

## Chaetognaths and ctenophores in the holoplankton of the Bristol Channel

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### Abstract

The geographical distributions, seasonal variations in numerical abundance and biomass ( $\text{mg C m}^{-3}$ ) of the predators of the holoplankton of the Bristol Channel, between November 1973 and February 1975, are described. The predator numbers and biomass were dominated by the chaetognath *Sagitta elegans* Verrill. This species represented 96% of the holoplankton carnivore biomass in the outer, seaward region of the Channel and 60% in the inner region; the remainder being ctenophores. The maximum numerical abundance of *S. elegans* occurred in September at 129 individuals  $\text{m}^{-3}$  ( $= 18 \text{ mg C m}^{-3}$ ). Juveniles ( $< 5 \text{ mm}$ ) reached maximum numbers of 55 individuals  $\text{m}^{-3}$  during June, August and September, demonstrating the reproductive activity of the population. The peak numbers were probably the result of the development of two major generations over the 90 d period from mid-June to mid-September. The tentaculate ctenophores were represented by *Pleurobrachia pileus* (O. F. Müller). The highest abundance was 81 individuals  $\text{m}^{-3}$  ( $= 3.0 \text{ mg C m}^{-3}$ ) at a single site in July in the South Central Channel. However, June was the only month when the ctenophores dominated the carnivore biomass in all regions of the Channel; thereafter, *S. elegans* was more abundant. Reproduction of the ctenophore occurred from April to September, with juveniles reaching maximum abundance in June at 12 individuals  $\text{m}^{-3}$ . The estimated food demand of the population in May for the outer region of the Channel was approximately 31% of the daily production of copepods. When the population reached its peak abundance in June, the estimated food requirement outstripped the daily production of copepods and a decline in both the prey and predator standing stocks was observed. Similar estimations were derived for the inner region of the Channel. *S. elegans* increased from a standing stock of  $0.038 \text{ mg C m}^{-3}$  in March to  $6.35 \text{ mg C m}^{-3}$  in September. Estimates of the copepod production compared with the derived demand of the chaetognath popu-

lation showed that the decline in the copepods in the late summer was the result of feeding by this predator. The holoplankton carnivore population was approximately 66% of the copepod standing stock for the 10 mo period November 1973 to September 1974 in the outer region of the Channel and 45% of that in the inner region. The carnivores formed the greater part of the total holoplankton biomass from September through the winter months to February, suggesting a predator-dominated community.

### Introduction

The communities of northern-latitude plankton ecosystems show complex seasonal successions and interactions between their component species. The spring bloom of phytoplankton is followed by an increase in the grazing herbivore populations which, in turn, are consumed by predators. It is assumed in this generalised succession that the resources are exploited up to the maximum carrying capacity for each component of the food web. This widely accepted and much quoted "classical" pattern of seasonal development of plankton from northern latitudes shows considerable geographical variation (Colebrook, 1979). One of the major factors affecting the rapid decline of the herbivore/omnivore populations in summer is the development of predator populations; this has been stated many times in the literature, but is very difficult to quantify. The foremost group of planktonic predators contributing to the seasonal decline of the copepod standing stock is the chaetognaths (Sameoto, 1972, 1973) which, together with the ctenophores, in near-shore environments make up the majority of carnivore biomass (Reeve and Baker, 1975; Reeve and Walter, 1978). The mysids are another important group in the Bristol Channel (Williams and Collins, 1984), interacting with both the copepods and the carnivores, but they will not be considered here. We wish to explore the feeding relationships which develop between the copepods and the chaetognath/ctenophore group. We suggest that the "success" of a particular



trophic level, or an ecosystem, is not so much limited by its maximum carrying capacity but that the whole resource exploitation is more susceptible to "control" by feed-back loops which develop within predator-prey relationships.

The objectives of this study were to (a) define the carnivore species (chaetognaths and ctenophores) of the holoplankton from an estuarine/near-shore locality, (b) describe their seasonal variations in abundance and geographical distribution, (c) select two contrasting regions within this locality for a more detailed study of predator-to-prey standing stocks (abundance and biomass) and their changing species composition throughout the year, and finally (d) examine feeding (predator-prey) relationships and explore the consequences of a predator-dominated community (i.e., resource exploitation by predators and the effects on the trophic relationships).

### Materials and methods

Twelve surveys of the Bristol Channel, carried out between November 1973 and February 1975 (Collins and Williams, 1981), were selected for detailed analysis of their omnivore and carnivore components. These surveys were part of a larger multi-disciplinary study of the Bristol Channel and Severn Estuary and were designed to provide data on geographical distribution, seasonal variation in abundance and community structure of the plankton for use in a Generalised Ecosystem Model of the Bristol Channel and Severn Estuary (GEMBASE, see Radford, 1979 a, b; Radford and Joint, 1980). The twelve surveys were based on a grid of 58 sampling sites (Fig. 1). At each site, a double oblique haul was taken using a 50.8 cm (20") diameter Lowestoft high-speed plankton sampler (Beverton and Tungate, 1967; Harding and Arnold, 1971) fitted with a 280  $\mu$ m mesh nylon net, to provide a zooplankton sample integrated over the whole water column. Chlorophyll *a* was also measured at each site. Sampling in November 1974 was restricted to 8 sites. The data were not contoured, but have been included in the figures where applicable; for further sampling details see Collins and Williams (1981).

