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# The relative importance of food and temperature to copepod egg production and somatic growth in the southern Benguela upwelling system

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**Abstract.** The fecundity and somatic growth rates of *Calanus agulhensis* and *Calanoides carinatus*, the dominant large calanoid copepods in the southern Benguela upwelling system, as well as the fecundity of several other common copepods, were measured between September and March of 1993/94 and 1994/95. Mean egg production of most copepods was low at <30 eggs female$^{-1}$ day$^{-1}$ (*Calanoides carinatus* 23.7, *Calanus agulhensis* 19.0, *Neocalanus tonsus* 16.1 and *Rhincalanus nasutus* 26.1), whereas the mean fecundity of *Centropages brachiatus* was significantly greater (83.6 eggs female$^{-1}$ day$^{-1}$). This study also presents the first comprehensive field estimates of the fecundity of *Nannocalanus minor* (mean: 26.1 eggs female$^{-1}$ day$^{-1}$, range: 0.0–96.2 eggs female$^{-1}$ day$^{-1}$) and of somatic growth of N6 and all copepodite stages of *Calanoides carinatus* (decreasing from 0.58 day$^{-1}$ for N6 to 0.04 day$^{-1}$ for C5). Somatic growth rates of *Calanus agulhensis* also declined with age: from 0.57 day$^{-1}$ for N6 to 0.09 day$^{-1}$ for C5. Data on growth rates were used to assess the relative importance of food [as measured by total chlorophyll (Chl) *a* concentration], phytoplankton cell size (proportion of cells >10 μm) and temperature to the growth of copepods. Multiple regression results suggested that fecundity and somatic growth rates were positively related to both Chl *a* concentration and phytoplankton cell size, but not to temperature. Although it was not possible to separate the effects of Chl *a* concentration and phytoplankton cell size, data from previous laboratory experiments suggest that copepod growth is not limited by small cells *per se*, but by the low Chl *a* concentrations that are associated with these particles in the field. Despite growth not being directly related to temperature, a dome-shaped relationship was evident in some species, with slower growth rates at cool (<13°C) and warm (>18°C) temperatures. The shape of this relationship mirrors that of Chl *a* versus temperature, where poor Chl *a* concentrations are associated with cool and warm temperatures. It is concluded that the effect of food limitation on growth of copepods outweighs that of temperature in the southern Benguela region. Sources of variability in relationships between growth and Chl *a* concentration are discussed.

## Introduction

Not only are copepods the most abundant metazoans on earth, but they also grow rapidly (see Humes, 1994). Davis (1987) argued that the only way to measure zooplankton production accurately is by estimation of species-specific growth rates. Field-based research on the growth of copepods has focused on female egg production (Durbin *et al.*, 1992; Plourde, 1993; Jónasdóttir *et al.*, 1995; McKinnon and Ayukai, 1996; Pond *et al.*, 1996), rather than juvenile growth, because of its ease of measurement using bottle incubations. Work on juvenile growth has been conducted in temperate and polar regions by following the progression of cohorts after spring or fall phytoplankton blooms (McLaren and Corkett, 1981; Middlebrook and Roff, 1986; McLaren *et al.*, 1989). Few studies have measured juvenile and adult growth rate simultaneously in dynamic regions such as upwelling areas

(Walker and Peterson, 1991; Verheye *et al.*, 1994; Hutchings *et al.*, 1995), where the use of distinct cohorts to estimate juvenile growth is difficult because female egg production is quasi-continuous.

Identifying factors that control the growth of copepods is essential to understanding nutrient and carbon fluxes in the marine environment. There has been considerable debate in the literature about the relative importance of the two main factors that control copepod growth, viz. food and temperature. Egg production (Durbin *et al.*, 1983; Kimmerer and McKinnon, 1987; Peterson *et al.*, 1991; Tourangeau and Runge, 1991; McKinnon and Ayukai, 1996) and somatic growth (Peterson and Hutchings, 1995; Webber and Roff, 1995) in natural copepod populations have been found to be limited by the quantity of available food. In terms of food quality, the nutritional value of phytoplankton has also been shown to influence growth (Ambler, 1985; Kleppel, 1993; Jónasdóttir *et al.*, 1995; Kleppel and Burkart, 1995). Another aspect of food quality, particle size, can also limit copepod growth because small particles are used inefficiently by many large species (Paffenhöfer, 1984; Berggreen *et al.*, 1988; Armstrong *et al.*, 1991). The influence of temperature on growth rates in the wild has been well documented, especially in temperate seas (Middlebrook and Roff, 1986; Davis, 1987; McLaren *et al.*, 1989). In their review of field measurements of growth rate, Huntley and Lopez (1992) concluded that copepods grow at maximum rates in the field, with an exponential increase in growth rate with temperature over a wide range of habitats. They suggested that food may not be limiting in nature, and the impression that food is limiting may be a consequence of sampling at incorrect scales.

The objectives of this study are two-fold. First, to estimate egg production and somatic growth of a number of common copepods from direct measurements using bottle incubations in the southern Benguela upwelling system. Second, to assess the relative importance of food quantity [expressed as chlorophyll (Chl) *a* concentration], phytoplankton cell size and temperature on rates of egg production and somatic growth of copepods in this system.

## Method

Rates of egg production (eggs female$^{-1}$ day$^{-1}$) were estimated for *Calanus agulhensis*, *Calanoides carinatus*, *Centropages brachiatus*, *Nannocalanus minor*, *Neocalanus tonsus* and *Rhincalanus nasutus*, as well as somatic growth rates (day$^{-1}$) and stage durations (days) for stages N6–C5 of *Calanus agulhensis* and *Calanoides carinatus*. The growth rate was estimated in the field using bottle incubation techniques, viz. egg production of females and moulting rate of pre-adult stages. 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 1993/94 and 1994/95. 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 (0.1–23.0 mg m$^{-3}$). The sampling grid and station positions are shown in Figure 1.

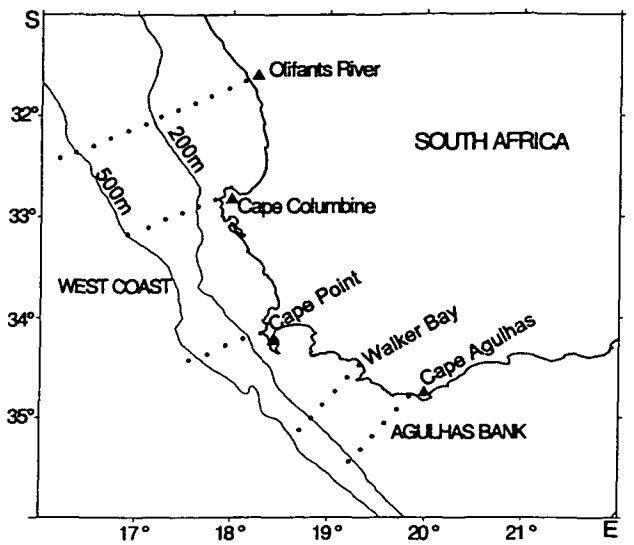


**Fig. 1.** The positions of stations in the SARP programme.

Copepods were collected using a 300-μm-mesh drift net, fitted with a 2 l 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 l of ambient sea water. Copepods were gently removed from this bucket using a sieve and washed into a Petri dish. Lively copepods were selected using a wide-mouthed dropper under a dissecting microscope at dim light conditions. The entire pre-incubation procedure lasted for <30 min.

