A. D. McKinnon · S. Duggan

Summer copepod production in subtropical waters adjacent to Australia's North West Cape

Abstract Growth and secondary production of pelagic copepods near Australia's North West Cape (21° 49′ S, 114° 14′ E) were measured during the austral summers of 1997/1998 and 1998/1999. Plankton communities were diverse, and dominated by copepods. To estimate copepod growth rates, we incubated artificial cohorts allocated to four morphotypes, comprising naupliar and copepodite stages of small calanoid and oithonid copepods. Growth rates ranging between 0.11 and 0.83 day^{-1} were low, considering the high ambient temperatures (23–28°C). Calanoid nauplii had a mean growth rate of 0.43 ± 0.17 day^{-1} (SD) and calanoid copepodites of 0.38 ± 0.13 day^{-1}. Growth rates of oithonid nauplii and copepodites were marginally less (0.38 ± 0.19 day^{-1} and 0.28 ± 0.11 day^{-1} respectively). The observed growth rates were suggestive of severe food limitation. Although nauplii vastly outnumbered copepodite and adult copepods, copepodites comprised the most biomass. Copepodites also contributed most to secondary production, although adult egg production was sporadically important. The highest copepod production was recorded on the shelf break (60 mg C m^{-2} day^{-1}). Mean secondary production over both shelf and shelf break stations was 12.6 mg C m^{-2} day^{-1}. Annual copepod secondary production, assuming little seasonality, was estimated as ~ 3.4 g C m^{-2} $year^{-1}$ (182 kJ m^{-2} $year^{-1}$).

Introduction

We know relatively little about the growth and production of juvenile copepods in nature, despite the fact that

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juvenile stages of copepods are usually the most abundant components of the mesozooplankton and copepod nauplii, the dominant metazoans of the microzooplankton, are the most abundant type of multicellular animal (Fryer 1986). These juvenile copepods constitute the principal trophic link between microbial food webs and larger zooplankton and nekton and are the principal food items of larval fish at first feeding. The greatest obstacle to the measurement of growth and production of juvenile copepods in oceanic waters is their sheer diversity. Oceanic and tropical coastal plankton samples can contain hundreds of species, usually without clear dominants on which to focus experimental studies.

The field measurements of mesozooplankton growth and production that have been made to date are predominately from upwelling zones and coastal areas with low species diversity. The plankton in upwelling systems is characteristically dominated by a few large copepod species, such as *Calanus agulhensis* in the southern Benguela system (Richardson and Verheye 1999), or *Calanoides carinatus* and *Eucalanus* spp. in the Arabian Sea (Smith 1995). Detailed measurements of these dominant species have provided robust estimates of secondary production in these systems. Many field experiments have been conducted using adult female copepods in a variety of habitats because they are easily identified and lend themselves to experimental studies. Juvenile growth rates, however, do not always correspond to those of the adults (Peterson et al. 1991; McKinnon 1996; Hopcroft and Roff 1998a). Though comparatively few measurements have been made in the tropics, the emerging picture is that tropical marine copepod production is often food-limited (McKinnon 1996; McKinnon and Ayukai 1996; Hopcroft et al. 1998a). The high metabolic costs associated with high water temperatures, and the generally low standing stocks of food resources in tropical waters, combine to limit tropical copepod growth.

Australia's North West Shelf (NWS) supports the highest zooplankton biomass in Australia (Tranter1962). Primary production rates in the vicinity of the present

study can exceed 1 g C m^{-2} day^{-1} despite low phytoplankton standing stocks (M. Furnas, personal communication). Despite such indications of high productivity, copepod egg production rates are low, and apparently limited by food availability (McKinnon and Ayukai 1996; McKinnon and Duggan 2001). The main source of new nutrients to the southern NWS must be oceanic, as there is little terrigenous input in the region. Intermittent upwelling events, tidal and internal tidal motions and tropical cyclones have been hypothesised to supply new nitrogen to the shelf (Holloway et al. 1985).

Zooplankton communities of the southern NWS are dominated by small copepods, such as the calanoid family Paracalanidae and the cyclopoid family Oithonidae. Wind and tidal currents mix adjacent water masses of quite different origin resulting in zooplankton communities that are a mixture of assemblages from the adjacent oligotrophic ocean and from inshore waters. The present data demonstrate mesozooplankton secondary production rates that are low compared to many temperate environments, but comparable to those of other tropical shelf systems.

Materials and methods

Growth experiments were conducted at representative stations on the shelf and adjacent continental shelf. At each station we sampled mesozooplankton community structure and biomass with triplicate bottom to surface vertical zooplankton hauls with a 0.5 m diameter net of 73 μm mesh fitted with a Rigosha flowmeter. We conducted growth experiments at five sites (Fig. 1). Most experiments were conducted at station E (∼75 m depth), a blue-water station on the continental shelf and station B (∼18 m), a station representative of turbid shelf waters. With one exception, four growth experiments were conducted on each of five monthly cruises over the austral summers of 1997/1998 and 1998/1999.

