Growth rates of copepods in the southern Benguela upwelling system: The interplay between body size and food

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Abstract

Copepod growth rates were estimated from shipboard measurements of egg production of adult female *Calanus agulhensis, Calanoides carinatus, Nannocalanus minor,* and *Centropages brachiatus* and molting rates of juvenile stages (N6–C5) of *C. agulhensis.* Data were obtained during austral spring and summer of 1989–1995 in the southern Benguela upwelling system. While maximum growth rates showed less than a threefold decline over the body-size range examined (525–2,763-μm total length), probably owing to allometric considerations, mean growth rate decreased by one order of magnitude, suggesting limitation of growth rate by an environmental factor. Most of this decline in mean growth rate was attributable to food limitation of large copepods. Frequency distributions of growth rate under low food densities were severely skewed toward slow growth rate for large copepods, whereas they were more symmetric for smaller copepods. In contrast, at high food concentrations, the frequency distributions had a high degree of symmetry for all copepods. These frequency distributions were interpreted in terms of a probabilistic model describing the encounter rate of copepods with suitably sized food particles. The effect of food limitation on growth rate was evaluated by regressing the coefficient of variation of growth rate against body size. A strong positive relationship was found ($r^2 = 0.94$, $P < 0.001$), indicating that small copepods were always growing well, whereas the growth rate of large copepods was more variable. It is suggested that this difference is a consequence of the ability of small copepods to consume small particles, which are present at a relatively constant background density.

The two main factors controlling growth of copepods are temperature and food. The influence of temperature on growth rates in the wild has been well documented, especially in temperate seas (*see* McLaren et al. 1989 and references therein). Huntley and Lopez (1992) concluded that copepods grow at maximum rates in the sea, with an exponential increase in growth rate with temperature over a wide range of habitats. In contrast, growth of copepods has been found to be more related to food rather than temperature in a variety of aquatic habitats, including freshwater systems (Hart 1991; Ban 1994), tropical seas (McKinnon and Thorrold 1993; Webber and Roff 1995), some temperate coastal regions (Bautista et al. 1994; Pond et al. 1996), and in an upwelling system (Peterson and Hutchings 1995; Richardson and Verheye 1998). In the latter system, the southern Benguela, the lack of dependence of growth on temperature is attributable to slower growth at warm (18–22°C) temperatures (Richardson and Verheye 1998), a consequence of very

low (usually <2 mg chlorophyll *a* [Chl *a*] m^{-3}) food concentrations at these temperatures (Pitcher et al. 1996).

Two studies in contrasting ecosystems suggest that the degree of food limitation in copepods may be related to body size, with larger species being more food limited. The first study, in the tropical ocean, shows that there is progressive food limitation of somatic growth and egg production with increasing body size (Chisholm and Roff 1990*b;* Webber and Roff 1995). In the second study, egg production by females in a temperate fjord was food limited, whereas the somatic growth of juveniles was not (Peterson et al. 1991). Moreover, in a recent global synthesis of copepod growth rates measured in the field, Hirst and Sheader (1997) suggested that food may be limited in a body-size dependent way, with larger individuals being more food limited. This contention requires testing in a variety of marine systems.

In the present study, we assess the hypothesis that food limits growth in a body-size dependent manner, using shipboard data on copepod growth rates collected in the southern Benguela upwelling region. Growth rates of copepods over a broad size range (525–2,763 μm) were measured, including somatic growth of preadult stages (662 molting rate experiments) and fecundity of several species (2,084 egg production experiments).

Methods

Copepod growth rate in the field was estimated using bottle incubation techniques, viz. egg production of females and
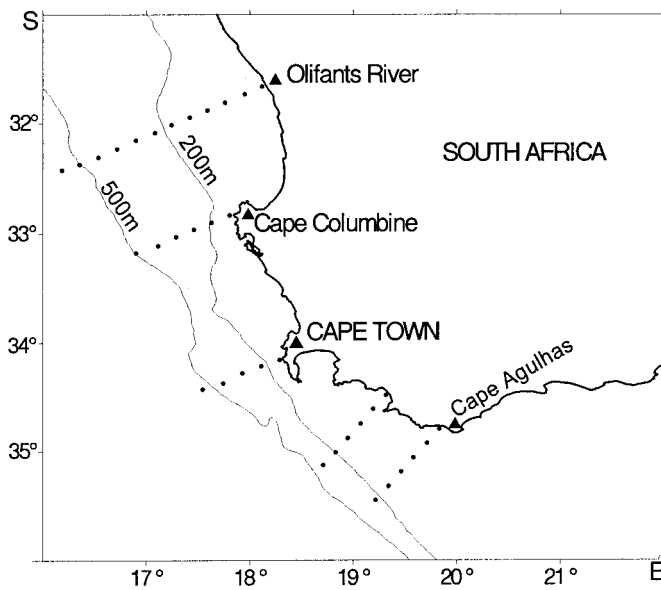
Fig. 1. The southern Benguela region off South Africa showing station positions during SARP.

molting ratio of juveniles. Data were obtained from shipboard measurements in the southern Benguela upwelling system during monthly South African SARP (Sardine and Anchovy Recruitment Programme) cruises between September and March 1993–1994 and 1994–1995. The station positions of the SARP survey are shown in Fig. 1. Additional data from annual surveys during November 1989–1992 between Cape Columbine and Cape Agulhas (Verheye et al. 1994) were also included in the analysis. Sampling extended from cool upwelling waters inshore to the 500-m isobath offshore, where warm oceanic conditions prevail, providing data over a broad range of temperatures (9–23°C) and Chl *a* concentrations (0.1–23 mg m^{-3}).

Copepods were collected using a 300-μm mesh drift net, fitted with a 2-liter plastic bottle as a cod-end, and allowed to drift for 10 min at the depth of maximum fluorescence determined from a vertical fluorescence profile. Upon retrieval, the sample was transferred into a bucket containing 20 liters of ambient seawater. Copepods were gently removed from this bucket using a sieve and washed into a petri dish. Lively copepods were selected with a wide-mouthed dropper under a dissecting microscope. For egg production experiments, individual females were placed in 1-liter bottles (usually 5–10 replicates per station) containing 63-μm filtered seawater from the depth of maximum fluorescence and incubated in on-deck darkened tubs that were kept at ambient temperatures by pumping seawater from a depth of 6 m (Hutchings et al. 1995). Although the bottles were not fitted with a screen to prevent females from ingesting their eggs, the low density of females used (one female per liter) minimized the effects of egg cannibalism (*see* Laabir et al. 1995).

After 24 h, the contents of each incubation bottle were poured through a 20-μm mesh, lively females and their eggs were preserved with 5% buffered formalin, and the number of eggs per bottle was counted. Experiments with dead or

moribund females were discarded. To enable direct comparison of female with juvenile growth rates, instantaneous weight-specific female growth rates were calculated according to Roff et al. (1995). As this study was performed as part of a routine monitoring survey and owing to the large number of females incubated, we used average female and egg masses (Table 1) for the calculation of female growth rate.

