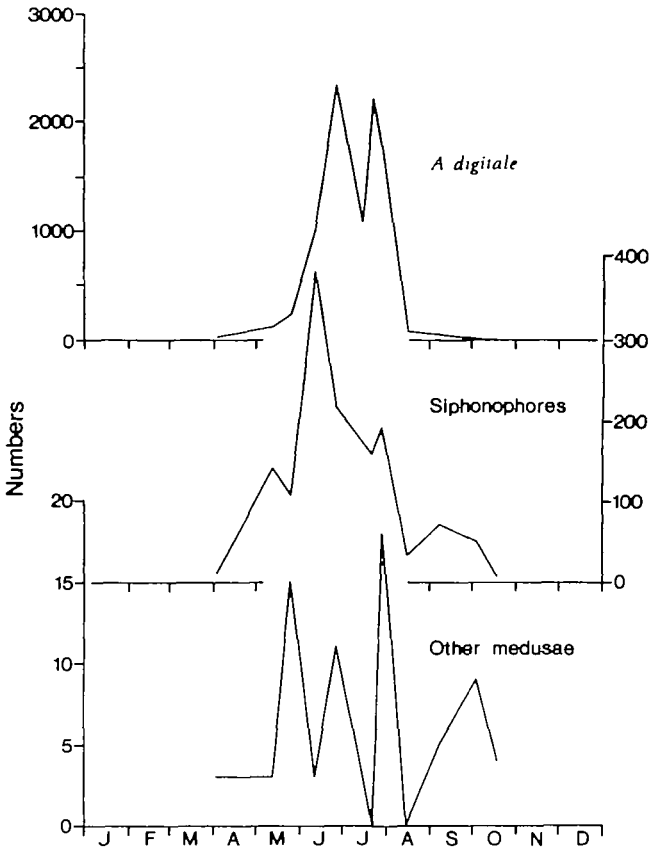

Fig. 3. Seasonal distribution and abundance of coelenterates from 12, 500 m LHPR hauls taken in 1973 at OWS "India" in the north-east Atlantic Ocean.

down to the limit of sampling (500 m). Analysis of the Hensen net hauls taken in autumn and winter of 1972/1973 revealed a few *A. digitale* in the upper 100 m, ranging in size from 7 to 18 mm. Small numbers of this overwintering population were found in the LHPR haul taken during late March (Figure 4) and the probable remnants (> 12mm) near the surface in late May. Small individuals (< 3 mm), originating from this overwintering stock, first appeared in early May and reached a peak of abundance in June. About 90% of *A. digitale* were between 2 and 7 mm in length (Figure 5) with a mean of 5 mm. Only 10% of the population were 8 mm or above at which size they are regarded as mature in the north-eastern Atlantic Ocean. The two most abundant siphonophores, *Dimophyes arctica* and *Nanomia cara*, (Figure 6) were deeper than the main population of *A. digitale*. The vertical distribution and abundance of all coelenterates identified from the LHPR hauls from 1971 to 1974 at OWS "India" are shown in Figure 7. The majority of the coelenterates were concentrated in the upper 100 m in the four years and although coelenterates from the hauls taken during 1971, 1972 and 1974 were not examined in precise taxonomic detail they were primarily small pre-adult *A. digitale*.

