

Egg production, somatic growth and productivity of copepods in the Benguela Current system and Angola-Benguela Front

A.J. Richardson^{a*}, H.M. Verheye^b, V. Herbert^c, C. Rogers^{b,c} and L.M. Arendse^b

Copepods form an important link between phytoplankton and fish, so estimates of their growth rates are essential for understanding their role in the marine food web. To date, no empirical estimates of copepod growth rate in the northern Benguela system off Namibia or the Angola-Benguela Front system off Angola have been published. To redress this situation, we used bottle incubation techniques to measure the daily growth rate of 13 copepod species from this region during two BENEFIT cruises in April/May 1997 and July/August 1999, in terms of egg production by adult females and somatic growth of copepodite stages. Mean growth rate was fast (0.13–0.24 d⁻¹) for small copepods (<1800 µm total length: *Calanoides carinatus* stages C3 and C4, and female *Centropages brachiatus*) and slow (<0.1 d⁻¹) for larger copepods (females of *Nannocalanus minor*, *Pleuromamma* spp., *Scolecithrix* spp., *Metridia lucens*, *Candacia armata*, *Euchaeta* spp., *Undinula vulgaris*, *Calanoides carinatus*, *Eucalanus* spp., *Rhincalanus nasutus*, Pontellidae spp. and *Eucalanus elongatus*). A strong negative relationship between mean growth rate (g) and mean body mass (BM) was found for the northern Benguela system ($g = 0.866 \times 10^{-0.075BM}$, $r^2 = 0.81$, $n = 15$). For comparison, an equation was also derived for the southern Benguela system ($g = 0.572 \times 10^{-0.042BM}$, $r^2 = 0.89$, $n = 21$) from previously published and unpublished data. These equations were used to calculate copepod production (growth rate \times biomass). The estimate for the northern Benguela system of 39 g C m⁻² yr⁻¹ is less than previous indirect values of 52–69 g C m⁻² yr⁻¹. The estimate of annual copepod production for the southern Benguela system of 99 g C m⁻² yr⁻¹ is at the upper end of previous estimates, which range from 11 to 120 g C m⁻² yr⁻¹. The considerably lower production calculated for the northern Benguela may reflect the inadequate estimates of size-differentiated biomass available. The application of our growth rate–body size relationship to biomass estimates is a simple means of estimating copepod production in the study region.

Introduction

Copepods are not only the most abundant metazoans on earth,¹ they also grow very rapidly. For instance, the number of copepods produced annually in the Baltic Sea has been estimated at 9 billion in 10 cubic metres.² Knowledge of their production is essential to understand nutrient and carbon fluxes in the marine environment, especially as copepods are the dominant trophic link between primary producers and fish. Copepod growth rates have been measured extensively in the southern

Benguela system off the west coast of South Africa since 1988.^{3–7} These growth rates have been used to calculate secondary production based on estimates of copepod biomass.^{4,8} There are no direct estimates from the northern Benguela and Angola Current systems, however, although Cushing⁹ derived crude estimates of annual mesozooplankton secondary production of 7.11–9.46 $\times 10^6$ t C yr⁻¹ (Orange River to Walvis Bay) and 10.8–14.4 $\times 10^6$ t C yr⁻¹ (Baia dos Tigros to Walvis Bay).

Previous work in the southern Benguela system showed that daily growth rate decreases with body size from ~ 0.5 d⁻¹ for small copepods (<1000 µm total length) to ~ 0.05 d⁻¹ for larger copepods (>2500 µm total length).^{6,7} This strong negative relationship is attributable not only to larger species that generally grow more slowly than smaller ones, but also to increased food limitation with size.^{6,7} This is because it is energetically more efficient for large copepods to capture large rather than small phytoplankton cells.^{10,11} Thus, large copepods grow optimally only when large cells are present, a condition that is met only during periodic diatom blooms.¹² By contrast, small copepods always grow at near-optimal rates because they feed on small cells that are omnipresent and ubiquitous.^{7,13} It is not known whether there is a similar relationship between mean growth rate and body size in the northern Benguela system.

