

The seasonal abundance and production of *Oithona nana* (Copepoda:Cyclopoida) in Southampton Water

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Recent studies indicate that Oithona spp. contribute significantly to total copepod biomass. Little is known, however, about their ecological significance, particularly in the case of the estuarine Oithona nana. A study comprising three sites within Southampton Water was conducted to evaluate the late-stage copepodite/adult (stages IV–VI) O. nana community, using 120-µm mesh nets. Although present throughout the estuary, there was a striking spatial gradient with O. nana most common in the upper estuary. A clear seasonal pattern was observed with O. nana as the most abundant copepod species from late summer until early winter. It comprised 61% of all copepods recorded, with a biomass of 757.22 mg C m⁻³. Production estimates of O. nana were derived from the ‘instantaneous-growth’ approach, using appropriate growth equations. The estimated production of O. nana ranged from 1.50 mg C m⁻³ year⁻¹ within the lower estuary to 146.77 mg C m⁻³ year⁻¹ in the upper estuary. In the upper estuary, this compares with production rates of 187.47 mg C m⁻³ year⁻¹ for all Acartia congeners (excluding nauplii), the most common calanoid genus. Throughout the estuary, O. nana annual production represented 18% of total copepod production clearly indicating that, at least in the upper estuary, O. nana production may be directly comparable with calanoid production.

INTRODUCTION

Southampton Water is a shallow, partially mixed coastal plain estuary (Dyer, 1973) located on the south coast of England (Fig. 1a). It is essentially marine in character, with little or no salinity variation near the mouth (~30). Stratification occurs mostly at the head of the estuary, where salinity values between 11 and 32 can be found (Hirst, 1996; Muxagata *et al.*, 2004). Water temperature within Southampton Water varies seasonally, with winter minima of <7°C and summer maxima of >17°C (Howard *et al.*, 1995; Hirst, 1996).

Several authors have described the mesozooplankton populations of Southampton Water highlighting aspects of the basic spatial and temporal patterns of the major groups of mesozooplankton; for chronology, see the work of Muxagata (Muxagata, 2005). Hirst *et al.* (Hirst *et al.*,

1999) and other authors (Zinger, 1989; Lucas, 1993; Hirst, 1996; Castro-Longoria, 1998) reported the mesozooplankton to be dominated by calanoid copepods of the genus *Acartia* for most of the year, with nauplii of *Balanus crenatus* and *Elminius modestus* numerically dominating during short periods in early spring (March–April) and summer (July–September), respectively (Muxagata *et al.*, 2004; Muxagata, 2005). Only Raymont and Carrie (Raymont and Carrie, 1964) and Castro-Longoria (Castro-Longoria, 1998), however, give some information on community structure in the upper reaches of this estuary, but they employed sampling devices that either under-sampled or missed the overall contribution of some components. The only assessment of copepod production within Southampton Water was conducted around Calshot, at the mouth of the estuary

(Fig. 1), and annual production of calanoid copepods, sampled using a 118- μm net, was estimated at $32.2 \text{ mg C m}^{-3} \text{ year}^{-1}$ (Hirst *et al.*, 1999). This was acknowledged to be relatively low compared with other copepod studies, and relative to both annual primary production (Iriarte and Purdie, 1994) and annual heterotrophic ciliate production (Leakey *et al.*, 1992).

There is now a growing body of information for coastal marine ecosystems on both the numerical importance of cyclopoid copepods, particularly the genus *Oithona*, and also their relative importance compared with calanoid copepods (Nielsen and Sabatini, 1996; Gallienne and Robins, 2001; Hansen *et al.*, 2004; Turner, 2004). Their range of natural diet, reported to include phytoplankton and raptorial consumption of copepod early stage nauplii and some copepodites (Lampitt, 1978; Lampitt and Gamble, 1982), calanoid faecal material (González and Smetacek, 1994) and some ciliates and dinoflagellates (Nakamura and Turner, 1997), also points to their potential role in pelagic carbon flux. There is still, however, relatively limited information on their ecological significance.

There are only a few occasions when cyclopoids have been reported in Southampton Water, with *Oithona similis* first identified (Raymont and Carrie, 1964; Hirst, 1996). More recently, Castro-Longoria (Castro-Longoria, 1998) provides the only information on *Oithona nana*, recording numerical abundance in the upper estuary with a seasonal peak in July (1507 individuals m^{-3}) and elevated numbers in autumn and winter, and lowest abundance in spring with 18 individuals m^{-3} . This study used a 210- μm net and acknowledges that actual numbers would be higher. Very small numbers, <1.0 individual m^{-3} , of *O. similis* were also recorded in winter. *Oithona nana* is a widespread neritic species (Digby, 1950; Lampitt, 1979; Ryan *et al.*, 1986; Paffenhöfer, 1993). It has been extensively reported in estuarine 'small' mesh sampling ($<200 \mu\text{m}$) (Reeve, 1975; Hopcroft *et al.*, 1998) although, because of its small size, it is consistently underestimated (Reeve, 1975; Hopcroft *et al.*, 1998; Gallienne and Robins, 2001; Hansen *et al.*, 2004).

In order to clarify the role of *O. nana* within Southampton Water, this article sets out to describe the spatial-temporal distribution of late-stage copepodite (IV and V) and adult (copepodite stage VI) *O. nana*. Biomass and production are estimated and compared with estimates of the major Southampton Water calanoid genus *Acartia*, to establish the relative importance of the potentially recent occurrence of *O. nana* for copepod secondary production through the estuary.

