Marine Biology 87, 297–306 (1985)

Marine Biology
International Journal on Life in Oceans and Coastal Waters

Demands of the herbivore community on phytoplankton production in the Celtic Sea in August

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Abstract

Zooplankton species diversity in the Celtic Sea in August 1982 was low; two species of copepod and two species of euphausiid accounted for 90 to 95% of the biomass sampled by a 280 μm-mesh net. Some 75% of the primary production was by phytoplankton smaller than 5 μm. The demands of both the macrozooplankton and the microzooplankton have been examined. If it is assumed that macrozooplankton cannot efficiently graze particles smaller than 5 μm, there was insufficient primary production to meet the demands of the copepods and euphausiids; however, there would have been sufficient if these animals could graze phytoplankton < 5 to $> 1\,\mu$m. Ciliates were in competition with the macrozooplankton for phytoplankton and could not have been significant grazers of bacterial biomass. The majority of microflagellates were autotrophic; less than 10% of the population did not possess a chloroplast and were presumably heterotrophs. Bacterial production was low and was insufficient to meet the demands of the heterotrophic microflagellates, but there was sufficient production by the picophytoplankton to meet microflagellate requirements. The data do not appear to support the ideas of a significant flow of energy through the "microbial loop" in the Celtic Sea in August.

Introduction

Qualitative schemes describing the trophic interactions that occur in the pelagic food web have been produced for many years and have fundamentally influenced biological oceanographic research. Descriptions of trophic relationships, such as that produced by Hardy (1924) for the feeding of the herring, have served as the basis for much of the research into trophic interactions and energy flow in the marine ecosystem. Yet results obtained in recent years no longer appear to support the traditional view of a food web based on large phytoplankton species. Small phytoplankton, in some cases of the size traditionally considered to be bacteria, are quantitatively the most important primary producers in many regions, and significant diatom production in temperate waters is often restricted to the few months of the spring. The role of bacteria, protozoans and microzooplankton has only recently been investigated. All of these factors have contributed to the current uncertainties about how the pelagic ecosystem functions.

The Institute for Marine Environmental Research at Plymouth began a programme of research in 1982 on a shelf–sea pelagic ecosystem, with the aim of relating primary, secondary and tertiary production. The area of study in the Celtic Sea has been described by Joint and Pomroy (1983). The water column is strongly stratified in the summer months, with values of the Simpson-Hunter stratification parameter greater than 2.5 (Simpson, 1976); in August 1982, a sharp thermocline of 7 C° difference in water temperature was recorded between 26 and 30 m, and the surface mixed-layer temperature was 16.3 °C. Nutrient and chlorophyll concentrations were low at this time, but there was significant primary production of between 600 and 700 mg C fixed $m^{-2}\,d^{-1}$ (Joint and Pomroy, 1983). There were no measurable fluctuations in vertical water structure, inorganic nutrient concentrations, phytoplankton biomass or production during either of two cruises of 14 d duration in early July and mid-August, and conditions in the surface mixed-layer approximated a steady state.

A significant proportion of the primary production in the summer months occurred in picoplankton and small nanoplankton (Joint and Pomroy, 1983). The first aim of the present paper is to consider the consequences of this small phytoplankton production for macrozooplankton production. The second aim is to prepare a budget which will attempt to relate the demands of the consumer community of macro- and microzooplankton to the measured primary production; it is not our intention to

construct a total ecosystem budget which will balance all flows of carbon within the ecosystem; rather, we will examine how much of the primary production might be available to the protozoans. The flow of carbon through the plankton is considered on one specific day, 21 August 1982.

Materials and methods

Data on water-column temperature, inorganic nutrients, chlorophyll concentration and primary production measurements have been reported by Joint and Pomroy (1983). Zooplankton were sampled using the double Longhurst-Hardy Plankton Recorder (LHPR), fitted with 280 and 53 μm mesh nets, as described by R. Williams *et al.* (1983). Samples were taken at ca. 6 h intervals during 21–22 August 1982 to study the diurnal variations in vertical migration. Data were lost at the midnight sampling period because of equipment failure, so data from midnight on the previous day are used; for convenience and ease of interpretation, the data are plotted in the sequence: midday, 18.00 hrs, midnight and 06.00 hrs.

Samples for particulate-carbon analysis were filtered through GFC glass-fibre filters and analysed in a Carlo Erba Elemental Analyser 1106; in some samples, particulate organic carbon was distinguished from total particulate carbon by combustion in a low-temperature plasma asher.

Results

Biomass of macrozooplankton species

Zooplankton species diversity was low at this station and four species accounted for 90 to 95% of the biomass sampled. Two species of copepod, *Calanus helgolandicus* and *C. finmarchicus,* comprised 57% of the biomass sampled by a 280 μm mesh net and two species of euphausiid, *Nyctiphanes couchi* and *Meganyctiphanes norvegica,* accounted for another 36% of the total; approximately 15 species made up the remaining 7% of the biomass. Table 1 shows the variation in total biomass (mg C m^{-2}) sampled and percentage composition at the four sampling times. The small number of species contributing to the major part of the biomass makes this system a convenient one with which to attempt to budget carbon flow.

The biomass of zooplankton retained by the 53 μm mesh net is also given in Table 1; the biomass was about 20% of that of the macrozooplankton, and the organic carbon content of this fraction was significantly lower, being only about 50% of that of the macrozooplankton. This low organic content suggests that a significant amount of inorganic detritus may have been present in this microzooplankton fraction.