The objectives of this study were threefold: first, to provide direct estimates of copepod growth rate in the northern Benguela and Angola-Benguela Front regions; second, to derive a relationship between growth rate and body size for this system, and to update the previous relationship between growth rate and body size for the southern Benguela system; last, to estimate copepod production (growth rate \times biomass) in both the southern and northern Benguela by calculating growth rate from body size and using data on size-differentiated copepod biomass.

Materials and methods

Data on copepod growth rate were obtained in both the northern Benguela and Angola-Benguela Front regions between Walvis Bay (Namibia) and Luanda (Angola) during two research cruises, namely, the first BENEFIT (BENGuela Environment Fisheries Interaction and Training) Research and Training Cruise aboard the Germany-chartered Russian RV *Petr Kottsov* in April/May 1997, and on Leg 2 of Cruise 3 of the BENEFIT Shipboard Research Training Programme for the SADC (Southern African Development Community) Region¹⁴ aboard the South African FRS *Africana* in July/August 1999 (see Fig. 4 in ref. 14). In the context of this study, we define the northern Benguela system as including the northern Benguela system proper as well as the Angola-Benguela Front region. These regions were not separated because of the paucity of growth rate data that could be collected. Sea-surface temperatures on the cruises ranged from 16 to 25°C (1997) and from 13 to 23°C (1999), and chlorophyll *a* concentrations varied between 0.25 and

^aMarine Remote Sensing Unit, Oceanography Department, University of Cape Town, Rondebosch, 7701 South Africa.

^bMarine and Coastal Management, Biological Oceanography, Private Bag X2, Rogge Bay, Cape Town, 8012 South Africa.

^cDepartment of Nature Conservation and Oceanography, School of Life Sciences, Cape Technikon, P.O. Box 652, Cape Town, 8000 South Africa.

*Author for correspondence. E-mail: arichard@physci.uct.ac.za

9.7 mg chl m^{-3} (1997) and between 1 and 9 mg chl m^{-3} (1999).

For comparison with growth rates from the northern Benguela system, published and unpublished estimates from the southern Benguela system were also used. To estimate growth rates in the southern region, copepods had been collected on monthly South African SARP (Sardine and Anchovy Recruitment Programme) cruises between September and March 1993/94 and 1994/95 and on annual Pelagic Spawner Biomass surveys in November 1988–1992. Surveys were conducted in the southern part of the southern Benguela, from Cape Agulhas to the Olifants River. Copepods were collected from cool upwelled waters inshore to warm oceanic waters offshore, providing data over a broad range of surface temperatures (9–23°C) and chlorophyll *a* concentrations (0.1–23.0 mg chl m^{-3}).⁶

For growth rate measurements, copepods were collected using a 300- μ m mesh drift net, fitted with a 2-litre plastic bottle as a cod-end, and allowed to drift for 10 minutes. Upon retrieval, the sample was transferred into a bucket containing 20 l of ambient seawater. Copepods were removed from this bucket using a sieve and gently washed into a Petri dish. Live copepods were selected under a dissecting microscope using a wide-mouthed dropper.

Female growth rates were estimated from daily rates of egg production that were measured using the bottle incubation technique.¹⁵ This involved placing individual females in sealed 1-litre bottles containing 63- μ m-filtered seawater and incubating them on-deck in darkened tubs kept at ambient temperature by pumping seawater from a depth of about 6 m through the containers.⁴ After 24 h, the contents of each incubation bottle were poured through a 20- μ m mesh and live females and their eggs were preserved in 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 per female per day) was calculated according to Peterson *et al.*¹⁶ as

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

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

To compare egg production and juvenile somatic growth, the former was converted to instantaneous mass-specific female growth (g_f , d^{-1}) by applying the following equation (modified from ref. 15):

$$g_f = \ln \left(\frac{W_e \times E}{W_f} + 1 \right)$$

where W_e = average egg mass (μ g dry mass) and W_f = average female body mass (μ g dry mass).

Implicit in this equation is that the addition of female body mass is negligible compared to the mass of eggs produced. Owing to the large number of females incubated, the combined average body masses of females and eggs (Table 1) were used to calculate growth rate.