For egg production experiments, individual females were placed in 1 l bottles (usually 5–10 per station) containing 63-μm-filtered sea water from the fluorescence maximum. Although the bottles were not fitted with a screen to prevent females from ingesting their eggs, the low density of females used (1 female $l^{-1}$) minimized the effects of possible egg cannibalism (see Laabir *et al.*, 1995). Bottles were incubated in on-deck darkened tubs which were kept at ambient temperatures by pumping sea water from a depth of 6 m through the incubators (as described by Hutchings *et al.*, 1995). After 24 h, the contents of each incubation bottle were poured through a 20-μm mesh, and lively females and their eggs were preserved with 5% buffered formalin. Experiments with dead or moribund females were discarded. In the laboratory, the number of eggs per bottle was counted and the daily egg production ($E$; eggs $female^{-1}$ $day^{-1}$) was calculated according to Peterson *et al.* (1991) as:

$$E = N_e \times \frac{24}{T}$$

where $N_e$ is the number of eggs and $T$ is the duration of the incubation experiment (h).

For moulting rate experiments for *Calanus agulhensis* and *Calanoides carinatus*, at least 15 (mean 26.3) individuals of a particular stage were incubated in a 2 l jar. After 24 h, the contents of the incubation bottle were preserved and the number of individuals that had and had not moulted to the next stage were counted. The moulting ratio ($MR_i$) of each juvenile stage $i$ was calculated after Peterson *et al.* (1991) as:

$$MR_i = \frac{N_{i+1}}{N_i + N_{i+1}}$$

where $N_i$ is the number of individuals in stage $i$ at the end of the experiment and $N_{i+1}$ is the number of individuals in stage $i + 1$ at the end of the experiment.

Exoskeletons were also counted and experiments were excluded from analyses if the difference between the moulting ratio calculated from the exoskeletons and that from the animals themselves was >10%. The daily stage-specific growth rate ($g_i$; day$^{-1}$) was calculated from the moulting ratio using masses from Table I and applying the following formula [modified from Peterson *et al.* (1991)]:

$$g_i = \ln\left(\frac{W_{i+1}}{W_i}\right) \times MR_i \times \frac{24}{T}$$

where $W_i$ is the average body mass of developmental stage $i$ and $W_{i+1}$ is the average body mass of developmental stage $i + 1$.

As this study was performed as part of a routine monitoring survey, and owing to the large number of individuals incubated for moulting rate experiments, we have made the assumption of mean growth rate increments. Although the mass of individual copepods and their growth increments are variable (Berggreen *et al.*, 1988; Paffenhöfer, 1994), we have assumed average masses because growth rates are more sensitive to changes in moulting ratios than growth increments (Webber and Roff, 1995). Stage durations were calculated as the reciprocal of the moulting ratios (Falkowski *et al.*, 1984). The average duration of each stage was

**Table I.** Average body mass (μg dry weight) of juvenile *Calanus agulhensis* and *Calanoides carinatus*

| Stage | *Calanus agulhensis* | *Calanoides carinatus* |
|---|---|---|
| N6 | 2[a] | 2[a] |
| C1 | 4[b] | 4[b] |
| C2 | 9[b] | 7[b] |
| C3 | 22[b] | 18[b] |
| C4 | 46[b] | 30[c] |
| C5 | 97[b] | 62[c] |

[a]Sea Fisheries Research Institute, unpublished data.
[b]Peterson *et al.* (1990).
[c]Verheye (1991).

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 fluorescence maximum was used as a measure of ambient food availability for copepods. Samples were size fractionated into two classes (<10 μm and total) using a 10 μm nylon mesh, filtered through Whatman GF/F filters, and analysed fluorometrically using a Turner Designs Model 10-000R fluorometer according to Parsons *et al.* (1984).

Relationships between growth and environmental variables such as Chl *a* concentration, phytoplankton cell size and temperature were assessed for *Calanus agulhensis* N6-female and *Calanoides carinatus* female, *Centropages brachiatus* female and *Nannocalanus minor* female. No such relationships were investigated for female *Neocalanus tonsus* and *R.nasutus* (see Table II), and juvenile *Calanoides carinatus* (see Table V), because of the paucity of data.

To assess the effect of phytoplankton cell size on fecundity and somatic growth, a measure of the dominance of large cells was derived. At each station, the proportion of cells that were >10 μm was calculated as the ratio of Chl *a* in the >10 μm fraction to the total Chl *a*. It has been suggested that Chl *a* in cells <10 μm is used inefficiently by many copepods (Peterson and Bellantoni, 1987; Berggreen *et al.*, 1988; Armstrong *et al.*, 1991).

Statistical differences among growth rates were evaluated by non-parametric tests because the data were heteroscedastic, preventing the use of parametric statistics (Zar, 1984). To identify significant differences in growth, one-way non-parametric ANOVA was conducted on rates of egg production and somatic growth using the Kruskal–Wallis test. A posteriori comparisons were then computed using the Mann–Whitney *U*-test. As a number of multiple comparisons were conducted, the Bonferroni adjustment was used, i.e. the type I error was divided by the number of comparisons (Harris, 1985).

To assess the relative effect of temperature, Chl *a* concentration and the proportion of large cells on fecundity and somatic growth, a multiple regression analysis was conducted for each species/stage. Backward multiple regression was performed, with non-significant variables removed sequentially until only significant factors remained. Standardized partial regression coefficients were calculated to highlight the relative importance of the independent variables to growth (Zar, 1984).

**Table II.** Egg production of copepods collected in the southern Benguela system during this study: mean ± SE (eggs female$^{-1}$ day$^{-1}$), range (eggs female$^{-1}$ day$^{-1}$) and the number of samples (*n*). Different superscripts indicate significant differences between means using the Mann–Whitney *U*-test at $P < \frac{0.05}{{}^{6}C_{2}} = 0.0\dot{3}$ (the Bonferroni adjustment)

| Species | Mean ± SE | Range | *n* |
|---|---|---|---|
| *Calanoides carinatus* female | 23.7$^{a}$ ± 1.6 | 0.0–143.5 | 350 |
| *Calanus agulhensis* female | 19.0$^{a}$ ± 0.6 | 0.0–130.8 | 1492 |
| *Centropages brachiatus* female | 83.6$^{b}$ ± 4.7 | 0.0–278.7 | 158 |
| *Nannocalanus minor* female | 26.1$^{a}$ ± 2.9 | 0.0–96.2 | 82 |
| *Neocalanus tonsus* female | 16.1$^{a}$ ± 4.3 | 0.0–98.2 | 33 |
| *Rhincalanus nasutus* female | 26.1$^{a}$ ± 4.2 | 0.0–61.2 | 19 |

## Results

### *Egg production rates*

Estimates of the egg production rates of six copepod species are summarized in Table II. The minimum egg production rate was zero for all species. Egg production rates were significantly different among species (Kruskal–Wallis ANOVA, $H = 244.4$, $n = 2144$, $P < 0.0001$). The mean egg production rate for *Calanus agulhensis*, *Calanoides carinatus*, *Nannocalanus minor*, *Neocalanus tonsus* and *R.nasutus* was small, below 30 eggs female$^{-1}$ day$^{-1}$, whereas that for *Centropages brachiatus* was significantly greater (83.6 eggs female$^{-1}$ day$^{-1}$).