Vertical distribution patterns

The system can be simplified further by considering the vertical distribution of the large herbivorous zooplankton. Fig. 1 shows the vertical distribution of *Calanus helgolandicus* Stages V and VI, *C. finmarchicus* Stages V and VI, and combined data on Stages I–IV of both species. During daylight, *C. helgolandicus* and early copepodites were found above the thermocline, with only a small proportion of the population being found below the thermocline at night. Similarly, *C. finmarchicus* was always below the thermocline, except for a small number in the surface mixed-layer at midnight. Therefore, there was almost a total segregation of these two *Calanus* species, with the

Table 1. Biomass (mg C m^{-2}) and percentage composition of zooplankton sampled by 280 and 53 μm mesh nets of the LHPR system at 0 to 100 m in the Celtic Sea, 21–22 August 1982

	Sampling time:			
	Midday	18.00 hrs	Midnight	06.00 hrs
280 μm net				
Copepods	1 173	1 753	1 097	1 537
Euphausiids	741	698	1 198	1 046
Carnivores	121	130	99	129
Limacina retroversa	8	77	22	138
Total	2 043	2 658	2 416	2 850
Copepods and euphausiids as % of total carbon biomass	93.7%	92.2%	95.0%	90.7%
Calanus spp. as % of total copepod carbon	97%	91%	100%	95%
53 μm net				
Total zooplankton	402	522	514	399
% organic carbon	43%	56%	30%	47%

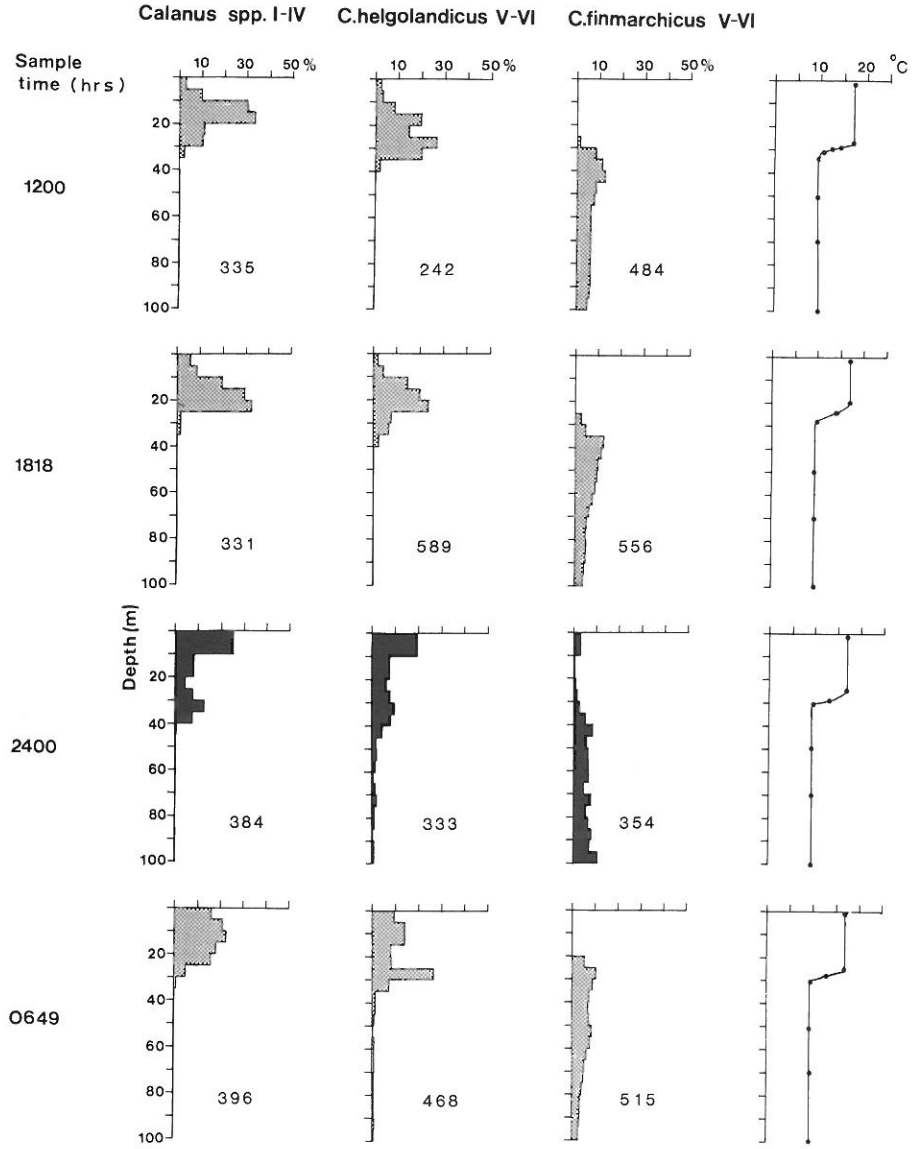

Fig. 1. *Calanus* species. Vertical distribution of *Calanus* spp. (I–IV), *C. helgolandicus* (V–VI) and *C. finmarchicus* (V–VI) sampled by the LHPR system at three times during daylight hours (light shading) and once at night (dark shading) on 21–22 August 1982. Values are mg C m^{-2} over the depth sampled for each profile; temperature profiles are also shown

