Annual pattern of calanoid copepod abundance, prosome length and minor role in pelagic carbon flux in the Solent, UK

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ABSTRACT: Investigation of the calanoid copepods at a coastal station in the Solent, UK, over a 14 mo period revealed a numerical dominance by species of the genus *Acartia* (comprising *A. bifilosa*, *A. clausi*, *A. discaudata* and *A. margalefi*), and the species *Temora longicornis* and *Centropages hamatus*, with sporadic appearances of *Paracalanus parvus* and *Pseudocalanus elongatus*. There was clear seasonality in the abundance of calanoids, with total numbers being highest from May onwards, and low after October. Stage-specific prosome lengths varied with season, and in most cases were negatively correlated with temperature. Individual weights and abundance of the copepods, together with measures of temperature, were used to predict weight-specific growth and production rates using a published empirical relationship. Comparisons of annual copepod production with previous measures of annual primary production and production of bacteria and ciliates at this same site were made, and a carbon flow diagram was constructed. Calanoid copepod annual production was 32.2 mgC m^{-3} yr^{-1}. This represents only 0.5% of the total annual primary production, and 0.6% of the annual primary production of algae >3 μm. Ciliate annual production was almost 2 orders of magnitude higher, and constituted 33% of the total annual primary production. In other neritic studies (with water column depths <200 m) annual production by copepods has varied between 21 and 177% of annual ciliate production, whereas at this Solent site the value was only 1.5%. It is suggested that the low biomass (and production) achieved by calanoid copepods was the consequence of population loss through high local flushing rates, unfavourable feeding conditions resulting from high suspended particulate matter, and high levels of hydrocarbon contaminants in the area.

KEY WORDS: Calanoid · Copepodite stage · Prosome length · Abundance · Production · Solent

INTRODUCTION

The Solent is a marine body of water situated at the opening of Southampton Water, on the south coast of the UK. The area is heavily industrialised, with major petroleum refinery installations on the west side of Southampton Water, and, to the north, the large city of Southampton. Although surveys of the mesozooplankton of Southampton Water have been undertaken by several workers over many years, comprehensive species-specific examinations of the zooplankton in this body of water have not been undertaken since those by Raymont & Carrie (1964). The Solent is situated to the north of the Isle of Wight, and is linked to the English Channel on either side of this island. Tidal features of the Solent are complex and characterised by a long stand of high water consisting of a double high tide, during which there is little water movement over a period of 2 to 3 h (Webber 1980). The Solent and Southampton Water are eutrophic, and the water column is partially to well mixed (Sylaios & Boxall 1998). The Calshot site investigated here is at the confluence of Southampton Water and the Solent (Fig. 1), and is

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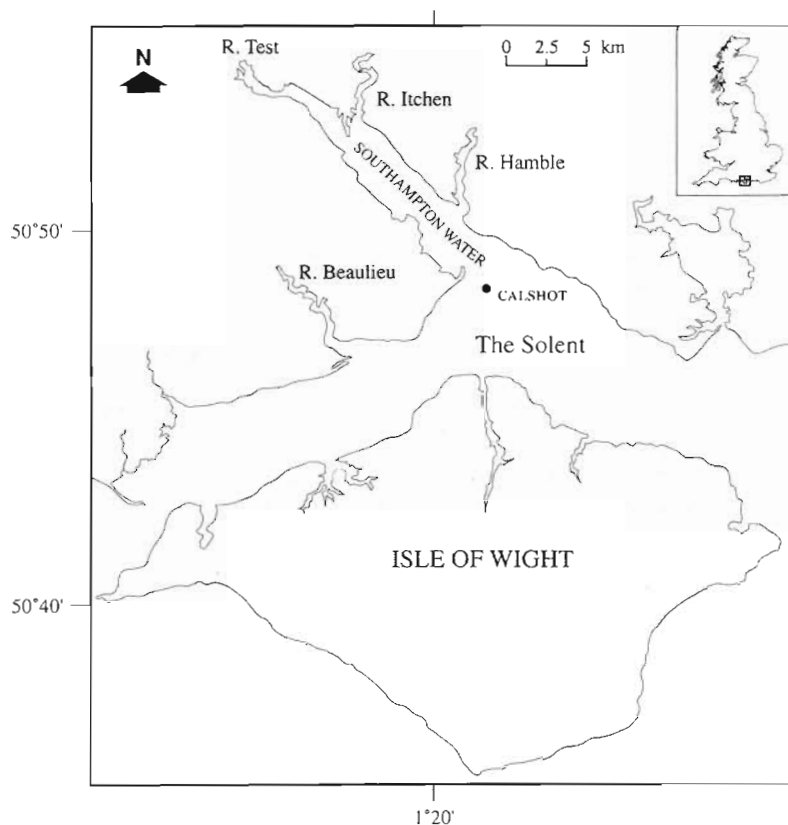
Fig. 1. Location of the Calshot site (the Solent, UK) investigated in the present study

located on the eastern limit of the dredged shipping channel.

This study forms part of an on-going investigation into the mesozooplankton of the area. The site has previously been used in examinations of the seasonal cycle, i.e. abundance, biomass and production rates of ciliates (Leakey et al. 1992), bacteria (Antai 1989) and size-fractionated primary production (Iriarte & Purdie 1994). The present investigation was designed to add to the body of information on pelagic carbon flux at this particular site by measuring abundances of the calanoid copepods and by estimating their contribution to pelagic carbon fluxes.

METHODS

Zooplankton were collected at 5 m from a 15 m deep site in the Solent, marked by the Calshot fixed shipping buoy (Fig. 1), over a 14 mo period (December 1992 to January 1994). Samples were taken at the high tide 'stand' during daylight hours, as close to spring tide as boat facilities and weather would allow. Plankton samples were collected using a 118 μm mesh non-filtering

cod-end net (mouth opening diameter 50 cm, net length 125 cm). The mesh size chosen ensured coverage of most of the copepodite stages, whilst minimising the reduction in filtering efficiencies during the periodic phytoplankton blooms which occur here. The net was towed horizontally at a speed of 2 knots for less than 5 min. A calibrated T.S Flowmeter (Tsurumi-Seiki Co. Ltd) was fixed in the mouth of the net to determine the water volume filtered. After towing the net was washed thoroughly, and the catch preserved in 4% formaldehyde-sea water. On 2 occasions (12 March 93 and 26 March 93) the usual net could not be used and a 200 μm mesh net was used as a replacement.

Temperature and salinity measurements were taken at 5 and 10 m depth, using a field T-S probe at each of the stations concurrently with the collection of zooplankton samples. Samples of water for pigment analysis were collected from 5 and 10 m, using a 5 l Niskin water bottle; samples were filtered through Whatman (GF/C) filters, and analysed fluorometrically for chlorophyll a and phaeo-pigments after 90% acetone extraction (protocol described in Kifle 1992).

After storage of the zooplankton material in excess of 6 mo, samples were concentrated to a fixed volume, and 2% sub-samples taken using a Stempel pipette. The sub-samples contained very large amounts of sediment, detritus and phytoplankton material, and zooplankton was therefore carefully separated out with the aid of a S-shaped Bogorov tray and binocular microscope. All zooplankton were enumerated and identified, although this study presents detailed results for only the dominant calanoid copepod component (other components described in Hirst 1996). Copepodites were identified to species level, although in the case of Acartia the non-adult copepodites were only classified to genus, and separated into the groups: C1, C2, C3, C4 (sexed when possible), C5 female and male, and C6 female and male. Naupliar stages were not identified to species level but were counted. Prosome lengths were measured for all individuals using a calibrated eye-piece graticule (where 1 division equalled 8.91 μm), at a standard magnification of 100×. No correction was made to these measurements as shrinkage due to preservation is minimal (Durbin & Durbin 1978). Prosome length measurements were made on a total of 3966 individuals, and although

a standard number were not measured for each copepodite stage, means often represent >20 individuals.