The results of the multiple regression analysis between fecundity and temperature, Chl *a* concentration and the proportion of large cells are shown in Table III. Fecundity was unrelated to temperature for all species. In contrast, fecundity was positively related to total Chl *a* concentration or the proportion of cells >10 μm in size (or both) for all species, although only poorly so for *Centropages brachiatus*. In *Calanus agulhensis* and *Calanoides carinatus*, the standardized partial regression coefficients show that egg production was more related to total Chl *a* concentration than to the proportion of cells >10 μm in size.

To aid interpretation of the multiple regression results, scatterplots of copepod egg production against temperature, Chl *a* concentration, and the proportion of cells >10 μm in size are shown in Figure 2. Although the multiple regression results suggested no relationship between egg production and temperature, this type of analysis only identifies linear relationships. A visual inspection of the plots between fecundity and temperature, however, suggests a dome-shaped relationship between these variables for some of the species. For example, egg production by *Calanus agulhensis* is ≤60 eggs female$^{-1}$ day$^{-1}$ for temperatures <13°C and >18°C, and up to 120 eggs female$^{-1}$ day$^{-1}$ between 13 and 18°C.

Scatterplots of egg production rate against Chl *a* concentration show saturation of egg production at high Chl *a* levels (Figure 2), suggesting that the linear relationship between growth rate assumed in the multiple regression is not the

**Table III.** Results of multiple regression analyses. In each multiple regression, the dependent variable is either fecundity (eggs female$^{-1}$ day$^{-1}$) or somatic growth rate (day$^{-1}$), and the independent variables are temperature (°C), Chl *a* concentration (mg m$^{-3}$) and the proportion of large cells. The standardized partial regression coefficients and the $r^2$ of the models are given, together with their respective significance level

| Species/stage | Temperature | Chl *a* | Proportion of cells >10 μm | $r^2$ |
|---|---|---|---|---|
| *Calanoides carinatus* female | n.s. | 0.457**** | 0.293**** | 0.39**** |
| *Calanus agulhensis* female | n.s. | 0.464**** | 0.192**** | 0.35**** |
| *Centropages brachiatus* female | n.s. | 0.274*** | n.s. | 0.07*** |
| *Nannocalanus minor* female | n.s. | n.s. | 0.506**** | 0.26**** |
| *C.agulhensis* N6 | n.s. | 0.500* | n.s. | 0.26* |
| *C.agulhensis* C1 | –0.311* | 0.348** | n.s. | 0.26*** |
| *C.agulhensis* C2 | n.s. | n.s. | 0.526**** | 0.27**** |
| *C.agulhensis* C3 | n.s. | 0.311** | 0.232* | 0.23**** |
| *C.agulhensis* C4 | n.s. | 0.314** | 0.333** | 0.33**** |
| *C.agulhensis* C5 | n.s. | n.s. | 0.396**** | 0.15**** |

n.s., non-significant; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; ****$P < 0.0001$.

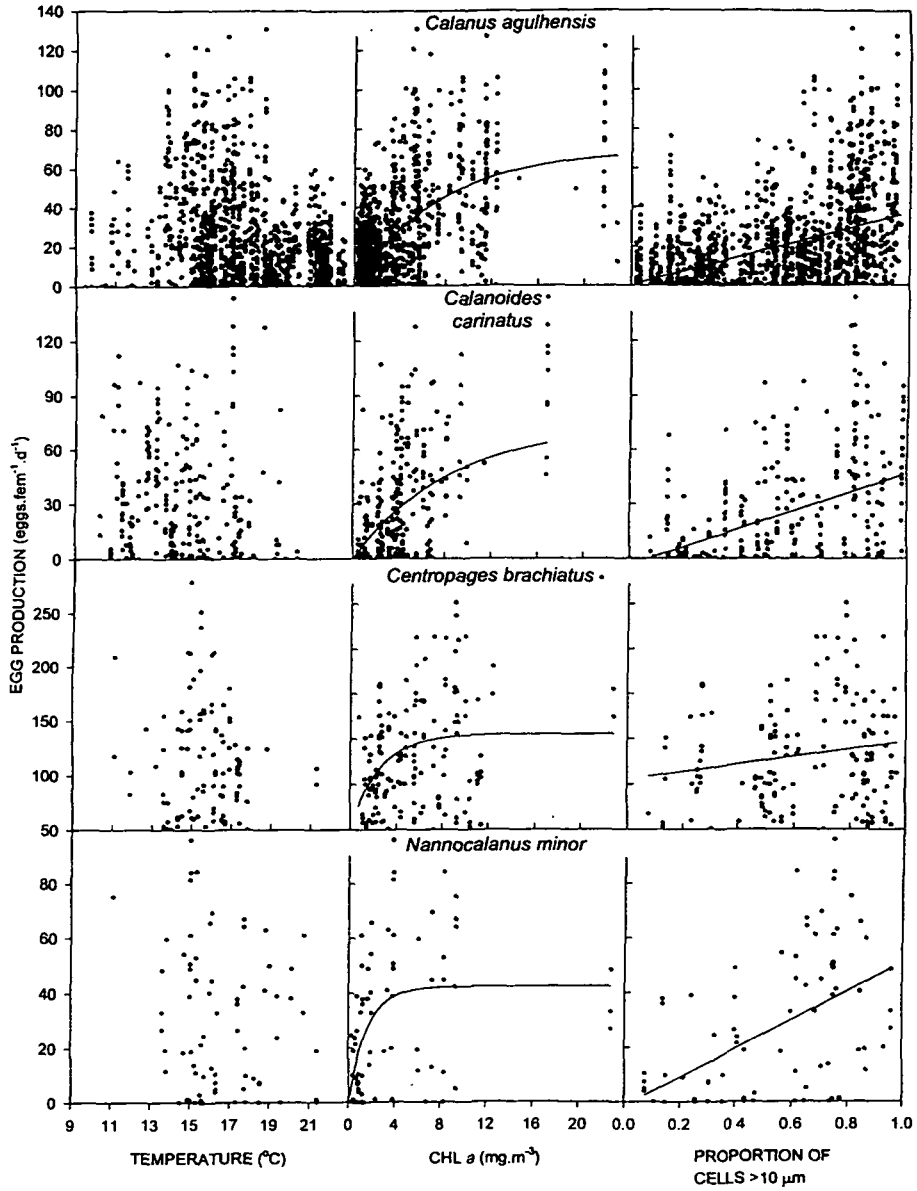


**Fig. 2.** Scatterplots of daily egg production rate of *Calanus agulhensis*, *Calanoides carinatus*, *Centropages brachiatus* and *Nannocalanus minor* versus sea surface temperature (left), Chl *a* concentration (centre, with Ivlev curves fitted; see Table IV for equations) and the proportion of phytoplankton cells >10 µm in size (right, with linear regressions fitted; see Table IV for equations). Note the different *y* scales.

most appropriate. Consequently, the functional response of fecundity to Chl *a* concentration was described by an Ivlev curve (Ambler, 1986; Hutchings *et al.*, 1995). The proportion of the variance explained by these curves was between 10 and 38% (Table IV).