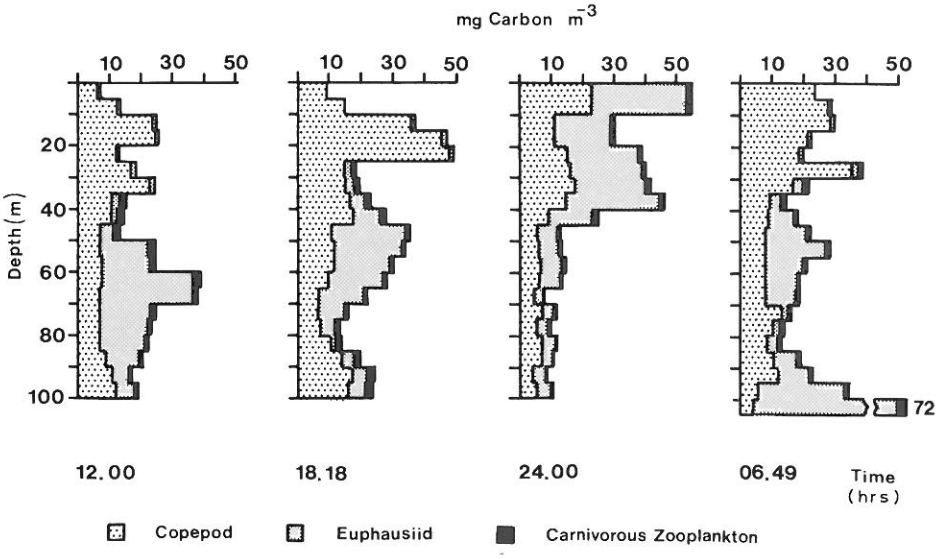

Fig. 2. Vertical distribution of copepods, euphausiids and carnivorous zooplankton in same samples as in Fig. 1

thermocline forming the boundary between their distributions (Williams, 1985).

The euphausiids showed large vertical migrations (Williams and Fragopoulu, in press); the biomass of copepods and euphausiids at the four sampling times is shown in Fig. 2. During the day, very few euphausiids were found in the surface mixed-layer and the major population was at 50 to 60 m; indeed, there is some evidence that part of the population was living close to the bottom because significantly higher numbers were sampled when the LHPR came within 10 m of the sea-bed at the 06.49 hrs sampling. There was, however, a large vertical migration into the surface waters at night.

Food requirements of the macrozooplankton

These vertical distributions have obvious implications for the food demand of the copepods and euphausiids. *Calanus finmarchicus* cannot feed on phytoplankton in the euphotic zone because it is not found in the surface layer at this time of year (Williams, 1985). Similarly, the period of time that euphausiids are present in the surface mixed-layer is restricted to the hours of darkness; in August, euphausiids can only feed on phytoplankton for a maximum of 6 to 8 h each day, and the rest of the time they are below the thermocline and out of the euphotic zone.

Experiments to establish the daily ration of *Calanus* species feeding on natural phytoplankton populations were unsuccessful; however, D. R. Robins (Institute for Marine Environmental Research, personal communication) measured feeding rates of *Calanus* spp. (Stage V and adult females) on the diatom *Thalassiosira weissflogii* in August 1982 at cell concentrations 6.25 times the concentration of natural particulates larger than 5 μm; these estimates of the food demand of *Calanus* species are shown in Table 2. We have attempted to extrapolate from the high experimental food concentration to natural particulate concentrations using data from Frost (1972), and the estimated grazing rates at natural concentrations are also given in Table 2. The food requirements of Stages II–IV were estimated using the data given by Paffenhöffer (1971) for the food required by *C. helgolandicus,* as a proportion of the body carbon required per day; this varied from 120% body carbon per day for Stage II to 63% per day for Stage IV.

We have no measurements of the grazing rate of the euphausiids. Lasker (1966) calculated that between 12 and 95 μg C mg^{-1} C d^{-1} were required by *Euphausia pacifica* feeding on phytoplankton and detritus to meet the metabolic demands of a natural population. The biomass of euphausiids in the Celtic Sea was between 700 and 1 200 mg C m^{-2} and, using the data of Lasker, would have a food requirement of between 9 and 114 mg C m^{-2} d^{-1}. However, euphausiids are omnivorous, and a significant proportion of their food requirements could be met by feeding on macrozooplankton; we have not attempted gut analysis to determine the food composition of the

Table 2. *Calanus* spp. Estimated food demand

Stage	Biomass (mg C m^{-2})	% biomass	Measured grazing rate (μg C mg^{-1} C d^{-1})	Estimated grazing rate (μg C mg^{-1} C d^{-1})	Water column demand (mg C m^{-2} d^{-1})
Calanus spp.					
II	1.2	0.4	ND	1 200[a]	1.4
III	72.7	21.7	ND	750[a]	54.5
IV	260.6	77.9	ND	630[a]	164.2
Total	334.5	100			220.1
C. helgolandicus					
V	181.6	75.3	192	29[b]	5.3[b]–34.9[d]
Female	46.1	19.1	88	14[b]	0.6[b]– 4.1[b]
Male	13.7	5.6	ND	14[c]	0.2[b]– 1.2[d]
Total	241.4	100			6.1[b]–40.2[d]
C. finmarchicus					
V	437.3	90.3	15	15[d]	6.6
Female	43.8	9	23	23[d]	1.0
Male	3.4	0.7	ND	23[d]	0.1
Total	484.5	100			7.7