MATERIALS AND METHODS

As part of a major mesozooplankton-sampling programme between January 2001 and July 2002, a total of 108 samples were collected at three fixed buoy sites within Southampton Water (Fig. 1a). To minimize the effects of tidal influence, the sites were sampled on the same day during the extended 2–3 h period of slack water between the double high-tide patterns of Southampton Water (Dyer, 1973). Sampling frequency at Cracknore and Calshot reflected a timescale comparable with the egg-to-adult development time (generation time) of the species, and sampling was carried out three to four times a month during spring and summer. In contrast, winter and autumn samples were collected one to two times monthly. Sampling at NW Netley station started in March 2001, and was only monthly until October 2001, and then at the same frequency as the other sites.

Mesozooplankton samples were collected from quantitative, 5-m double oblique tows using conventional cod-end plankton nets of 120- μm mesh. Towing times varied according to season, but the sampled volume, on average, was $\sim 50 \text{ m}^3$ on each tow. All samples were preserved in 4% formaldehyde-seawater buffered with borax (Steedman, 1976) until processing. Concurrent temperature and salinity measurements were recorded at 1 m depth intervals. Replicate water samples were collected from surface and 2 and 8 m depths for chlorophyll *a* (Chl *a*) analysis.

Subsamples between 0.39 and 12.5% of the original sample were made. Copepods were identified as species and categorized as adults and copepodites, and all nauplii were combined. The counting error was based on the number of all individuals counted following a Poisson distribution (Postel *et al.*, 2000) and averaged $\pm 10\%$ for all samples.

Adult (VI) and late-stage (IV and V) copepodites of *O. nana* were combined together as a single value for biomass and production estimates. Annual production estimates were derived using the 'instantaneous-growth' approach and using a number of growth equations. *Oithona nana* was considered to have a mean weight of $0.54 \pm 0.07 \mu\text{g}$ dry weight (DW) obtained after weighing replicated samples ($n = 11$), each containing 100–2500 individuals, irrespective of stage. This was acknowledged to potentially introduce some error, as both stage size and individual size may vary with season. Regarding the striking seasonal signal of *O. nana* and the way the raw abundance data were combined, this procedure was considered acceptable. To enable comparison with other production values, we estimated a range of growth rates from equations proposed by Huntley and Lopez