For molting rate experiments, at least 15 individuals (mean = 30.1) of a particular stage of *C. agulhensis* were incubated in a 2-liter jar. After 24 h, the contents of the incubation bottle were preserved. In the laboratory, the ratio of individuals that had molted to the total number incubated was determined. This was combined with stage-specific body mass values (Table 1) to calculate growth rates according to Peterson et al. (1991). Although the mass of individual copepods and their growth increments are variable (Berggreen et al. 1988; Paffenhöfer 1994), we have used average stage-specific body masses to calculate somatic growth because of the large number of individuals incubated and because growth rates are more sensitive to changes in molting ratios than growth increments (Webber and Roff 1995). Stage duration was calculated as the reciprocal of the molting ratio (Falkowski et al. 1984). Average duration of each stage was then estimated using a geometric mean to give each ratio (stage duration) equal weight (Zar 1984).

At each station, the concentration of Chl *a* at the depth of maximum fluorescence was used as a measure of ambient food availability for copepods. Samples for total Chl *a* were filtered through Whatman GF/F filters and analyzed fluorometrically using a fluorometer (model 10-000R, Turner Designs) (Parsons et al. 1984). The functional response of copepod growth rate to food availability was described by an Ivlev curve (Hutchings et al. 1995). In addition, stations were categorized into low (≤2 mg Chl *a* m^{-3}) and high (>2 mg Chl *a* m^{-3}) food availability for copepods, based on the critical Chl *a* concentration of 2 mg Chl *a* m^{-3} for initiation of egg production (Hutchings 1992). Frequency distributions of growth rate under low and high food conditions could then be examined. The food available to copepods was also measured in terms of particle volume in 5-μm intervals (5–75-μm equivalent spherical diameter [ESD]) using a multisizer (Coulter) fitted with a 140-μm aperture tube.

Results

Growth rates (mean ± SD and range) and average stage durations are given in Table 1. Mean growth rates decreased by more than one order of magnitude with increasing copepod size, from 0.545 d^{-1} for *C. agulhensis* N6 (525-μm TL) to 0.053 d^{-1} for *C. agulhensis* females (2,763-μm TL). A negative exponential function best described the relationship between mean growth rate and mean body size (Fig. 2; $r^2 = 0.96$, $n = 10$, $P < 0.0001$). This decrease corresponded to a marked increase in stage duration of *C. agulhensis,* from 1.27 d for N6 to 8.48 d for C5.

In contrast, maximum growth rate exhibited less than a threefold decline over the above size range, from 0.849 d^{-1} (*C. agulhensis* C2) to 0.328 d^{-1} (female *C. agulhensis;* Table

Table 1. Average body mass, egg mass, total length (TL), growth rate (mean ± SD and range), and the geometric mean of stage duration (*D*), for the copepods examined in this study, ranked from the smallest to the largest. Also shown is the asymptotic growth rate (g_a) and the rate at which growth approaches this asymptote (*k*) for Ivlev curves [$g = g_a(1 - e^{-k \times c})$] fitted to copepod growth rate (*g*) vs. Chl *a* (*c*). The proportion of variance explained (r^2) and the Chl *a* at which 90% of maximum growth rate is obtained ($c_{0.9g_a}$) are also given. *n* = the number of samples.

Species/Stage	Body mass (μg dry weight)	Egg mass (μg dry weight)	TL (μm)	Mean ± SD	Range	*D*	g_a	*k*	r^2	$c_{0.9g_a}$	*n*
Calanus agulhensis N6	2*	—	525**	0.545 ± 0.110	0.204–0.693	1.27	0.550	4.827	0.05	0.5	36
C. agulhensis C1	4†	—	785††	0.510 ± 0.206	0.116–0.811	1.59	0.612	1.970	0.11	1.2	92
C. agulhensis C2	9†	—	939††	0.421 ± 0.195	0.027–0.849	2.12	0.551	1.435	0.17	1.6	114
C. agulhensis C3	22†	—	1,193**	0.278 ± 0.164	0.000–0.709	2.65	0.400	1.035	0.22	2.2	126
C. agulhensis C4	46†	—	1,700††	0.240 ± 0.162	0.000–0.720	3.11	0.396	0.591	0.26	3.9	150
Centropages brachiatus ♀	25†	0.075‖	1,756††	0.214 ± 0.138	0.000–0.608		0.257	0.475	0.09	4.8	158
Nannocalanus minor ♀	35‡	0.25¶	1,800‡‡	0.159 ± 0.152	0.000–0.523		0.253	0.662	0.31	3.5	82
C. agulhensis C5	97†	—	2,309††	0.097 ± 0.096	0.000–0.468	8.48	0.144	0.895	0.06	2.6	143
Calanoides carinatus ♀	123§	0.5‖	2,640§	0.086 ± 0.104	0.000–0.460		0.194	0.160	0.24	14.4	350
C. agulhensis ♀	202†	0.6#	2,763††	0.053 ± 0.062	0.000–0.328		0.180	0.150	0.38	15.4	1,492

* From Sea Fisheries Research Institute (SFRI) unpubl. data.
† From Peterson et al. (1990).
‡ Converted from PL (prosome length): ln(dry weight) = 2.74 ln(PL) − 16.41 (Chisholm and Roff 1990*a*), where PL = (TL − 52.4)/1.198 (van der Lingen unpubl. data).
§ From Verheye (1991).
‖ From Peterson (1989).
¶ From egg diameter (ED): ln(dry weight) = −3.578 + 0.0147 × ED (van der Lingen unpubl. data), assuming egg size for *N. minor* is 150 μm (excluding perivitelline space).
# Using egg mass of *Calanus finmarchicus* (McLaren et al. 1989).
** Huggett (unpubl. data).
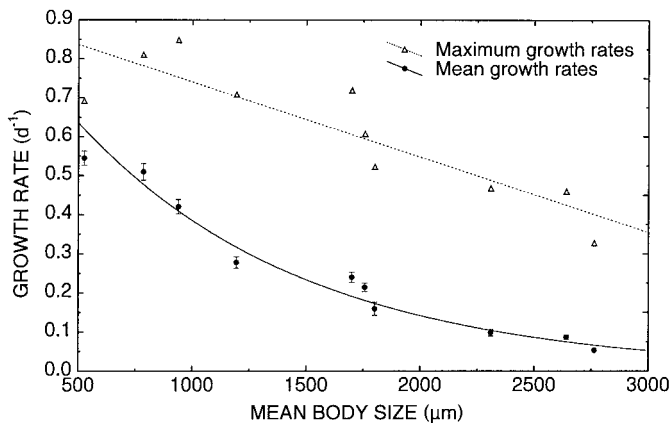†† From Stuart and Huggett (1992).
‡‡ From Rose (1933).

Fig. 2. The relationship of mean (±SE) and maximum copepod growth rates vs. mean body size in the southern Benguela system. The equation fitted to maximum growth rates is $y = 0.93363 - 0.00019x$, $r^2 = 0.79$, $n = 10$, $P < 0.001$. The equation fitted to mean growth rates is $y = 1.0485445e^{-0.001001x}$, $r^2 = 0.96$, $n = 10$, $P < 0.0001$. The n for each species is shown in Table 1.