[a] Estimated from data from Paffenhöffer (1971) for *C. helgolandicus*
[b] Experiments performed at food concentration of 2.5 ppm (by vol) and adjusted to the concentration of natural particulates > 5 μm in August (0.4 ppm), using the data of Frost (1972)
[c] Assumed to be the same rate as *C. helgolandicus* female
[d] Using measured grazing rate, uncorrected for lower food concentration

euphausiids of the Celtic Sea in 1982, but feeding experiments with *Nyctiphanes couchi* carried out in the Celtic Sea in 1981 showed grazing throughout the particle size spectrum, with a preference for particles in the range 20 to 40 μm (J. A. Lindley, Institute for Marine Environmental Research, personal communication). Similarly, we do not know how much feeding these euphausiids do when they are below the thermocline; in constructing a carbon budget, we assume that most of the euphausiid feeding occurs in the surface mixed-layer at night and that they graze on phytoplankton.

We have no data on the food requirement of microzooplankton which is retained on 53 μm mesh. The biomass of these microzooplankton was between 10 and 20% of the macrozooplankton biomass. We cannot estimate the food demand of these animals but, given the inverse relationship between organism size and metabolic activity, they could have a food demand equivalent to the macrozooplankton. We have not included microzooplankton in our calculations of a carbon budget because we have no data on the metabolic activity of these small animals and young stages.

The "microbial loop"

We also wish to consider the part of the pelagic ecosystem that involves bacteria and microzooplankton. These organisms have recently been recognised as very important in the flow of carbon in the pelagic ecosystem (Williams, 1981); the pathways involved have been termed the "microbial loop" (Azam et al., 1983). Fig. 3 shows the vertical distribution of bacteria, microflagellates and ciliates on 21 August 1982. The microflagellate counts include photosynthetic flagellates, which were the organisms responsible for primary production in the > 5 to < 1 μm size fraction (Joint and Pipe, 1984), and so not all of these organisms would be involved in the heterotrophic microbial loop.

There were 10^6 bacteria ml^{-1} above the thermocline and these were almost all small cells of 0.2 to 0.3 μm diam; assuming that each cell contains 1.7×10^{-15} g C (Watson *et al.*, 1977) the biomass of bacteria above the thermocline was 1.7 μg C l^{-1} and below the thermocline was 0.68 μg C l^{-1}. Joint and Pomroy (1983) measured the incorporation of ^{3}H thymidine and estimated a bacterial production rate of between 0.24 and 0.32 μg C l^{-1} d^{-1} for bacteria above the thermocline and 0.06 to 0.08 μg C l^{-1} d^{-1} below the thermocline. The carbon requirement of the bacteria depends on the efficiency with which they utilize dissolved organic carbon. A minimum requirement of 0.48 μg C l^{-1} d^{-1} is obtained by assuming an assimilation efficiency of 50% and using the minimum estimate of bacterial production; taking an assimilation efficiency of 10% and the higher estimate of production results in a carbon demand of 3.2 μg C l^{-1} d^{-1}.

We have no estimates of the proportion of microflagellates that are heterotrophic, and the numbers shown in Fig. 3C include autotrophic forms. Indeed, the majority of microflagellates present in August possessed photosynthetic membranes (Joint and Pipe, 1984); although it is difficult to be quantitative with transmission electron micrographs, about 90% of the cells > 2 μm diam possessed chloroplasts. It is possible that microflagellates possessing chloroplasts are capable of feeding on bacteria but, for the purposes of constructing a carbon budget, we assume that the total biomass of bactivorous microflagellates is 10% of the total shown in Fig. 3C, i.e., about 500 ml^{-1}. Sieburth and Davis (1982) measured the numbers of heterotrophic nanoplankton in the North Atlantic

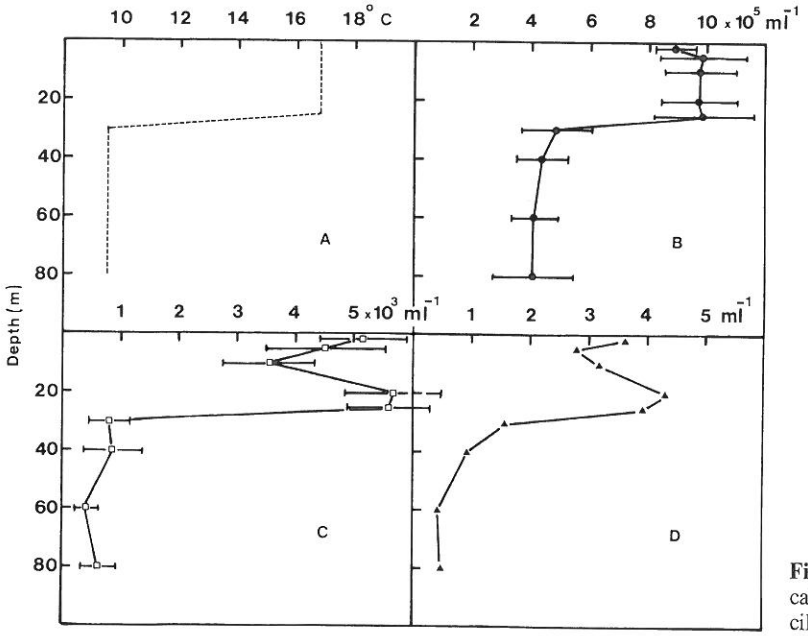

Fig. 3. Continuous profile of temperature (A) and vertical distribution of bacteria (B), microflagellates (C) and ciliates (D) on 21 August 1982