Southampton Water

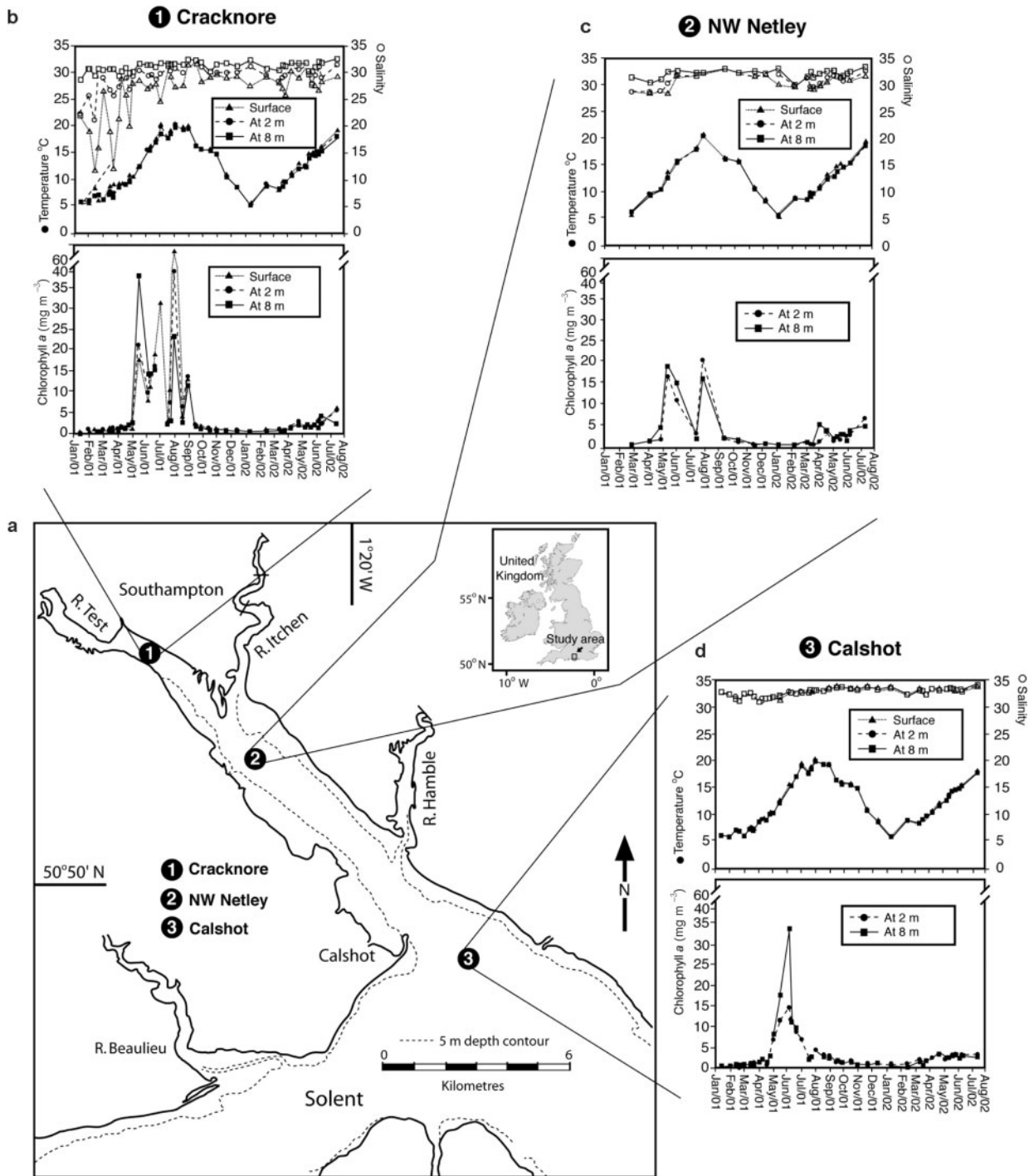


Fig. 1. Southampton Water: the seasonal (2001/02) temperature, salinity and chlorophyll *a* profiles at Cracknore (1), NW Netley (2) and Calshot (3) sampling stations.

(Huntley and Lopez, 1992), Hirst and Lampitt (Hirst and Lampitt, 1998), Hirst and Bunker (Hirst and Bunker, 2003) and Hirst *et al.* (Hirst *et al.*, 2003). Considering

that abundance values were from combined values of late copepodite and adult stages, the equations selected (Table I), best accommodated the data. Production

Table I: Production equation and equations used to estimate *Oithona nana* growth

$\Sigma P = B \times g$		
Growth equation	Stage applied to	Reference
(a) $g = 0.0445 \times e^{0.111 \times (T)}$	All	Huntley and Lopez (1992)
(b) $\text{Log}_{10}(g) = -1.1408 + [0.0208 \times (T)] - [0.3221 \times \text{log}_{10}(w_{ic})]$	Br + S (adults + juveniles)	Hirst and Lampitt (1998)
(c) $\text{Log}_{10}(g) = -1.7255 + [0.0464 \times (T)]$	S (adults + juveniles)	Hirst and Lampitt (1998)
(d) $\text{Log}_{10}(g) = -1.591 + [0.0182 \times (T)] + [0.193 \times \text{log}_{10}(w_{ic})] + [0.195 \times \text{log}_{10}(\text{Chl } a)]$	S (adults)	Hirst and Bunker (2003)
(e) $\text{Log}_{10}(g) = -1.528 + [0.0333 \times (T)] + [-0.163 \times \text{log}_{10}(w_{ic})]$	S (juveniles)	Hirst and Bunker (2003)
(f) $\text{Log}_{10}(g) = -1.209 + [0.0186 \times (T)] + [-0.288 \times \text{log}_{10}(w_{ic})] + [0.417 \times \text{log}_{10}(\text{Chl } a)]$	All data	Hirst and Bunker (2003)
(g) $\text{Log}_{10}(g) = -1.529 + [0.0345 \times (T)] - [0.128 \times \text{log}_{10}(w_{ic})]$	All Br + S	Hirst <i>et al.</i> (2003)

P, average production of a particular size class/stage in mg dry weight m⁻³ day⁻¹; *B*, biomass (i.e. $N_i \times w_i$); N_i , number of organisms m⁻³ at stage *i*; w_i , the average dry weight at stage *i* (in µg individual⁻¹); *g*, growth rate day⁻¹ (for adults it is considered as the specific egg/spermatophores production rate day⁻¹); Chl *a*, chlorophyll *a* concentration (mg Chl *a* m⁻³); w_{ic} , the average carbon weight at stage *i* (in µg individual⁻¹); *T*, temperature in °C; Br, broadcast-spawners; S, sac-spawners.

calculated using the appropriate growth equations of Hirst and Bunker (Hirst and Bunker, 2003), which incorporate body weight, temperature and Chl *a*, was selected to illustrate the daily contribution of *O. nana* at each station and also that of *Acartia* spp., the main calanoid component of the estuary. Calculated daily production and biomass for a particular sample date were considered to be the mean of the time interval between the two successive midpoints of the inter-sample period. Conversion to carbon assumed a DW/carbon ratio of 0.4 (Omori and Ikeda, 1992; Postel *et al.*, 2000).

Fluorometric determination of Chl *a* (Welschmeyer, 1994) was used. Differences between Chl *a* replicates varied, and the average error for all measurements, calculated as a percentage of the mean, was ± 3.9 %. Owing to the oblique zooplankton tows used, water column temperature, salinity and Chl *a* data for each tow were averaged before statistical analysis.

Pearson's product-moment correlation coefficient *r* was used to measure the intensity of the association between the biotic and abiotic variables. To stabilize the variance of the data, we log₁₀(*x* + 1) transformed *O. nana* abundance, biomass and production, and average Chl *a* value was log₁₀(*x*) transformed before analysis (Prepas, 1984; Zar, 1999).

RESULTS

As expected, temperature varied with season, with winter (January–March) minima, and maxima from mid-summer through to early autumn (July–September) (Fig. 1b–d). The minimum temperature recorded was 5.3°C in January 2002 and the maximum 20.4°C in August 2001. No significant difference in temperature was

recorded with depth at any site. Salinity did not show any clear seasonal variation but showed an increasing gradient towards Calshot (Fig. 1d). There was some vertical stratification at NW Netley and particularly at Cracknore, where the lowest salinity values were recorded (Fig. 1b and c). Southampton Water therefore divides into two distinct zones, a well-mixed zone with almost no temperature and salinity variation with depth generally found at mid-estuary and more established towards Calshot at the mouth of the estuary. In contrast, a weak/partially stratified zone, with some surface temperature and salinity stratification, was usually found at the head of the estuary at Cracknore and also detected towards mid-estuary at NW Netley (Fig. 1b–d).