All zooplankton were counted, identified to species and in many cases to developmental stage (including sex). Copepod species and their developmental stages were divided into three groups, Copepodite Stages I–III, IV–V and VI (adults). Chaetognaths (*Sagitta elegans*) were separated into two size groups, less than and greater than 5 mm total length. Ctenophores (*Pleurobrachia pileus*) were similarly separated into two size groups, less than and greater than 5 mm body diameter. Ten species of copepods were allocated, according to their mode of feeding, into an omnivore group; the chaetognaths and ctenophores comprised the holoplankton carnivore group. Each size category was given a carbon value ( $\mu$ g C) based on our own determinations carried out on frozen material or derived from the literature (Table 1). The mean biomass ( $\text{mg C m}^{-3}$ ) for the two trophic types and each size category within each type have been estimated for the sub-

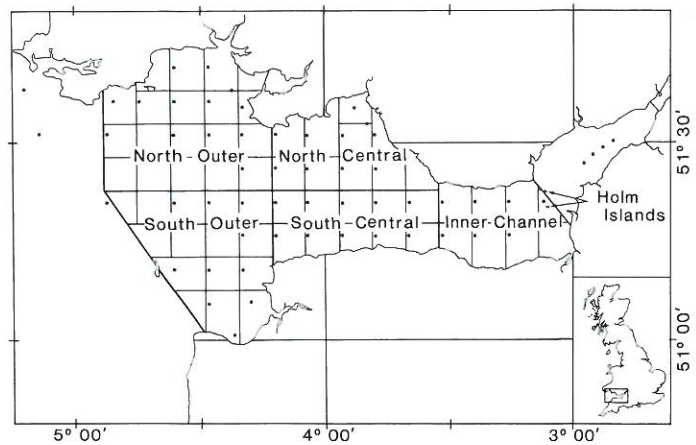


Fig. 1. Bristol Channel and Severn Estuary showing the 58 sampling sites (●), the arbitrary 5-mile grid, and the sub-regions

Table 1. Mean lengths and total carbon values (inorganic plus organic) used for the species and developmental stages in the two trophic groups studied

Species	Stage	Mean length (mm)	Mean carbon ( $\mu$ g C)
<b>Omnivores</b>			
<i>Acartia bifilosa</i>	I–III	0.45	0.56
	IV–V	0.69	1.10
	VI	0.83	2.35
<i>Calanus helgolandicus</i>	I–III	1.02	4.70
	IV–V	1.79	29.40
	VI	2.28	62.40
<i>Centropages hamatus</i>	I–III	0.52	1.70
	IV–V	0.72	2.97
	VI	1.04	5.55
<i>Eurytemora affinis</i>	I–III	0.36	0.29
	IV–V	0.64	1.57
	VI	0.77	2.57
<i>Acartia clausi</i>	I–III	0.45	0.56
	IV–V	0.69	1.10
	VI	0.83	2.35
<i>Centropages typicus</i>	I–III	0.58	1.16
	IV–V	0.99	5.51
	VI	1.09	11.30
<i>Metridia lucens</i>	VI	1.73	27.00
<i>Paracalanus parvus</i>	I–III	0.37	0.31
	IV–V	0.52	0.85
	VI	0.77	2.60
<i>Pseudocalanus elongatus</i>	I–III	0.45	0.56
	IV–V	0.74	2.36
	VI	0.83	3.32
<i>Temora longicornis</i>	I–III	0.40	0.25
	IV–V	0.62	1.85
	VI	0.82	6.34
<b>Carnivores</b>			
<i>Sagitta elegans</i>	< 5 mm	5.00	6.80
	> 5 mm	15.50	183.00
<i>Pleurobrachia pileus</i>	< 5 mm	3.53	36.80
	> 5 mm	6.59	121.31

regions of the Channel (Fig. 1) for these surveys. Two sub-regions, the North Outer Channel and the Inner Channel, were chosen for detailed comparison of omnivore to carnivore biomass. The biomass means for the sub-regions were derived in two ways: either using the computer program SACM (Surface Approximations and Contour Mapping: Applications Consultants Inc., Houston, Texas, USA) or by direct averaging. The contouring procedure required the site positions to be corrected to their hypothetical locations at the nearest times of high and low water (Collins and Williams, 1981). Biomass values for each category at each site were contoured at both high and low water positions. The contoured data and the depth of water were then used to produce mean mid-tide biomass values ( $\text{mg C m}^{-3}$ ) integrated over each sub-region. The direct averaging method converted numbers per cubic metre for each category at each site to  $\text{mg C m}^{-3}$  and calculated an average from all sites (corrected to high water) within each sub-region.

Each biomass category was integrated over an interval of 307 d from 4 November 1973 to 6 September 1974 to provide an estimate of the total standing stock ( $\text{mg C m}^{-3}$ ) for the 10 mo period. This period was chosen because we were unable to sample the North Outer Channel in

November 1974 but wished to keep the same time interval for comparison of the two sub-regions (February was excluded to avoid the bias that would have resulted from the inclusion of two winter periods).

## Results

The predators of the holoplankton of the Bristol Channel were numerically dominated by chaetognaths. Only one chaetognath species was identified, *Sagitta elegans* Verrill. Its congener *S. setosa* J. Müller, which is abundant in the mixed waters of the English Channel (Southward, 1962, 1984) was not recorded (D. V. P. Conway, personal communication). The geographical distributions and seasonal variations in abundance of total *S. elegans* (all stages) are shown in Fig. 2; the maximum abundance of 129 individuals  $\text{m}^{-3}$  occurred in September. The juveniles ( $<5$  mm) occurred predominantly in November 1973, June, August and September 1974 at a maximum density of 55 individuals  $\text{m}^{-3}$ . The increase in the population in the spring and early summer was the result of development of the indigenous population in the Channel and not of increased numbers being advected from the thermally stratified waters of the adjacent Celtic Sea. The South