Growth rates of easily identifiable juvenile stages of the large copepod *Calanoides carinatus* were estimated using the 'artificial cohort' incubation technique.^{15–17} This involved creating cohorts of at least 15 individuals of a particular stage and incubating them in 2-litre bottles. After 24 h, the contents of the bottles were preserved in 5% buffered formalin and the moulting ratio (MR_i), i.e. the ratio of individuals that had moulted to the next stage to the total number incubated, was calculated.

Exoskeletons were also counted and results of experiments were excluded from analysis if the difference between the

moulting ratio calculated from the exoskeletons and that from the animals themselves was greater than 10%. The daily stage-specific growth rate (g_i , d^{-1}) was calculated from the moulting ratio using masses from Table 1 and applying the following formula (modified from ref. 16):

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

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

Mean masses of copepodites were used because growth rates are more sensitive to changes in moulting ratios than growth increments.¹³

Data from the southern Benguela system included published growth rate measurements of female *Centropages brachiatus*, *Nannocalanus minor*, *Calanoides carinatus*, *Calanus agulhensis*, *Neocalanus tonsus* and *Rhincalanus nasutus*, and juvenile *Calanus agulhensis* and *Calanoides carinatus*,^{6,7} the dominant large copepods in the region (Table 2). Previously unpublished data on mean growth rates of *Paracalanus parvus*, *Pleuromamma* spp. and *Candacia armata* were also included.

As there is little information on egg and body masses of most of these species, egg mass was estimated from egg diameter, and body mass was estimated from prosome length, using published regression relationships (Table 1). Egg and body sizes were measured separately for the two regions whenever possible, in case the same species differed between systems.

Relationships between mean growth rate and mean body size for each of the northern and southern Benguela systems were derived using regression analysis. Mean growth rates were used rather than individual measurements in order to give each species equal weighting, as there was a large discrepancy in the number of samples of each species. For instance, we recorded 1496 egg production measurements for *Calanus agulhensis* in the southern Benguela and fewer than 10 for several other species.

Calculation of copepod production requires data on both the biomass and the growth rate of copepods. In the southern Benguela, measurements of copepod biomass in the upper 200 m were obtained from vertical Bongo net (200- μ m mesh) tows during 45 cruises (1988–1997) conducted throughout the year ($n = 2471$ samples). Data on species (i.e. size) composition were available for each cruise. Copepod production was estimated as the product of biomass for each species/stage of the calanoid copepods and the corresponding size-based growth rate, using the growth rate–body size relationship derived for the southern Benguela system. For non-calanoid copepods, a published relationship for adult sac-spawners was used to estimate growth rate,²⁴ assuming a temperature of 20°C.

We could not find a suitable published estimate of size-differentiated copepod biomass in the upper 200 m for the northern Benguela system. The only previous size-based estimate was made using a different mesh size (300 μ m). Furthermore, mesozooplankton (mainly copepod) biomass was categorized into only three size classes,²⁵ which was too coarse for the current analysis. For the purpose of estimating copepod production, therefore, the size structure of the northern Benguela copepod community was assumed to be the same as in the southern Benguela and copepod biomass was taken as the average of the only published estimate of mesozooplankton biomass from Namibian waters.²⁶ Growth rate was then estimated from the growth rate–body size relationship for the northern Benguela system. The equation²⁴ for adult sac-spawners at 20°C was also used here to estimate growth rates of non-calanoid copepods. As estimates for both copepod biomass

Table 1. Parameter values used to calculate growth rate for different copepod species and developmental stages in the southern Benguela (SB) and the northern Benguela (NB) systems: total length (TL, μm), prosome length (PL, μm), body mass (BM, μg dry mass), egg diameter (ED, μm) and egg mass (EM, μg dry mass). Species/taxa are in ascending order of body size. Egg diameter excludes the perivitelline space, where present. Values without superscripts were obtained in this study (the number of samples is shown in brackets).