Ocean and also found 500 ml^{-1}. The mean cell volume of the microflagellates, determined by scanning electron microscopy, was 13.3 μm^3, but there is uncertainty over this estimate because some shrinkage may have occurred during sample preparation. Holligan *et al.* (1984 a) found the mean volume of microflagellates in the stratified regions of the English Channel to be between 20 and 44 μm^3, with a mean carbon content per cell of between 4.2 and 8.8 pg C $cell^{-1}$. If these values are taken as minimum and maximum estimates, the biomass of heterotrophic microflagellates above the thermocline in the Celtic Sea is calculated to be between 2.1 and 4.4 μg C l^{-1}; below the thermocline, all of the microflagellates are assumed to be heterotrophic and the estimated biomass is the same as in the surface mixed-layer.

The numbers of ciliates were small, so sampling error is large and there is some uncertainty in the estimate of ciliate biomass (Fig. 3 D). Typical cell diameter of these ciliates was 24 μm, giving a cell volume of 7 240 μm^3; assuming that 1 ml cell volume is equivalent to 0.071 g C (Fenchel and Finlay, 1983), the biomass of ciliates is about 2 to 2.5 μg C l^{-1}.

Food requirements of the microzooplankton

Microflagellates are reported to grow quickly with high efficiency when presented with abundant food; Fenchel (1982) found a maximum food consumption for six microflagellate species of 60% of the cell volume per hour. Of the six species he studied, the small choanoflagellate *Monosiga* sp. was of the same size as the microflagellates in the Celtic Sea, and these are the most appropriate data to use in this budget. *Monosiga* sp. had a maximum uptake of 27 bacteria h^{-1}; however, Fenchel's experiments were done with cultures feeding on bacterial suspensions that were two orders of magnitude more dense than the bacterial population found in the Celtic Sea, and caution is required in extrapolating from these laboratory experiments to the natural environment. Nevertheless, these data are the best available and can be used to give a maximum estimate of microflagellate grazing rate in the Celtic Sea. The rate is calculated to be equivalent to a consumption of 3.25×10^5 bacteria ml^{-1} d^{-1} by 500 heterotrophic microflagellates. Bacterial numbers of ca. 10^6 ml^{-1} were constant over the period of the cruise; since the measured generation time of bacteria was between 4 and 7 d (Joint and Pomroy, 1983), this estimate of microflagellate grazing is close to that required to control the observed bacterial population, especially if microflagellates can also utilise some of the autotrophic picoplankton production. Therefore, for this carbon budget, we assume a maximum grazing rate of 27 bacteria per microflagellate per hour and calculate a food requirement of 0.55 μg C l^{-1} d^{-1}. However, the grazing rate of *Monosiga* sp. at the bacterial densities found in the Celtic Sea would not be this high. Grazing rates at natural population densities can be estimated from the Monod plot of specific growth rate against bacterial concentration given by Fenchel (1982). At a bacterial concentration of 10^6 ml^{-1}, specific growth rate (and presumably grazing rate) would be 5% of the maximum. If allowance is made for the small size of Celtic Sea bacteria, which have a cell volume of 5% that of the bacteria used by Fenchel in his experiments, the grazing rate may be less than 1% of the maximum calculated above; microflagellates would then have an insignificant impact on bacterial biomass. Since we have no data for the actual grazing rate of the Celtic Sea microflagellate population, for the purposes of calculating a carbon budget we have used the maximum value of 0.55 μg C l^{-1} d^{-1} for microflagellate grazing.

Fenchel (1980) states that, at the densities of bacteria that are found in the sea, ciliates are unlikely to be important in controlling the bacterial population. Jørgensen (1983) has pointed out that ciliates adapted to feed on particles of bacterial size have a low capacity for water-processing because of the high flow-resistance of the filter and, therefore, require high bacterial concentrations of 10^7 to 10^8 ml^{-1}. Ciliates from oceanic environments have porous filters which can process larger volumes of water and are adapted to retain phytoplankton-sized particles. Therefore, we assume that the consumption of bacteria and autotrophic picoplankton by ciliates is negligible, but that ciliates could graze on particles $> 5\ \mu m$. There is a paucity of data on ciliate grazing on natural particulate concentrations; the most comprehensive data are those of Fenchel (1980), who found that under ideal conditions small ciliates (of the size found in the Celtic Sea) could ingest 80 to 120% of their cell volume per hour, with a generation time of 2 to 4 h. However, the food concentrations used in the experiments would never be found in the Celtic Sea, and these rates are unrealistic for present purposes.

Available food – primary production

Picoplankton and small nanoplankton were responsible for most of the primary production at this station in the summer months. Fig. 4 shows the percentage carbon fixed in three size-fractions and the dissolved fraction for August 1982; the data obtained in July and October are also included to demonstrate the continuing quantitative importance of small phytoplankton to the primary production of this region. The daily primary production rates, as measured by ^{14}C fixation, were 631.38 and 624.38 mg C m^{-2} d^{-1} on 22 and 23 August, respectively, and these values are typical of the other measurements of primary production made in August (Joint and Pomroy, 1983). On these two days, production was, respectively, 113.69 and 129.63 mg C m^{-2} d^{-1} in the $> 5\ \mu m$ size fraction, with 214.75 and 219.19 mg C m^{-2} d^{-1} in the < 5 to $> 1\ \mu m$ fraction, and 199.25 and 193.00 mg C m^{-2} d^{-1} in the < 1 to $> 2\ \mu m$ fraction.