Artificial cohort experiments

Water from beneath the vessel was pumped with a hand-operated bilge pump. The hose intake was covered with 37-μm plankton mesh that excluded all copepod life stages from the incubation water, but potentially removed larger food particles. For each experiment, five replicate 20-l cubic containers were filled with the 37-μm filtered water. Total Chlorophyll a (hereafter Chl) in the incubation water was measured at the beginning of the incubation and from two containers at the end of the incubation. The water

Fig. 1 Location of stations at which growth experiments were conducted on the north-west coast of Australia
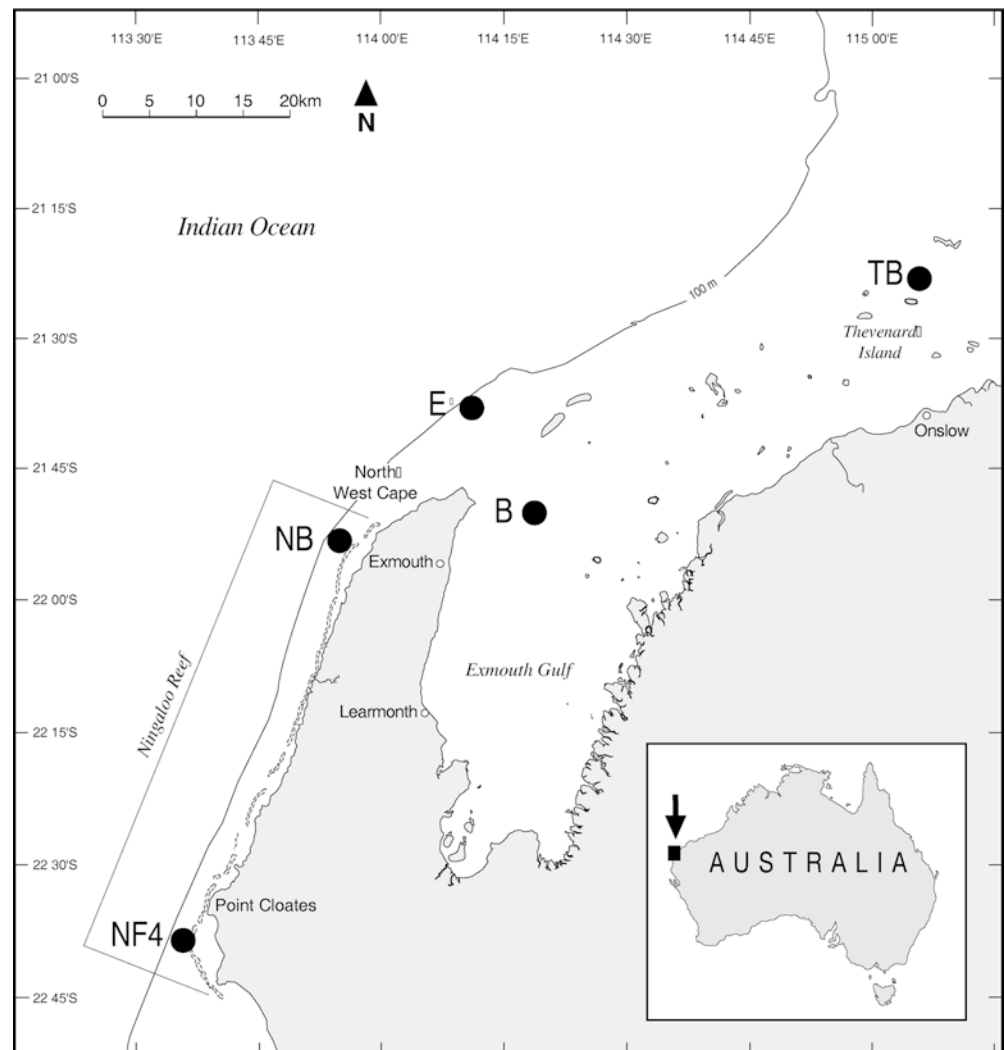
samples were filtered on to GF/F filters, which were then frozen (−10°C) and stored until subsequent grinding and extraction in 90% acetone and analysis by fluorometry (Parsons et al. 1984).

We collected live plankton for growth experiments by drifting 0.5-m plankton nets of 53-μm and 100-μm mesh at a depth of 5–10 m. The cod end contents were immediately transferred into a 20-l bucket containing surface water. A PVC cylinder with mesh of either 80-μm or 150-μm aperture covering the bottom was slowly lowered into the bucket containing the plankton sample, and water containing animals smaller than the size of the mesh was siphoned out of the cylinder. This process was repeated to give two "artificial cohorts" (sensu Kimmerer and McKinnon 1987), one with animals nominally between 53 μm and 80 μm in size, and the other between 100 μm and 150 μm. Aliquots of screened plankton from each size fraction were then placed in each of five containers, and sets of five time-zero samples fixed in formaldehyde. The containers were closed and placed in seawater-cooled deck incubators covered with a neutral density mesh (∼30% light transmittance). Limited mixing of the containers was provided by the often sprightly ship's motion, and there was no obvious settling of seston. Incubator water temperature was recorded at 10-min intervals.

Our intention in using two size fractions was to measure naupliar and copepodite growth of the most abundant small copepods in the mesozooplankton. The 53–80 μm size fraction contained mostly nauplii and was incubated for ∼24 h, whereas the 100–150 μm fraction contained mostly copepodites and was incubated for ∼48 h. Each size-based cohort contained copepod juveniles of many species. In some experiments ($n = 7$) adults of some of the smaller species of *Oithona* occurred in the 100–150 μm size fraction, and since adults do not moult (and increase in weight cannot be calculated from metrics) the results from these experiments were discarded. At the conclusion of these incubation periods, the mesozooplankton in each container were concentrated on 37-μm mesh and preserved with formalin.