In winter, Chl *a* at all three sites was typically <2 mg m⁻³ (Fig. 1b–d). After May, and until the end of August, the concentration increased averaging 15 mg m⁻³ at Cracknore, 13 mg m⁻³ at NW Netley and 8 mg m⁻³ at Calshot, with a more sustained Chl *a* signal recorded up the estuary. In September, concentrations returned to levels <2 mg m⁻³. Chl *a* was essentially uniform with depth, but during May through to September the concentrations were usually higher in the upper layers.

Copepod abundance varied with season, with the lowest values recorded during winter. Generally, abundance starts to increase at all three sample sites from early spring, reaching maximum values during the summer (Fig. 2). The majority of copepods identified were holoplanktonic, and differences in abundance between sites were clear, with Cracknore having the highest abundance, followed by NW Netley and Calshot, respectively. In terms of total numerical dominance, calanoids, with an average of 2608 individuals m⁻³ for all sites over the survey period, were followed by copepod nauplii (2243 individuals m⁻³) and cyclopoids (1891 individuals m⁻³).

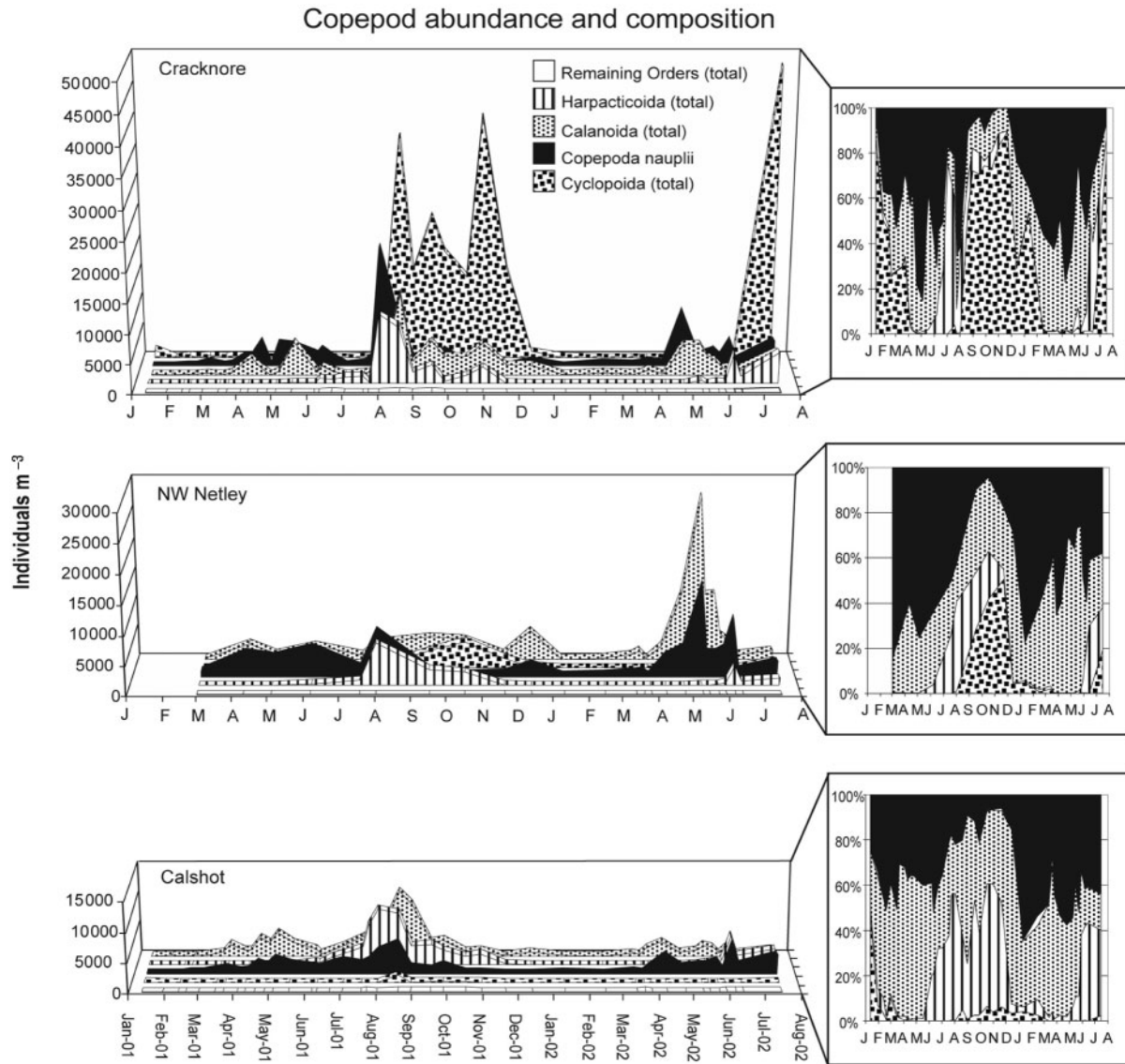


Fig. 2. Temporal composition and abundance of the different copepod orders at Southamton Water sampling stations.

Nauplii and calanoids, with *Acartia* spp. averaging 93% of the calanoids, were the most common groups in the estuary at any period, and particularly during winter and spring (Fig. 2).