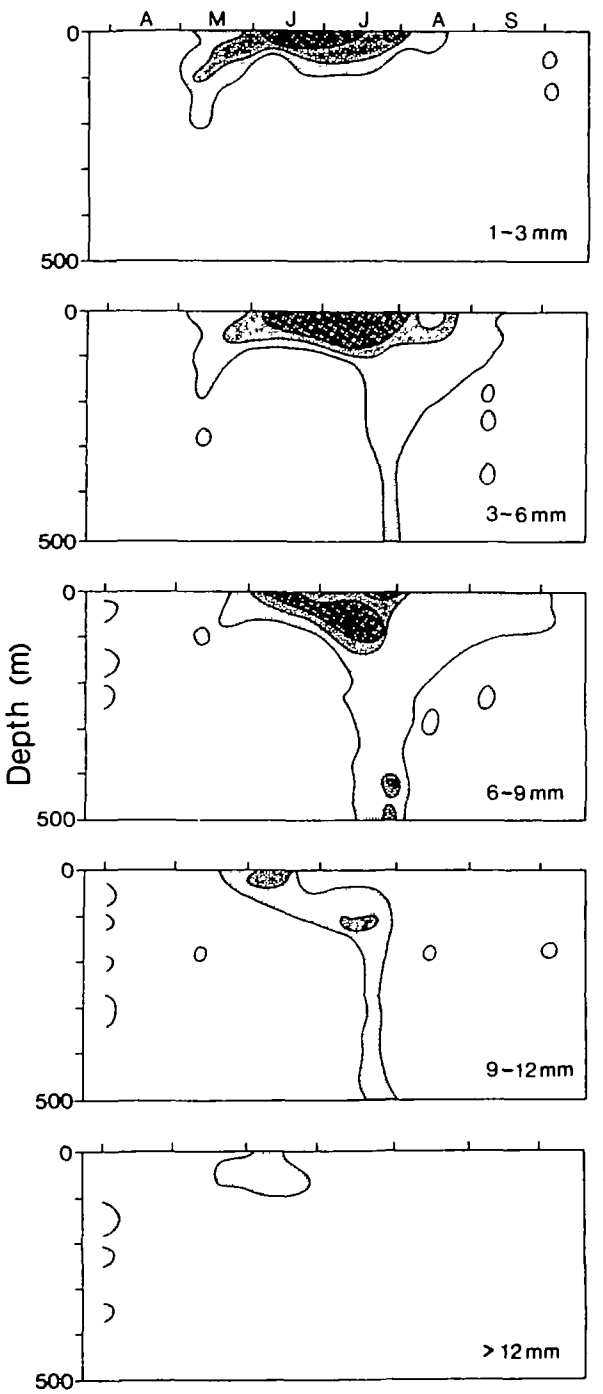

Fig. 4. *Aglantha digitale*. Vertical distributions and seasonal abundance of the various size categories from 12 LHPR hauls at OWS "India" taken during 1973. Contour drawn at 1:10:50 individuals 10 m^{-3}.

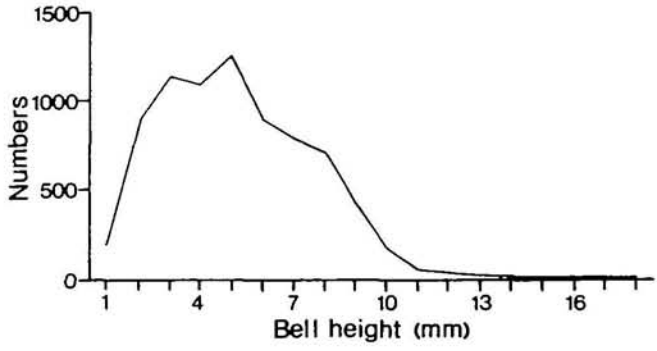

Fig. 5. *Aglantha digitale.* Size distribution (bell-height) of the population identified from 12 LHPR hauls taken during 1973.

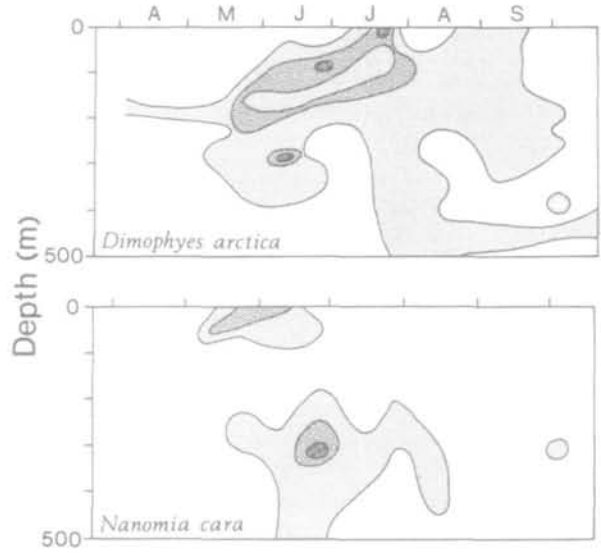

Fig. 6. *Dimophyes arctica* and *Nanomia cara.* Vertical distribution and seasonal abundance from 12 LHPR hauls at OWS "India" during 1973. Contours drawn at 1:2:4 individuals 10 m^{-3}.