Calculation of growth rates

Mesozooplankton communities in the North West Cape area are diverse: we have identified over 130 species of copepods in our samples to date. It is therefore extremely difficult—and operationally impractical—to identify developmental stages of individual species, or even genera. For simplicity we have confined our analysis of the artificial cohorts to copepod morphotypes. Insofar as body plan reflects ecological role, these groups of taxa constitute functional groups. We classified nauplii and copepodites in the preserved samples into assemblages of small calanoid and cyclopoid copepods. The families Paracalanidae (∼14 spp.) and Clausocalanidae (∼6 spp.) dominated the calanoids, whereas the cyclopoids were all Oithonidae (∼12 spp.). Once sorted, animals were stained with Chlorazol Black and examined with an inverted microscope fitted with an image analysis system (Optimas 6.2), which approximated the shape of each copepod to an ellipse and calculated the length of the major and minor axes for each. These data were used to calculate the total length and width of nauplii and the prosome length and width of copepodites.

Because our morphotypes comprise numerous taxa of different shape, the calculation of biomass from the various metrics was first calculated as wet weight (WW) according to Svetlichny (1983):

$$WW = K_c * prosome\ length * width^2$$

We used values of the constant K_c of 0.6 for the calanoids, and 0.705 for the cyclopoids. Wet weight (μg) was then converted to carbon (μg) with a conversion factor of 0.06 (dry weight = 0.135 WW, Postel et al. 2000; carbon = 0.42 dry weight, Beers 1966). The biomass values obtained in this way were checked against directly measured values from preliminary experiments, and with biomass measurements of adult copepods.

We analysed a minimum of three of the five replicate containers from each growth experiment. When calculated biomass changes were non-significant ($P > 0.05$) on the basis of three replicates in

one or more of the four morphotypes, we analysed all five replicates. From these results we calculated growth rates (g, day^{-1}) as:

$$g = (\ln W_t - \ln W_0)\ t^{-1}$$

where W_0 and W_t are the mean carbon weights of an individual copepod at the beginning and end of the incubation period t (days).

Calculation of secondary production

The biomass of copepods attributable to each morphotype was calculated as the product of the geometric mean carbon content at each date, taken from the time-zero measurements for each growth experiment, and the numerical abundance of appropriate life stages from microscope counts of the copepods from vertical hauls taken when the experiments were started. The contribution of adult paracalanids to secondary production was calculated as the product of biomass and specific egg production rate. Biomass was estimated as the total abundance of all species multiplied by the median adult weight. The best coverage of specific egg production rate data we have is for *Paracalanus indicus* (McKinnon and Duggan 2001). Since there was little difference in specific egg production rates between paracalanid species, we took these data as representative of all. Male paracalanids were rare in comparison to the females, but for consistency we assumed male production (of spermatophores) to be equivalent to female specific egg production (see Escaravage and Soetaert 1993). Also, our calculations of secondary production do not include exuvial production, which may comprise 8.4% of somatic production (Chisholm and Roff 1990). Areal secondary production was then calculated as the product of the date-specific growth rate (μg C m^{-3} day^{-1}), the average biomass (m^{-3}) and the water depth (m), assuming a depth of 18 m for station B and 75 m for station E. Carbon-specific production was converted to energy, assuming an energy density of 25 kJ g^{-1} AFDW (Chisholm and Roff 1990), a ratio of 0.89 of AFDW to DW (Båmstedt 1986), and 0.42 for carbon to DW (Beers 1966).

Results

Water temperature increased during each summer (Table 1). Despite generally higher ambient temperatures in 1998/99 than in 1997/98 (McKinnon and Duggan 2001), incubator temperatures covered a similar range in each summer: 21.4°–30.8° in 1997/1998 and 20.7°–30.5° in 1998/1999 (Table 1). Chl concentrations at the start of the incubations were always below 0.7 μg Chl *a* l^{-1}, and were usually higher at station B than at station E (Table 1). Chl concentrations of < 37 μm incubation water were not significantly different to whole-water surface samples taken at the same time and place (*t*-test). Variance of the size distribution of the artificially created cohorts increased at the conclusion of all our experiments (Fig. 2). Typically, the calculated copepod wet weight in both experimental size fractions increased two- to three-fold over the incubations.
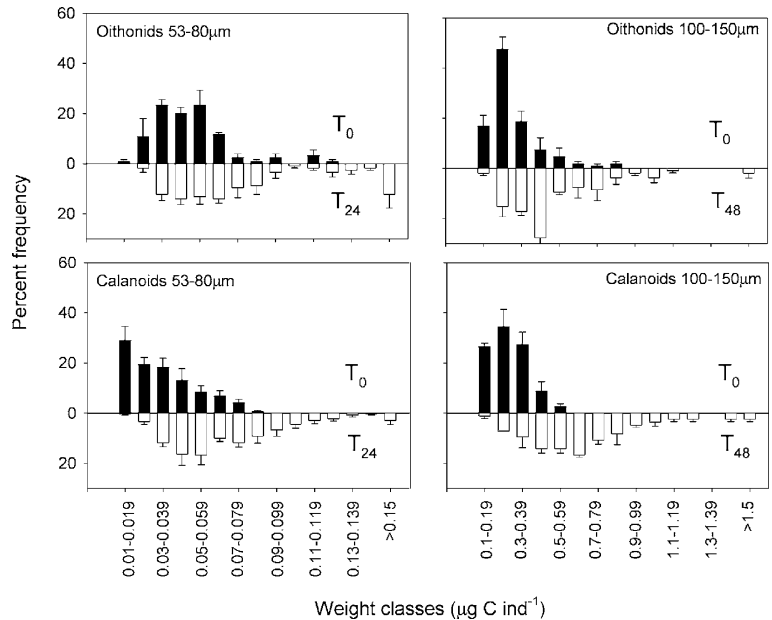
Growth rates

Growth rates ranged between 0.11 and 0.83 day^{-1} (Fig. 3). Overall mean growth rates were 0.43 ± 0.17 day^{-1} (SD) and 0.38 ± 0.13 day^{-1} for calanoid nauplii and copepodites respectively, and 0.38 ± 0.19 day^{-1}