Oithona nana was found all year round at the three sites, especially during summer and extending until early winter. *Oithona nana* accounted for 99.9% of all cyclopoids recorded in Southampton Water and occurred in 77% of all samples and represented 18.9% of the total copepods sampled throughout the estuary. It was recorded in high numbers only within the upper reaches, where it was the dominant copepod species at Cracknore over the sample period, occurring in 90% of samples and accounting for

50% of all copepods. From late summer until late autumn, *O. nana* accounted for 61% of all copepods found in the zooplankton at Cracknore and averaged 18 192 individuals m^{-3} (3.93 mg C m^{-3}). Peaks of 36 916 (7.97 mg C m^{-3}), 23 880 (5.16 mg C m^{-3}) and 40 092 individuals m^{-3} (8.66 mg C m^{-3}) were recorded in August, September and October/November 2001, respectively, and 48 199 individuals m^{-3} (10.41 mg C m^{-3}) in July 2002 (Fig. 3a). This high abundance starts to decline by November/December, reaching winter–spring low values around January/February.

At NW Netley and Calshot, *O. nana* showed the same general seasonal pattern but accounted, numerically, for

Abundance, biomass and production of *Oithona nana* in Southampton Water

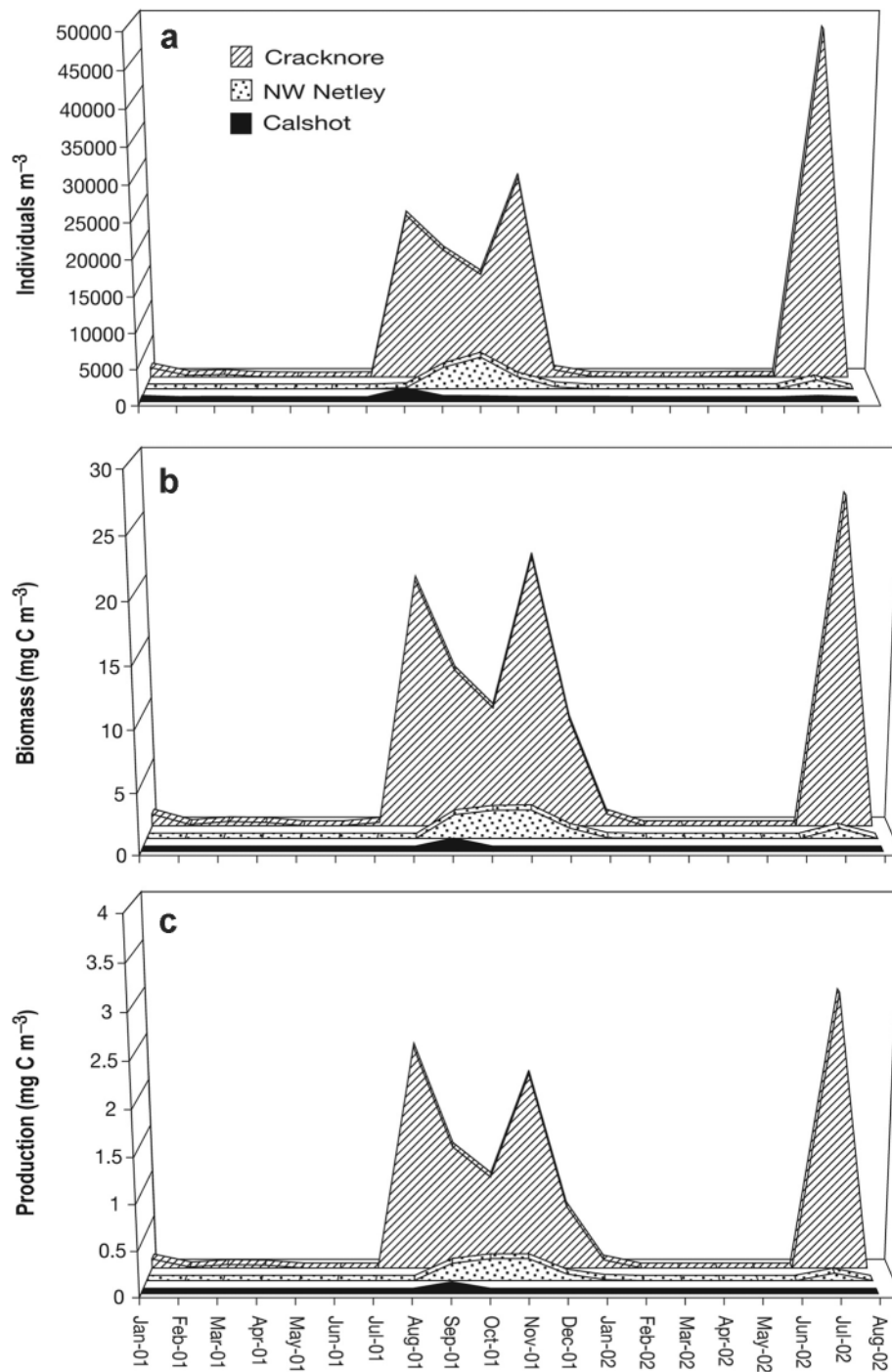


Fig. 3. Temporal variability of *Oithona nana* abundance (a), biomass (b) and production (c) at Southampton Water sampling sites.

only 5.4 and 1.4% of the total copepods and 96.8 and 99.5% of all cyclopoids (Fig. 3a). From late summer until late autumn, it averaged 1970 (0.43 mg C m⁻³) and 236 individuals m⁻³ (0.05 mg C m⁻³), representing 25.2 and 3.4% of the copepods at NW Netley and Calshot, respectively.