How much confidence can be placed on these estimates of primary production in view of the considerable speculation that the ^{14}C method may seriously underesti-

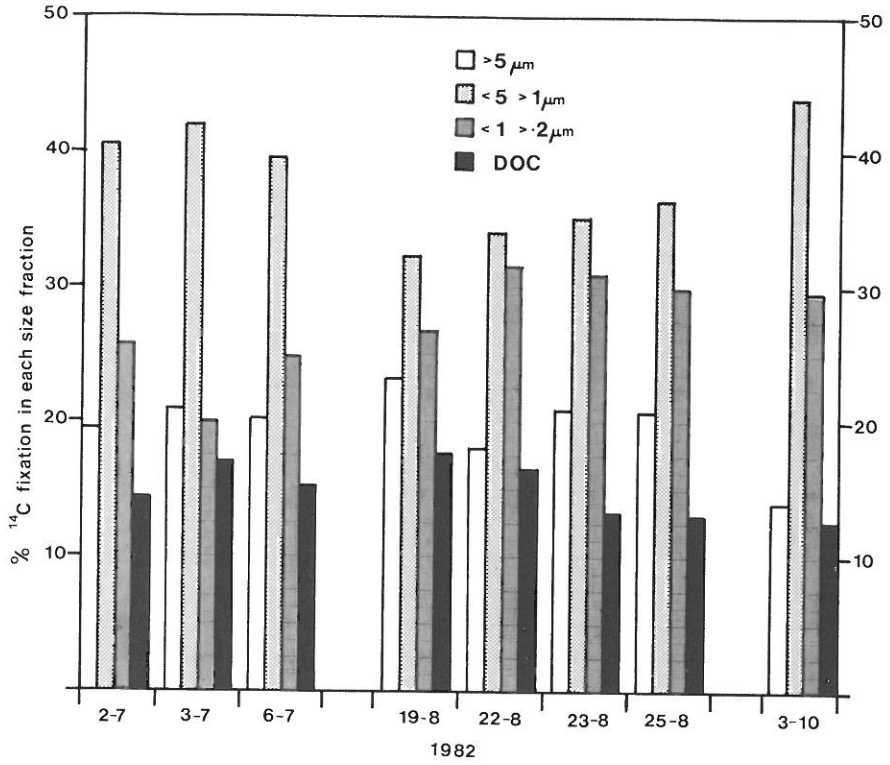

Fig. 4. Percentage carbon fixed by phytoplankton of > 5 μm, < 5 to > 1 μm, and < 1 to > 0.2 μm and exuded as dissolved organic carbon (DOC) in July, August and October 1982

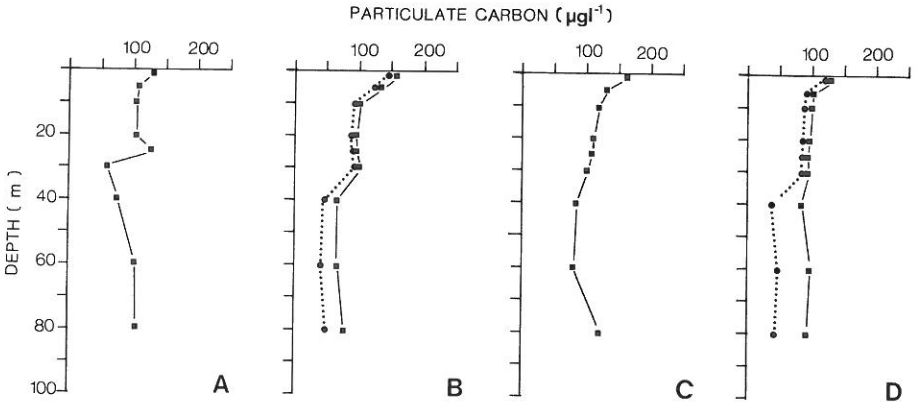

Fig. 5. Distribution of total particulate carbon (continuous lines) and organic carbon (dotted lines) at (A) midday, (B) 18.18 hrs, (C) midnight and (D) 06.49 hrs

mate primary production? Recently, P. J. LeB. Williams *et al.* (1983) have shown close agreement between estimates of primary production derived by the ^{14}C method and high-precision oxygen measurements for oligotrophic waters; Davies and Williams (1984) reached the same conclusion for coastal waters. These results suggest that the ^{14}C method may give accurate estimates of primary production. In contrast, Holligan *et al.* (1984b), using the same techniques, concluded that the ^{14}C method underestimated gross photosynthesis in the English Channel by up to 50%; however, they did not measure label in dissolved organic carbon produced by the phytoplankton, and this may account for at least some of the discrepancy. Therefore, it seems reasonable to assume that the production estimates of Joint and Pomroy (1983) are close to the actual production values, with any underestimation unlikely to be more than 30%; it is appropriate to use these values in a budget of carbon flow.