Table 1 Cruise dates, mean temperature during growth incubations, and average chlorophyll concentrations at the commencement of incubations of artificial cohorts of copepods collected at either station B or station E

Cruise	Date	Temperature °C	Chl at stn B µg l^{-1}	Chl at stn E µg l^{-1}
1	25/10/97–3/11/97	23.00	0.200	0.195
2	26/11/97–6/12/97	23.92	0.210	0.348
3	26/12/97–4/1/98	23.45	0.135	0.695
4	23/1/98–1/2/98	23.58	0.215	0.143
5	21/2/98–2/3/98	27.95	0.123	0.120
6	16/10/98–24/10/98	22.91	0.135	0.135
7	16/11/98–23/11/98	24.22	0.360	0.200
8	16/12/98–23/12/98	26.24	0.150	0.095
9	13/1/99–22/1/99	26.70	0.168	0.060
10	10/2/99–19/2/99	28.21	0.165	0.170

Fig. 2 Examples of frequency distributions of biomass in artificially created cohorts at the beginning and end of incubation

and 0.28 ± 0.11 day^{-1} for oithonid nauplii and copepodites respectively. There was no discernable difference in growth rates between stations, between cruises or between years. We were unable to detect any consistent pattern of change in Chl concentration within our containers during the course of growth experiments (Fig. 4). Chl increased in half the incubations, and decreased in 42% of the incubations, with no change in the remainder. Where changes in Chl occurred, the magnitude was usually less than two-fold, and always less than four-fold (Fig. 4). Naupliar growth rates showed significant Michaelis-Menten relationships to Chl concentration, but no significant relationship to temperature (Fig. 4). Copepodite growth rates and adult specific egg production rates were decoupled from both temperature and Chl (Fig. 4).

Secondary production

Copepods comprised 61–98% (median 79%) of > 73 µm mesozooplankton numbers at stations B and E. The mean abundance of copepods at station B increased over the summer of 1997/1998 from 2,400 m^{-3} in October to 33,000 m^{-3} in January and February (Fig. 5). In 1998/1999 there was no similar increase in abundance at station B; mean copepod abundance was 7,800 m^{-3}. Copepod abundance at station E did not increase during 1997/1998, but was higher, on average than in 1998/1999 (7,500 m^{-3} vs 3,100 m^{-3}). Oithonid nauplii were relatively more abundant at station B than at station E, whereas station E had more copepods not assigned to any of the four morphotypes ("other"; Table 2).

The numerical dominance of juvenile copepods contributed to their dominance in biomass, but the smaller numbers of adults were increased in importance by their greater individual mass (Table 2, Fig. 5). Standing stocks of copepods (no. m^{-2}) were similar at stations B and E, the difference in water depth compensating for differences in volumetric abundance (station B, 6–91 mg C m^{-2}; station E, 8–100 mg C m^{-2}). One anomalously high value (341 mg C m^{-2}) occurred in November 1997 at station E, when *Paracalanus indicus* adults were unusually abundant (1,300 m^{-3}).

Estimated copepod production at stations B and E ranged between $2 - 18$ mg C m^{-2} day^{-1}, and 3–61 mg C