Individual carbon weights were estimated from prosome lengths using the regressions of Klein Breteler et al. (1982) for southern North Sea *Acartia clausi*, *Centropages hamatus* and *Temora longicornis*, while their equation for *Pseudocalanus* sp. was used to estimate weights of *Paracalanus parvus* and *Pseudocalanus elongatus*. Ash-free dry weight was converted to dry weight by assuming that ash represented 10.4% of the dry weight in *T. longicornis*, 8.9% in *Acartia* spp., 8.5% in *Pseudo/Paracalanus* and 4.1% in *C. hamatus* (Laurence 1976). Carbon weights were calculated assuming these to be 40% of dry weight (Omori & Ikeda 1984, Båmstedt 1986). Adult *Acartia* weights were determined using the appropriate speciesspecific equation, whilst for non-adult copepodites the length-weight equation for whichever *Acartia* species was numerically dominant in the adult stage was applied. As there was no equation available for *A. discaudata* and *A. margalefi*, the equations for *A. bifilosa* and *A. clausi* respectively were applied (as body form is similar between these species). *A. bifilosa* weights were determined using the equation describing carbon weight (C, µgC) as a function of prosome length (PL, µm), where $\log_e C = -2.285 + 0.003793\,PL$ (M. Koski pers. comm.). Unfortunately, given the variation in stage abundances resulting from the mixing in the area, and the resolution of sampling, we made no attempt to describe growth using cohort methods. As an alternative, growth of copepods was estimated using the globally predictive equation of Hirst & Lampitt (1998):

$$\log_{10} g = 0.0208(T) - 0.3221(\log_{10} BW) - 1.1408$$

where g (d^{-1}) is weight-specific growth, T (°C) is temperature, and BW (µgC ind.$^{-1}$) is individual body weight, adult males were assumed not to grow. Individual weights rather than mean values, and the temperature at the time of sample collection were utilised. Production was determined by multiplying weight-specific growth (g) for each individual by its calculated *in situ* biomass (µgC m^{-3}), given the sub-sample size and volume of water filtered. Annual production was derived for each species separately, except for *Acartia* spp. where all species were considered together, using trapezoidal integration between points. Total production was derived simply as the sum of production for each of the copepod species.
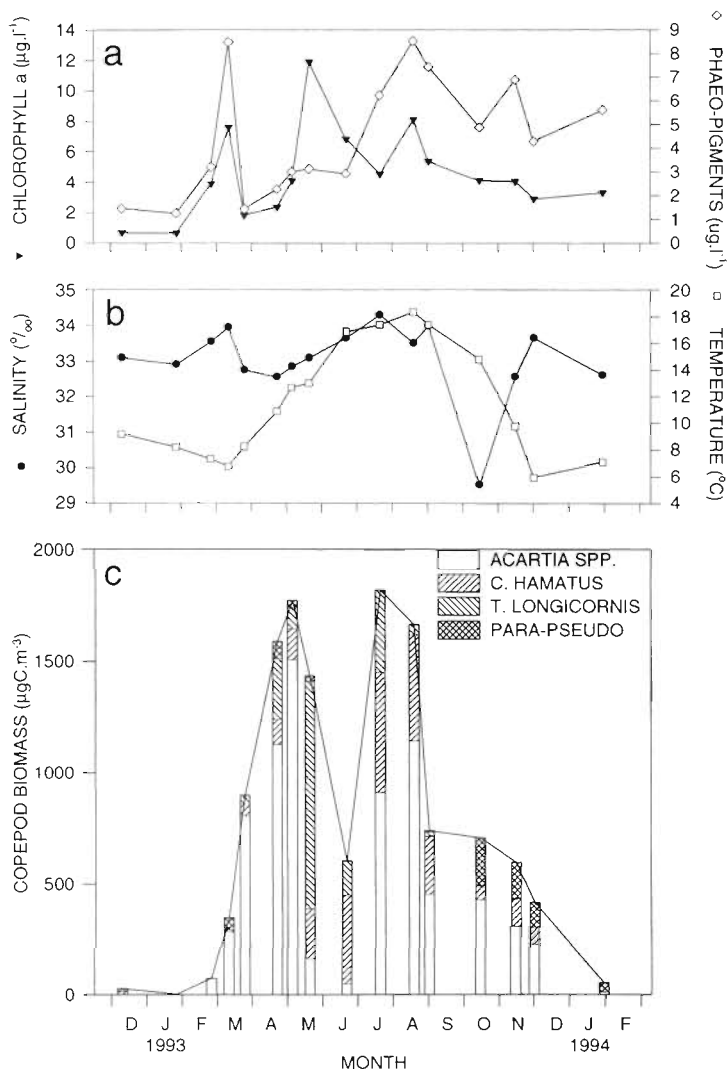

Fig. 2. Seasonal patterns at the Calshot site. (a) Chlorophyll *a* and phaeo-pigment concentrations; (b) temperature and salinity; and (c) biomass of copepods. Physical-chemical measurements are averages of values at 5 and 10 m depth

RESULTS

Temperature, salinity, chlorophyll *a* and phaeo-pigment measurements over the 14 mo investigation are presented in Fig. 2. Temperature shows a cyclical annual pattern with the highest temperatures recorded in mid-August at 18.4°C, and the minimum at the beginning of December at 6.0°C. Chlorophyll *a* peaked at 11.9 µg l^{-1} in May, and on only 3 occasions fell below 2 µg l^{-1}, in December, January and April. Phaeo-pigments concentrations peaked in March at >8 µg l^{-1}, and also later in the year during August at >8 µg l^{-1}. October 1993 was a period of particularly heavy rainfall, and this explains the unusual low salinity (29.5‰) observed at the Calshot site. Salinity on all the other occasions it was measured was fairly stable, varying between 32.6 and 34.3‰.
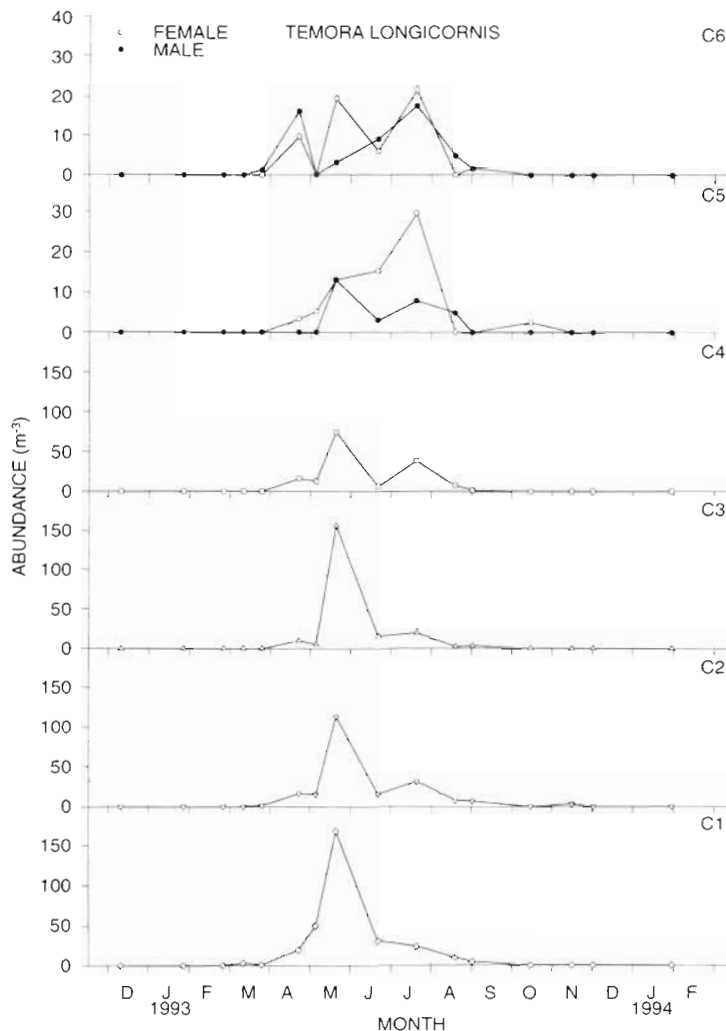
Fig. 3. Abundance of *Temora longicornis* (C1 to C6) over the 14 mo investigation (note scale change)