1). There was a significant linear decline of maximum growth rate with increasing size (Fig. 2; $r^2 = 0.79$, $n = 10$, $P < 0.001$). It should be noted that the maximum growth rate for *C. agulhensis* N6 and C1 was underestimated because all individuals had molted within the 24-h duration of the experiments. Often, large copepods did not molt or lay eggs within this period, whereas the minimum growth rate of smaller copepods was always above zero.

The coefficient of variation (C.V.), the ratio of the standard deviation to the mean, was used to compare the variability in growth rate of copepods of different size. A strong positive relationship between the C.V. of growth and body size was evident ($r^2 = 0.94$, $n = 10$, $P < 0.0001$). Thus, small copepods were consistently growing rapidly (small C.V.), whereas the growth rate of large copepods was more variable.

Growth rates were positively related to total Chl a concentration (Fig. 3). Parameters for each Ivlev curve, the r^2, and the concentration of Chl a at which 90% of the maximum asymptotic growth rate was achieved are given in Table 1. Although <40% of the variability in the growth rate of each species was explained by total Chl a, several general patterns are evident from the Ivlev parameters. First, the asymptotic growth rate (g_a) was negatively related to body size ($r^2 = 0.86$, $n = 10$, $P < 0.0001$). This suggests that food-saturated growth rate decreased with increasing body size. Second, the rate at which growth approaches the asymptotic rate (k) decreased with increasing body size ($r^2 = 0.59$, $n = 10$, $P < 0.01$). Thus, maximum growth rate was attained at lower Chl a for smaller copepods, as was evident from the lower Chl a at which 90% of the maximum growth rate was achieved (Table 1). Lastly, the r^2 generally increased with body size, although this relationship was not significant when all copepods were included ($P > 0.05$). The small r^2 for *C. agulhensis* C5 and female *C. brachiatus* did not fit this trend. This lack of dependence of growth rate on Chl a may be because *C. brachiatus* is omnivorous (compared with the other copepod genera, which are predomi-

nantly herbivorous; *see* Boyd et al. 1980; Turner 1984), and C5 copepodites often store food reserves in the form of lipids in preparation for their final molt to adulthood (Borchers and Hutchings 1986). After removing these two copepods from the analysis, the r^2 was positively related to copepod size ($r^2 = 0.74$, $n = 8$, $P < 0.01$). Collectively, the trends described above imply a greater dependence of growth rate of large copepods on chlorophyllous phytoplankton.

The growth rate of copepods under conditions of low (≤2 mg m⁻³) and high (>2 mg m⁻³) Chl a for the different species is shown in Fig. 4a. Growth rate increased substantially under high Chl a relative to low Chl a. This proportional increase in growth rate from low to high Chl a was positively related to body size (Fig. 4b; $r^2 = 0.78$, $P < 0.001$), indicating that the degree of food limitation, as measured by Chl a, was greater for larger copepods. A further implication may be that smaller copepods utilize nonchlorophyllous food sources.

Marked differences in the frequency distributions of growth rate under low and high Chl a were apparent for species of different sizes (Fig. 5). Under low Chl a, the frequency distributions of small copepods (e.g., *C. agulhensis* N6, C1, and C2) were more symmetric than those of large copepods (e.g., C5 and female *C. agulhensis* and female *C. carinatus*), which were heavily skewed toward slow growth rates. Further, the frequency distributions showed a progressive increase in skewness toward slower growth rates as body size increased. This suggests that most small copepods were growing rapidly, even under low Chl a, and that proportionately more individuals were growing poorly as body size increased. It is noteworthy that the change in the shape of the distributions from low to high Chl a was related to body size. For large copepods, the distributions under low and high Chl a were skewed toward slower growth rates, with greater bias at low Chl a. For small copepods, the distributions under low and high Chl a had greater symmetry than large copepods, although the mode of the distribution did shift toward faster growth rates under high Chl a. (Note that the frequency distribution for *C. agulhensis* N6 was truncated at a growth rate of 0.6–0.7 and for *C. agulhensis* C1 at 0.8–0.9, because all individuals had molted within 24 h.) For copepods intermediate in size, there were striking changes in shape of the frequency distribution of their growth rate, from being skewed toward a slow growth rate at low Chl a to greater symmetry at high Chl a. These changes can be summarized by calculating the skewness of each distribution. Skewness is zero for a symmetrical distribution and is positive when it is biased toward slow growth rates. The degree of skewness was positively related to copepod body size under both low ($r^2 = 0.76$, $P < 0.001$) and high ($r^2 = 0.62$, $P < 0.01$) Chl a. Furthermore, the frequency distributions for all copepods (except *C. agulhensis* N6) were more skewed under low than high Chl a.

The more extensive data set for the two largest copepods, female *C. agulhensis* and *C. carinatus*, enabled the effect of increasing Chl a on the frequency distributions of growth rate for large copepods to be explored in more detail (Fig. 6). The frequency distributions for both species were markedly skewed toward slow growth rate for Chl a ≤2 mg m⁻³ (Fig. 6a,f). As Chl a increased to 6 mg m⁻³, the distributions
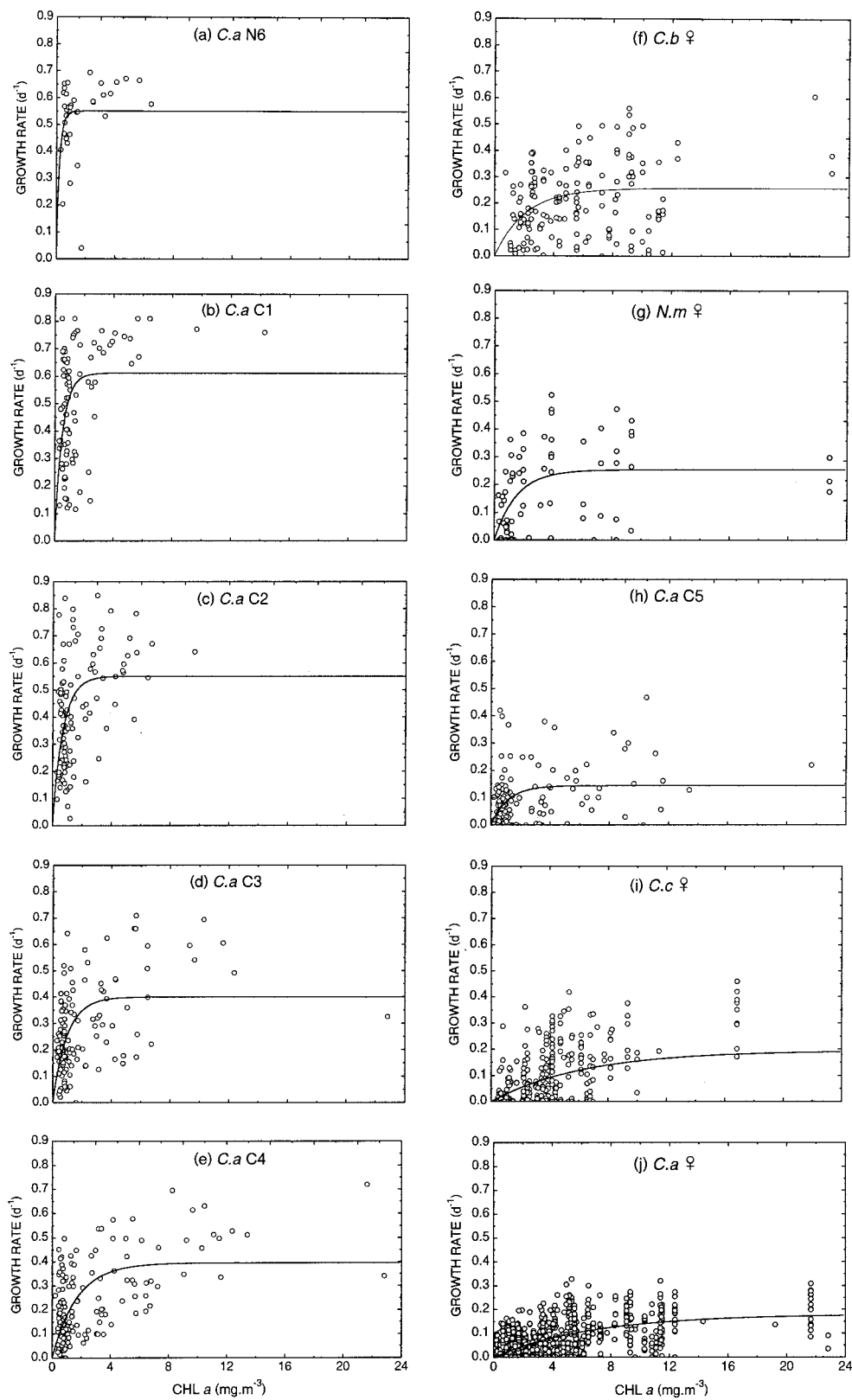
Fig. 3. Growth rates against Chl *a* for (a) the smallest, to (j) the largest copepod examined. Ivlev curves were fitted (*see Table 1 for details of equations*). *C.a* = *C. agulhensis, C.b* = *C. brachiatus, N.m* = *N. minor,* and *C.c* = *C. carinatus.*