Fig. 3 Growth rates (mean and 95% confidence limits) of copepod morphotypes at station B (*left panel*) and station E (*right panel*). Duplicate experiments were conducted for each month of sampling; results are not shown for experiments where growth rate was not significantly different from zero. Individual experiments at station TB, and the Ningaloo Reef stations NB and NF4 are shown in the *centre panel*
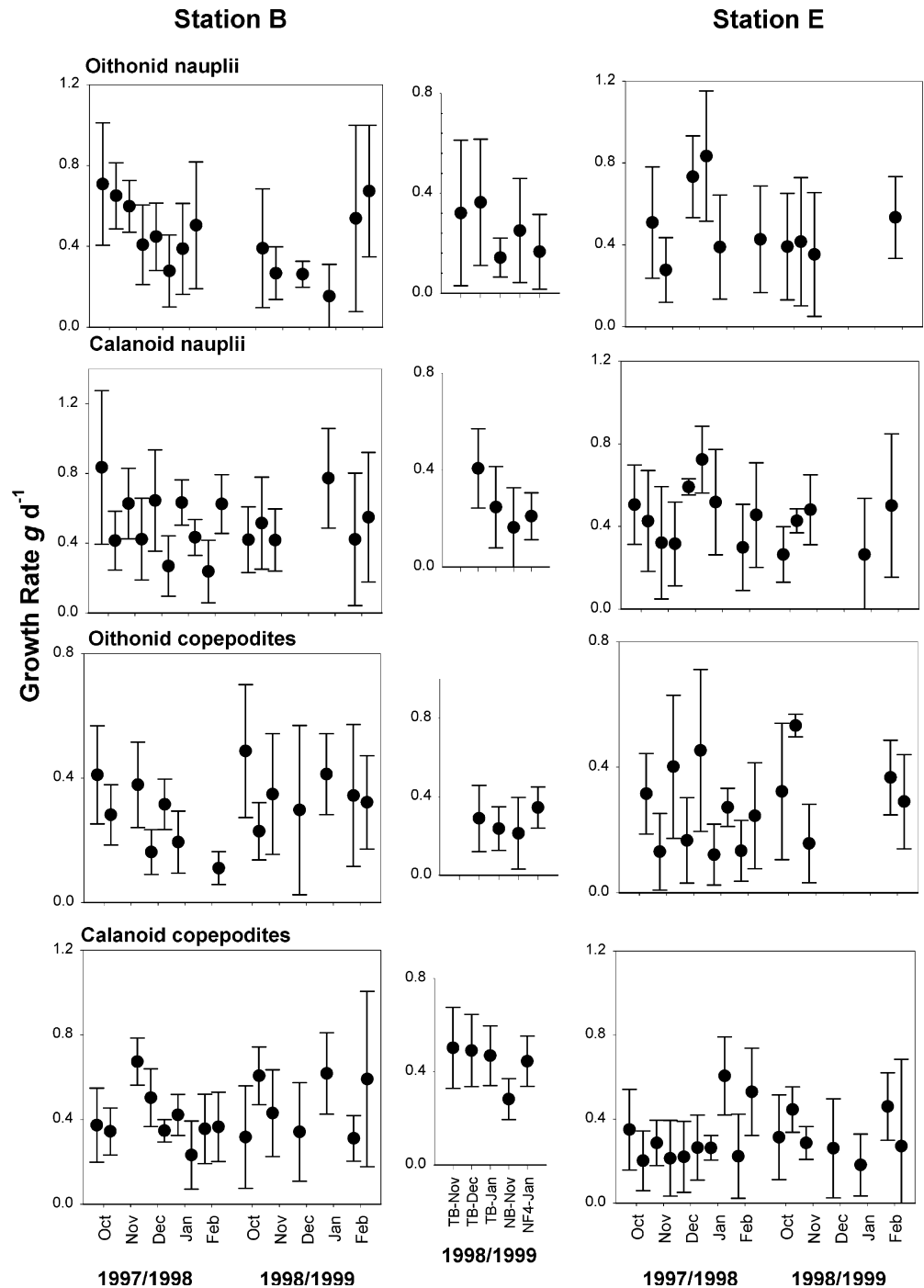
m^{-2} day^{-1} respectively (Fig. 5). Overall, copepod production at station E was higher in 1997/1998 than in 1998/99 (16.2 vs 6.2 mg C m^{-2} day^{-1}). At station B, calanoid juveniles made the greatest contribution to production, whereas oithonid juveniles made a larger contribution at station E (Table 2). However, oithonid juveniles made a lower contribution to production in the summer of 1998/1999 than they did in 1997/1998 (Fig. 5). Adult growth (derived from specific egg production rate) comprised a larger fraction of production in 1997/98 than in 1998/1999.

During the summer of 1998/1999, we conducted three growth experiments near Thevenard Island (station TB; 15 m depth), and two experiments in the front of Ningaloo Reef (stations NB, 45 m depth and NF4, 60 m depth). In the January 1999 experiment oithonid copepodites and "other" copepods were more abundant at station TB, than at station B. However, station TB resembled station B in biomass and production in the same months (Fig. 5). The Ningaloo stations had a clearly different community than our other stations, with lower copepod abundances, yet broadly similar biomass

Fig. 4 Growth rates of copepod morphotypes and specific egg production rates of *Paracalanus indicus* versus Chl (*left panel*) and temperature (*right panel*). Chl data relate to the concentration occurring in the containers at the beginning and at the end of each incubation. Temperature data are the mean and range of temperatures within the incubators used for growth rate incubations. Fitted curves are Michaelis-Menten relationships $[g = Chl(g_{max})/Chl + K_m]$ of growth rate to the mean Chl concentration during the incubation
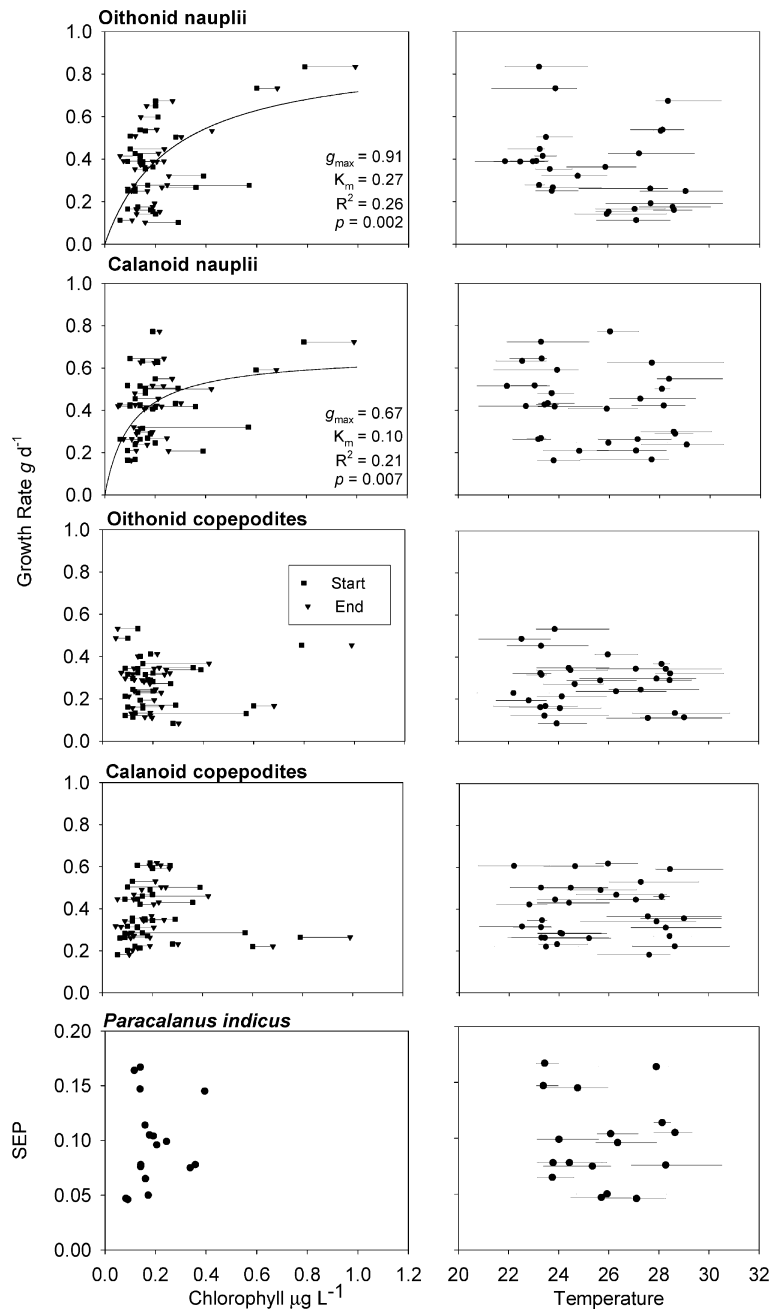
and production to station E on the same months. This indicates that the copepods were of larger size than at our other stations.