Abundance patterns

Abundances of copepodite stages over the 14 mo investigation at Calshot are presented in Figs. 3 to 6. Although other calanoid copepod species not presented in detail here were occasionally present, these were always very rare, and their appearance sporadic. *Temora longicornis* was most abundant from April through to August, and typically absent during the winter months October to February (Fig. 3). Maximum concentrations of males and females were found in July when together they totalled 39 ind. m^{-3}, C5 abundances also peaked at this point, while the densities of all the earlier copepodite stages peaked in May. *Centropages hamatus* copepodites were abundant from April until November, and rare or absent during the late winter and spring (Fig. 4).

Adult concentrations peaked in July at 53 ind. m^{-3}. Abundances of stages generally fell rapidly after August, although abundance of C3s and C4s showed small secondary peaks in November. *Acartia* spp. were dominant throughout much of the year, with peaks in numbers during both April-May and July-August (Fig. 5). The peak in *Acartia* adult numbers occurred during April, this peak being predominantly *A. bifilosa* (Fig. 6). *A. bifilosa* was numerically the dominant *Acartia* adult during the first 5 mo of the year, with *A. discaudata* and *A. clausi* dominating from July until November-December. *A. bifilosa* adults reached abundances of almost 600 ind. m^{-3}. *A. clausi* adults reached a maximum of 140 ind. m^{-3} in July, while *A. discaudata* adults reached a maximum density of 166 ind. m^{-3} in August. *A. margalefi* were rare or absent throughout most of the year; the maximum abundance of adults occurred in May and August-September, although density never exceeded 18 ind. m^{-3}. *Paracalanus parvus* adults were most abundant during November, when they reached 34 ind. m^{-3}. *Pseudocalanus elongatus* adults were much rarer than *P. parvus*, and were recorded in November to January and in April. Maximum adult abundance of *P. elongatus* was just 10 ind. m^{-3} in January.

Seasonal variations in size

Mean prosome lengths for copepodites stages (C1 to C6) of *Temora longicornis* decreased in all stages from a March to May maximum to a minimum in August to October (Fig. 7). There was a general absence of *T. longicornis* after September The pattern of change in length of *Centropages hamatus* was very similar to that for *T. longicornis*, with a decrease in size from spring (most values being highest in March to May) to summer and early autumn (the smallest individuals found in August to October). There was a general increase in size of *C. hamatus* after September, although not for C1 or C2. Copepodite stages C1 to C5 of *Acartia* spp. showed clear changes in mean prosome length, with increasing size from their first appearance in January-February until a minimum in March. After this peak, prosome lengths for all stages of this genera progressively decreased until September, when the minimum prosome length was recorded for all stages. Subsequently, mean prosome lengths generally increased

once again. The older stages of all the species showed greater absolute size changes over the course of the investigation than the younger stages.

Acartia bifilosa adults demonstrated clear changes in mean prosome length (Fig. 8). Lengths increased from January to an annual maximum in March of 0.85 mm (±0.027 [±SD]) and 0.87 mm (±0.046) in males and females respectively. After this, prosome lengths decreased until July, when female lengths were the shortest recorded, but no males were found. *A. bifilosa* adults were absent after July until their re-appearance in November and December when their lengths were close to, but lower than, those recorded during the previous winter. *A. discaudata* adult prosome lengths were highest for males in April to May, after which they were only recorded again in mid-July, when their size had decreased dramatically to 0.63 mm (±0.016) in females and 0.63 mm (±0.005) in males. From September until December size increased in both sexes. In *A. clausi* size was fairly constant from July to October, with mean prosome lengths of females ranging from 0.79 mm (±0.052) to 0.81 mm (±0.039), and for males between 0.75 (±0.022) and 0.78 mm (±0.020). Following this period of stability, the mean prosome length increased into winter. A single large female of 1.0 mm prosome length was found in May 1993. The sporadic appearance and scarcity of *A. margalefi* adults made it impossible to describe the seasonal trend. Prosome lengths never exceeded 0.60 mm in this species, and means were as low as 0.52 mm (±0.042) in females and 0.54 mm (±0.034) in males during September.

Comparisons of prosome lengths with temperature were made using correlation analysis on data collected on the same date. As lengths and weights of the older stages of copepods depend on their temperature history, analysis was also carried out regressing prosome length against temperature measured on the previous sampling date (i.e. typically 2 or 4 wk before). Correlations between concurrent temperature and prosome length data were not significant (p > 0.05) in all cases for all stages and sexes (Table 1), although in many cases there were significant relationships. In all cases where the relationship was significant the slope was negative, i.e. mean prosome length decreased with increasing temperature. Often the relationship between prosome length and temperature on the previous sampling occasion was more highly significant than the relationship with the concurrent temperature.
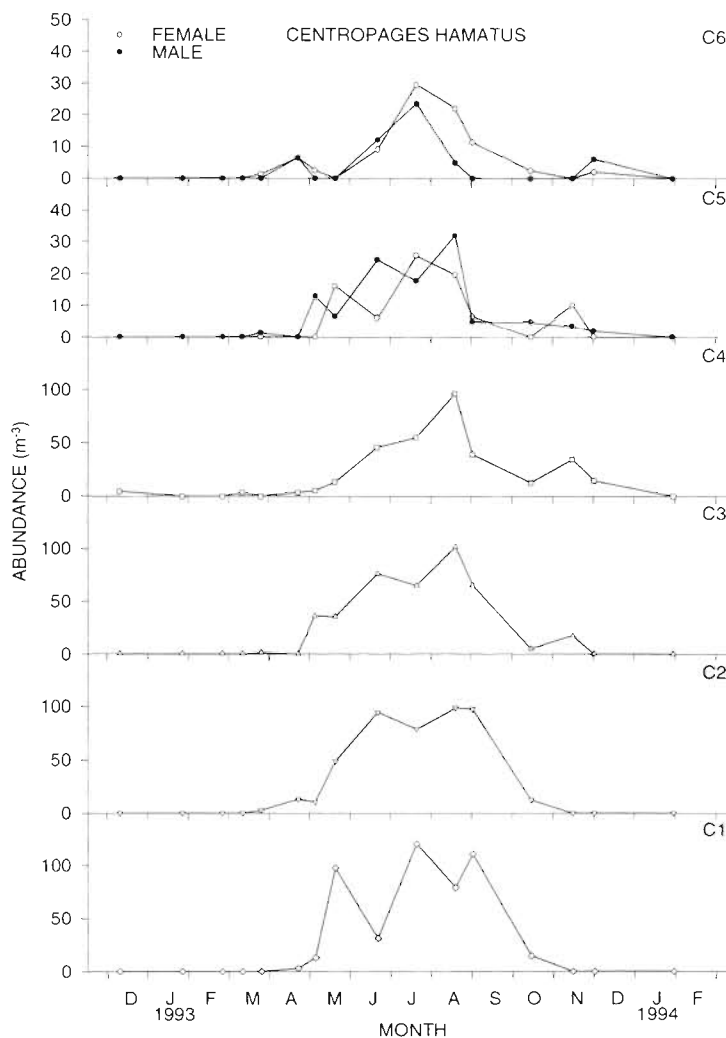