The fecundity of each species increased linearly with the proportion of cells >10 μm in size (Figure 2). Despite the multiple regression selecting either the concentration of Chl *a* or the proportion of cells >10 μm in size as the variables most related to egg production for a particular species, it can be seen that both variables are always positively related to fecundity (Table IV).

### *Somatic growth rates*

Somatic growth rates of *Calanus agulhensis* and *Calanoides carinatus* are given in Table V. Both species exhibit a similar trend, with older stages generally growing

**Table IV.** Egg production and somatic growth related to Chl *a* concentration (Ivlev curve) and the proportion of cells >10 μm in size (linear equation). The parameters of the respective curves are shown, together with the proportion of the variance explained ($r^2$). Also shown for the linear equation is the significance level. Note that no significance level is possible using non-linear equations. The number of samples is the same as in Tables II and V

| Species/stage | Growth versus Chl *a* $g = g_a(1 - e^{-k*c})$ | | | Growth versus cell size $Y = a + bX$ | | |
|---|---|---|---|---|---|---|
| | $g_a$ | $k$ | $r^2$ | $a$ | $b$ | $r^2$ |
| *Calanoides carinatus* female | 73.698 | 0.117 | 0.27 | -3.378 | 49.929 | 0.21**** |
| *Calanus agulhensis* female | 69.371 | 0.135 | 0.38 | 0.322 | 36.814 | 0.20**** |
| *Centropages brachiatus* female | 105.133 | 0.401 | 0.10 | 55.652 | 41.396 | 0.03* |
| *Nannocalanus minor* female | 42.335 | 0.630 | 0.30 | -1.308 | 52.015 | 0.26**** |
| *C.agulhensis* N6 | 0.593 | 4.641 | 0.27 | 0.514 | 0.094 | 0.09$^{n.s.}$ |
| *C.agulhensis* C1 | 0.635 | 2.580 | 0.13 | 0.417 | 0.278 | 0.18*** |
| *C.agulhensis* C2 | 0.552 | 2.010 | 0.19 | 0.304 | 0.367 | 0.27**** |
| *C.agulhensis* C3 | 0.373 | 1.222 | 0.15 | 0.161 | 0.257 | 0.16*** |
| *C.agulhensis* C4 | 0.399 | 0.648 | 0.24 | 0.105 | 0.318 | 0.27**** |
| *C.agulhensis* C5 | 0.124 | 0.998 | 0.04 | 0.028 | 0.133 | 0.15**** |

n.s., non-significant; *$P < 0.05$; ***$P < 0.001$; ****$P < 0.0001$.

**Table V.** Somatic growth rates (day$^{-1}$) of *Calanus agulhensis* and *Calanoides carinatus*: mean ± SE (day$^{-1}$), range (day$^{-1}$), geometric mean of stage duration ($D$, days) and the number of samples ($n$). Different superscripts indicate significant differences at $P < \frac{0.05}{{}^6C_2} = 0.03\dot{3}$ (Mann–Whitney $U$-test). There were insufficient data for *C.carinatus* to test differences among mean growth rates

| Stage | *Calanus agulhensis* | | | | *Calanoides carinatus* | | | |
|---|---|---|---|---|---|---|---|---|
| | Mean ± SE | Range | $D$ | $n$ | Mean ± SE | Range | $D$ | $n$ |
| N6 | 0.566$^a$ ± 0.015 | 0.406–0.665 | 1.235 | 21 | 0.584 | – | 1.188 | 1 |
| C1 | 0.557$^a$ ± 0.023 | 0.152–0.811 | 1.557 | 59 | 0.533 | – | 1.050 | 1 |
| C2 | 0.462$^a$ ± 0.020 | 0.097–0.838 | 2.114 | 82 | 0.451 ± 0.079 | 0.082–0.802 | 2.519 | 9 |
| C3 | 0.278$^b$ ± 0.017 | 0.000–0.709 | 3.101 | 90 | 0.135 ± 0.022 | 0.097–0.215 | 3.967 | 5 |
| C4 | 0.260$^b$ ± 0.016 | 0.000–0.720 | 3.463 | 105 | 0.199 ± 0.024 | 0.091–0.272 | 3.906 | 8 |
| C5 | 0.089$^c$ ± 0.009 | 0.000–0.420 | 7.365 | 108 | 0.044 ± 0.014 | 0.000–0.167 | 9.318 | 15 |

more slowly than their younger conspecifics. Growth rates of *Calanus agulhensis* stages were significantly different from one another (Kruskal–Wallis ANOVA, $H = 262.8$, $n = 465$, $P < 0.0001$). From a posteriori multiple comparisons using the Mann–Whitney *U*-test (Table V), somatic growth rates of *Calanus agulhensis* N6, C1 and C2 were found to be not significantly different, but were faster than for the older stages. In addition, stages C3 and C4 also had similar growth rates, but these were significantly slower than for stages N6 to C2. The growth rate of C5 was significantly slower than that of all other stages.

Multiple regression analyses reveal that somatic growth rates ($day^{-1}$) were generally independent of temperature (Table III), except for *Calanus agulhensis* C1 where the relationship was negative. Somatic growth for all stages was positively related to either Chl *a* concentration (N6 and C1) or the proportion of cells >10 μm in size (C2 and C5), or both (C3 and C4; Table III).

Scatterplots of somatic growth against temperature, Chl *a* concentration and the proportion of cells >10 μm in size are shown in Figure 3. Interestingly, the relationship between somatic growth and temperature for the larger stages (C3–C5) appeared dome shaped (Figure 3), similar to that observed for female fecundity. For example, growth rates of *Calanus agulhensis* C5 were generally slow (<0.2 $day^{-1}$) for temperatures <13°C and >18°C, and faster (up to 0.4 $day^{-1}$) for temperatures between 13 and 18°C.

As the scatterplots of growth rate against Chl *a* concentration showed saturation (Figure 3), Ivlev curves were again fitted (Table IV). Somatic growth rates of all *Calanus agulhensis* stages accelerated with increasing concentrations of Chl *a*. The proportion of the variance explained was between 4 and 27%.

Somatic growth rates of all stages increased linearly as the proportion of cells >10 μm in size increased (Table IV). Despite the multiple regression selecting either the concentration of Chl *a* or the proportion of cells >10 μm in size as the variables most related to somatic growth, it can be seen that both variables are always positively related to growth (Table IV). This suggests that Chl *a* concentration and the proportion of cells >10 μm in size are highly correlated, an assertion that is confirmed by Figure 4.