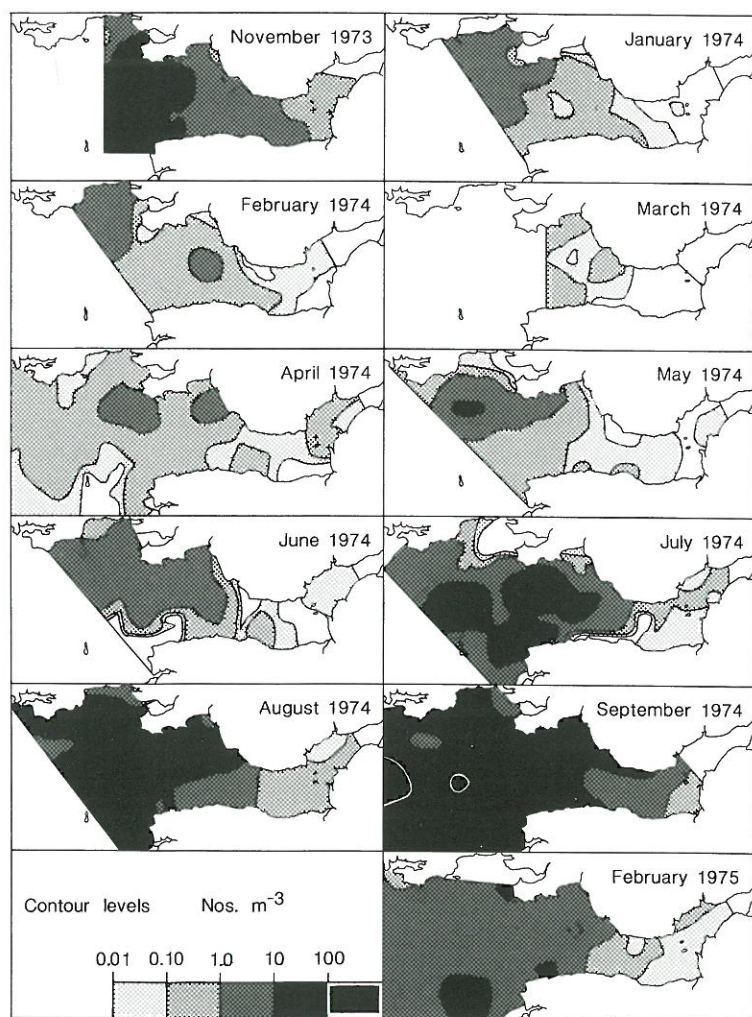


Fig. 2. *Sagitta elegans*. Distribution and abundance for the eleven surveys of the Bristol Channel from November 1973 to February 1975



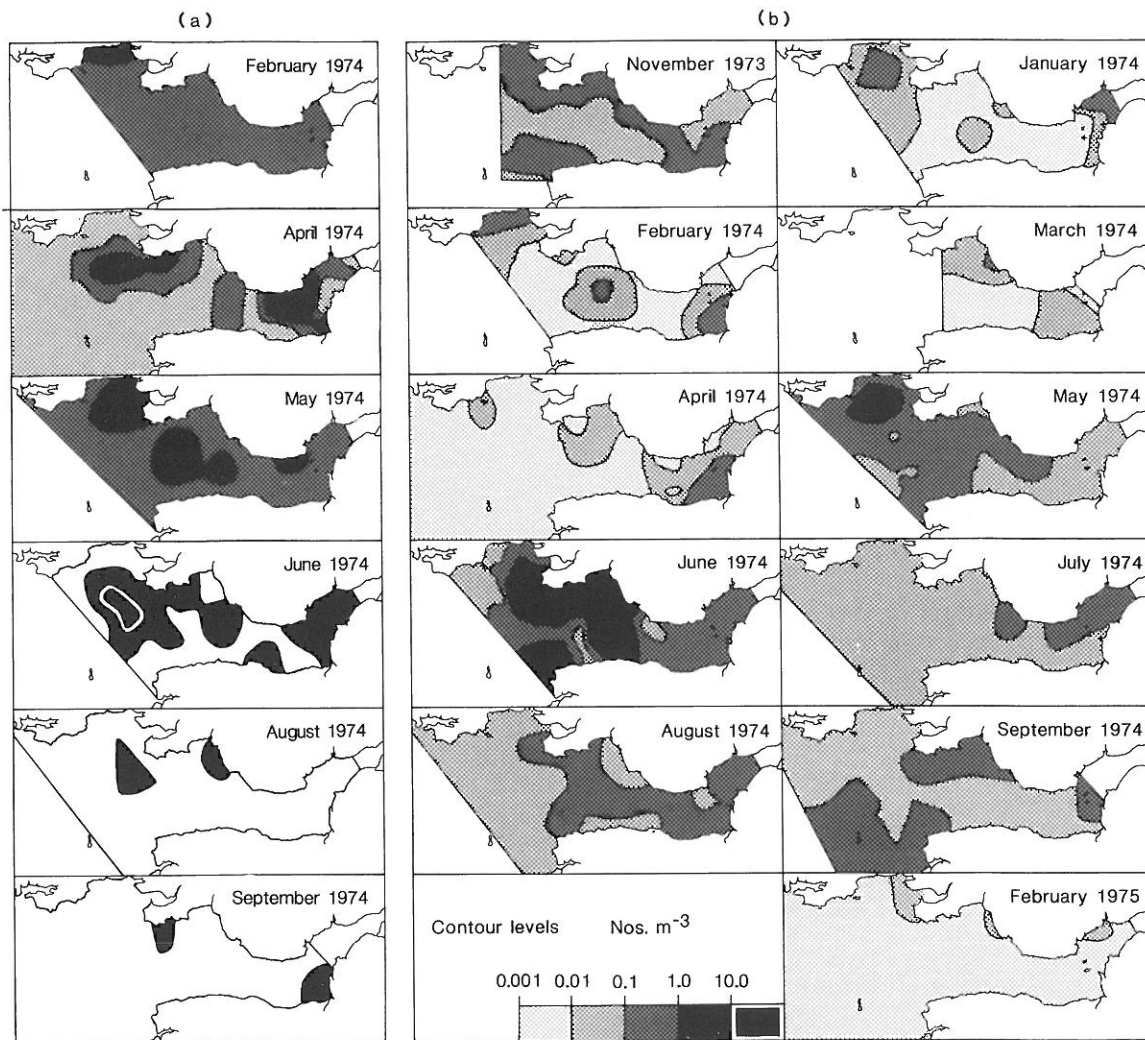


Fig. 3. *Pleurobrachia pileus*. (a) Distribution and abundance for the six surveys of the Bristol Channel in 1974 when specimens  $< 5$  mm were recorded; all numbers recorded in June, August and September were either 0 or  $\geq 1$   $m^{-3}$ . (b) Distribution and abundance of specimens  $> 5$  mm for the eleven surveys from November 1973 to February 1975

Outer sub-region (Fig. 1) had low numbers (0.1 individuals  $m^{-3}$  April to June, Fig. 2) of chaetognaths associated with the higher salinity water penetrating into the Channel along the southern shore (Collins and Williams, 1981).