Fig. 4. Abundance of *Centropages hamatus* (C1 to C6) over the 14 mo investigation (note scale change)

Biomass and production

Acartia spp. was the single most dominant group in terms of biomass throughout much of the year (Fig. 2c), typically having greater biomass than all the other calanoids together. The *Para-Pseudocalanus* group and *Centropages hamatus* had higher biomass than *Acartia* spp. in winter, and the biomass of *C. hamatus*, and also *Temora longicornis*, was higher in May and June. *Acartia* biomass was at its highest in early May when it reached 1508 µgC m^{-3}, and in August when it reached 1144 µgC m^{-3}. *C. hamatus* biomass increased from February, when no individuals were found, to the end of July when its biomass reached its maximum at 541 µgC m^{-3}. There were 3 discrete peaks of *T. longicornis* biomass, in April (273 µgC m^{-3}), in May (1021 µgC m^{-3}) and in July (365 µgC m^{-3}). *Para-Pseudocalanus* biomass was highest in October, at
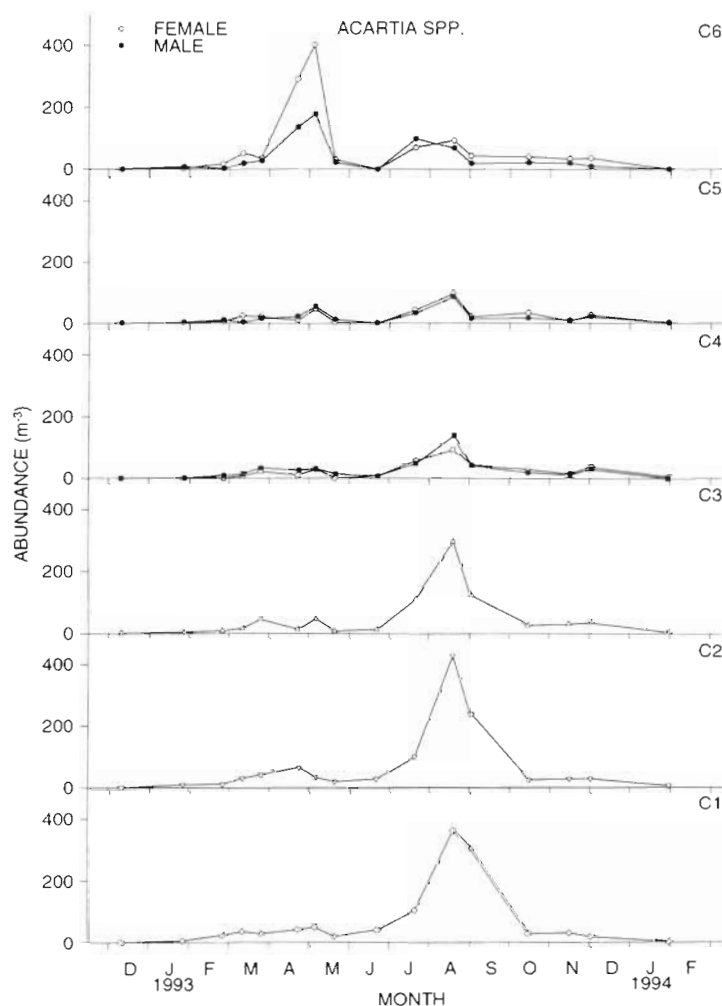
Fig. 5. Abundance of *Acartia* spp. (C1 to C6) over the 14 mo investigation

215 µgC m⁻³. Total calanoid copepod biomass was lowest in January at <1 µgC m⁻³, then increased until May when it reached 1772 µgC m⁻³. There was a subsequent fall, with a mid-year low in June, after which it rose once again reaching 1818 µgC m⁻³ in July. Although biomass fell after this point values were above 400 µgC m⁻³ until after early December 1993.

The contribution of each of the calanoid copepods to the total annual production varied dramatically (Fig. 9, Table 3), and was predominantly a reflection of their total biomass dominance. *Acartia* spp. had the highest annual production of 17.62 mgC m⁻³ yr⁻¹, *Centropages hamatus* had an annual production of 8.16 mgC m⁻³ yr⁻¹, while *Temora longicornis* had an annual rate of 4.77 mgC m⁻³ yr⁻¹ The *Paracalanus parvus* and *Pseudocalanus elongatus* group had the smallest contribution at 1.67 mgC m⁻³ yr⁻¹. The sum of these components gave a total annual production by the calanoid copepods of 32.2 mgC m⁻³ yr⁻¹.

DISCUSSION

Abundance patterns

In the present investigation calanoid numbers and biomass at the Calshot site were dominated by just 7 species; *Acartia clausi*, *A. bifilosa*, *A. tonsa*, *Centropages hamatus*, *Temora longicornis*, *Paracalanus parvus* and *Pseudocalanus elongatus*. Although there has been some confusion over the morphology and classification of *A. bifilosa* and its varieties, the description of the individuals from this area has been documented by Hirst & Castro-Longoria (1998) as part of a detailed examination of its classification.

Acartia tonsa accounted for up to 4% of the total *Acartia* population abundance at a single point in time at Calshot in a previous study (Conover 1957). It was not found during the present study, but it is still found in reduced salinity areas of the river Test (Castro-Longoria 1998). Its sporadic appearance may be the result of inter-annual changes in physical parameters such as temperature and salinity, or the degree of estuarine flushing. As *A. margalefi* is morphologically similar to *A. clausi*, and was only described recently by Alcaraz (1976), it is not surprising that it was not reported in this area until the 1990s (Castro-Longoria & Williams 1996). When both of these species occurred together here, *A. margalefi* always had a mean prosome length between 66% and 72% that of *A. clausi*, this was one of the most obvious differences between the 2 species.