Discussion

At OWS "India" coelenterates were abundant from May to September in the upper 100 m and reached peak numbers in the summer months (June, July and August) when concentrations of 40 individuals m^{-3} were recorded. The timing of their seasonal occurrence and the species composition has remained relatively stable since sampling commenced in 1952. For all years sampled the hydromedusa *Aglantha digitale* numerically dominated the coelenterate population and accounted for the majority of the dry weight biomass of coelenterates; over 80% from 1971 to 1974 at OWS "India". A few species of siphonophores were also numerically important in the samples but the detailed analysis of the samples taken in 1973 has shown that they were more evenly spread through the water column than *A. digitale*. At OWS "India" the majority of *A. digitale* with bell

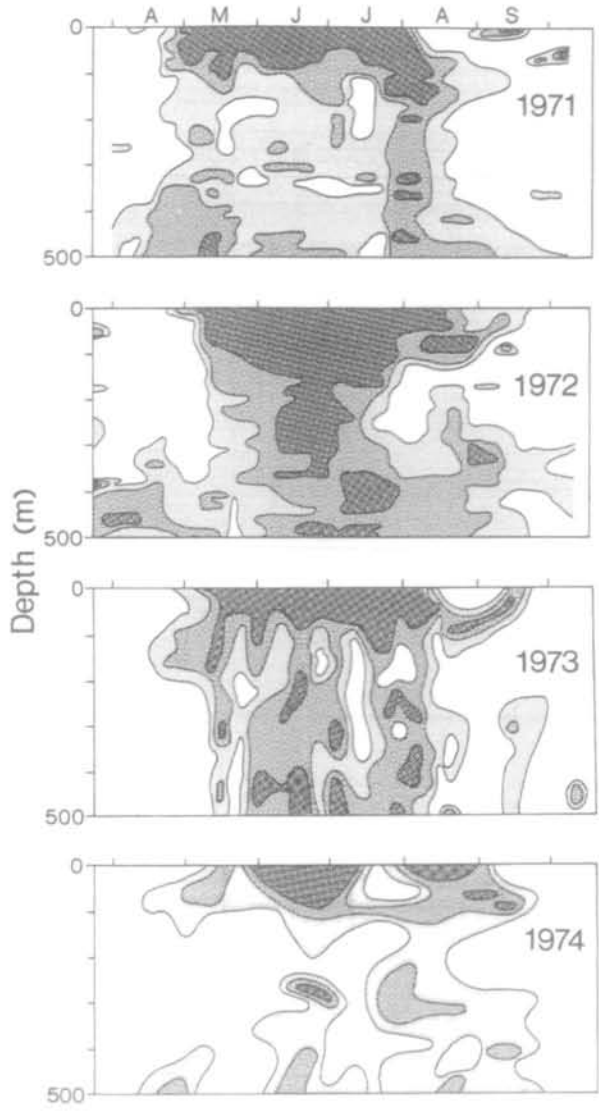

Fig. 7. Vertical distribution and seasonal abundance of coelenterates at OWS "India", 1971 to 1974, in the north-east Atlantic Ocean. Contours drawn 4:8:16 individuals 10 m^{-3}.

heights 6 mm and less were concentrated in the 0 to 100 m (Figure 4) and migrated to greater depths as they matured. Those found between 0-400 m in late March and early April, 1973, (Figure 4), had bell heights between 8 to 15 mm and these together with the specimens (> 12 mm) in the upper 100 mm in May and June, were assumed to be the remnants of the overwintering population from the previous year. *Aglantha* occurred in low numbers, in September and October of 1972 in the upper 500 m (Figure 7); in the absence of sampling below this depth, it

is possible only to speculate that larger specimens may have migrated below 500 m (a few individuals of 7 to 18 mm were caught in the upper 100 m, in Hensen net hauls in February, 1973).

Our observations of the vertical distribution of *Aglantha digitale* support those made by Östvedt (1955) from the Norwegian Sea and Beyer *et al.*, (1967) and Smedstad (1972) from the shallower waters of the Oslofjord, who observed that smaller specimens were found nearer the surface and only penetrated to greater depths as they grew and matured. Östvedt (1955) collected *A. digitale* at all depths (10 to 1000 m) during his investigations at OWS "Mike" (66°00'N 02°00'E) and found small individuals between the surface and 50 m and full grown specimens below 100 m. Russell (1938) observed that the adults in the shallow shelf waters off Plymouth, England spawned in late March, the offspring matured in May, and were followed by three to four generations in a single year; the summer medusae were 5 to 7 mm. From his field data, Russell (1938) estimated that the development of egg to mature adult took approximately one month. In contrast to Russell's estimate, Kramp (1927) concluded that *A. digitale* had one generation per year in the North Sea and Skagerrak. Smedstad (1972) estimated that the species took 11 weeks to reach maturity at 6 to 7 mm and reached a size of 9 mm after 14 weeks. The estimates of development times by Kramp and Smedstad fit our interpretation of the field data from OWS "India" in the north-east Atlantic Ocean.