The tentaculate ctenophores in the Channel were represented by *Pleurobrachia pileus* (O. F. Müller). The geographical distributions and seasonal variations in abundance of the juveniles ( $< 5$  mm diameter) and adults ( $> 5$  mm diameter) of *P. pileus* are shown in Fig. 3. Small ctenophores ( $< 5$  mm) occurred in February, when they were evenly distributed throughout the Channel (Fig. 3a). This could be an indication of reproductive activity, but it is thought to be unlikely at this time of year when food supplies are at their lowest levels. It is more credible that the overwintering ctenophores had utilised their body tissue for metabolism and had therefore shrunk in size (Greve, 1972; Kremer, 1976). In June, the maximum number of juveniles and adults was 12 and 10 individuals  $m^{-3}$ , respectively, the highest abundance at one site was 18 individuals  $m^{-3}$  (9 juveniles and 9 adults) (Fig. 3). Both

juveniles and adults were most abundant in the North Outer and Central Channel sub-regions. From June to September, juveniles occurred in localised high densities (maximum of 81  $m^{-3}$ ,  $\approx 3.0$  mg C  $m^{-3}$ , occurred in July at a single site in the South Central sub-region and was not included in Fig. 3a) and were absent elsewhere in the Channel. The mean numerical abundance of this ctenophore over the whole North Outer Channel sub-region reached a peak of 5.6 individuals  $m^{-3}$  in June (Table 2) and the Inner Channel sub-region reached peaks in April, June and September of 2.1, 3.0 and 2.8 individuals  $m^{-3}$ , respectively (Table 2). The Inner Channel has an approximate water volume for average tides of  $1.4 \times 10^{10}$   $m^3$ , which compares with a volume of approximately  $5.3 \times 10^{10}$   $m^3$  for the North Outer Channel; this gives an indication of the potential size of the ctenophore populations in these regions.

The biomass (mg C  $m^{-3}$ ) of carnivorous holoplankton (*Sagitta elegans* and *Pleurobrachia pileus*) for the five sub-regions of the Bristol Channel is shown in Fig. 4. Chaetog-

**Table 2.** Holoplankton monthly mean data for two sub-regions of the Bristol Channel for the period November 1973 to September 1974. All weights in mg C m<sup>-3</sup>; numbers are m<sup>-3</sup>. Int. = biomass values integrated over period 4 November 1973 to 6 September 1974. Average depths: North Outer Channel = 33 m, Inner Channel = 18 m. Dash indicates no data

Month	Holoplankton carnivores					Copepods				Prey: predator ratio
	Total	<i>Sagitta elegans</i>		<i>Pleurobrachia pileus</i>		Total	<i>C. hamatus/ A. bifilosa</i>			
	wt	wt	nos	wt	nos	wt	nos	wt	nos	
North Outer Channel										
								<i>Centropages hamatus</i>		
Nov.	2.410	2.394	15.2	0.016	0.1	0.372	70.5	0.241	43.0	0.154
Jan.	1.020	1.010	5.5	0.010	0.1	0.252	51.3	0.210	37.8	0.247
Feb.	0.325	0.311	1.7	0.014	0.3	0.074	14.2	0.043	8.0	0.288
Mar.	0.039	0.038	0.2	0.001	0.01	—	—	—	—	—
Apr.	0.186	0.165	0.9	0.021	0.6	0.973	182.8	0.292	61.3	5.231
May	0.330	0.232	1.3	0.098	1.3	6.127	1 234.5	2.029	407.0	18.567
June	0.590	0.256	4.2	0.334	5.6	1.553	262.2	0.145	29.1	2.632
July	1.143	1.142	6.2	0.001	0.01	7.994	2 034.0	3.066	601.6	6.994
Aug.	5.811	5.731	34.2	0.080	1.0	3.831	911.3	1.332	243.8	0.659
Sep.	6.371	6.352	37.6	0.019	0.3	1.334	239.2	0.494	90.9	0.209
Int.	435.8	417.8		17.8		656.9		231.6		
Inner Channel										
								<i>Acartia bifilosa</i>		
Nov.	0.185	0.170	1.1	0.015	0.1	0.038	13.5	0.019	9.5	0.205
Jan.	0.007	0.006	0.03	0.001	0.01	0.005	1.8	0.001	0.2	0.714
Feb.	0.019	0.011	0.1	0.008	0.2	0.038	9.2	0.001	0.4	2.000
Mar.	0.002	0.0	0.0	0.002	0.02	—	—	—	—	—
Apr.	0.095	0.009	0.1	0.086	2.1	0.093	18.5	0.021	8.6	0.979
May	0.028	0.004	0.02	0.024	0.5	0.406	92.9	0.100	40.8	14.500
June	0.141	0.009	0.05	0.132	3.0	0.326	114.3	0.180	73.6	2.312
July	0.033	0.016	0.1	0.017	0.1	0.687	185.7	0.162	66.2	20.818
Aug.	0.121	0.093	0.5	0.028	0.3	0.280	94.1	0.112	45.4	2.314
Sep.	0.628	0.516	3.6	0.112	2.8	0.152	55.3	0.105	43.4	0.242
Int.	26.8	16.1		10.7		59.4		19.2		

naths were dominant from July to September. June is the only month when ctenophores predominated in all sub-regions. There was an order of magnitude difference between the biomass of the carnivores in the Outer and Inner Channel sub-regions, which was accounted for by the increased numbers of chaetognaths in the former (Fig. 4 and Table 2). The total holoplankton carnivore biomass in Table 2 is the sum of the values for *S. elegans* and *P. pileus*.

The omnivore and carnivore holoplankton biomass values for the two sub-regions chosen for study are shown in Figs. 5 and 6. The seasonal abundance (biomass mg C m<sup>-3</sup>) of total copepods and *Centropages hamatus* (Lilljeborg), the most abundant copepod, in the North Outer Channel are shown in relation to the two predators (*Sagitta elegans* and *Pleurobrachia pileus*) in Fig. 5. The peaks of abundance of copepods occurred in May and July, whilst *P. pileus* reached maximum abundance in June and *S. elegans* peaked in September. The main carnivore biomass reached a peak three months after the copepods and thereafter dominated the biomass throughout the winter months. The integrated standing stocks for the two groups are given in Table 2, which shows that the holoplankton

carnivores reached about 66% of the copepod standing stock for the 10 mo period. From feeding studies of chaetognaths (Rakusa-Suszczewski, 1969; Pearre, 1973; Tungate, 1975; Pearre, 1980) we can assume that the developmental stages of the calanoid copepods are the main food source for *S. elegans* within the Channel. The copepod *C. hamatus* was the representative species of the euryhaline marine assemblage defined by Collins and Williams (1982).