became progressively less skewed for both species (Fig. 6b,c,g,h). For Chl *a* concentrations of 6–8 mg m^{-3}, the distribution changed shape (Fig. 6d,i), with more individuals producing more eggs, especially in the case of *C. agulhensis*. Above Chl *a* concentrations of 8 mg m^{-3}, the shape of the distributions for both species tended toward symmetry (Fig. 6e,j). The skewness of the distributions did decrease significantly with increasing Chl *a* for both *C. agulhensis* (r^2 = 0.86, n = 5, P < 0.05) and *C. carinatus* (r^2 = 0.92, n = 5, P < 0.01). These findings are compatible with the concept of food limitation of large copepods at low Chl *a*.

Analysis of particle spectra reveals that the study area is dominated by particles <25-μm ESD (Fig. 7a), with those <15-μm ESD occurring at a consistent background density, as indicated by a lower C.V. of particle volume than for particles >15-μm ESD (Fig. 7b).

Discussion

Body size—Growth rates of copepods in the southern Benguela upwelling system decreased with increasing body size. This decline may be a general phenomenon and has been documented in both field (Peterson et al. 1991; Hutchings et al. 1995) and laboratory studies in terms of stage duration (Peterson et al. 1990), somatic growth (Paffenhöfer 1976; Vidal 1980), and egg production (Ambler 1985). Allometric relationships, which describe many biological rate processes such as size-specific growth rates in copepods (Banse and Mosher 1980; McLaren et al. 1989; Hirst and Sheader 1997), may account for the less than threefold decline in maximum growth rates between the largest (female *C. agulhensis*) and the smallest copepods (*C. agulhensis* N6) in this study (Table 1). Mean growth rate, however, was one order of magnitude slower for the largest copepod compared with the smallest one, implying that an environmental factor may limit growth.

Food limitation—It is suggested that the primary factor responsible for the decrease in mean growth rate with size in the southern Benguela upwelling region is food limitation, the degree of which increases with body size. A very similar situation has been observed in the tropical ocean, with larger copepod species being food limited above copepodite C1 in size and smaller species above C2 (Webber and Roff 1995). A recent global synthesis of growth rate data has also shown that weight-specific fecundity of female copepods declines with increasing body weight (Kiørboe and Sabatini 1995). Moreover, the growth rate of *C. carinatus,* a common large copepod in the southern Benguela region, also declines with increasing body size (Richardson and Verheye 1998). These strong declines in growth rate with size contrast with Vidal's (1980:111) conclusion from laboratory experiments that "extrapolation of growth rates from one species to another on the basis of similarity in body size is not justified." Because food limitation appears similar for species of the same size in the southern Benguela system, it is postulated that growth rates of calanoid copepods in this system can be estimated from body size.

The phenomenon of increased food limitation with copepod body size supports the assertion of Verheye et al. (1994),
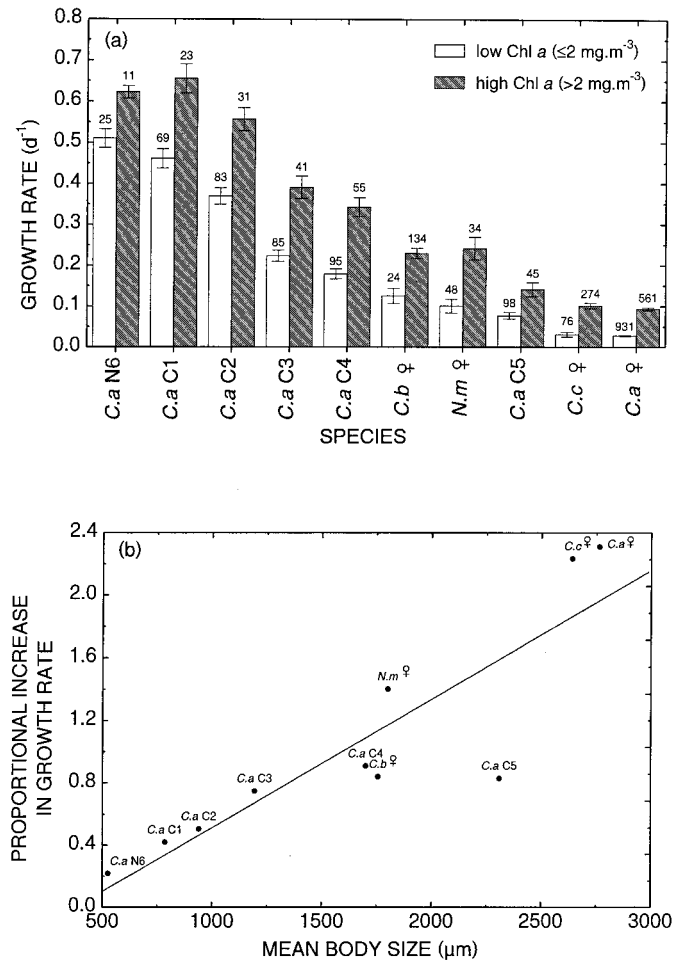

Fig. 4. (a) Growth rate of copepods under conditions of low and high Chl *a*. Standard errors and the number of samples are shown. (b) The proportional increase in growth rate of each species from low to high food conditions against mean body size. *C.a* = *C. agulhensis, C.b* = *C. brachiatus, N.m* = *N. minor,* and *C.c* = *C. carinatus.*

which is that there is intraspecific size-based food partitioning in *C. agulhensis,* and extends it to include interspecific food partitioning based on size. A consequence of progressive food limitation of *C. agulhensis* as body size increases is that juvenile growth is unrelated to female growth in the southern Benguela system (*see also* Hutchings et al. 1995). Thus, juvenile growth rate cannot be estimated from that of females, although there may be less variability in growth of small copepods than previously thought.