Of the *Acartia* species, *A. bifilosa* was numerically dominant during January to May; *A. discaudata* and *A. clausi* were co-dominant from July to September, and then *A. clausi* was dominant until December (with *A. discaudata* still the second most abundant). After December *A. discaudata* became dominant (Fig. 6). The successional pattern described by Conover (1957) during October 1954 to June 1955, for a site at the entrance to Southampton Water, was similar to that found in the present investigation. Conover (1957) found *A. clausi* and *A. discaudata* were the co-dominant *Acartia* species over the winter months of November to January, after which *A. bifilosa* became dominant. From May, *A. clausi* was again the most abundant *Acartia* species. It is of interest to compare our results with those of Raymont & Carrie (1964) collected in the 1950s, at a site not more than 2.5 km from the current site, using a pump and hose system with screening onto a No. 10 nylon net (i.e. ~135 µm mesh;
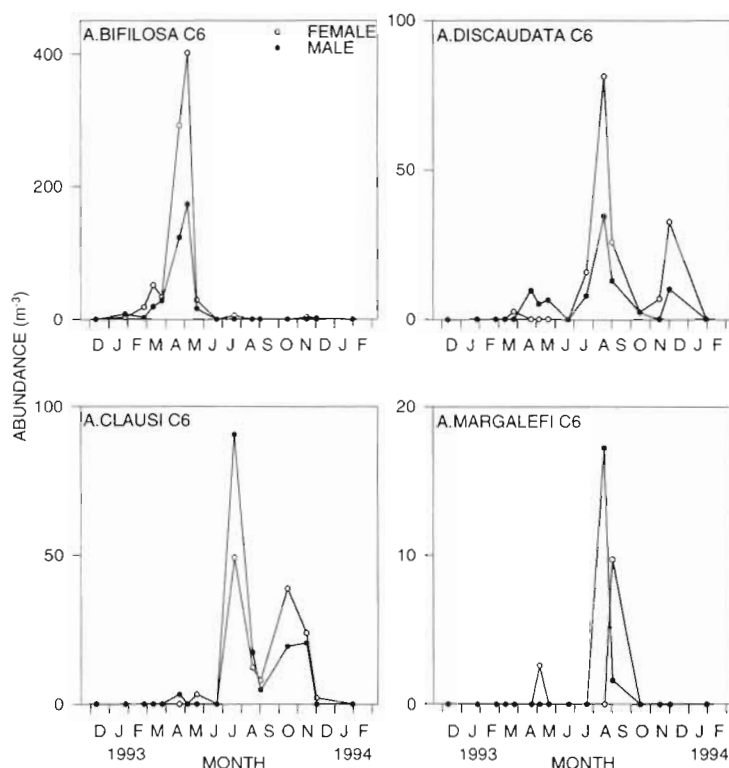
Fig. 6. Abundance of the adult *Acartia* species found at the Calshot site (note scale change)

and 1959, but 5000 ind. m⁻³ in 1956 and 1958. In 1993 the calanoid peak in spring was 1065 ind. m⁻³, with maximum annual numbers in August of 2155 ind. m⁻³. Raymont & Carrie (1964) found mean densities of calanoids between September and December to vary between 433 and 1263 ind. m⁻³; in the present investigation average calanoid copepodite numbers during the same period fell between this range at 900 ind. m⁻³.

Seasonal variations in size

Seasonal variations in size and weight have often been recorded in marine invertebrates including copepods. Copepod body sizes, as in the current investigation, are usually inversely related to temperature in nature (Uye et al. 1982, Liang & Uye 1996). Regressions of prosome lengths, for each separate stage and sex, against temperature were carried out for each of the species at Calshot. Previously, such relationships have been reported to be more marked in older stages (see Uye et al. 1982, Jerling & Wooldridge 1991, Liang & Uye 1996, Liang et al. 1996), and seasonal changes in prosome length in the current investigation were also greater in many of the older stages, although for *Acartia bifilosa* and *A. clausi*, neither adult females nor males showed a significant relationship between prosome length and temperature. Changes in body size of copepods may also be positively related to food concentration (Moraïtou-Apostolopoulou 1975, Landry 1978, Evans 1981, Durbin et al. 1983, Berggreen et al. 1988, Christou & Verriopoulos 1993). In Southampton Water, as chlorophyll *a* concentrations change dramatically on a very short time scale (Kifle 1992), the changes of prosome length with chlorophyll concentration were not examined here, as these were believed not to accurately reflect any real relationships given our sampling frequency.

Pelagic carbon flux

The values for calanoid copepod production (32.2 mgC m⁻³ yr⁻¹) are included together with previous estimates of bacterial, ciliate, and size-fractioned primary production for the Calshot site in a carbon flow diagram (Fig. 9). Primary production was measured at the Calshot site from April to October 1990 using a C¹⁴ incubation technique (Iriarte & Purdie 1994), and a total annual rate of 6667 mgC m⁻³ yr⁻¹ was derived.

Heinle 1966). They reported that *Centropages hamatus* was the most dominant calanoid after the *Acartia* group. This species was reported as rare before March-April, but moderately common from May and throughout the summer. It was described as generally persisting through the autumn, and disappearing in late December. This pattern is similar to that found in the present investigation; the species was the most abundant after *Acartia* spp. *Temora longicornis* was found by Raymont & Carrie (1964) to be less common than *C. hamatus* at Calshot, and to be more restricted in timing, not appearing until April and then being plentiful until August. It was also much less common than *C. hamatus* in the autumn. Again this situation is similar to that found in the current study, with *T. longicornis* appearing in April; it was more abundant than *C. hamatus* in May, but after this the latter became more abundant. They also found *Paracalanus parvus* and *Pseudocalanus elongatus* to be sporadic in appearance at Calshot, the former species being more abundant than the latter. *P. parvus* was also found in greater densities than *P. elongatus* in the present investigation, and their appearance was certainly variable. Raymont & Carrie (1964) observed greater peak densities of calanoids over the 6 yr of their study than those found in the present investigation. They report spring maxima of around 2000 to 2500 ind. m⁻³ in 1954, 1957
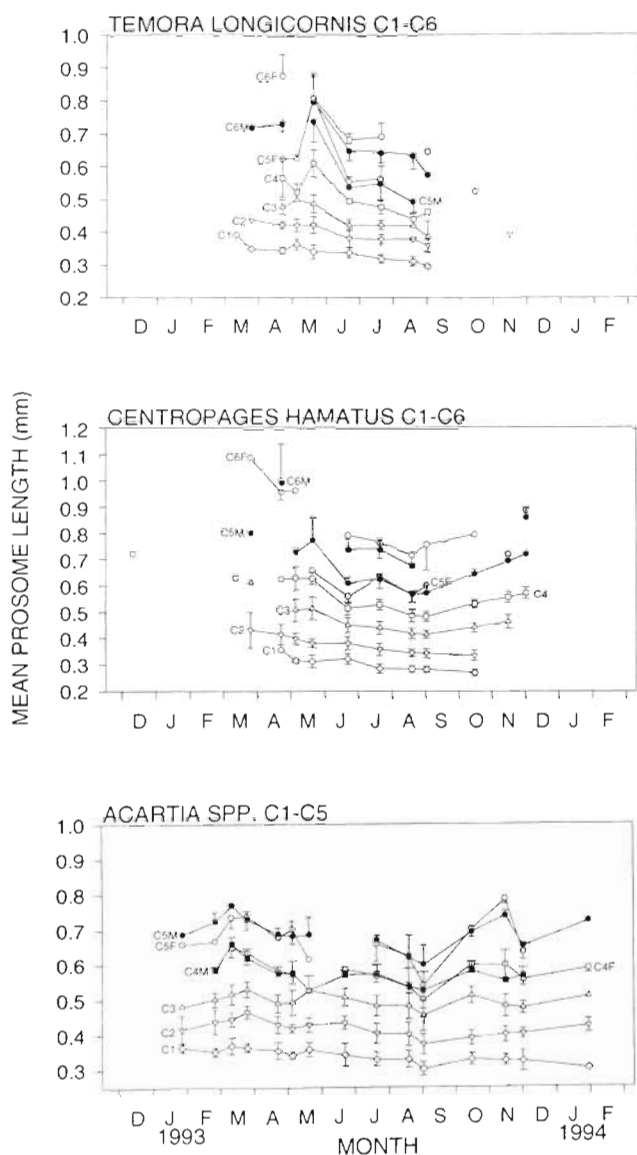
Fig. 7. Mean prosome lengths of *Temora longicornis* (C1 to C6), *Centropages hamatus* (C1 to C6) and *Acartia* spp. (C1 to C5) over the 14 mo investigation. Error bars give standard deviation of measurements, lines joining symbols are only given when individuals were found in consecutive samples
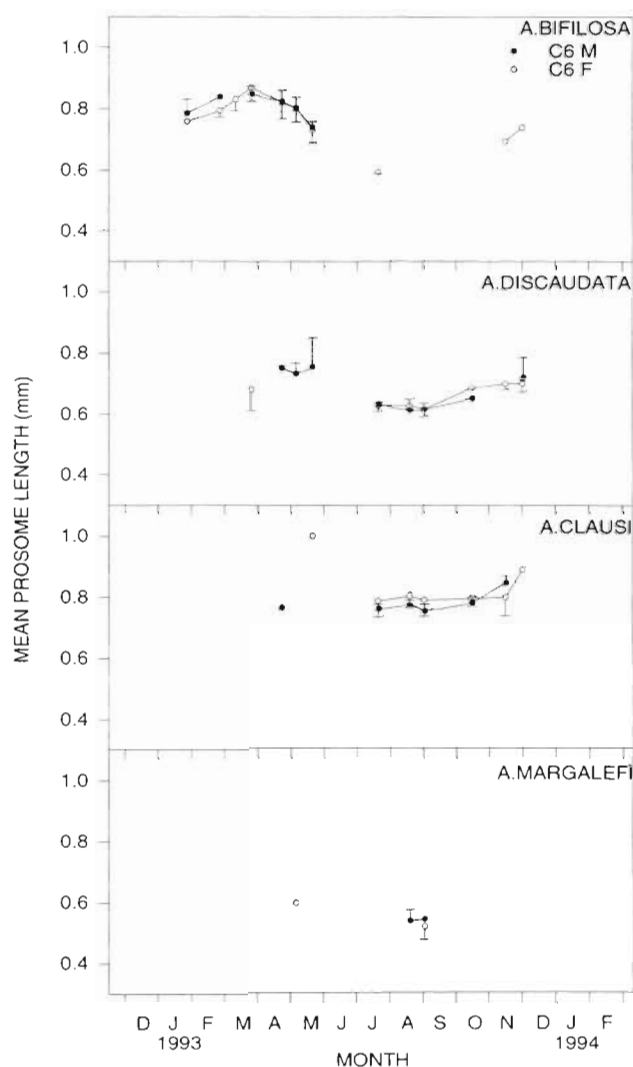