The seasonal abundance of total copepods and *Acartia bifilosa* var. *inermis* Rose in the Inner Channel are shown in relation to the two predators (*Sagitta elegans* and *Pleurobrachia pileus*) in Fig. 6. In the Inner Channel, the numerically dominant copepod species was *A. bifilosa*, which was the representative copepod species of the estuarine and marine assemblage defined by Collins and Williams (1982). The remainder of the omnivore biomass consisted of mysids and euphausiids (Williams and Collins, 1984). From March to June, *P. pileus* dominated the carnivore biomass and occurred in equal abundance to *S. elegans* in July. The integrated standing stock of the holoplankton carnivores reached 45% of the omnivore standing stock over the 10 mo period (Table 2).

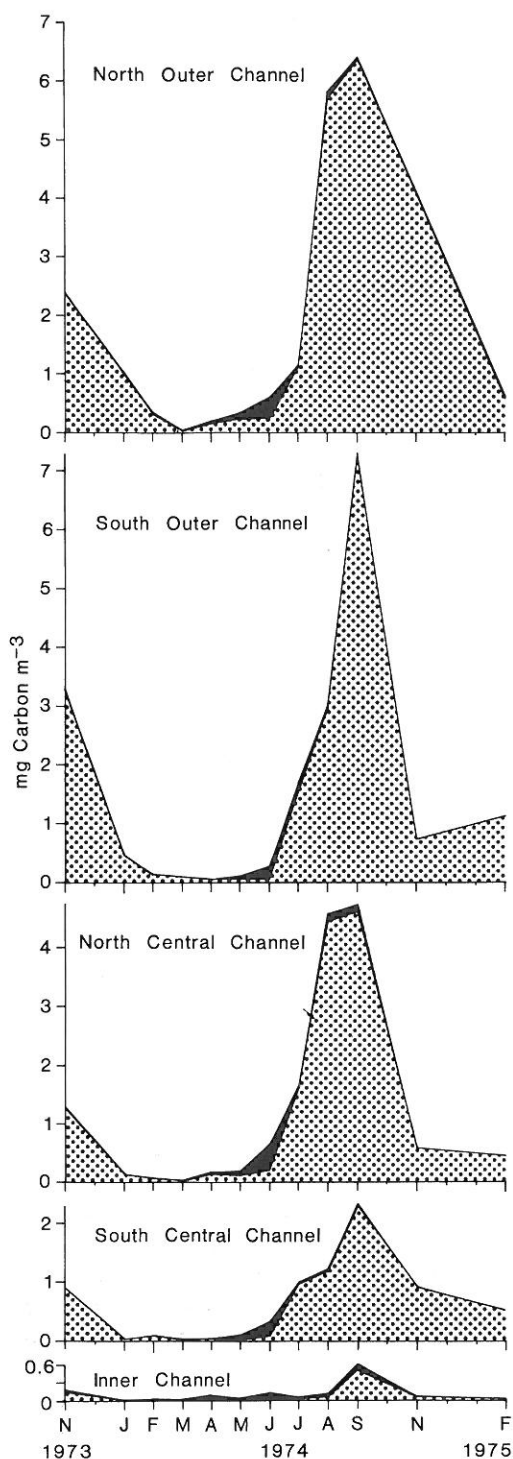


Fig. 4. *Sagitta elegans* (stippled) and *Pleurobrachia pileus* (black). Biomass for the five Bristol Channel sub-regions over the period November 1973 to February 1975

## Discussion

The Inner Channel is an area of high tidal energy which ensures thorough vertical mixing in all but exceptional conditions (Radford, 1979a; Joint and Pomroy, 1981; Uncles and Joint, 1983). We assume, therefore, that the zooplankton were evenly distributed throughout the water

column and that numbers  $m^{-3}$  was a valid estimate of the zooplankton population. Similar assumptions have been made for the North Outer Channel, to which they are perhaps less applicable. The North Outer Channel has an average depth of 33 m and shows some indication in summer of temporary structure in the temperature and salinity profiles. This structure could possibly be reflected in vertical stratification of the zooplankton populations similar to that observed in the summer months in the stratified waters of the Celtic Sea (Williams and Conway, 1984).

Figs. 4, 5, 6 and Table 2 illustrate that the chaetognath *Sagitta elegans* dominated the carnivore biomass of the holoplankton of the Bristol Channel. *S. elegans* represented 96% of the carnivore biomass ( $mg\ C\ m^{-3}$ ) over the sampling period in the North Outer Channel and 60% in the Inner Channel, the remainder being *Pleurobrachia pileus*. Although the proportion of *P. pileus* of total holoplankton carnivore biomass was ten times greater in the Inner Channel than in the North Outer Channel, the

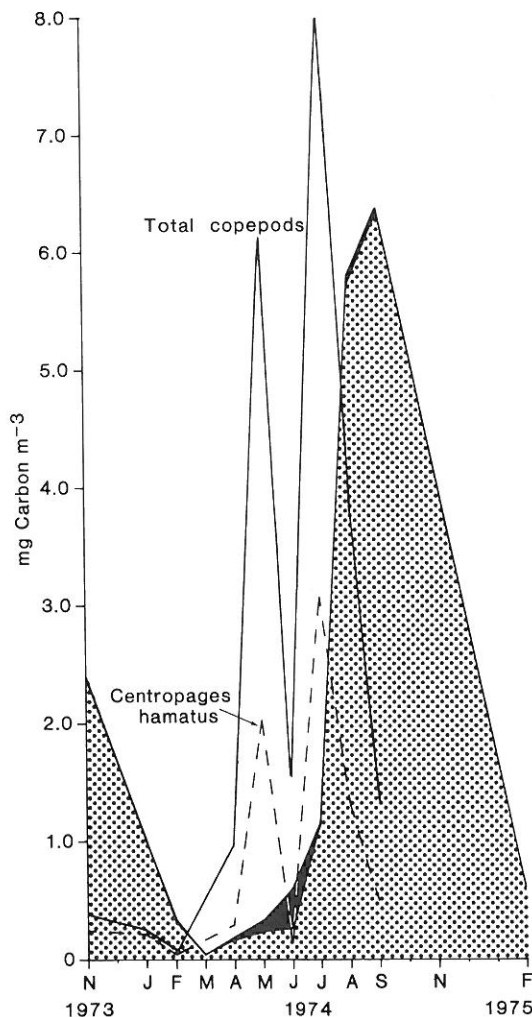


Fig. 5. *Sagitta elegans* (stippled) and *Pleurobrachia pileus* (black). Biomass for the North Outer Bristol Channel sub-region over the period November 1973 to February 1975. Biomass graphs for total copepods and *Centropages hamatus* are also shown