Discussion

The copepod community in the vicinity of North West Cape, Western Australia, is highly diverse. In attempting to measure secondary production with existing techniques it is necessary to choose between conducting experiments using representative species and then applying the results to the whole community, or to adopt a community-level approach that aggregates the responses of multiple species. The former approach allows detailed study of a small subset of the community, and makes the assumption that those particular species will be present on most occasions, and that their growth rates will be representative of the total community. The latter approach captures the full range of variability of the plankton, whatever its composition may be on the particular day of sampling. However, in applying a single experimental protocol across a large number of taxa there is a concomitant loss of resolution. Irrespective of this, in view of the diversity of the copepod community of North West Cape and the lack of clear dominants, we adopted the community level approach. Our study is the first to apply the artificial cohort technique to multi-species groups.

Fig. 5 Abundance (*top panel*), biomass (*middle panel*) and secondary production (*bottom panel*) of the copepod community for stations B (*left panel*) and station E (*right panel*) and stations TB, NB and NF4 (*centre panel*)
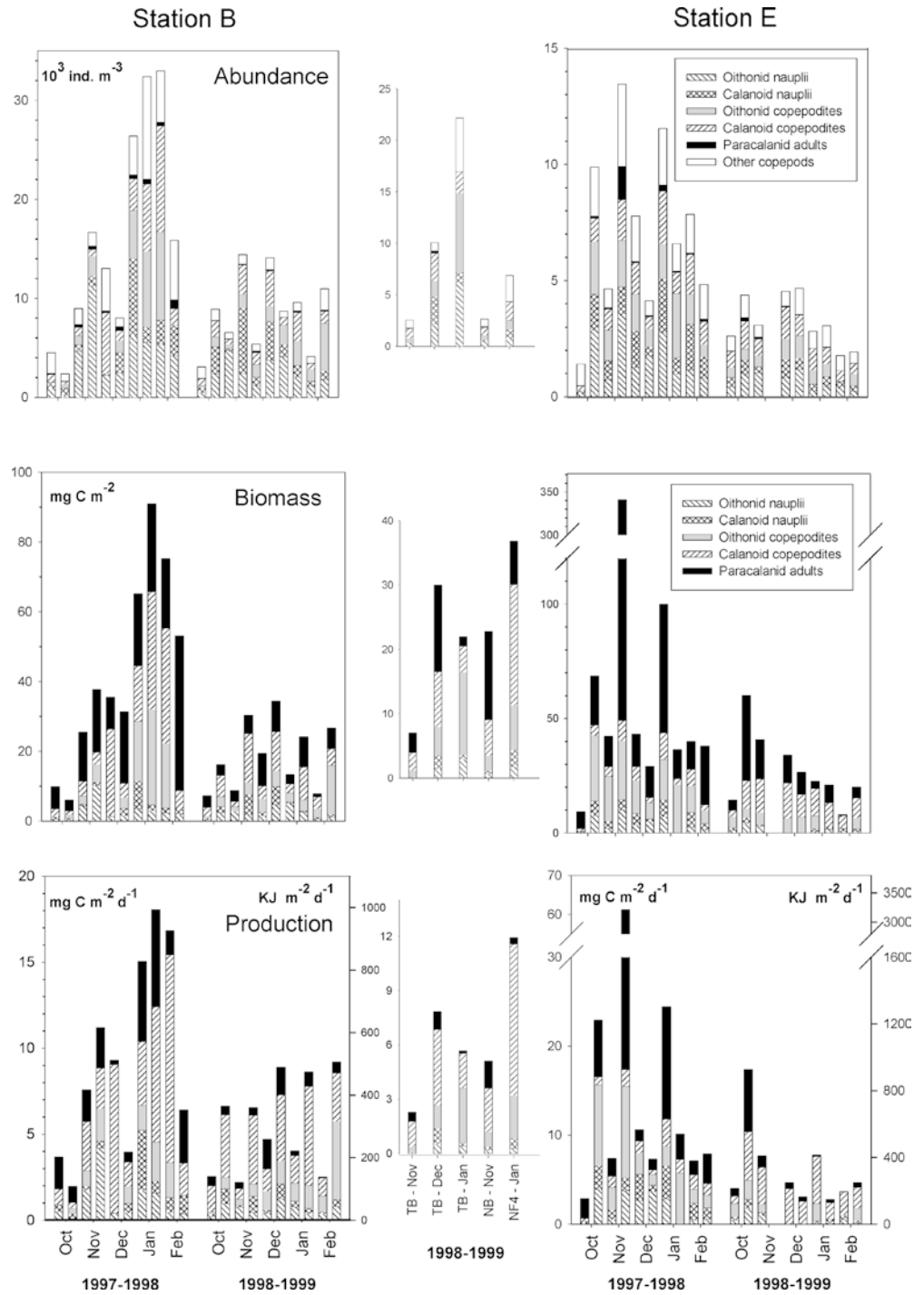