Available food-organic detritus

In addition to phytoplankton biomass, there is a considerable quantity of organic detritus that may be exploited by the zooplankton. Certainly, the population of *Calanus finmarchicus* must be utilising a food source other than growing phytoplankton because the copepods are always below the euphotic zone in the summer months. Fig. 5 shows the vertical distribution of particulate organic carbon in samples taken at the same time as the LHPR profiles were made; samples from two of the profiles were pretreated in a low-temperature plasma asher to give an estimate of the organic carbon content of the particulate carbon. Above the thermocline there was very little difference between the two measurements, and the concentration was ca. 100 $\mu g\, C\, l^{-1}$, with a slight increase in the surface samples. Below the thermocline there was a significant difference in the two estimates, which suggests

that a higher concentration of inorganic carbon was present. Particulate organic carbon concentration was approximately half that in the surface mixed-layer, although the concentration of total particulate carbon was not significantly different. Coulter Counter analysis showed no variation in particle size above the thermocline, and 60% (by vol) of particles were between 5 and 10 μm; below the thermocline there were more large particles, particularly in the deepest samples, which were presumably the result of resuspension of bottom sediment. The size distribution of particles suggests a population of large particles of < 5 μm diam, but the primary production data show that only ca. 120 mg C m^{-2} d^{-1} is fixed by phytoplankton of this size, with 65% of the primary production occurring in organisms smaller than 5 μm.

Minimum particle size retained by macrozooplankton

In view of the substantial primary production by small phytoplankton in the Celtic Sea, it is important to know the smallest size of particle that can be captured by the macrozooplankton. Conover (1981) describes the mechanisms involved in feeding on small particles; he concludes that interception of food particles by the structural parts of the feeding apparatus, acting as a sieve or filter, explains most food capture by suspension-feeding animals. With 65% of the primary production occurring in phytoplankton that are smaller than 5 μm diam, it becomes very important to know the smallest size of particle that can be captured by the copepods and euphausiids.

The elegant experiments of Koehl and Strickler (1981) demonstrated that the feeding appendages of copepods do not act as simple sieves, but function to entrain water flow past the animal; the second maxillae act as sieves only in the final stages of the feeding process when water is squeezed from the water parcel that contains the food particles. Nevertheless, the setule spacing must control the size of particle that is retained in the feeding basket. We have measured the minimum distance between setules on the second maxillae of adult *Calanus helgolandicus* to be between 2.5 and 4 μm, and for *Nyctiphanes couchi* between 3 and 4 μm. Marshall and Orr (1956) measured similar distances in nauplii and adult *C. helgolandicus,* but found that particles of this size were rarely, if ever, retained. Similarly, Conover (1978), in a study using natural particulates as food, found that particles less than 2 to 3 μm are not ingested by neritic copepods. In a study on *Paracalanus parvus,* which has a feeding mode similar to *Calanus* spp., Bartram (1980) found that capture efficiency decreased with particles < 12 μm and was less than 30% with cells 5 μm diam. However, small cells may be captured by *Calanus* species. Johnson *et al.* (1982) reported picoplankton cells within the faecal pellets of *C. finmarchicus,* but the cells did not appear to be degraded and presumably could not have contributed to the nutrition of the copepod. For the purposes of this model, we will consider that the macrozooplankton can only utilize phytoplankton > 5 μm diam, and that cells < 5 μm are either not captured efficiently or are not utilized.

Carbon budget for the Celtic Sea pelagic ecosystem

Table 3 summarises the data discussed above; primary production and the estimated demand of the various components of the system are shown and the range of biomass measured is indicated. The maximum and minimum values obtained on 21 August define the range in biomass of the macrozooplankton, bacteria, flagellates and ciliates. Throughout the period of the cruise, the biomass values obtained for each of these categories did not vary and were not significantly different from the ranges shown in Table 3; as far as the biomass estimates indicated, the pelagic ecosystem in August appeared in quasi-steady state and variations were presumably the result of patchiness in distribution. The ranges of carbon demand shown in Table 3 arise from taking the highest and lowest values in the assumptions discussed earlier ("Results – The "microbial loop"; Table 2).

There appears to be insufficient primary production by phytoplankton > 5 μm to meet the requirements of the macrozooplankton; however, if the production by phytoplankton of < 5 to > 1 μm is assumed to be directly available, there may be sufficient primary production. There is some uncertainty, because the greatest demand in our estimate was by the young stages of *Calanus* spp., which require 220 mg C m^{-2} d^{-1} (Table 2); this estimate is based on literature values of *Calanus* spp. grazing on optimal food concentrations. In August, particle concentrations in the

Table 3. Production by different phytoplankton size-fractions and the herbivore demand on that production in the surface 30 m. Columns refer to production by phytoplankton of different sizes or to herbivore demand on that size of phytoplankton. Production and demand are in mg C m^{-2} d^{-1}, values in parentheses are biomass in mg C m^{-2}

	Phytoplankton size-fraction:			DOC
	> 5μm	< 5– > 1 μm	< 1– > 0.2 μm	
Phytoplankton production	120	215	195	95
Herbivore demand				
Macrozooplankton				
Calanus spp. I–IV (335)	221	?	?	–
Calanus spp. V–VI (242)	6– 40	?	?	–
Euphausiids (700–1 200)	9–114	?	?	–
Protozoans				
Ciliate (60–75)	?	?	–	–
Microflagellate (63–132)	–	–	16.5	–
Bacteria (51)	–	–	–	14–96

Celtic Sea were low and it is unlikely that young *Calanus* spp. could feed at optimal rates. We are unable to estimate the food requirement of microzooplankton sampled by the 53 μm mesh net, or to speculate on the size of phytoplankton cells that these animals could feed on, but this microzooplankton might exert a significant additional demand on primary production by the largest phytoplankton size-fraction.