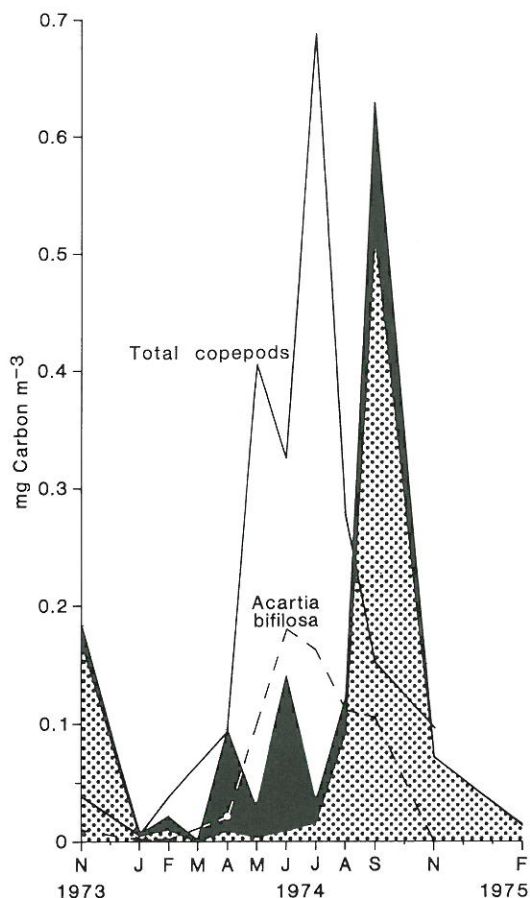


Fig. 6. *Sagitta elegans* (stippled) and *Pleurobrachia pileus* (black). Biomass for the Inner Bristol Channel sub-region over the period November 1973 to February 1975. Biomass graphs for total copepods and *Acartia bifilosa* var. *inermis* are also shown

integrated mean values shown in Table 2 illustrate that numerically the ctenophore was nearly twice as abundant in the North Outer Channel. Moving further westward out of the mixed waters of the Bristol Channel into the Celtic Sea the numbers of ctenophores decrease markedly, although chaetognaths remain the dominant carnivore group in the plankton of the Celtic Sea. Ctenophores are generally more abundant in estuarine and near-shore waters (Mortensen, 1912; Kramp, 1913) than oceanic waters, where they rarely exceed 0.1 individuals  $m^{-3}$  (Harbison *et al.*, 1978; Greze and Bileva, 1980; Biggs *et al.*, 1981). The tentaculate ctenophores become so numerous at times that they deplete copepod populations (Kamshilov, 1960; Fraser, 1961, 1970; Yip, 1980; Harris *et al.*, 1982). Ctenophores were responsible for 52% mortality of *Acartia tonsa* Dana in the Patuxent River (Heinle, 1966; Bishop, 1967). The major predators of these ctenophores are another class of ctenophores (Nuda) of which the principal genus is *Beröe* spp. (Lebour, 1922; Russell, 1933; Fraser, 1970; Greve, 1970); they are eaten by cod, herring and mackerel (Scott, 1913, 1924; Jensen and Hansen, 1931; Hansen, 1949; Kamshilov, 1961). Kamshilov (1961) first suggested the ecological feedback system where *Beröe cucumis* Fabricius, feeding and controlling the numbers of

the tentaculate ctenophore *Bolinopsis infundibulum* (O. F. Müller), affected and modified indirectly the population dynamics of the copepod *Calanus finmarchicus* (Gunnerus). Further evidence of this feedback interaction was given by Greve (1971) for *Beröe gracilis* Kunne and *P. pileus* in the German Bight and by Swanberg (1974) for *Beröe ovata* Bosc and *Bolinopsis vitrea* (Agassiz) off the Great Bahama Bank. *Beröe* spp. was not observed in our surveys, although it has been occasionally recorded in the Bristol Channel (W. Greve personal communication). The only predator capable of consuming the larger specimens of *P. pileus* were the summer populations of the scyphomedusa *Aurelia aurita* (L.).

In June, *Pleurobrachia pileus* had a maximum abundance of at 18 individuals  $m^{-3}$  (9 juveniles and 9 adults = 1.4 mg C  $m^{-3}$ ), which, for the depth of water sampled (22 m) was equivalent to 395 individuals  $m^{-2}$ . This value per  $m^3$  compares favourably with the maximum numbers of ctenophores observed by Greve (1971) of twenty *P. pileus*  $m^{-3}$  in the German Bight, by van der Veer and Sadée (1984) of seventeen *P. pileus*  $m^{-3}$  in the Dutch Wadden Sea, and by Hirota (1974) of twenty *P. bachei* Agassiz  $m^{-3}$  in the southern Californian Bight.

There are considerable discrepancies in the percentages of organic carbon to dry weight of ctenophores reported in the literature (Reeve and Walter, 1978). These authors, quoting a variety of sources, gave an organic carbon range of 2 to 4% of dry weight for *Pleurobrachia* spp. Unless measured for the particular population under study, the value chosen can have drastic effects upon the value of the final estimate of organic carbon present in the water column. Van der Veer and Sadée (1984), using a value of 4.5% carbon content, calculated 10 to 12 mg C  $mg^{-3}$  for approximately the same number of individuals  $m^{-3}$  as we observed at our maximum level, but using our carbon values these numbers were equivalent to 1.8 mg C  $m^{-3}$ . Applying the formula given by Reeve and Walter (1976) of:

$$\log_{10}(\text{dry weight [mg]}) = -1.54 + 2.65 [\log_{10}(\text{polar length [mm]})]$$

and the conversion formula of Oorthuyzen and Sadée (1982) quoted by van der Veer and Sadée (1984) of:

$$\text{polar length} = 1.25 \times \text{diameter}$$

with the two estimates of organic carbon content of 2 and 4% to our mean diameter data, we arrived at the values shown in Table 3. These values can be compared to the carbon values determined from our own total carbon estimates.