The total seasonal biomass of *O. nana* was 757.22, 76.34 and 8.64 mg C m⁻³ for Cracknore, NW Netley and Calshot, respectively, and the daily contribution at each site is illustrated in Fig. 3b. Estimated production of *O. nana* based on abundance, biomass and a range of growth rate approaches is summarized in Table II. Production estimates derived from growth equations specifically directed at sac-spawners clearly result in lower estimates than more generic equations combining both brood- and sac-spawners, irrespective of the complexity of the equation (Table II). Equally, estimated production using equation (a), that provides an approximation to food satiated rates, gives a higher value to that of the equivalent, but more sophisticated model (f), which incorporates a variable feeding (Chl *a*) parameter. Considering the original compilation of *O. nana* abundance values in this study, with late-stage copepodites and adults summed, and the sophistication of the growth models (Table I), growth equation (f) best approximates the daily contribution of *O. nana* at each station (Fig. 3c). The overall annual production for the three stations was calculated as 161.75 mg C m⁻³ year⁻¹ (Table II).

The numbers of *O. nana* recorded at Cracknore during this study represented 50% of total copepods and gave an estimated production equivalent to 146.77 mg C m⁻³ year⁻¹ (Fig. 3c). This value is 74% of that calculated for *Acartia* spp. (187.47 mg C m⁻³ year⁻¹) for the same period and sampling site, and using equivalent growth equations. *Acartia* spp. represented, in turn, 18% of the total copepods and 96% of the calanoids. In contrast, the relative importance of *Oithona* in the lower estuary, where it accounted for only 1.4% of the total copepods at Calshot, is indicated by a production of only 1.50 mg C m⁻³ year⁻¹, or 1.4% of that of the *Acartia* spp. 105.8 mg C m⁻³ year⁻¹.

Physicochemical parameters together with potential food sources, copepod nauplii and *Acartia* copepodites, were analysed as forcing variables of *O. nana* distribution

(Table III). The negative correlation between *O. nana* and Chl *a*, together with the positive correlation with early copepodite stages, may indicate a dietary relationship for late summer *O. nana* in Southampton Water.

DISCUSSION

The seasonal pattern of temperature, salinity and Chl *a* found during this investigation agrees with values reported during other studies at these sites and within the estuary (Zinger, 1989; Lucas, 1993; Hirst, 1996) and highlights the potentially productive nature of Southampton Water. There is a clear and numerically significant presence of *O. nana* within the upper estuary, with a progressive decrease in abundance towards the mouth of the estuary (Figs 2 and 3). *Oithona nana* is a widespread neritic species, and the late summer pattern of occurrence observed in Southampton Water is similar to that previously reported. Despite the use of a 120- μ m mesh in the present study, the abundance of *O. nana* recorded (Fig. 3a) compares with the 5000 individuals m⁻³ reported by Ryan *et al.* (Ryan *et al.*, 1986) using a 90- μ m mesh, where *O. nana* was considered the most abundant copepod in the Irish inlet of Killary Harbour. Abundance levels of 112 individuals L⁻¹ were reported for *O. nana* in the lower Westerschelde using a 55- μ m mesh during late summer and autumn (Soetaert and Van Rijswijk, 1993). In contrast, *O. nana* was recorded as relatively constant throughout the year in a Mediterranean hypersaline lagoon (Gilbert, 2001), although it did contribute significantly to a 'massive proliferation of copepods' in winter. Other studies have reported oithonids to show a similar seasonal cycle, with *O. similis* contributing significantly to total copepod biomass in late summer through winter in the North Sea (Hay *et al.*, 1991) and Kattegat (Kjørboe and Nielsen, 1994), and *Oithona davisae* and *O. similis* occurring during

Table II: Annual production estimates (in mg C m⁻³ year⁻¹) of *Oithona nana* at sites in Southampton Water, using the growth equations summarized in Table I

Equation	Cracknore	NW Netley	Calshot	Total
(a)	167.60	16.18	1.97	185.75
(b)	128.34	13.55	1.47	143.36
(c)	55.12	5.35	0.65	61.12
(d)	22.49	2.25	0.25	24.99
(e)	66.83	6.77	0.77	74.37
(f)	146.77	13.48	1.50	161.75
(g)	66.21	6.69	0.77	73.67
Average	93.34	9.18	1.05	103.57

Table III: Pearson's product–moment correlation of biotic and abiotic parameters from data collected in Southampton Water

	T (°C)	Salinity	Chlorophyll a	<i>Oithona nana</i> abundance
Temperature	1.00			
Salinity	0.33**	1.00		
Chlorophyll a	0.72**	0.20*	1.00	
<i>O. nana</i> (abundance)	0.18	–0.13	–0.25**	1.00
<i>O. nana</i> (biomass)	0.28**	–0.03	0.01	0.73**
<i>O. nana</i> (production)	0.29**	–0.02	0.04	0.68**
Total <i>Acartia</i> copepodite	0.53**	0.27**	0.34**	0.26**
<i>Acartia</i> C5	0.17	0.25**	0.02	0.26**
<i>Acartia</i> C4	0.32**	0.23*	0.16	0.28**
<i>Acartia</i> C3	0.44**	0.14	0.32**	0.24*
<i>Acartia</i> C2	0.57**	0.25**	0.39**	0.21*
<i>Acartia</i> C1	0.75**	0.29**	0.44**	0.34**
Copepoda nauplii	0.54**	0.17	0.59**	–0.09

*Significant at $P < 0.05$.