Table 2 Median percentage contribution of each morphotype to abundance, biomass and production at stations B and E. *ON Oithona* nauplii,*OC Oithona* copepodites, *O adult Oithona* adults,*CN* calanoid nauplii, *CC* calanoid copepodites, *Pc adult* paracalanid adults, *n.d.* not determined

Morphotype	Station B			Station E		
	Abundance	Biomass	Production	Abundance	Biomass	Production
ON	23	7	10	17	7	8
OC	17	13	14	18	24	17
O adult	4	n.d.	n.d.	4	n.d.	n.d.
CN	14	4	6	15	7	11
CC	17	24	39	22	18	21
Pc adult	2	34	17	1	36	21
Other	10	n.d.	n.d.	19	n.d.	n.d.

Growth rates

Juvenile copepod growth rates were usually not significantly different (apparent from the comparison of confidence intervals; Fig. 3). The overall similarity of growth rates was also a characteristic of our parallel egg production experiments (McKinnon and Duggan 2001). We believe that two factors contribute to the variance observed in our measurements of growth rate.

Firstly, because the physical oceanography of the area is dynamic, there is no doubt that different species assemblages, and indeed different populations, were used to start the experiments. In this highly diverse system, it was impractical to identify the juvenile copepods further than the level of morphotype. However, in the case of the nauplii, many of which would be less than a day old, it is reasonable to expect that the composition of the nauplii would reflect that of the adults taken at the same station. For instance, in one of the few cases where significant differences in growth rates occurred on the same cruise (February 1998 at station B for calanoid nauplii), mean growth rates increased from 0.24 day^{-1} when *Parvocalanus* spp. dominated the assemblage to 0.62 day^{-1} when *Paracalanus* species were co-dominant.

Secondly, we speculate that differences in feeding history of the animals used in the incubations contribute to variability in growth rate. Indeed, field-based growth rate measurements repeated at similar sites within a few days support the supposition that differences in feeding history influence growth rates of planktonic copepods. Peterson et al. (1991) conducted artificial cohort experiments at a series of stations across the Skagerrak over the course of 10 days, and recorded up to three-fold differences in growth rate for *Temora* and *Pseudocalanus* (their Fig. 8). Similar degrees of difference in the moulting rate of *Calanus finmarchicus* nauplii and copepodites were observed by Campbell et al. (2001) on Georges Bank. In both cases, temperature differences between experiments were minimal. In our case particularly, but also more generally, we expect that resource availability must influence copepod growth rates in the field.

Our overall mean growth rates (0.27 day^{-1} for oithonid copepodites, 0.38 day^{-1} for oithonid nauplii and calanoid copepodites, and 0.43 day^{-1} for calanoid nauplii) may be compared with data for similar species assemblages from Jamaican coastal waters. Chisholm and Roff (1990) reported growth rates of 0.63 day^{-1} for *Centropages velificatus* and *Paracalanus aculeatus*, and 0.48 day^{-1} for *Temora turbinata*. Hopcroft and Roff (1998b) measured growth rates of oithonid and paracalanid nauplii at ~28°C of 0.49 day^{-1} and 0.81–0.90 day^{-1}, respectively. *Oithona nana* copepodites grew at 0.46–0.65 day^{-1}, and paracalanid copepodites at 0.69–0.78 day^{-1} (Hopcroft et al. 1998a). These rates were estimated when Hopcroft et al. (1998a) removed *O. simplex* from their multi-species analyses, on the basis of its having anomalously low growth rates (0.25 day^{-1}).

On average, our growth rates are about half those measured for single species in the Caribbean, and one half to two thirds of those predicted on the basis of temperature and body weight according to the global model of Hirst and Lampitt (1998). At the upper end of the temperature range our values are about one third of those predicted on the basis of temperature alone, according to the model of Huntley and Lopez (1992).

The higher growth rates estimated in the Caribbean experiments compared to those observed at North West Cape may have occurred because resources were typically less limiting to growth rate. However, even under these circumstances, Hopcroft and Roff (2003) found that Chl increased by up to 2 orders of magnitude when nutrients were added, and copepodite growth rates increased by 32% (Hopcroft et al. 1998a). In coastal waters of North-Eastern Australia, McKinnon (1996) reported growth rates of *Acrocalanus gibber* of 0.49–0.72 day^{-1} at temperatures of 24°-29°C. Though *A. gibber* apparently had access to substantially higher resource concentrations than found in the present study, growth was still food-limited. For instance, Chl concentrations in McKinnon's (1996) study were on average five-fold higher than reported here. It therefore appears that our experiments were conducted under limiting trophic conditions. Indeed, this seems to be the emerging picture of planktonic rate processes from earlier work in the same area (McKinnon and Ayukai 1996; Ayukai and Miller 1998; McKinnon and Duggan 2001). In the case of copepodids, the lack of correlation of growth with either temperature or Chl found in the present study was also characteristic of McKinnon's (1996) study, and underscores the inadequacy of these as predictors of copepod growth in tropical environments characterised by the dominance of microbial processes. However, the significant Michaelis-Menten relationships found between naupliar growth rates and Chl suggest a greater reliance on herbivory by nauplii than for the later stages, which may feed more as carnivores or detritivores.