Growth rates of *C. agulhensis* N6 were fast, consistent (small C.V.), and independent of Chl *a*. This is despite the maximum growth rate of *C. agulhensis* N6 in this study being underestimated because the duration of the incubation (24 h) is the minimum stage duration that can be estimated. Stage durations in the field for calanoid nauplii can be <1 d (Webber and Roff 1995), and in some of our experiments, all the nauplii had indeed molted within 24 h. Nauplii of freshwater and coastal marine copepods are known to have fast and consistent growth rates (Hart 1990). This is a con-
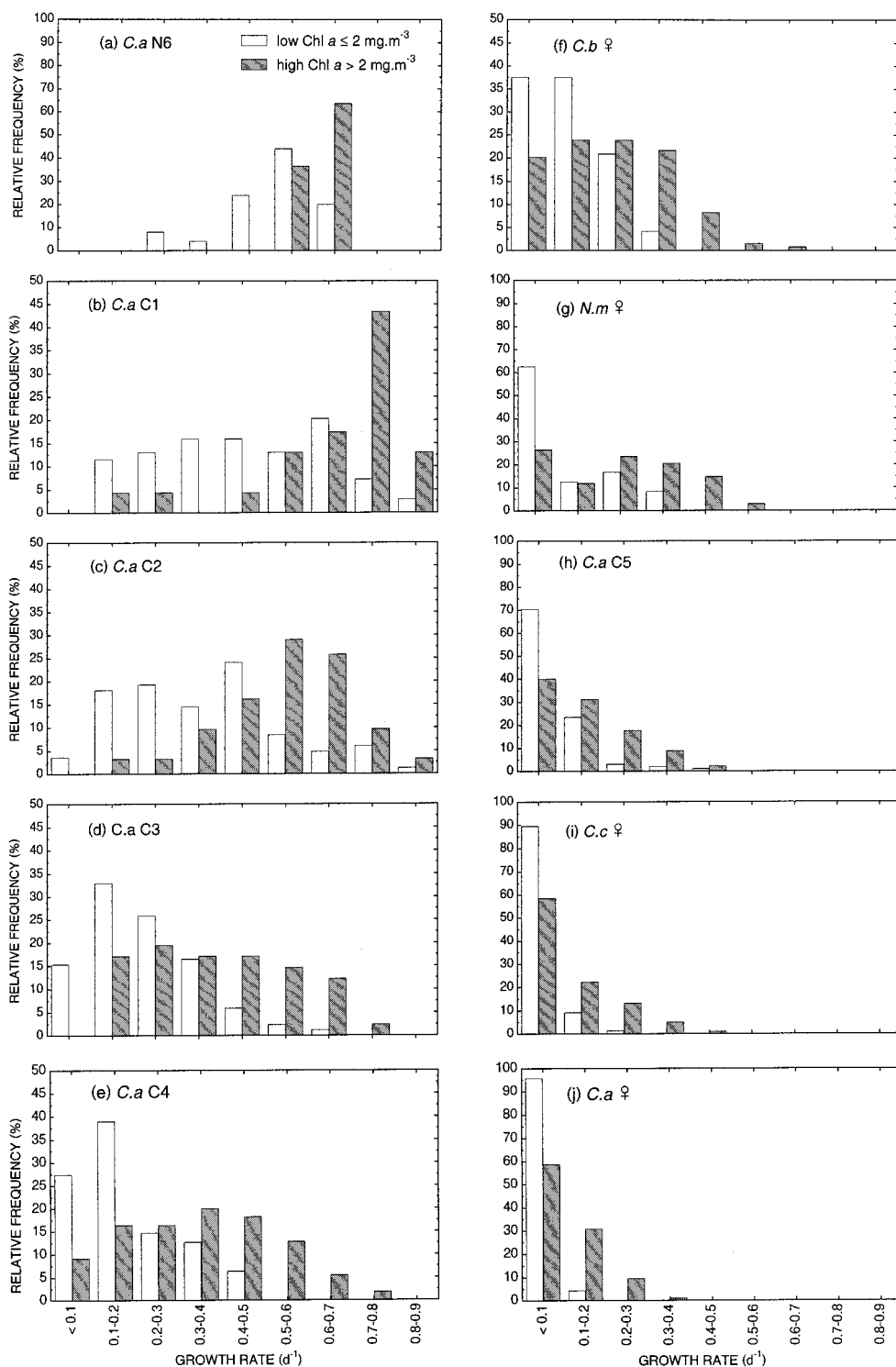
Fig. 5.   Frequency distributions of growth rate under conditions of low and high Chl *a* for (a) the smallest, to (j) the largest copepod. Note the different y-scales. *C.a = C. agulhensis, C.b = C. brachiatus, N.m = N. minor,* and *C.c = C. carinatus.* The number of samples are the same as Fig. 4.
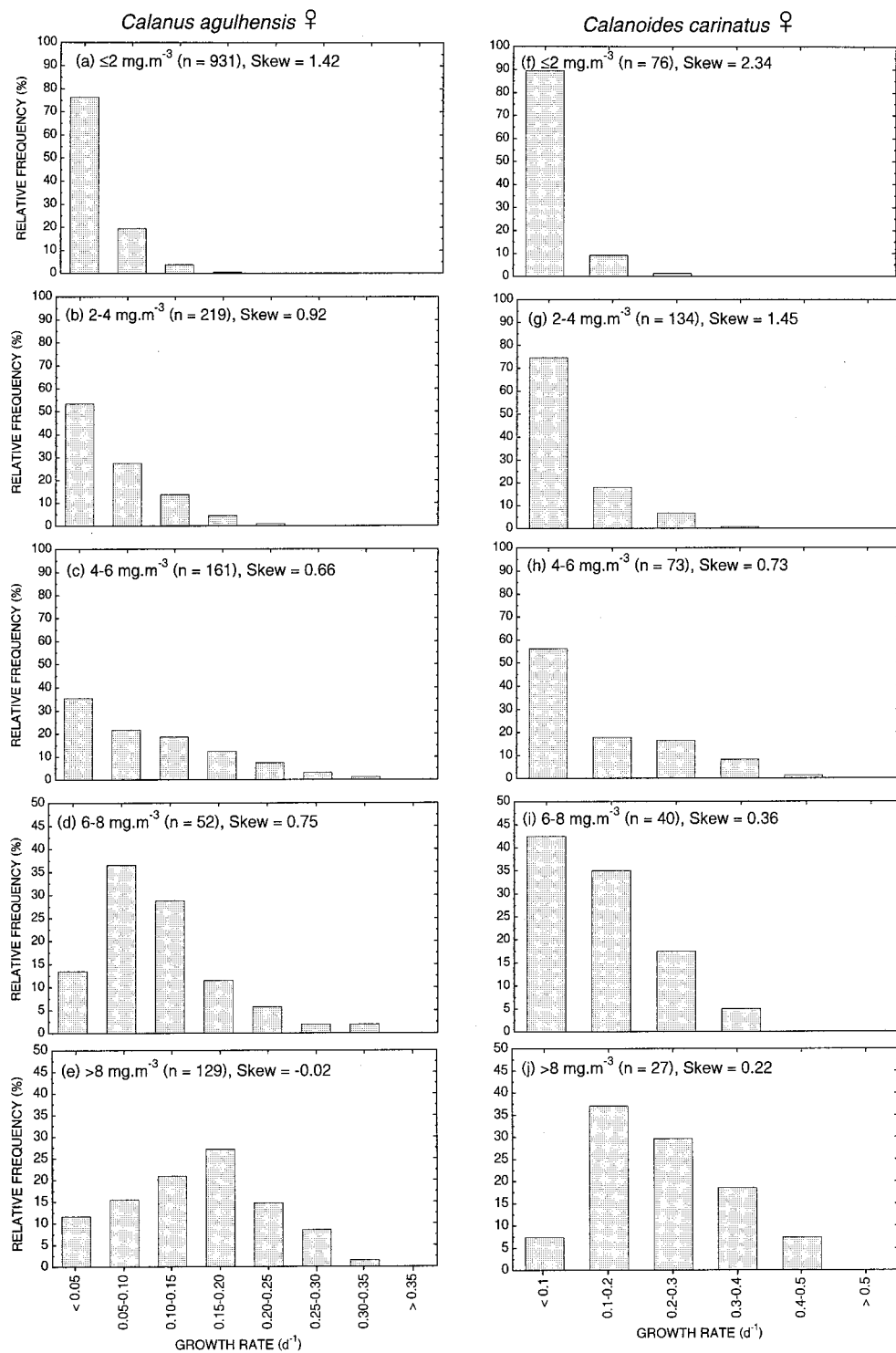
Fig. 6. Frequency distributions of growth rate of *C. agulhensis* (a)–(e) and *C. carinatus* (f)–(j) for five Chl *a* concentrations. The number of samples is in brackets. Note two y-scales are used and that the x-scales are different for the two species because more samples were available for *C. agulhensis,* allowing greater resolution.
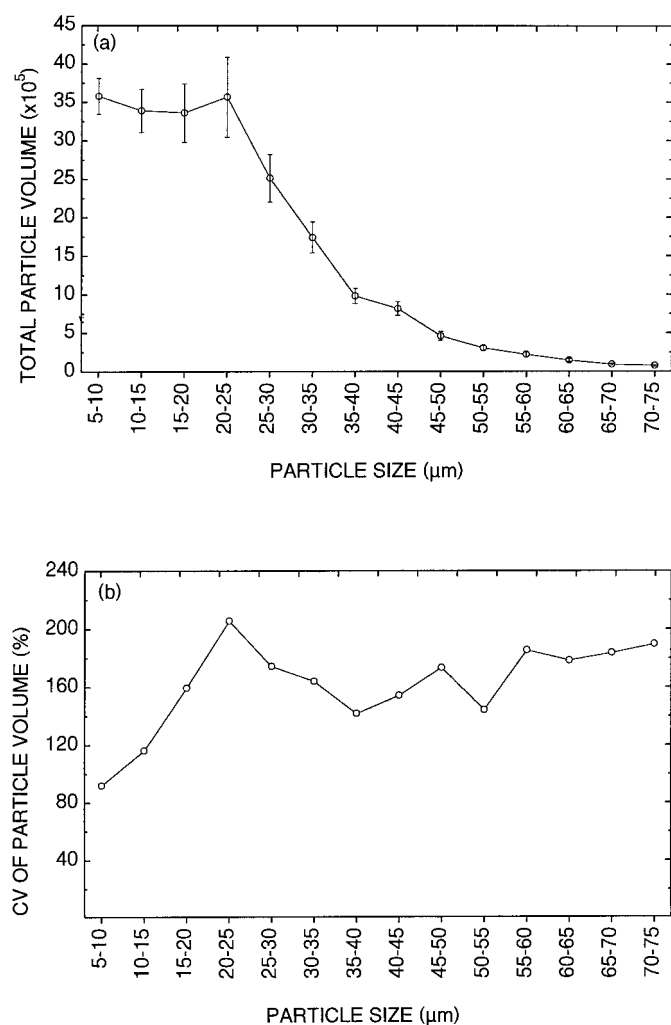
Fig. 7. (a) Mean (±SE) of total particle volume (cubic micrometers) against particle size in 5-μm intervals, and (b) the C.V. of particle volume against particle size. Standard errors are shown in (a). The number of samples for each interval is 168.