Fig. 8. Mean prosome length measurements for adult males and females of each *Acartia* species during the 14 mo investigation. Error bars represent standard deviation of measurements, lines linking symbols are only given when individuals were found in consecutive samples

Annual bacterial production was measured at Calshot from January 1987 to January 1988, and is given as 8300 mgC m^{-3} yr^{-1} (Antai 1989). The bacterial production, which exceeds primary production, may be met by additional allochthonous inputs, with a potential supply from terrestrial inputs as well as from lateral movements of material of marine or estuarine origins. Material may also recycle through the bacterial compartment so as to inflate the bacterial production value with respect to primary production. Estimates of the mean annual production of heterotrophic ciliates at

this location were derived by Leakey et al. (1992) for the period June 1986 to January 1987, using an equation that predicts ciliate growth from individual size and temperature (i.e. Montagnes et al. 1988). We have estimated the ingestion demand of ciliates from their production by assuming a gross growth efficiency (GGE) of 30% (Straile 1997). Similarly, annual ingestion demand by the copepods was derived assuming for this group a GGE of 26% (Straile 1997). This efficiency may be too high given the conditions in the estuary, where sediment and detritus concentrations are elevated.

Combining production estimates for various components collected over several years has the disadvan-

Table 1. Regression analysis of mean prosome length versus concurrent temperature and versus temperature on the previous sampling occasion. Equations are only given where the relationship is significant ($p < 0.05$). n is the number of observations, PL is the prosome length (mm), T is temperature (°C). ns: not significant

Species/stage	Concurrent temperature (°C)				Previous temperature (°C)			
	n	r^2	p	Equation	n	r^2	p	Equation
Acartia spp.								
C1	15	0.111	ns	–	14	0.180	ns	–
C2	15	0.250	ns	–	14	0.573	<0.01	PL = 0.4694 − 0.0044T
C3	15	0.086	ns	–	14	0.236	ns	–
C4F	12	0.348	<0.05	PL = 0.6435 − 0.0052T	12	0.433	<0.05	PL = 0.6502 − 0.0058T
C4M	13	0.334	<0.05	PL = 0.6314 − 0.0048T	13	0.398	<0.05	PL = 0.6401 − 0.0056T
C5F	13	0.234	ns	–	12	0.324	ns	–
C5M	14	0.478	<0.01	PL = 0.7720 − 0.0074T	13	0.545	<0.01	PL = 0.7806 − 0.0079T
Acartia bifilosa								
C6F	10	0.384	ns	–	9	0.836	<0.001	PL = 1.0122 − 0.0244T
C6M	6	0.424	ns	–	5	0.922	<0.01	PL = 0.9740 − 0.0176T
Acartia discaudata								
C6F	7	0.757	<0.05	PL = 0.7473 − 0.0064T	7	0.535	ns	–
C6M	8	0.592	<0.05	PL = 0.8396 − 0.0114T	8	0.830	<0.01	PL = 0.8759 − 0.0139T
Acartia clausi								
C6F	7	0.182	ns	–	7	0.287	ns	–
C6M	6	0.445	ns	–	6	0.200	ns	–
Centropages hamatus								
C1	8	0.500	<0.05	PL = 0.4155 − 0.0074T	8	0.913	<0.001	PL = 0.4098 − 0.0074T
C2	9	0.737	<0.01	PL = 0.4983 − 0.0085T	9	0.974	<0.001	PL = 0.4826 − 0.0079T
C3	9	0.767	<0.01	PL = 0.6813 − 0.0145T	9	0.780	<0.01	PL = 0.6702 − 0.0143T
C4	12	0.474	<0.05	PL = 0.7230 − 0.0116T	11	0.670	<0.05	PL = 0.7176 − 0.0120T
C5F	6	0.806	<0.05	PL = 0.8732 − 0.0161T	6	0.355	ns	–
C5M	10	0.640	<0.01	PL = 0.8798 − 0.0152T	10	0.714	<0.01	PL = 0.9101 − 0.0175T
C6F	9	0.651	<0.01	PL = 1.1625 − 0.0224T	9	0.843	<0.001	PL = 1.1945 − 0.0255T
C6M	5	0.561	ns	–	5	0.835	<0.01	PL = 1.1752 − 0.0284T
Temora longicornis								
C1	9	0.712	<0.01	PL = 0.4151 − 0.0056T	9	0.724	<0.01	PL = 0.4067 − 0.0054T
C2	9	0.647	<0.01	PL = 0.4797 − 0.0058T	9	0.748	<0.01	PL = 0.4729 − 0.0057T
C3	7	0.792	<0.01	PL = 0.6398 − 0.0128T	7	0.685	<0.05	PL = 0.5753 − 0.0094T
C4	7	0.738	<0.05	PL = 0.7798 − 0.0177T	7	0.560	ns	–
C5F	6	0.251	ns	–	6	0.154	ns	–
C5M	4	0.780	<0.05	PL = 1.3331 − 0.0459T	4	0.436	ns	–
C6F	5	0.976	<0.01	PL = 1.2226 − 0.0318T	5	0.773	<0.05	PL = 1.0375 − 0.0213T
C6M	7	0.522	ns	–	7	0.486	ns	–

tage that there may be inter-annual variability in the production of individual components, but this method provides a first step towards assessing the possible general importance of each of the compartments. The likely ingestion food sources for the copepods are algae >3 µm, detrital material, allochthonous inputs and ciliates. The ingestion demand of the copepods was 2.2% of the production by the >3 µm algae, while the ingestion demand of ciliates was almost 60 times greater, at 110% of total primary production. This suggests ciliates may have met their demands by ingesting material which was allochthonous to the site, although production and ingestion demands for ciliates were probably too high, because the equation of Montagnes et al. (1988) used to estimate growth was derived under conditions where food was not limiting This

may not always accurately reflect the situation in the natural environment.