Differences in the nutritional status of the animals, either before or during the incubation, can influence growth rate (e.g. Hopcroft et al. 1998a). We had no control over food resources available to the juvenile copepods during the incubations. Though there were no consistent trends in resource availability (measured as Chl) in the containers, founder effects could have led to differences in the nature of resources utilised by the copepods. It is conceivable that in some cases differences in the community composition of protists could have developed during the course of the incubation, and that this could result in differences in food quality. Our method of filling containers was by upward filtration through a 37-μm mesh and a gentle hand pump, which ought not to disrupt delicate food organisms such as protists, though some losses of aloricate ciliates will occur (Gifford 1993). Nevertheless, such effects are implicit in incubation experiments, which are by nature static, and fail to simulate the dynamic natural envi-

ronment. In this sense, the development of new retrospective methods which infer the growth rates that would have occurred in the natural environment are attractive (e.g. Roff et al. 1994; Hernández-León et al. 1995; Sastri and Roff 2000).

Secondary production

We have used the biomass distribution recorded in our time-zero samples to calculate the biomass of nauplii and copepodites in net tows. Our measurements of pelagic biomass and secondary production are therefore confined to the small copepods which typically dominate mesozooplankton communities in the tropics (McKinnon and Thorrold 1993, Hopcroft et al. 1998b). Although this will underestimate community biomass by disregarding the contribution of rare large copepods, the community data to hand suggest this is an acceptable compromise. In any event, it is important to recognise that our measurements do not include larger copepods, such as the families Calanidae and Eucalanidae, and other zooplankton such as Appendicularia that are occasionally abundant.

Though nauplii were numerically dominant in our samples, copepodites contributed most to community biomass and production. Adult paracalanid copepod abundance was low, but their greater mass resulted in their contribution to community biomass being larger,

and at station E in 1997/1998 their contribution to community production rivalled that of the copepodites. Overall, the contribution of each copepod life stage to total production is very similar to those found by Hopcroft et al. (1998b): 11% by nauplii, 59% by copepodites and 30% as adult egg production, in keeping with the axiom that ~50% of planktonic secondary production occurs as egg production and naupliar growth (Mullin 1988). This generality almost certainly has its origins in the broad similarity of zooplankton community composition in coastal waters worldwide.

Daily copepod production at our stations was low in comparison with similar measurements taken in other environments (Table 3). The data of Hopcroft et al. (1998b) and Newbury and Bartholomew (1976) are from more resource-rich tropical environments (Chl ~ 2 μg l^{-1}), though both included many species also found in our study. Our data are similar to rates of production recorded from a temperate Australian bay when summer temperatures reached 22° (Kimmerer and McKinnon 1987). Copepod production on the Agulhas Bank, a temperate upwelling system, is 4- to 40-fold higher on average than occurred in our study (Peterson and Hutchings 1995).

Taking the grand mean of copepod secondary production at both stations over both summers (500 J m^{-2} day^{-1}) and calculating annual production (assuming little seasonality) yields a value of 182 kJ m^{-2} year^{-1} (Table 4). This rate is comparable to that measured

Table 3 A comparison of daily copepod production

Location	Water depth (*m*)	Temperature (°C)	mg C m^{-2} day^{-1}	J m^{-2} day^{-1}	Environment	Reference
Station B	18	23–28	7.5	397	Subtropical shelf	This study
Station E	75	23–28	11.5	609	Subtropical shelf-break	This study
Kingston Harbour	15	27–30	–	4,600	Tropical bay	Hopcroft et al. 1998b
Kaneohe Bay	14	27–29	151	8,000	Tropical bay	Newbury and Bartholomew 1976
Westernport Bay	10	11–22	7.5	400	Temperate bay	Kimmerer and McKinnon 1987
Western Agulhas Bank	40–200	17–18	40	2,120	Upwelling shelf	Peterson and Hutchings 1995
Eastern Agulhas Bank	40–200	17–18	400	21,200	Upwelling shelf	Peterson and Hutchings 1995

Table 4 A comparison of annual copepod production in shelf systems. Measurements marked with an asterisk have been converted from units of g C m^{-2} year^{-1} by multiplication by a factor of 53, derived from the conversion factors given in Materials and methods

Location	Water depth (m)	Temperature (°C)	kJ m^{-2} year^{-1}	Reference
NW Cape, Australia	18–75	23–28	182	This study
Discovery Bay, Jamaica	60	27–30	160	Webber and Roff 1995
Discovery Bay, Jamaica	200	22–30	304	Webber and Roff 1995
Kingston Harbour, Jamaica	15	27–30	688	Chisholm and Roff 1990
Kingston Harbour, Jamaica	15	27–30	1,679	Hopcroft et al. 1998b
Passamaquoddy Bay, USA	28	2–12	850[*]	Middlebrook and Roff 1986
Kattegat	28	5–19	636[*]	Kiørboe and Nielsen 1994
Inland Sea of Japan	33	10–24	2,745[*]	Uye and Shimazu 1997
Benguela System, S. Africa	40–200	10–19	900–7,950[*]	Hutchings et al. 1995
Scotian Shelf	89	3–17	984	McLaren et al. 1989
Scotian Shelf	89	1–21	530[*]	Tremblay and Roff 1983
Solent, UK	15	6–18	26[*]	Hirst et al. 1999
Northumberland, UK	54	6–14	164[*]	Evans 1977

in a similar offshore environment off Discovery Bay, Jamaica, but substantially lower than in within Kingston Harbour (Table 4). Temperate shelves and can be equally productive, though highest rates occur in upwelling systems such as the Benguela (Table 4).

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