Ctenophores have high ingestion rates at elevated food levels which lead to high growth rates and fecundity (Greve, 1970). These attributes, together with short generation times, mean that this carnivore species can reach large population densities when sufficient food is available. Greve (1970) showed that adult *Pleurobrachia pileus* produced fertilised eggs within 2 d of excessive feeding and took 60 d to develop from egg to 11 mm adult at a sea



**Table 3.** *Pleurobrachia pileus*. Determinations of dry weight and carbon content using the formula of Reeve and Walter (1976):  $\log_{10}(\text{dry weight [mg]}) = -1.54 + 2.65 \times [\log_{10}(\text{polar length [mm]})]$  and the conversion formula of Oorthuyzen and Sadée (1982) quoted by van der Veer and Sadée (1984):  $\text{polar length} = 1.25 \times \text{diameter}$

Nominal categories (mm)	Mean diam (mm)	Polar length (mm)	Total dry wt (mg)	Derived organic C ( $\mu\text{g}$ )		Observed total C values ( $\mu\text{g}$ )
				2%	4%	
< 5	3.53	4.41	1.29	26	51	36
> 5	6.59	8.24	7.71	154	308	121

temperature of 9°C. For adults of the ctenophore *Mnemiopsis mccradyi* Mayer, Reeve *et al.* (1978) demonstrated that the species did not grow at prey densities of 1 copepod  $\text{l}^{-1}$  ( $1000 \text{ m}^{-3}$ ), while *M. leidyi* Agassiz lost weight at 10 copepods  $\text{l}^{-1}$  and gained weight at 100 copepods  $\text{l}^{-1}$  ( $10^5 \text{ m}^{-3}$ ) (Kremer, 1976).

The peak numbers of copepods corresponding to the main reproductive period of *Pleurobrachia pileus* in the North Outer Channel were  $1234 \text{ m}^{-3}$  (May) and  $2034 \text{ m}^{-3}$  (July). Thus, we cannot demonstrate from our sampling methods the high densities of prey which have been deduced as the requirements for growth of ctenophores from laboratory feeding experiments (Reeve *et al.*, 1978). All laboratory studies carried out to date on ctenophores have been carried out at these very high prey densities and the results have been rationalised to prey densities observed in the sea in the same way as we have in the following sentences. It has to be remembered however, that the mesh size of our nets was  $280 \mu\text{m}$  and that copepods can aggregate into much higher densities on a smaller scale than we effectively sampled. The filtering mesh biased our sampling for Stage V copepodites and adults; nauplii and Stages I–III were poorly sampled. The densities of copepods in May and July are based on copepodite Stages IV to V and adults of *Centropages*, *Acartia* and *Temora* spp. If we consider the nauplii and early copepodite stages (I–III), then the numbers recorded throughout the water column of  $30$  to  $60 \times 10^3$  individuals  $\text{m}^{-2}$  could be increased by one or two orders of magnitude, although the biomass of plankton  $\text{m}^{-2}$  would not be greatly altered by the inclusion of these smaller developmental stages.

Using the data from Greve (1972) and van der Veer and Sadée (1984), we calculated the daily production of the ctenophore population in the two sub-regions of the Bristol Channel. In the North Outer Channel, *Pleurobrachia pileus* became dominant in June with a mean standing stock for the sub-region of  $0.334 \text{ mg C m}^{-3}$  (Table 2). The estimated daily production of this stock would be  $0.080 \text{ mg C m}^{-3}$  (i.e., 24%). Assuming a net growth efficiency of 10% (Reeve and Walter, 1978) this relates to a food demand of  $0.802 \text{ mg C m}^{-3} \text{ d}^{-1}$ . The standing stock of

the copepods was  $1.553 \text{ mg C m}^{-3}$ , with an estimated daily production of  $0.194 \text{ mg C m}^{-3} \text{ d}^{-1}$  (i.e., 12.5%). In this month the copepod production would only satisfy about 20% of the daily demand of the ctenophore population. A similar calculation for May, when the population of *P. pileus* was increasing, shows that they would be consuming 31% of the daily production of copepods. By June, when the ctenophore juvenile and adult populations reached maximum abundance, we can infer from these estimates that the predator demand outstripped the food source and the ctenophore populations should show a decline; which in fact they do for the North Outer Channel (Table 2). These are very gross estimates and rely on the assumption that all food is available to the ctenophore. If the food organisms are evenly distributed throughout the water column then, even when the ctenophore is at its maximum June density, i.e., 18 individuals  $\text{m}^{-3}$ , the population cannot filter and remove all the copepods  $\text{m}^{-3}$ . Postulating a maximum water clearance rate for *P. pileus* of 20 litres  $\text{d}^{-1}$ , then the population at its maximum numerical abundance would clear 360 litres  $\text{m}^{-3} \text{ d}^{-1}$  (36%). Reeve and Baker (1975) made this calculation for the *Mnemiopsis mccradyi* population in Biscayne Bay and arrived at a maximum rate of removal of copepod standing stock of 10% (Reeve *et al.*, 1978). As the population of ctenophores declined in the North Outer Channel, the *Sagitta elegans* population gradually increased, replacing the ctenophores in July and for the remainder of the year as the dominant predator. In the Inner Channel, *P. pileus* was also dominant in June with a mean standing stock of  $0.132 \text{ mg C m}^{-3}$ . Using the same calculation, the daily demand of the ctenophore population would be  $0.317 \text{ mg C m}^{-3}$  and the daily production of copepods would be estimated at  $0.041 \text{ mg C m}^{-3}$ . Therefore the production of copepods would meet only a fraction (13%) of the daily requirement of the ctenophores. Similarly, in May, the daily demand of the ctenophores was  $0.058 \text{ mg C m}^{-3} \text{ d}^{-1}$  with a daily copepod production of  $0.051 \text{ mg C m}^{-3}$ , i.e., ctenophores require more than the daily copepod production. The mean sea temperatures in May and June were 11° and 13°C, respectively, which would give an estimated generation time for *P. pileus* from egg to 11 mm adult of 55 and 37 d, respectively (after Greve, 1972). These estimates agree very well with the modality of the population graphs given in Figs. 5 and 6.