## Discussion

This study provides the most comprehensive set of estimates of copepod egg production rates from any upwelling region (2134 experiments), as well as of somatic growth rates of *Calanus agulhensis* in the southern Benguela system (465 experiments). Moreover, the first extensive field estimates of somatic growth rate of N6 (0.58 $day^{-1}$) to C5 (0.04 $day^{-1}$) of *Calanoides carinatus* (39 experiments) are presented, although there are a few previous measurements from the same region, viz. ~0.36 $day^{-1}$ for C2 ($n = 1$), 0.20 $day^{-1}$ for C3 ($n = 3$) and 0.13 $day^{-1}$ for C4 ($n = 3$) estimated from Figure 10 in Walker and Peterson (1991). Somatic growth of both *Calanus agulhensis* and *Calanoides carinatus* declined sharply with age (Table V), as has been noted previously (Peterson and Painting, 1990; Hutchings *et al.*, 1995; Peterson and Hutchings, 1995). Such a decline in growth rate with body size may be a general phenomenon, and has been documented in both field

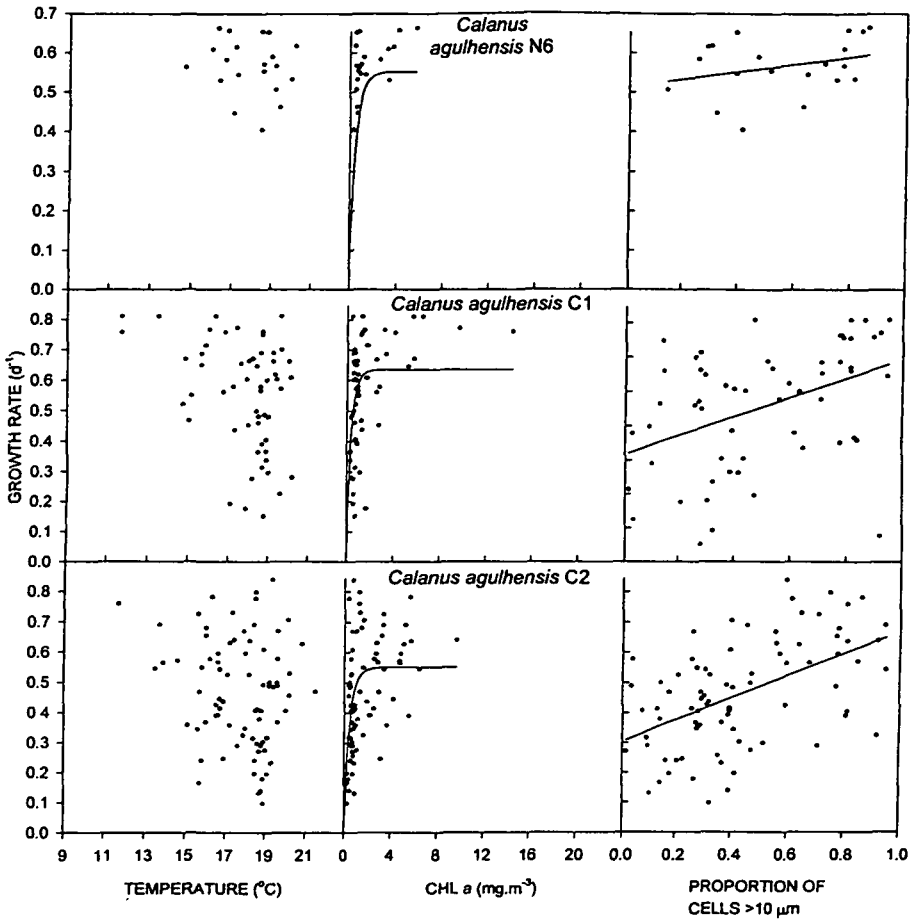


**Fig. 3.** Scatterplots of daily somatic growth rate of nauplius N6 and copepodites C1–C5 of *Calanus agulhensis* versus sea surface temperature (left), Chl *a* concentration (centre, with Ivlev curves fitted; see Table IV for equations) and the proportion of phytoplankton cells >10 µm in size (right, with fitted linear regressions; see Table IV for equations). Note the different *y* scales.

(Greze, 1978; Peterson *et al.*, 1991) and laboratory studies in terms of stage duration (Peterson and Painting, 1990) and somatic growth (Harris and Paffenhöfer, 1976; Paffenhöfer, 1976; Vidal, 1980). This decrease may not only reflect allometry (Peters, 1983; McLaren *et al.*, 1989), however, but may also be a consequence of increased food limitation of larger copepods (Webber and Roff, 1995). This contention is explored further by Richardson and Verheye (in press).

To our knowledge, the rates of egg production for *Nannocalanus minor* presented in this study (mean: 26.1 eggs female$^{-1}$ day$^{-1}$, range: 0–96.2 eggs female$^{-1}$ day$^{-1}$, $n$ = 82) are the first comprehensive estimates for this species from any marine system. In a preliminary study of copepod growth in the northern Benguela system, the egg production rate of this species was found to be substantially lower