Annual size fractioned primary production estimates, together with ciliate, tintinnid, bacterial and copepod production values for other shallow nearshore locations with water column depths <200 m are compiled in Table 2. These previous investigations have shown copepod annual production to be typically lower than that of ciliates (but not Uye & Shimazu 1997), although the 2 values are usually within an order of magnitude of one another, i.e. in the Gulf of Maine, USA (Montagnes et al. 1988), Lime Cay, Jamaica (Roff et al. 1990), and the Southern Kattegat (Kiørboe & Nielsen 1994, Nielsen & Kiørboe 1994). The present study is unusual in that copepod annual production and ingestion demand are very much lower

Table 2. Production rates of microbial and metazoan zooplankton populations in pelagic neritic areas of less than 200 m water column depth. Units are mgC m^{-3} yr^{-1} integrated over the entire water column depth. Values in brackets are percentage of total primary production

Primary production		Secondary production				Site	Source
Size fractioned	Total	Total ciliate	Tintinnid	Bacteria	Zooplankton		
>10 µm 9798.7 (81.0); <10 µm 2298.5 (19.0)	12097.2 (100)	132.7 (1.1)[a]	–	2419.4 (20)	176.4 (1.5)	Gulf of Maine, USA	Montagnes et al. (1988)[b]
>20 µm 2278.2 (28.5); 2–20 µm 2601.8 (32.5); <2 µm 3118.2 (39.0)	7998.2 (100)	525.1 (6.6)	59.4 (0.7)	1199.7 (15)	878.4 (11.0)[c]	Lime Cay, Jamaica	Roff et al. (1990)[b]
>10 µm 19250 (50.0); <10 µm 19250 (50.0)	38500 (100)	–	3300 (8.6)	–	4745 (12.3)[d]	Narragansett Bay, USA	Verity (1987)
	10357 (100)	2036 (19.7)	–	–	429 (4.1)[e]	Southern Kattegat	Kiørboe & Nielsen (1994), Nielsen & Kiørboe (1994)
	8742 (100)	896 (10.2)[e][f]	–	–	1589 (18.2)[g]	Inland Sea of Japan	Uye & Shimazu (1997)
>3 µm 5520 (82.8)[h]; 1–3 µm 727 (10.9)[h]; <1 µm 420 (6.3)[h]	6667 (100)[h]	2200 (33.0)[a]	333 (5.0)[f]–624 (9.4)[k]	8300 (124.5)[l]	32.2 (0.5)[e]	Calshot, Solent, UK	This study

[a] Montagnes et al. (1988) equation used to estimate growth rates

[b] Phytoplankton kJ converted to carbon assuming 1 mgC = 0.055 kJ [calculated from Richman (1958), and assuming 1 g phytoplankton = 15.8 kcal (Platt 1971)] and 1 kcal = 4.1855 kJ. Ciliate and tintinnid values were converted from kJ to mgC by assuming 20.15 J per mgDW (Finlay 1978), 0.17 g DW (ml cell volume)$^{-1}$ (Laybourn & Finlay 1976) and that 1 ml protoplasm contains 0.071 gC (Fenchel & Finlay 1983)

[c] Zooplankton production was summed for all metazoans, excluding carnivores, miscellaneous crustacea, chaetognaths, coelenterates and fish groups. The total was converted from kJ assuming 1 gDW = 6 kcal (Tremblay & Roff 1983), 40 % of DW is carbon (Omori & Ikeda 1984, Båmstedt 1986), and 1 kcal = 4.1855 kJ

[d] Annual zooplankton production rate was derived from the average daily copepod production rate (i.e. *Acartia hudsonica* and *Acartia tonsa*, the dominant zooplankton in the estuary, derived over March to October using maximal laboratory rates) multiplied by 365

[e] Includes only planktonic copepods

[f] Includes production of microzooplankton (tintinniids, naked ciliates and copepod nauplii), although crustacea are only a minor component

[g] Group defined as herbivorous or suspension feeding mesozooplankton

[h] Iriarte & Purdie (1994)

[j] Leakey et al. (1992)
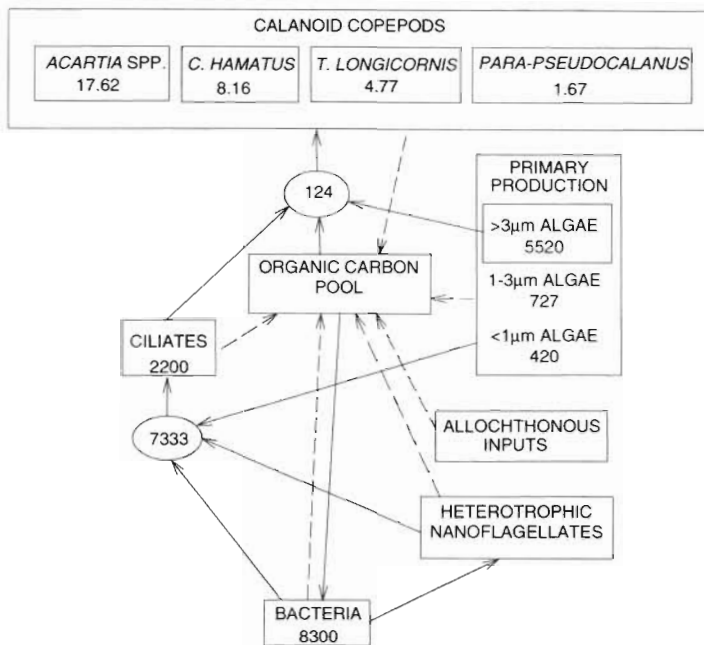
[k] Burkill (1982)

[l] Antai (1989)

Fig. 9. Pelagic carbon flux through the biological community at the Calshot site; all values are integrated over the entire water column depth. Values in boxes are production estimates, those in ellipses are ingestion demands (units: mgC m^{-3} yr^{-1}). Solid arrows represent ingestion of carbon; dashed arrows represent movement to a non-living organic carbon 'pool'

than those of the ciliates. In the other shallow water neritic studies, annual production by copepods was between 21 and 177 % that of the ciliates, while at Calshot the proportion was only 1.5 %. Copepod secondary production as a percentage of total primary production is also relatively low at the Calshot site, 0.5 %. In the other studies compiled here, this value was between 1.5 and 18.2 %. A great many investigations of neritic and coastal water copepod production have demonstrated rates in excess of 100 to 1000 mgC m^{-3} yr^{-1} when integrated over total water column depth (e.g. Landry 1978, Uye 1982, Kimmerer & McKinnon 1987, Uye et al. 1987, Roff et al. 1988, McLaren et al. 1989, Chisholm & Roff 1990, Jerling & Wooldridge 1991, Kiørboe & Nielsen 1994, Escaravage & Soetaert 1995, Uye & Liang 1998); given the value was only 32.2 mgC m^{-3} yr^{-1} at the Solent site, it must be regarded as having unusually low copepod production.