The population of *Sagitta elegans* increased to a single population maximum in August/September (Fig. 4) and dominated the biomass of the holoplankton carnivores throughout the Bristol Channel. The growth and development of *S. elegans* is well documented (Sameoto, 1973) and its generation time from egg to mature adult can be estimated from sea-temperature data. At a mean sea temperature of 12°C (May to June) the generation time is about 60 d, while at 16°C (July to September) the generation time is about 40 d. The mean length of adult *S. elegans* sampled throughout the year was 15.5 mm, although the modal length of the population in late summer was nearer 12 mm. Using the regression equation given by Sameoto



(1973) of

$$y = 47.73/x^{0.53},$$

where  $y$  is the mean length at maturity and  $x$  is the mean sea temperature, the mean length at maturity can be calculated. At a temperature of 12 °C, length at maturity is 12.5 mm; at 16 °C, it is 10.7 mm; this fits reasonably well with our data. The use of a single weight factor for individuals >5 mm possibly may have biased our estimates of the chaetognath population in summer.

The spacing of our sampling does not allow us to separate the generations making up the single biomass peak, but from the generation times it is highly likely that it is composed of a number of sub-populations. The development of these sub-populations contribute towards the increase in the standing stock from 0.038 mg C m<sup>-3</sup> in March to 6.35 mg C m<sup>-3</sup> in September (Table 2). Young stages are found in the plankton from June to September and demonstrate the reproductive activity of the indigenous population. The period between mid-June and mid-September covered the main growth and production of the species in the Bristol Channel and probably resulted from the development of two generations over the 90 d period.

The maximum numerical abundance of *Sagitta elegans* observed in our plankton hauls occurred in September 1974 at 129 individuals m<sup>-3</sup> (31 < 5 mm; 98 > 5 mm length); which was equivalent to 18 mg C m<sup>-3</sup>. It has to be remembered that these values were derived by integrating over the depth of water sampled, which in this particular haul was 60 m. Therefore, the total number of *S. elegans* identified from the haul was 129 × 60 = 7 740 individuals m<sup>-2</sup> (= 1 080 mg C m<sup>-2</sup>).

*Sagitta elegans* occurred at an abundance greater than 30 individuals m<sup>-3</sup> over the North Outer Channel in August/September (Table 2) which represents a mean numerical abundance for this region of 990 individuals m<sup>-2</sup> (= 200 mg C m<sup>-2</sup>), while in the Inner Channel the population peaked in September at 3.6 individuals m<sup>-3</sup> (60 individuals m<sup>-2</sup>, = 9 mg C m<sup>-2</sup>); approximately 1/20 of the population in the North Outer Channel. The biomass of the chaetognaths in the North Outer Channel (417.8 mg C m<sup>-3</sup>, integrated over 307 d) was greater by more than an order of magnitude than that found in the Inner Channel (16.1 mg C m<sup>-3</sup> 307 d<sup>-1</sup>); a similar difference was observed in the biomass of the copepods (Table 2).

The increase in the standing stock of *Sagitta elegans* in the North Outer Channel in the summer months was 6.09 mg C m<sup>-3</sup> (6.35 minus 0.26, Table 2); taking this period to be 90 d, this increase in weight is equivalent to 0.068 mg C m<sup>-3</sup> d<sup>-1</sup>. To produce and sustain this net growth of the chaetognath, assuming a mean gross growth efficiency of 34.5% (Reeve, 1970; for *S. hispidus*), the carnivore would have to consume a minimum of 17.65 mg C m<sup>-3</sup> of copepods over the 90 d. The estimated daily copepod production in July was 0.194 mg C m<sup>-3</sup> d<sup>-1</sup> at the peak of copepod standing stock. If this net growth of copepods was sustained over the summer months, the

increase to the population would be 17.46 mg C m<sup>-3</sup>. This value is very close to the derived demand of the chaetognath carnivores. The ctenophore was at its lowest numerical density in July, therefore the main predator pressure was from *S. elegans*. Similar gross calculations can be made for the Inner Channel, but it is clear that the decline of the copepods in the Bristol Channel in late summer (Figs. 5 and 6) was the result of feeding by this chaetognath.

Throughout the main period of spawning of *Pleurobrachia pileus* in the Channel in 1974 (April to July), the prey:predator ratio varied from 2.6 to 18.6 in the North Outer Channel (April to July) and 1.0 to 20.8 in the Inner Channel (February to July). The prey:predator ratio peaked in May in the North Outer Channel at 18.6 and reached a maximum in the Inner Channel of 20.8 in July. In the North Outer Channel the chaetognath contributed the majority of the carnivore biomass except for June, while in the Inner Channel *P. pileus* made a larger contribution than *Sagitta elegans* during April to July. These high prey:predator ratios emphasise the presence of excess food available to the holoplankton predators in these particular months; especially as the two species were reproducing in these months. Both *S. elegans* and *P. pileus* exploit the same food resource, primarily copepods, and should therefore be in competition with each other. *P. pileus* has specific attributes which make it ideally suited to exploit food resources of short temporal persistence. The greatest population increase of the ctenophore should, therefore, coincide or be closely associated with the maximum abundance of the copepods (see Figs. 5 and 6). Reeve and Baker (1975) suggested there are periods in the year when food density is below that required by *P. pileus* but is sufficient for an increase in the chaetognath population to occur. Chaetognaths, which have longer generation times, build-up to a single population maximum in the Channel following the period of highest copepod numbers. If chaetognaths do not require the prey density of ctenophores, they will be adapted to the food levels which occur in northern latitudes in the latter half of the year and should therefore show persistence through the winter period. From July to September the chaetognath population increased, reaching peaks of 6.4 and 0.52 mg C m<sup>-3</sup>, respectively, in the North Outer Channel and the Inner Channel. In November and January the levels were still quite high, equivalent or greater than the values recorded in July in the North Outer Channel. The prey to predator ratios from August through the winter months were less than 1.0, implying the predominance of the *Sagitta elegans* population. The seasonal development of the two species within the carnivore populations is a possible adaptation that ensures that interspecific competition is minimised and habitat utilisation is maximised. This pattern of changing dominance over the seasons between these two genera has been observed before by Sameoto (1971a, b), Reeve and Baker (1975), Tungate (1975) and Reeve and Walter (1978) and is typical of northern hemisphere shallow-water holoplankton communities.

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