Similarly, we cannot make a realistic estimate of the food demand of ciliates, and there is an urgent need for ciliate grazing rates to be determined at natural particle concentrations so that the role of these organisms can be assessed. However, it does seem clear that pelagic ciliates, as well as being a potential food of the macrozooplankton organisms, must compete with them for nanophytoplankton-sized organisms; at the concentrations of bacteria in the Celtic Sea, ciliates cannot have a significant effect on bacterial biomass.

Discussion

Our first objective was to assess whether the demands of the macrozooplankton in the Celtic Sea could be satisfied by the measured primary production in August. The answer is equivocal; if the lower size limit for zooplankton grazing is 5 μm, there does not appear to be sufficient production by phytoplankton larger than 5 μm. However, if copepods and euphausiids can utilize phytoplankton of < 5 to > 1 μm, albeit at lower efficiencies, then the demands of the macrozooplankton could be met. It is possible that the presence of flagella that are significantly longer than the cell dimensions of the microflagellates might result in capture by the feeding appendages of the macrozooplankton. Clearly, this must be tested experimentally before we can conclude that primary production by phytoplankton of < 5 to > 1 μm is directly available to the crustacean zooplankton.

On the second question of the significance of the microbial loop in the Celtic Sea, again the answer is equivocal, but the data seem to suggest that there is no large flow of energy through the bacteria and heterotrophic microflagellates. This conclusion follows because bacterial production is low and there is apparently only a small population of non-photosynthetic microflagellates. Bacterial production in August 1982 was 0.25 to 0.32 μg C l^{-1} d^{-1} (Joint and Pomroy, 1983), and specific growth rate varied between 0.14 and 0.22 d^{-1}. Most published estimates of bacterial production have been made in temperate coastal waters and are between 1 and 100 μg C l^{-1} d^{-1} (Azam and Fuhrman, 1984). How much confidence can be placed on the estimate of Joint and Pomroy (1983)? The most likely cause of error would be if the factors used to convert uptake rate of ^{3}H thymidine to bacterial production are not appropriate to the bacteria of the Celtic Sea, but this seems unlikely. Why should bacterial production be low in the Celtic Sea? Unlike the environments quoted by Azam and Fuhrman, the Celtic Sea is away from coastal influences and does not have a significant allochthonous input of organic matter. We have used epifluorescence microscopy to determine if phytoplankton are colonized and, therefore, directly utilized by bacteria, but have only rarely found bacteria on the surface of phytoplankton. We conclude that algal cells are not directly available to bacteria and, in cases where bacterial production is a significant proportion of phytoplankton production, there must be a mechanism which affects the integrity of the algal cell and makes the organic matter available to the bacteria. Three mechanisms are possible: There could be a high rate of exudation from growing phytoplankton but, unless the nitrogen content of the exudate was high, or unless nutrients were available from the water column, this need not result in significant bacterial production (Joint and Morris, 1982). Secondly, during the grazing of herbivores on phytoplankton a significant proportion of the organic matter of the algal cell might be lost. Thirdly, herbivore excretion and faeces production supply organic matter that could be utilised by bacteria. In the absence of allochthonous sources of organic matter, high bacterial production would only seem possible if one, or all, of these mechanisms act. Phytoplankton exudation accounted for about 15% of the primary production in the Celtic Sea (Joint and Pomroy, 1983) and, in these calculations, we have assumed that this is the major source of organic substrates for bacteria. The two other mechanisms rely on herbivore activity; therefore, bacteria cannot be considered in competition with herbivores for the phytoplankton since herbivores consume intact algal cells and bacteria do not appear to colonize growing phytoplankton in the Celtic Sea. Bacterial production is the consequence of the release of organic matter from phytoplankton cells or from herbivore activity.

The estimate of low heterotrophic microflagellate activity depends on the assumptions we have made about the proportion of flagellates that do not possess chloroplasts and that are presumed to be heterotrophic. For the August samples we have used an estimate which is based on examination by transmission electron microscope, and this showed that more than 90% of the cells of microflagellate size possessed a large chloroplast and were presumably autotrophic. We did not examine fresh samples with epifluorescence microscopy in 1982 but, in subsequent years, we have found that greater than 95% of the microflagellate population possessed the characteristic red chlorophyll fluorescence. Clearly, photosynthetic flagellates dominated the microflagellate population. Photosynthetic microflagellates might be capable of grazing bacteria, but we have no evidence that this occurs; we assume that the majority of microflagellates are photosynthetic and that autotrophic nutrition dominates.

The low estimate of bacterial production is consistent with a small population of heterotrophic flagellates because the calculated demand of the microflagellates in August is almost in balance with the estimated bacterial

production. If bacterial production is greater than our estimate, there would then be insufficient microflagellate activity to keep the bacterial numbers constant. If only 10% of the total microflagellate population was indeed heterotrophic, then it is difficult to see how there could have been a significant flow of material through the "microbial loop" in the Celtic Sea.

Acknowledgements. This work forms part of the Shelf-Sea Ecology Programme of the Institute for Marine Environmental Research, a component of the Natural Environment Research Council, and is part of a multidisciplinary study of the Celtic Sea.

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Date of final manuscript acceptance: April 11, 1985.
Communicated by J. Mauchline, Oban