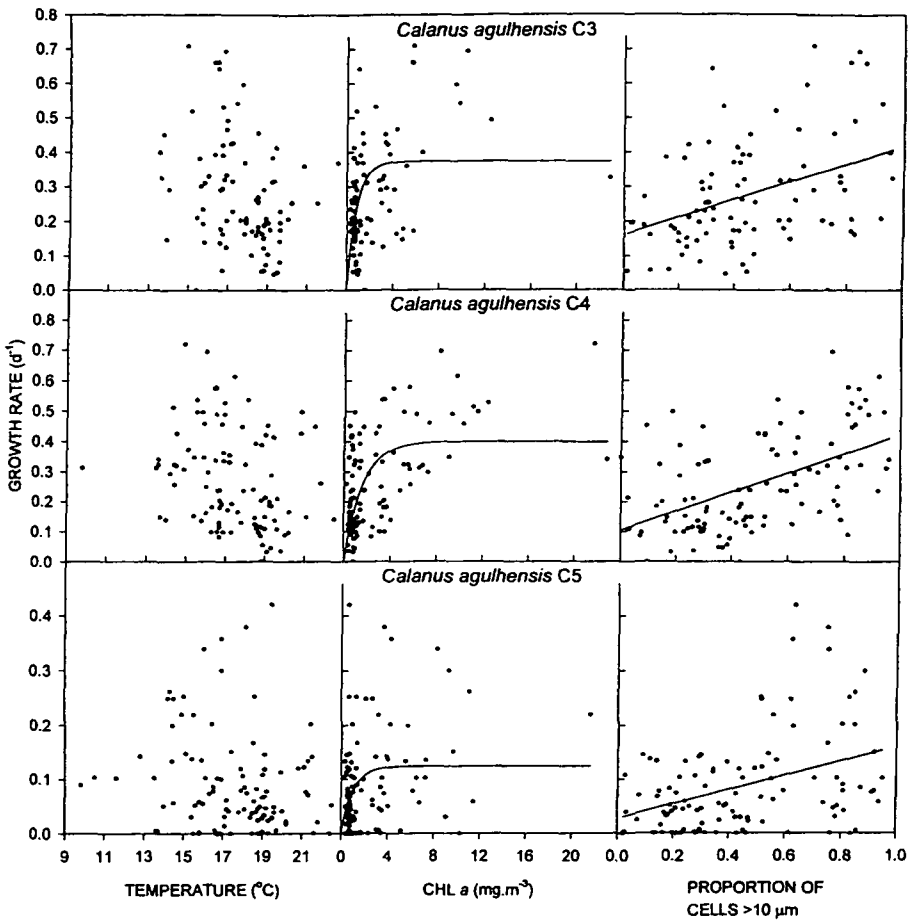


**Fig. 3.** Continued.

(mean = 2 eggs female$^{-1}$ day$^{-1}$, range: 0–8 eggs female$^{-1}$ day$^{-1}$, $n$ = 14; Verheye *et al.*, 1998) than those reported here, perhaps owing to the smaller data set in that study. *Nannocalanus minor* is an important species globally, being distributed widely within tropical and temperate regions of the Atlantic, Pacific and Indian oceans, and showing a preference for warm water (Unterüberbacher, 1964; De Decker, 1973). It is also an important food item of mesopelagic fish such as myctophids (Kinzer and Schultz, 1985).

### *Maximum growth rates*

Maximum growth rates of copepods are important because they define the upper limit of growth under given environmental conditions (Kleppel *et al.*, 1996). As such, they allow the degree of limitation of growth by factors such as food and

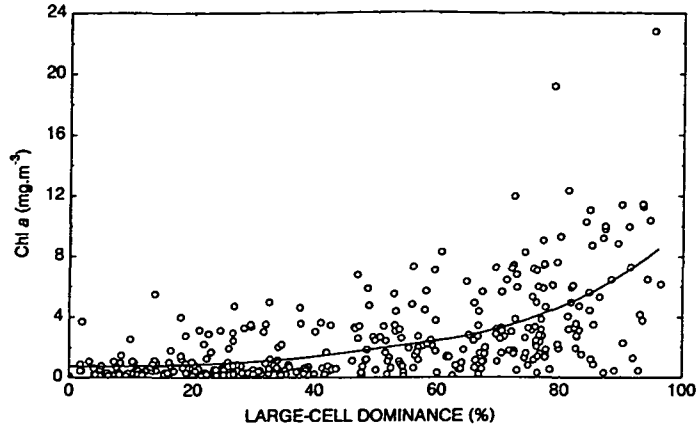


**Fig. 4.** The relationship between Chl *a* concentration and the dominance of large phytoplankton, expressed as the percentage contribution of cells >10 μm in size to the total Chl *a* concentration. A distance-weighted least squares line was fitted (StatSoft, 1996).

temperature to be assessed. The rates of egg production and somatic growth of copepods reported here for the southern Benguela upwelling region are high, probably a consequence of the large Chl *a* concentrations and fast primary production that are encountered during bloom conditions in upwelling regions (Mitchell-Innes and Pitcher, 1992).

The maximum estimate of fecundity for *Calanoides carinatus* was 143 eggs female$^{-1}$ day$^{-1}$, substantially greater than a previous estimate in the southern Benguela system of 40 eggs female$^{-1}$ day$^{-1}$ (Armstrong *et al.*, 1991). This difference may be attributable to the larger number of samples collected over a wider variety of food types in the present study. Our estimate is similar to that of 150 eggs female$^{-1}$ day$^{-1}$ in the laboratory under excess food conditions (Borchers and Hutchings, 1986). Presumably, *Calanoides carinatus* is sometimes not food limited in the field.

The maximum egg production rate of 130 eggs female$^{-1}$ day$^{-1}$ estimated for *Calanus agulhensis* was more than three times that measured under excess food conditions in the laboratory (Attwood and Peterson, 1989). Although it is possible that the food resource [*Thalassiosira weissflogii*, 14 μm equivalent spherical diameter (ESD)] used in that study was of a suboptimal size for growth of female *Calanus agulhensis*, a smaller flagellate (*Pseudoisochrysis paradoxa*, 4 μm ESD) provided in excess was a suitable food resource for *Calanoides carinatus* (Borchers and Hutchings, 1986), which is similar in size to *Calanus agulhensis*. It is therefore more likely that *T.weissflogii* is not a nutritious food for *Calanus agulhensis*, or that experimental conditions were inadequate. This highlights that laboratory estimates of egg production should only be applied to natural populations with caution.

No previous estimates of maximum egg production of *R.nasutus* (61.2 eggs female$^{-1}$ day$^{-1}$) are available in the literature. The maximum egg production by *Centropages brachiatus* was 278 eggs female$^{-1}$ day$^{-1}$, substantially greater than its

maximum of 95 eggs female$^{-1}$ day$^{-1}$ observed in the upwelling zone off Chile (Peterson *et al.*, 1988). This discrepancy may be due to the larger number of samples collected in the present study. The estimate of maximum egg production presented here is similar to a recent estimate from the northern Benguela region of 225 eggs female$^{-1}$ day$^{-1}$ (Verheye *et al.*, 1998) and that of 200 eggs female$^{-1}$ day$^{-1}$ for the closely related species *Centropages typicus* in the laboratory (Dagg, 1978).

The maximum egg production of *Neocalanus tonsus* was 98 eggs female$^{-1}$ day$^{-1}$. This is very similar to the 95 eggs female$^{-1}$ day$^{-1}$ measured during spring in the southern Pacific Ocean when *T.weissflogii* was added to the experimental incubations (Ohman, 1987). *Neocalanus tonsus* is a sub-Antarctic species that is only found periodically in the southern Benguela system after intrusion of cold water (De Decker, 1984). It is noteworthy that *N.tonsus* is fecund in the southern Benguela upwelling system because some copepods do not lay eggs outside of their typical area of distribution (Williams and Conway, 1988).

Maximum somatic growth rates presented here for *Calanus agulhensis* are similar to those reported by Hutchings *et al.* (1995) for the Agulhas Bank, South Africa. However, the estimates of (N6) naupliar growth in both studies (~0.6 day$^{-1}$) are lower than those for calanoid nauplii (0.85 day$^{-1}$) in the tropical ocean (Roff *et al.*, 1995). Although this difference could be attributable to the warmer water temperature in the latter study, maximum growth rates of *Calanus agulhensis* N6 in the present study and that by Hutchings *et al.* (1995) were probably underestimated. This is 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 less than a day (Webber and Roff, 1995), and in some of our experiments all the nauplii had moulted within 24 h.

### *Relationship between growth and Chl a*

The significant relationships between growth and both Chl *a* concentration and the proportion of cells >10 μm in size imply that the growth rate is often food limited in the southern Benguela system. Thus, although maximum growth rates are sometimes fast (as discussed above), copepods only grow at these rates relatively infrequently. The predictability of egg production and somatic growth from Chl *a* concentration (most below 30%) for the species and life history stages examined was similar to that reported in other studies in upwelling regions (Peterson *et al.*, 1988; Armstrong *et al.*, 1991; Hutchings *et al.*, 1995).