The only observations on the spawning of *Aglantha digitale* were made by Hargitt (1917) who considered that the eggs were shed over a period of one to two weeks. A pulsed or a slow release of eggs from mature adults at OWS "India" in spring would greatly extend the breeding season and lengthen the period when young specimens (1 mm) of *A. digitale* would be found in the upper 50 m. In 1973 (see Figure 4) the overwintering population (> 6 mm) presumably start to spawn in late April-early May, at a temperature of 9°C (Williams and Hopkins, 1975), and continue until mid-June, that is six to seven weeks. The frequency data of the various sizes of *A. digitale* do not suggest a single release of eggs from the adult population but a prolonged spawning period; although this does not preclude a spawning period of one to two weeks for an individual adult, as suggested by Hargitt (1917). From the date of the first release of eggs to sexual maturity at 7 mm, we assume a 2½ month development period, or generation time. Numbers of adults should therefore peak again after 11 weeks in late July-early August, that is the approximate date when the larger individuals penetrated deeper in the water column at OWS "India" (Figure 4). Within the productive season of the year there is sufficient time to enable the adults of the first generation to spawn again in late July early August. If favourable conditions were available to the offspring it would enable them to develop until late September or early October.

During the growth of *Aglantha digitale* there were considerable changes in the ratios of wet to dry weights. At bell height of 1 mm, the mean dry weight of the medusae which had been preserved for five years in neutral formalin, was 0.09 mg and 22% of the mean wet weight. When the medusae reached 8 mm the mean dry weight was 0.29 mg and was less than 5% of the mean wet weight. The largest specimen weighted had a bell height of 25 mm, and a weight of 4 mg and the percentage dry weight to wet weight had reduced to 2%. This

change in the composition during growth may be reflected in changes in chemical composition of the medusae and are subject to further investigations. Examination of the stomach contents of a few individuals within the size range of *Aglantha digitale* caught in 1973 revealed a considerable size spectrum of particles consumed by the medusae. Tintinnids and diatoms were found in the stomachs of the smaller specimens (2 to 4 mm) while eggs and young copepodites of *Calanus finmarchicus* (Gunnerus) were found in slightly larger specimens (5 mm.). The adult medusae contained primarily copepods; *Oithona* sp., and *Meridia lucens* Boeck were identified in specimens larger than 8 mm. These copepods were the most abundant species found at OWS "India" during the summer months (Williams and Hopkins, 1975). Smedstad (1972) found *Oithona* and *Oncaea* to be the most important food source of *A. digitale* in the Oslofjord and Lebour (1922) observed adult *C. helgolandicus* Claus in the stomachs of medusae in the English Channel.

Aglantha digitale reached its maximum abundance in 1973 on 21 July with 2227 individuals m^{-2} from 0-500 m (dry weight = 546 mg m^{-2}); maximum densities of 40 individuals m^{-3} (equivalent to 15 mg m^{-3}) occurred in the upper 100 m; the haul also included 150 siphonphores. The importance of gelatinous zooplankton (coelenterates and salps), as a source of nitrogen for phytoplankton has been demonstrated from measurements made by Biggs (1977) who suggested that the excretion of ammonia from gelatinous zooplankton accounted for a large percentage of the ammonium requirements of phytoplankton in the Sargasso Sea. Calculations on the respiration and excretion of siphonophores from the Sargasso Sea showed that 1 animal m^{-3}, containing approximately 5 mg of body proteins, excreted 7 ng - atoms NH_4^+- N litre $^{-1}$ day^{-1}. This excretion level was sufficient, according to Biggs using the ammonium assimilation rate of phytoplankton derived by Eppley *et al.*, (1973), to supply 39 to 63% of the ammonium requirements of the phytoplankton in the Sargasso Sea. The presence and abundance of large numbers of *A. digitale* in the euphotic zone during the summer at OWS "India" would presumably be an important source of nitrogen for the production of phytoplankton.

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