**Significant at $P < 0.01$.

summer/autumn and winter, respectively, in inlet waters around Japan (Ueda, 1991). Considering the use of different mesh sizes in the studies detailed, Hansen *et al.* (Hansen *et al.*, 2004) reporting levels of copepodite I–VI *O. similis* in the Baltic during spring/summer made the interesting comment that copepodites were better retained by a 150- μm mesh than a 50- μm mesh. The widespread use of 200- μm mesh as the ‘standard net’ for mesozooplankton (Bé *et al.*, 1968) should, however, certainly now be reconsidered. In the particular case of *O. nana*, >80% of adults and copepodites can pass through a 200- μm mesh (Richard and Jamet, 2001).

The relatively constant presence of many oithonids in the water column (Gallienne and Robins, 2001), and their success in late summer to winter, has been attributed to their relatively lower metabolic rate (Lampitt and Gamble, 1982; Castellani *et al.*, 2005) and also to their wide-ranging dietary preferences. Lampitt and Gamble (Lampitt and Gamble, 1982) reported *O. nana* as a raptorial feeder, with an opportunistic diet, able to consume particulates from detritus to phytoplankton, including earlier stages of calanoid nauplii and even copepodite stages (Lampitt, 1979). Equally, oithonids have been reported to feed on calanoid faecal material and *O. similis* can meet 20–30% of its daily carbon requirements from faecal matter alone (González and Smetacek, 1994), and in the Weddell Sea, *Oithona* can subsist and reproduce entirely from faecal material.

Current opinion suggests *Oithona* to be a protozooplankton predator. Nielsen and Sabatini (Nielsen and Sabatini, 1996), while pointing out a food size-spectrum

overlap between calanoids and oithonids, suggest a positive trend of selecting protozoan prey in oithonids. Similarly, Nakamura and Turner (Nakamura and Turner, 1997) report that *O. similis* had a diet based on autotrophic/heterotrophic (dino)flagellates, ciliates and nauplii, with heterotrophic dinoflagellates and ciliates its main food source. *Oithona davisae* is reported not to feed on diatoms but to prefer motile flagellates (Uchima and Hirano, 1986).

Food preferences may go some way to explaining both the striking spatial and seasonal pattern of *O. nana* in Southampton Water, with its relatively lower abundances in the mid and lower part of the estuary (Fig. 3a). Although spring to autumn Chl *a* values are essentially constant throughout the estuary (Iriarte and Purdie, 1994), there is a strong gradient of microheterotroph abundance (Leakey *et al.*, 1992). Significantly higher numbers of heterotrophic ciliates were recorded in the mid-upper estuary, with annual potential production values of 2 and 9 mg C L^{–1} year^{–1} in the lower and mid-upper estuary, respectively. In addition, abundance of nanoflagellates was greater in late summer and autumn, 3000 individuals mL^{–1}, compared with winter to spring values of 1000 individuals mL^{–1}. The potential annual heterotroph production was considered to be equivalent to between 34 and >100% of the energy requirements of metazoan plankton in the area (Leakey *et al.*, 1992). This late summer, mid-upper estuary distribution of microheterotrophs certainly reflects *O. nana* distribution.

Feeding preferences could also be reflected in the negative correlation between *O. nana* abundance and

Chl *a* (Table III). Although the impact of grazing could produce this relationship, *O. nana* maintained high, late autumn abundances of >13 000 individuals m^{-3} (average of 8.04 mg DW m^{-3}), for more than 3 months after the last phytoplankton bloom, with Chl *a* concentrations, on average, only 1.19 mg m^{-3} . No significant correlation was found between copepod nauplii and *O. nana* (Table III), but there was a strong correlation with the smallest copepodite stages of *Acartia* spp. sampled, which are within the recorded upper dietary size limit of *O. nana* (Lampitt and Gamble, 1982).

Considering other potential factors responsible for the striking spatial distribution of *O. nana* in Southampton Water, there is a strong correlation between the salinity profile of the estuary and abundance. There is, however, no record of *O. nana* having significant ontogenetic spatial (horizontal) patterns of distribution which might be associated with the physical structure of the water column, although the vertical displacement of *O. similis* in the central Baltic is constrained by the lower limit of the surface halocline (Hansen *et al.*, 2004). Feeding and respiratory rate patterns of late-stage copepodites and adult *O. nana* show a wide tolerance to salinity and temperature (J. A. Williams, unpublished), which suggests that the physical environment is not responsible for their sharp spatial distribution pattern. It has been suggested that low, mid-summer levels of *O. davisae* are related to ctenophore predation (Uye and Sano, 1998). The potential pressure of gelatinous predators in Southampton Water, although occurring in early summer, is balanced throughout the estuary (Lucas and Williams, 1994; Lucas *et al.*, 1995) and would not account for the distribution observed. An investigation of salinity influences on reproductive indices such as brood size and egg hatch success may provide an insight into the spatial pattern observed.