There are a number of possible reasons for the relatively poor correlations between growth and Chl *a* concentration in this study. First, copepods have different modes of nutrition (Mullin, 1966; Turner, 1984), so that Chl *a* is not always the best measure of food. Egg production is only weakly related to Chl *a* concentration for the omnivorous (Boyd *et al.*, 1980) *Centropages brachiatus* [$r^2$ = 10%, Table IV; $r^2$ = 3% in Peterson *et al.* (1988)], compared with the predominantly herbivorous species *Calanus agulhensis* [belonging to a mainly herbivorous genus (Turner, 1984)] and *Calanoides carinatus* (Schnack, 1982) ($r^2$ = 38 and 27% respectively, Table IV). Second, some species of phytoplankton

are a more nutritious food source than others (Cahoon, 1981; Napp *et al.*, 1988; Kleppel and Burkart, 1995), so that estimates of Chl *a* concentration as a bulk index of food may not adequately reflect the actual nutritive value of the food. For instance, dinoflagellates, which are common in upwelling regions, have relatively more carbon than diatoms for a given Chl *a* concentration (Chan, 1980). Moreover, Kleppel and Burkart (1995) concluded that dietary diversity, which is not reflected in a single Chl *a* value, increases copepod production. Third, weak coupling between growth and food supply in upwelling areas could be attributable to wind-driven advection causing spatial mismatch between vertically migrating copepods, which can maintain themselves within their preferred habitat, and their food resource, which remains in the upper mixed layer and is subject to surface advection (Peterson *et al.*, 1988; Armstrong *et al.*, 1991).

Fourth, the relationship between growth and ambient food concentration is likely to be poorer in dynamic upwelling regions where the Chl *a* concentration is changing rapidly, because of the lag between the ingestion of food and its conversion to production. Moreover, this time lag varies for different species, with the lag ranging from 9.5 to 91 h for five species of marine copepods (Tester and Turner, 1990). The effect of this time lag on the relationship between growth and Chl *a* concentration can be illustrated by a simple model (Figure 5). It is assumed that growth (somatic growth or fecundity) is only a function of Chl *a* concentration, although it is lagged by a variable amount. Phytoplankton growth and decay in the southern Benguela system is represented by a sine wave with a bloom development time of 8 days (Brown and Hutchings, 1987). Sampling is simulated by repeatedly recording the growth and Chl *a* concentration throughout the development and decay of the phytoplankton bloom. Growth and the concentration of Chl *a* are perfectly correlated when there is no time lag between growth and Chl *a* concentration (Figure 5a). With a 1 day lag between ingestion and assimilation into growth, two very different rates of growth occur for the same Chl *a* concentration (Figure 5b). Faster growth is observed during the decay phase of the bloom because of the prior high Chl *a*, and slower copepod growth during the earlier growth phase of the bloom. As the time needed for conversion into production increases to one-quarter of the bloom development time (2 days), the relationship between growth and Chl *a* concentration deteriorates so that there is no relationship (Figure 5c). At a time lag of 3 days, the relationship becomes negative (Figure 5d), and at a 4 day time lag there is a perfect negative relationship (Figure 5e). Thus, the instantaneous growth rate is not directly related to the contemporaneous food density.

Fifth, the lag between growth and Chl *a* concentration may not be constant within a species. The time needed for rates of egg production to recover to their maximum is related to the duration of starvation (Attwood and Peterson, 1989; Calbet and Alcaraz, 1996). For instance, in *Calanus agulhensis*, restoration to maximum fecundity following a 1 day starvation period is ~1 day, whereas after 1 week of starvation recovery takes 5 days (Huggett, 1996). Correlations between growth and food conditions would be expected to be weaker in physically dynamic regions such as upwelling areas than in more stable ones. This may

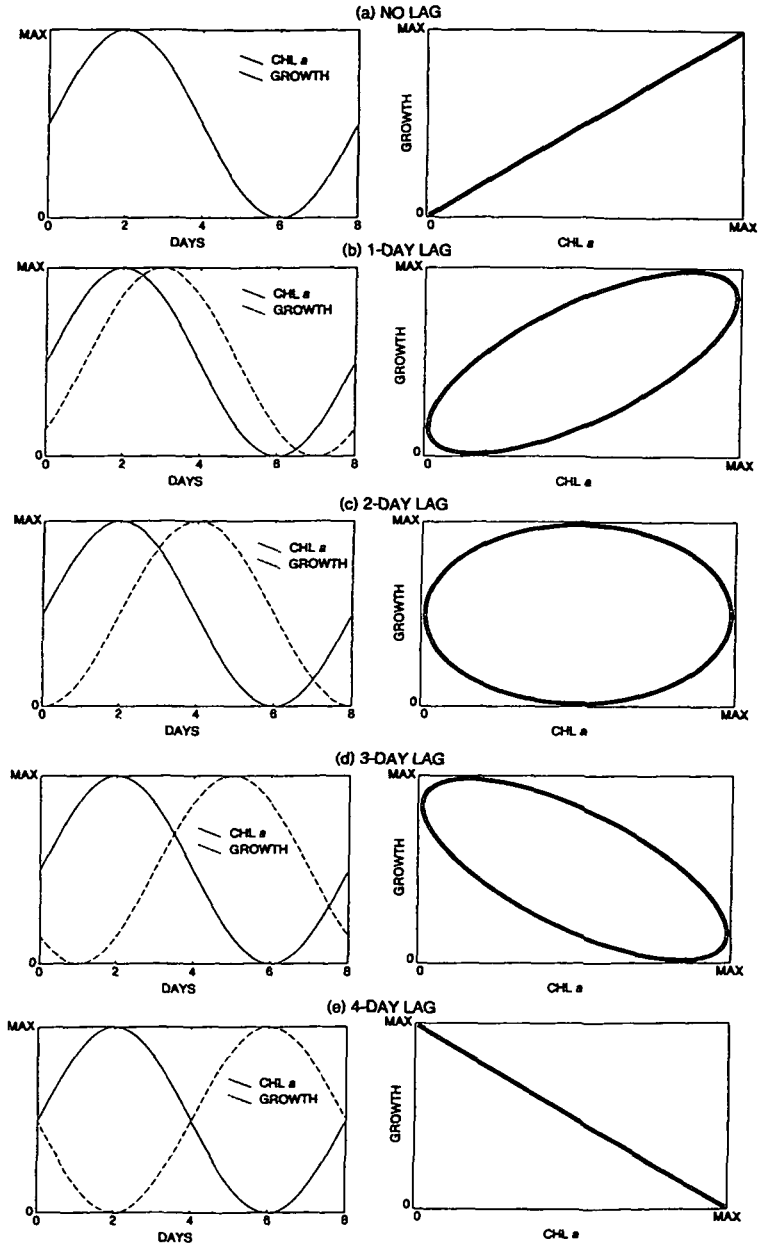


**Fig. 5.** (a–e) The relationship between copepod growth rate and Chl *a* concentration, assuming that growth is dependent upon Chl *a* concentration which varies as a sine wave with a period of 8 days. Time lags (in days) between growth and Chl *a* concentration vary from (a) 0 to (e) 4 days. Time series of copepod growth and Chl *a* concentration (left), and the relationship between growth and Chl *a* concentration (right), are shown.

partially account for the very poor correlations between growth rates and food availability that have been found in upwelling regions in this and other studies (Peterson *et al.*, 1988; Armstrong *et al.*, 1991; Hutchings *et al.*, 1995).