Fig. 8. Probability distributions of a Poisson variable for encounter rates (λ) of 1, 2, and 5. Note that the unit of time for the x-axis scale is arbitrary.

sequence of their slow metabolic rates (Paffenhöfer 1976) and their ability to ingest picoplankton (Roff et al. 1995). The role of the microbial community in supporting fast growth rates of copepods has been recognized in oligotrophic seas (Webber and Roff 1995), where the numbers of bacteria and picoplankton are less variable than larger sized nano- and netplankton (Hopcroft and Roff 1990).

Growth rates of other small copepods (particularly *C. agulhensis* C1 and C2) were also consistent and largely independent of Chl *a,* even at very low Chl *a,* implying little or no food limitation. This may be owing to their preference for smaller food particles. The optimal size of food particles for copepods has been estimated to be 2–5% of their prosome length (Berggreen et al. 1988). This translates into an optimal food size range of 8–20, 12–31, and 15–37 μm for *C. agulhensis* N6, C1, and C2, respectively. Thus, the range of optimal food particle sizes for these small copepods includes microflagellates, which are ubiquitous and abundant throughout the southern Benguela region (Fig. 7; Painting et
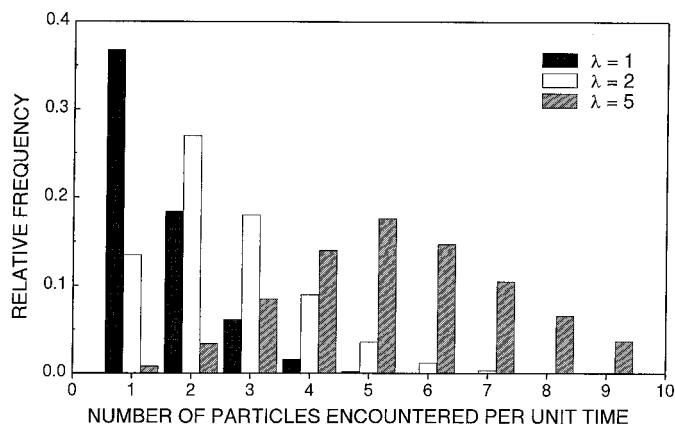
al. 1993). The concept that eutrophic upwelling areas are dominated by large diatoms (Cushing 1989) needs to be broadened to include the microheterotrophic pathways (Hutchings 1992). Fast growth rates of copepods can therefore be achieved by being small and by feeding on small phyto- and zooplankton (Webber and Roff 1995). Moreover, the suggestion that young stages are more susceptible to starvation than older ones (Paffenhöfer 1976; Borchers and Hutchings 1986; Hutchings 1992) may not be valid in upwelling areas such as the southern Benguela system. The growth rate of small copepods in other aquatic systems that have a consistent microheterotrophic food web may also be relatively constant.