This study fundamentally alters the accepted, narrow calanoid-dominance pattern of copepods in Southampton Water. The previously unconsidered production of *O. nana* (Table II) supports the growing literature on the importance of oithonids in pelagic community structure and, more importantly, adds to the discussion of the relative significance of cyclopoid biomass and production compared with calanoid species. The copepod secondary production estimate of 32.2 mg C m^{-3} year^{-1} within the lower reaches of Southampton Water (Hirst *et al.*, 1999), which was exclusively based on calanoid copepods, is comparable with *Acartia* spp. production of 89.28 mg C m^{-3} year^{-1} calculated using the same growth model (Muxagata, 2005). Given the abundance levels of *O. nana* recorded in the lower estuary, neither estimate would be significantly enhanced by the inclusion of *O. nana* production (1.5 mg C m^{-3} year^{-1}) identified in this study. However, in

contrast, *O. nana* production in the upper estuary (146.77 mg C m^{-3} year^{-1}), compared with equivalent *Acartia* spp. estimates, suggested that *O. nana* production was 74% of that of *Acartia* spp., or 43% of major copepod production in the upper estuary. This is a significant contribution to total copepod production. In terms of total annual production throughout the estuary, *O. nana* with 161.75 mg C m^{-3} year^{-1} represents 22% of the total *Acartia* spp. production of 727.8 mg C m^{-3} year^{-1} and 18% of total calculated copepod production (Muxagata, 2005).

There are very few critical assessments of oithonid production, but allowing for the effect of mesh size and methods of calculation, production estimates of *O. nana* in the upper reaches of Southampton Water compare with values reviewed by Nielsen and Sabatini (Nielsen and Sabatini, 1996). Values for oithonids in the North Sea range between 1.0–1.4 g C m^{-2} year^{-1} (Tremblay and Roff, 1983; McLaren *et al.*, 1989) and 1.8–2.2 g C m^{-2} year^{-1} (Nielsen and Sabatini, 1996), which represent a relative contribution of between 13 and 40% to annual copepod production. In fact, *Oithona* spp. sometimes contribute as much as 50–70% to summer copepod production, depending on region and associated calanoid species (Nielsen and Sabatini, 1996). *Oithona nana* biomass in the upper estuary (Fig. 3b) falls within the seasonal range of *O. davisae* (copepodite stages I–VI) biomass of between 2.18 mg C m^{-3} (April) and 92.2 mg C m^{-3} (June), reported from a temperate eutrophic inlet (Uye and Sano, 1998). As a consequence, *O. davisae* production, at an integrated annual value of 650 mg C m^{-3} year^{-1} and making up 26% of annual copepod community production, is substantially higher than the 161.75 mg C m^{-3} year^{-1} production estimate for Southampton Water. The average summer biomass and gross production of *O. similis* in the Baltic, ranging between 16–305 mg C m^{-2} and 2.2–53.5 mg C m^{-2} day^{-1} , respectively, reflects that, on average, the abundance of *O. similis* is considered to be 50% of that of the standing stock of *Pseudocalanus* spp. and *Acartia* spp. and 25% of that of the dominant *Temora longicornis* (Hansen *et al.*, 2004). It is clear that production estimates for *O. nana* are lower than for many other oithonids, but per cent production relative to major calanoid species is at comparable levels with other studies, particularly in the upper estuary.

The lower production estimates of *O. nana* in Southampton Water can, in part, be accounted for by sampling methodologies, with *O. davisae* (Uye and Sano, 1998) and *O. similis* (Nielsen and Sabatini, 1996) collected using 62- and 50- μm mesh, respectively, compared with the 120- μm net used in this study. Despite this, it is clear that *O. nana* is a significant member of the total copepod community in the upper

estuary, and it is expected that production here, and in Southampton Water as a whole, will be much higher if nauplii and stage I–III copepodites are assessed, and the weight at each developmental stage is factored into calculations. With this, it is anticipated that *O. nana* will exceed production of calanoid copepods in the upper estuary.

Considering the chronology and methodologies of mesozooplankton sampling in Southampton Water (Muxagata, 2005), it is impossible to definitely state if *O. nana* is, indeed, a recent introduction into the estuary or whether it was simply ‘overlooked’ in previous studies using >200- μm nets (Raymont and Carrie, 1964; Zinger, 1989; Lucas, 1993). Additionally, these earlier studies tended to concentrate on the middle and lower reaches of the estuary. The absence of *O. nana* within Southampton Water was specifically mentioned by Raymont and Carrie (Raymont and Carrie, 1964) as it was abundant off the Isle of Wight (Fig. 1a). It was first reported in Southampton Water by Castro-Longoria (Castro-Longoria, 1998) using a 220- μm mesh net, though no estimate of its impact on total copepod abundance in the estuary was made. Hirst (Hirst, 1996) employed 118- μm mesh nets to sample the lower part of Southampton Water and reported the seasonal occurrence of cyclopoids in similar proportions, $\sim 2.7\%$ of total copepod abundance at Calshot, as the present *O. nana* pattern.

The occurrence of *O. nana* could be related to detrimental environmental or biological changes in the estuary. Richard and Jamet (Richard and Jamet, 2001) suggested the presence of *O. nana* as a biological indicator of increasingly anthropogenic-perturbed systems. Uye (Uye, 1994) also reported that increasing eutrophication and nutrient loading promoted a shift from diatoms to flagellates, thus favouring *O. davisae*, which feeds on flagellates (Uchima and Hirano, 1986). There is, however, no evidence to suggest that water/sediment quality conditions in Southampton Water are decreasing (Statham, 2000), and it is not considered an eutrophic environment (Hydes, 2000).

It is most probable that the apparent recent appearance of *O. nana* in Southampton Water is simply a reflection of sampling methodology, more specifically inappropriate mesh size. Whatever its previous history, it is clear from the present study that as a species, and in comparison with the main calanoid group within Southampton Water, *O. nana* has a substantial role in total copepod production, and therefore carbon flux in the water column. In the mid-upper estuary, preliminary production estimates suggest it may be the dominant copepod species.

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