Last, a large portion of the variability in relationships between growth and food is related to individual variation in growth. For example, egg production of *Calanus agulhensis* at one station with a Chl *a* concentration of 21 mg $m^{-3}$ ranged from 30 to 120 eggs $female^{-1}$ $day^{-1}$ and that of *Calanoides carinatus* ranged from 45 to 145 eggs $female^{-1}$ $day^{-1}$ at a Chl *a* concentration of 17 mg $m^{-3}$ (see Figure 2). This individual variability may be partially attributable to the number of particles encountered by individual copepods (Richardson and Verheye, in press).

### *The effect of cell size*

The copepod growth rate was faster when there were more large than small cells present. This confirms earlier work in the southern Benguela system. For instance, during a 27 day anchor station study in the St Helena Bay region, *Calanoides carinatus* produced more eggs during a bloom of the large diatom *Coscinodiscus gigas* (250 μm diameter) than during a microflagellate bloom (<6 μm) between upwelling events (Armstrong *et al.*, 1991). Along a cross-shelf transect in the same region, Walker and Peterson (1991) found a 3- to 5-fold improvement in egg production of *Calanoides carinatus*, *Calanus agulhensis* and *Centropages brachiatus* in areas dominated by large cells.

Large copepods such as females feed more efficiently on large cells (Frost, 1977), particularly cells >20 μm ESD (Berggreen *et al.*, 1988), obtaining their maximal daily ration at relatively small carbon concentrations (Frost, 1972). It is known from laboratory experiments, however, that copepods can grow rapidly on small cells at very large densities. Borchers and Hutchings (1986) found high egg production (150 eggs $female^{-1}$ $day^{-1}$) by *Calanoides carinatus* fed excess concentrations of the small flagellate *Pseudoisochrysis galbana* (4 μm ESD). Peterson *et al.* (1990) also reported high egg production by *Calanoides carinatus* (mean 74.5 eggs $female^{-1}$ $day^{-1}$) on a diet of the small diatom *T.weissflogii* (12 μm ESD; Sea Fisheries Research Institute, unpublished data) at a density of 8000 cells $ml^{-1}$, equivalent to a Chl *a* concentration of 78 mg $m^{-3}$ (using their C:Chl *a* ratio of 23.7). It should be noted that in these laboratory experiments, cell concentrations were used that are rarely encountered in the field (Brown *et al.*, 1991). Small cells are normally associated with poor Chl *a* conditions, because the concentration of Chl *a* increases as phytoplankton cell size increases in the southern Benguela system (Figure 4; also see Mitchell-Innes and Pitcher, 1992). This makes the relative importance of cell size and Chl *a* concentration to growth rate difficult to distinguish in the field. By interpreting the data from this study in terms of previous laboratory experiments, it is suggested that copepod growth in the field may not be limited by cell size when small phytoplankton cells dominate the phytoplankton assemblage, but by the typical concentrations of these cells.

*Effect of temperature on growth*

Many biological rates such as fecundity generally increase with temperature, within the tolerance range of an organism (Kinne, 1970). For *Calanus agulhensis* and *Calanoides carinatus*, laboratory studies under conditions of excess food have shown substantially faster growth rates at warmer temperatures (Peterson and Painting, 1990). In cool temperate coastal regions where much of the scientific research on copepods has focused, temperature is considered the main factor controlling growth (McLaren and Corkett, 1981; Davis, 1987; McLaren *et al.*, 1989). When other factors such as food are limited, however, temperature does not accurately predict growth rate (Middlebrook and Roff, 1986; Kleppel *et al.*, 1996). The growth rates of copepods in the present study were not directly related to temperature over the range examined (9–23°C). This lack of a positive relationship has been noted previously on the Agulhas Bank (Hutchings *et al.*, 1995). In the southern Benguela system, favourable food conditions are restricted spatially to the narrow upwelling belt inshore, and temporally to quiescent conditions between upwelling events (Brown *et al.*, 1991; Richardson *et al.*, in press). Thus, growth rates estimated in the laboratory under food-saturated conditions at specific temperatures are not always representative of field values. Undoubtedly, the growth rate is dependent upon temperature on a global scale, although the assertion that copepods may not be food limited in nature (Huntley and Lopez, 1992) is clearly overstated (Kleppel *et al.*, 1996).

The growth rate of copepods in a variety of aquatic habitats is controlled by food rather than temperature, including freshwater systems (Hart, 1991; Ban, 1994), tropical seas (McKinnon and Thorrold, 1993; Webber and Roff, 1995), and some temperate coastal regions (Peterson, 1985; Peterson and Bellantoni, 1987; Armstrong *et al.*, 1991; Bautista *et al.*, 1994; Peterson and Hutchings, 1995; Pond *et al.*, 1996). The domed relationship between growth rate and temperature that was discernible in some plots (Figures 2 and 3) may be a consequence of the domed association between Chl *a* concentration and temperature (Figure

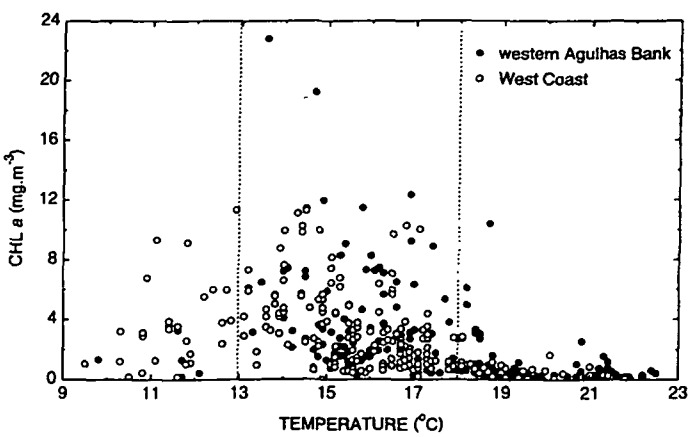


**Fig. 6.** Chl *a* concentration against sea surface temperature. A dome-shaped relationship is evident.

6). This pattern is typical of the southern Benguela upwelling system (Mitchell-Innes and Pitcher, 1992; Pitcher *et al.*, 1996). The domed relationship in the present study, however, is shifted towards warmer temperatures, probably because of the inclusion of the warmer western Agulhas Bank region in this study (Figure 6). Cool temperatures (<13°C) indicate water that is newly upwelled with a poor Chl *a* concentration. As the water warms, the concentration of Chl *a* increases as diatoms dominate initially, followed by dinoflagellates. Above 18°C, there is a change from a diatom/dinoflagellate-dominated phytoplankton community of large biomass to a microflagellate-dominated microbial community of small-biomass (Mitchell-Innes and Pitcher, 1992). Impoverished food conditions, therefore, limit copepod growth at both cool and warm temperatures, so that growth cannot be assumed to be a function of temperature alone in upwelling regions, as it has been in models of other systems (Miller and Tande, 1993).

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