Although large copepods can also ingest small cells (Borchers and Hutchings 1986; Peterson et al. 1990), the concentrations of small cells in the southern Benguela region are usually not adequate to support fast growth rates of large copepods (Richardson and Verheye 1998). Their growth rates are frequently food limited because they preferentially ingest particles >20 μm in size (Berggreen et al. 1988). They feed more efficiently on these large cells (Frost 1977), obtaining their maximal daily ration at relatively low carbon concentrations (Frost 1972). In the southern Benguela system, the concentration of Chl *a* is positively related to the proportion of large cells (Mitchell-Innes and Pitcher 1992; Richardson and Verheye 1998). Thus, there is sufficient Chl *a* to ensure fast growth rates by large copepods only when there are large cells present.

Encounter rate model—The degree of food limitation is related to the availability of appropriately sized food particles for a copepod of a particular size. The effect of food limitation on individual copepods in the southern Benguela region was reflected in the shape of the frequency distributions of growth rate (Figs. 5, 6). The changes in shape of these distributions may be a result of the different amounts of food ingested by each copepod in a population under different food densities. A conceptual model is developed here to explain the different frequency distributions of growth rate for copepods of varying size. The total number of particles ingested is related to the density and size of particles avail-

able and can be described by the following Poisson distribution:

$$f(x) = \frac{\lambda^x e^{-\lambda}}{x!} \quad \text{(Evans et al. 1993),}$$

where $f(x)$ is the probability function, λ is the expected value of x, and $x!$ is $x \times (x - 1) \times (x - 2) \times \ldots \times 1$. In this probabilistic model, λ can be interpreted as the average encounter rate by a copepod with particles of an appropriate size for it to feed on, and x as the number of particles actually encountered and eaten by a particular copepod. For small copepods, their food source (small cells) is always abundant (Fig. 7b), and thus, they always have a high encounter rate, independent of the total concentration of Chl *a*. Therefore, in terms of the population, the distribution of the number of particles ingested by the copepods is symmetric and approximates normality (Fig. 8: $\lambda = 5$). The shape of this distribution is similar to the frequency distribution describing growth rate for small copepods (Fig. 5b,c), because growth rate is a function of the total number of particles ingested.

At low Chl *a*, phytoplankton is generally dominated by microflagellates with few large cells present (Mitchell-Innes and Pitcher 1992). Large copepods therefore encounter low numbers of large particles, and the distribution of total particles encountered is severely skewed toward low numbers (Fig. 8: $\lambda = 1$). Because copepods must obtain a minimum amount of energy to initiate egg production (Hutchings 1992) or to molt, the distribution is skewed toward slow growth at low encounter rates (Fig. 6a,f). At elevated Chl *a*, the greater proportion of large cells (Richardson and Verheye 1998) increases the probability of large copepods encountering particles of a suitable size. A sufficient food ration can now be obtained by most individuals for initiation of egg production or ecdysis, and the distribution is less skewed (cf. Fig. 8: $\lambda = 2$ with Fig. 6d,j). As the Chl *a* and hence encounter rate increase further, there is sufficient food for all individuals to grow (cf. Fig. 8: $\lambda = 5$ with Fig. 6e). The distribution is symmetric, and at high encounter rates, it approximates the normal distribution (Evans et al. 1993). A similar frequency distribution was reported by Peterson (1988) for *Calanus marshallae* fed excess food in the laboratory. Therefore, calanoid copepod growth rates in the southern Benguela region appear to be controlled by the interplay between body size, food size, and food density.

The consistency of the relationships between copepod growth rate and body size identified in this study using two independent field techniques, the broad size range of the copepods examined (525–2,763 μm) and the varied environmental conditions (9–23°C, 0.1–23 mg Chl *a* m^{-3}) over which the data were collected, suggest that the progressive food limitation of growth rate as body size increases may apply to the entire community of calanoid copepods in the southern Benguela system. Moreover, this phenomenon may also occur in other aquatic systems with a significant microbial component.

References

AMBLER, J. W. 1985. Seasonal factors affecting egg production and viability of eggs of *Acartia tonsa* Dana from East Lagoon, Galveston, Texas. Estuarine Coastal Shelf Sci. **20:** 743–760.

BAN, S. 1994. Effect of temperature and food concentration on post-embryonic development, egg production and adult body size of the calanoid copepod *Eurytemora affinis*. J. Plankton Res. **16:** 721–735.

BANSE, K., AND S. MOSHER. 1980. Adult body mass and annual production/biomass relationships of field populations. Ecol. Monogr. **50:** 355–379.

BAUTISTA, B., R. P. HARRIS, V. RODRIGUEZ, AND F. GUERRERO. 1994. Temporal variability in copepod fecundity during two different spring bloom periods in coastal waters off Plymouth (SW England). J. Plankton Res. **16:** 1367–1377.

BERGGREEN, U., B. HANSEN, AND T. KIØRBOE. 1988. Food size spectra, ingestion and growth of the copepod *Acartia tonsa* during development: Implications for determination of copepod production. Mar. Biol. **99:** 341–352.

BORCHERS, P., AND L. HUTCHINGS. 1986. Starvation tolerance, development time and egg production of *Calanoides carinatus* in the southern Benguela Current. J. Plankton Res. **8:** 855–874.

BOYD, C. M., S. L. SMITH, AND T. J. COWLES. 1980. Grazing patterns of copepods in the upwelling system off Peru. Limnol. Oceanogr. **25:** 583–596.

CHISHOLM, L. A., AND J. C. ROFF. 1990a. Size-weight relationships and biomass of tropical neritic copepods off Kingston, Jamaica. Mar. Biol. **106:** 71–77.

———, AND ———. 1990b. Abundances, growth rates, and production of tropical neritic copepods off Kingston, Jamaica. Mar. Biol. **106:** 79–89.

CUSHING, D. H. 1989. A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. J. Plankton Res. **11:** 1–13.

EVANS, M., N. HASTINGS, AND B. PEACOCK. 1993. Statistical distributions, 2nd ed. Wiley.

FALKOWSKI, P. G., J. VIDAL, T. S. HOPKINS, G. T. ROW, T. E. WHITLEDGE, AND W. G. HARRISON. 1984. Summer nutrient dynamics in the Middle Atlantic Bight: Primary production and utilization of phytoplankton carbon. J. Plankton Res. **5:** 515–537.

FROST, B. W. 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. Limnol. Oceanogr. **17:** 805–815.

———. 1977. Feeding behavior of *Calanus pacificus* in mixtures of food particles. Limnol. Oceanogr. **22:** 472–491.

HART, R. C. 1990. Copepod post-embryonic durations: Pattern, conformity, and predictability. The realities of isochronal and equiproportional development, and trends in the copepodid–naupliar duration ratio. Hydrobiologia **206:** 175–206.