Although production by nauplii is not included in the present study, this does not typically exceed 25 % of copepod total production (Mullin 1988, Laing et al. 1996, Liang & Uye 1996). The inclusion of estimates of production for meroplanktonic larvae and other holoplankton at the Calshot site would increase the mesozooplankton production value. In addition, the harpacticoid copepod *Euterpina acutifrons* made up a

significant fraction of total copepod numbers. Its abundance in the net samples was similar to that of the total calanoid abundance. As the adults of this species have a comparable weight to that of the calanoids, ~1 µgC (Conway et al. 1993), then their total biomass would have also been similar. Given the abundance of the other meroplankton and holoplankton groups (Table 3) and that they have similar body sizes, and assuming similar weight-specific growth and ingestion rates, then it is still unlikely that the role of the total mesozooplankton, either as producers or consumers, would have been more than 3.5 times greater than that of the calanoids whose mean annual abundance was 29 % of the total.

Zooplankton may not in fact be the main consumers of suspended particulate carbon (including phytoplankton) in shallow coastal areas where benthic organisms can play an important role (Williams & Collins 1986). Hirst (1996) made some estimates of macro-faunal production using data collected near Calshot during 1979 by Oyenekan (1981). Preliminary results suggested that macro-benthic production is lower than that of the calanoid copepods on an area basis. The benthic community has, however, seen a massive shift from biomass dominance by the bivalve *Mercenaria mercenaria* in 1979, to the virtual absence of this species during this zooplankton investigation (M. Sheader pers. obs.). Unfortunately no values are available for meiofaunal or microbenthos production in this area.

Table 3. Geometric mean abundance (trapezoidal integration) and range of the dominant zooplankton at Calshot during the 14 month investigation (calculated from the data of Hirst 1996)

Group	Geometric mean abundance (ind. m^{-3})	Range min–max (ind. m^{-3})
Holoplankton		
Calanoid copepodites	642.2	8.6 – 2255.2
Cyclopoid copepodites	3.1	0.0 – 19.2
Ostracods	1.2	0.0 – 6.5
Oikopleura spp.	109.5	0.0 – 1172.1
Euterpina acutifrons	650.5	0.0 – 2524.3
Meroplankton		
Cirripede larvae	432.4	52.6 – 1242.1
Polychaete larvae	40.6	4.4 – 188.7
Bivalve larvae	70.7	0.0 – 313.0
Bryozoan larvae	60.9	0.0 – 175.5
Ascidian larvae	4.6	0.0 – 30.4
Gastropod larvae	128.3	0.0 – 421.2
Harpacticoid copepodites (excluding *Euterpina acutifrons*)	59.5	4.4 – 466.5

Although the estimate of ciliate production for Calshot is at the higher end of values for studies elsewhere (Table 2), their relative dominance over copepods is more extreme at the Calshot site because of the very low production by the calanoid copepods. Growth rates for copepods were determined from an empirical relationship which provides 'typical growth rates', and the low production rates are therefore a consequence of low biomass, with the maximum biomass reaching only 1818 µgC m^{-3}. This is in contrast to other temperate estuarine and shelf waters maximum annual copepod or metazoan zooplankton biomass levels which often exceed 10 or even 100 mgC m^{-3} (Curl 1962, Durbin & Durbin 1981, Tremblay & Roff 1983, Kiørboe & Nielsen 1994, Uye & Liang 1998). Williams & Collins' (1986) 12 mo investigation of the Bristol Channel (UK) did, however, give comparable maximum biomass levels, with the inner channel holoplankton biomass reaching an annual maximum of ~1800 µgC m^{-3}, and when including meroplankton the total biomass did not exceed 2800 µgC m^{-3}.

The question must be posed as to why copepod biomass and abundance were so low at the Calshot site while chlorophyll levels were high, typically >2 µg l^{-1}. There are several plausible reasons which may, acting in unison, bring about the untypical situation. Certainly flushing rates from the Solent are high, and whereas microbial populations have high rates of growth and hence are better able to cope with population loss, the low biomass presented by the calanoid copepods may be a direct consequence of an environment with high flush out. Information on the physics of the Solent is generally sparse, but the net change in tidal volume (i.e. the change in water volume between high and low water) for the Solent has been estimated at 540 × 10^6 m^3 and 270 × 10^6 m^3 for typical spring and neap tides respectively (Blain 1980). The annual inflow of freshwater to the Solent has been computed to be of the order 10^9 m^3, which is equivalent to 1.4 × 10^6 m^3 per tidal cycle but varies considerably depending upon time of year. Tidal streams in the Solent to the west of Calshot are up to 4 knots, and to the east 2.5 knots (Webber 1980). There are no estimates of flushing time for the Solent although for Southampton Water estimates range from 3 to 5 d in winter and 20 d in summer (see Zinger 1989), this could result in major population losses. Species of the families Acartiidae, Temoridae and Centropagiidae all produce resting eggs which can survive deposition in the sediments (Uye 1985), and these eggs may be the major contributors to the new population following winter (Marcus 1984). Winter residual population levels have been implicated as having significant control over the potentially achievable abundances later in the year (Roff et al. 1988), and loss during winter may be particularly important. The

tides are strong in the area, and ebb tides are stronger than flood tides so that re-suspension of sediments could result in major washout of over-wintering eggs.

Measurements of suspended particulate matter within the mouth of the estuary were taken over the period May 1994 to May 1995 (Hirst 1996). Dry weight values of SPM were fairly constant at around 40 mg l^{-1}, while the ash weight of SPM was typically ~10 mg l^{-1}. It has previously been suggested that suspended seston of low food value could disrupt feeding, or reduce the feeding or digestion efficiency in some manner (Burkill & Kendall 1982). High suspended sediment concentrations have been shown to reduce the total survival of Acartia tonsa nauplii, as well as inhibiting development rate and fecundity of survivors (Sellner et al. 1987), while Calanus helgolandicus has reduced growth, reduced survival, lower stage weights and reduced ovary development rates under conditions of high sediment concentrations (Paffenhöfer 1972). Irigoien & Castel (1995) described important effects of suspended particulate on the feeding and growth success of A. bifilosa in a turbid estuarine environment, and although the values of chl a/SPM found by Hirst (1996) were generally higher (and therefore assumed not to be as inhibiting), they did fall to levels which can be considered to result in reduced growth rates.

Southampton Water is highly industrialised, the city of Southampton is to the north, and major chemical and oil refineries are based on the western shore of Southampton Water. In the mid to late 1980s, levels of non-volatile petroleum hydrocarbons (PHC) in sea water from the main Southampton Water channel ranged between ~40 and 500 µg l^{-1}, while in sediments they were between 80 and 1200 µg (g sediment dry weight)$^{-1}$ (Bianchi 1993). The viability of copepod eggs deposited in marine sediments has been linked to the degree of hydrocarbon pollution in that sediment (Lindley et al. 1998), and waterborne concentrations of ~100 µg l^{-1} total oil have been found to lead to dramatic reductions in viability of calanoid copepods in large enclosures (Davies et al. 1980). Oil concentrations below 1000 µg l^{-1} produce sub-lethal responses by zooplankton under laboratory conditions, and sub-lethal damage may occur when exposure is for days or weeks at oil concentrations between 50 and 300 µg l^{-1} (NRC 1985). If hydrocarbon levels in the area at the time of our investigation were similar to those in the 1980s then they are certainly within the range which would have adversely affected the local zooplankton.

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