———. 1991. Food and suspended sediment influences on the naupliar and copepodid durations of freshwater copepods: Comparative studies on *Tropodiaptomus* and *Metadiaptomus*. J. Plankton Res. **13:** 683–689.

HIRST, A. G., AND M. SHEADER. 1997. Are *in situ* weight-specific growth rates body-size independent in marine planktonic copepods? A reanalysis of the global syntheses and a new empirical model. Mar. Ecol. Prog. Ser. **154:** 155–165.

HOPCROFT, R. R., AND J. C. ROFF. 1990. Phytoplankton size fractions in a tropical neritic ecosystem near Kingston, Jamaica. J. Plankton Res. **12:** 1069–1088.

HUNTLEY, M. E., AND M. D. G. LOPEZ. 1992. Temperature-dependent production of marine copepods: A global synthesis. Am. Nat. **140:** 201–242.

HUTCHINGS, L. 1992. Fish harvesting in a variable, productive environment—searching for rules or searching for exceptions? *In* A. I. L. Payne, K. H. Brink, K. H. Mann, and R. Hilborn [eds.], Benguela trophic functioning. South Afr. J. Mar. Sci. **12:** 297–318.

———, H. M. VERHEYE, B. A. MITCHELL-INNES, W. T. PETERSON, J. A. HUGGETT, AND S. J. PAINTING. 1995. Copepod production

in the southern Benguela system. ICES J. Mar. Sci. **52:** 439–455.

KIØRBOE, T., AND M. SABATINI. 1995. Scaling of fecundity, growth and development in marine planktonic copepods. Mar. Ecol. Prog. Ser. **120:** 285–298.

LAABIR, M., S. A. POULET, AND A. IANORA. 1995. Measuring production and viability of eggs in *Calanus helgolandicus*. J. Plankton Res. **17:** 1125–1142.

MCKINNON, A. D., AND S. R. THORROLD. 1993. Zooplankton community structure and copepod egg production in coastal waters of the central Great Barrier Reef lagoon. J. Plankton Res. **15:** 1387–1411.

MCLAREN, I. A., M. J. TREMBLAY, C. J. CORKETT, AND J. C. ROFF. 1989. Copepod production on the Scotian Shelf based on life-history analyses and laboratory rearings. Can. J. Fish. Aquat. Sci. **46:** 560–583.

MITCHELL-INNES, B. A., AND G. C. PITCHER. 1992. Hydrographic parameters as indicators of the suitability of phytoplankton populations as food for herbivorous copepods. *In* A. I. L. Payne et al. [eds.], Benguela trophic functioning. South Afr. J. Mar. Sci. **12:** 355–365.

PAFFENHÖFER, G-A. 1976. Feeding, growth, and food conversion of the marine planktonic copepod *Calanus helgolandicus*. Limnol. Oceanogr. **21:** 39–50.

———. 1994. Variability due to feeding activity of individual copepods. J. Plankton Res. **16:** 617–626.

PAINTING, S. J., M. I. LUCAS, W. T. PETERSON, P. C. BROWN, L. HUTCHINGS, AND B. A. MITCHELL-INNES. 1993. Dynamics of bacterioplankton, phytoplankton and mesozooplankton communities during the development of an upwelling plume in the southern Benguela. Mar. Ecol. Prog. Ser. **100:** 35–53.

PARSONS, T. R., Y. MAITA, AND C. M. LALLI. 1984. A manual of chemical and biological methods for seawater analysis, 14th ed. Pergamon.

PETERSON, W. T. 1988. Rates of egg production by the copepod *Calanus marshallae* in the laboratory and in the sea off Oregon, USA. Mar. Ecol. Prog. Ser. **47:** 229–237.

———. 1989. Zooplankton feeding and egg production in comparison to primary production along the west coast of South Africa, p. 1–5. *In* Proceedings of the Plankton Dynamics Minisymposium, May 1989. BEP Rep. 17.

———, AND L. HUTCHINGS. 1995. Distribution, abundance and production of the copepod *Calanus agulhensis* on the Agulhas Bank in relation to spatial variations in hydrography and chlorophyll concentration. J. Plankton Res. **17:** 2275–2294.

———, S. J. PAINTING, AND L. HUTCHINGS. 1990. Diel variations in gut pigment content, diel vertical migration and estimates of grazing impact for copepods in the Southern Benguela upwelling region in October 1987. J. Plankton Res. **12:** 259–281.

———, P. TISELIUS, AND T. KIØRBOE. 1991. Copepod egg production, moulting and growth rates, and secondary production, in the Skagerrak in August 1988. J. Plankton Res. **13:** 131–154.

PITCHER, G. C., A. J. RICHARDSON, AND J. L. KORRÛBEL. 1996. The use of sea temperature in characterizing the mesoscale heterogeneity of phytoplankton in an embayment of the southern Benguela upwelling system. J. Plankton Res. **18:** 643–657.

POND, D., R. HARRIS, R. HEAD, AND D. HARBOUR. 1996. Environmental and nutritional factors determining seasonal variability in the fecundity and egg viability of *Calanus helgolandicus* in coastal waters off Plymouth, UK. Mar. Ecol. Prog. Ser. **143:** 45–63.

RICHARDSON, A. J., AND H. M. VERHEYE. 1998. The relative importance of food and temperature to copepod egg production and somatic growth in the southern Benguela upwelling system. J. Plankton Res. **20**: 2379–2399.

ROFF, J. C., J. T. TURNER, M. K. WEBBER, AND R. R. HOPCROFT. 1995. Bacterivory by tropical copepod nauplii: Extent and possible significance. Aquat. Microb. Ecol. **9:** 165–175.

ROSE, M. 1933. Faune de France. 26 Copépodes Pélagiques, 1st ed. Lechevalier. [In French]

STUART, V., AND J. A. HUGGETT. 1992. Prey selection by *Euphausia lucens* (Hansen) and feeding behaviour in response to a mixed algal and animal diet. J. Exp. Mar. Biol. Ecol. **164:** 117–133.

TURNER, J. T. 1984. The feeding ecology of some zooplankters that are important prey items of larval fish. NOAA Tech. Rep. NMFS **7:** 1–28.

VERHEYE, H. M. 1991. Short-term variability during an anchor station study in the southern Benguela upwelling system: Abundance, distribution and estimated production of mesozooplankton with special reference to *Calanoides carinatus* (Krøyer, 1849). Prog. Oceanogr. **28:** 91–119.

———, L. HUTCHINGS, J. A. HUGGETT, R. A. CARTER, W. T. PETERSON, AND S. J. PAINTING. 1994. Community structure, distribution and trophic ecology of zooplankton on the Agulhas Bank with special reference to copepods. South Afr. J. Sci. **90:** 154–165.

VIDAL, J. 1980. Physioecology of zooplankton. I. Effects of phytoplankton concentration, temperature, and body size on the growth rate of *Calanus pacificus* and *Pseudocalanus* sp. Mar. Biol. **56:** 111–134.

WEBBER, M. K., AND J. C. ROFF. 1995. Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. Mar. Biol. **123:** 481–495.

ZAR, J. H. 1984. Biostatistical analysis, 2nd ed. Prentice-Hall.