Species/taxon	Stage	Region	TL	PL	BM	ED	EM
<i>Calanus agulhensis</i>	N6	SB	585 ^a	–	2 ^g	–	–
<i>Calanoides carinatus</i>	N6	SB	585 ^b	–	2 ^b	–	–
<i>Calanus agulhensis</i>	C1	SB	780 ^c	650 ^c	4 ^g	–	–
<i>Calanoides carinatus</i>	C1	SB	788 ^d	614 ^e	4 ^g	–	–
<i>Calanus agulhensis</i>	C2	SB	950 ^c	800 ^c	9 ^g	–	–
<i>Paracalanus parvus</i>	Fem	SB	1004 (17)	772 (17)	6 ^h	76 (71)	0.101 ⁱ
<i>Calanoides carinatus</i>	C2	SB	1010 ^d	796 ^e	7 ^g	–	–
<i>Calanoides carinatus</i>	C3	SB	1253 ^d	1002 ^e	18 ^g	–	–
	C3	NB	1253 ^d	1002 ^f	18 ^f	–	–
<i>Calanus agulhensis</i>	C3	SB	1350 ^c	1090 ^c	22 ^g	–	–
<i>Calanoides carinatus</i>	C4	SB	1653 ^d	1336 ^e	30 ^g	–	–
	C4	NB	1653 ^d	1336 ^f	30 ^f	–	–
<i>Calanus agulhensis</i>	C4	SB	1700 ^c	1400 ^c	46 ^g	–	–
<i>Centropages brachiatus</i>	Fem	SB	1790 ^c	1220 ^c	25 ^g	76 (57)	0.101 ⁱ
	Fem	NB	1677 (17)	1211 (22)	21 ^h	76 ^f	0.101 ⁱ
<i>Nannocalanus minor</i>	Fem	SB	1903 (23)	1507 (23)	34 ^h	124 (32)	0.200 ^j
	Fem	NB	2035 (23)	1614 (25)	46 ^h	122 (15)	0.195 ^j
<i>Calanoides carinatus</i>	C5	SB	2095 ^d	1705 ^e	60 ^g	–	–
<i>Pleuromamma</i> spp.	Fem	SB	2107 (19)	1362 (23)	29 ^h	146 (55)	0.274 ⁱ
	Fem	NB	2137 (20)	1462 (22)	35 ^h	188 (1)	0.500 ^j
<i>Scolecithrix</i> spp.	Fem	NB	2150 (8)	1698 (8)	53 ^h	260 (1)	1.401 ^j
<i>Metridia lucens</i>	Fem	NB	2294 (18)	1517 (19)	39 ^h	153 (9)	0.303 ^j
<i>Calanus agulhensis</i>	C5	SB	2300 ^c	1780 ^c	97 ^g	–	–
<i>Candacia armata</i>	Fem	SB	2405 (5)	1831 (13)	66 ^h	160 (23)	0.335 ^j
	Fem	NB	2283 (5)	1821 (5)	65 ^h	134 (11)	0.231 ^j
<i>Euchaeta</i> spp.	Fem	NB	2413 (8)	1770 (8)	59 ^h	279 (28)	1.838 ^j
<i>Undinula vulgaris</i>	Fem	NB	2427 (7)	1867 (8)	69 ^h	120 (10)	0.189 ^j
<i>Calanoides carinatus</i>	Fem	SB	2498 ^d	2041 ^e	124 ^g	151 (32)	0.295 ^j
	Fem	NB	2445 (19)	1971 (22)	80 ^h	165 (6)	0.360 ^j
<i>Calanus agulhensis</i>	Fem	SB	2760 ^c	2130 ^c	202 ^g	166 (62)	0.365 ^j
<i>Eucalanus</i> spp.	Fem	NB	2903 (24)	2533 (24)	158 ^h	215 (71)	0.736 ^j
<i>Neocalanus tonsus</i>	Fem	SB	3601 (19)	2774 (19)	203 ^h	138 (62)	0.245 ^j
<i>Rhincalanus nasutus</i>	Fem	SB	4411 (22)	3815 (22)	486 ^h	212 (58)	0.705 ^j
	Fem	NB	4319 (7)	3743 (7)	461 ^h	203 (17)	0.620 ^j
Pontellidae spp.	Fem	NB	4777 (5)	3873 (4)	506 ^h	143 (10)	0.263 ^j
<i>Eucalanus elongatus</i>	Fem	NB	6541 (18)	5916 (17)	1617 ^h	197 (10)	0.569 ^j

^aMean of N4–N6 and C1 masses. ¹⁹ ^bAssumed the same as for *Calanus agulhensis*. ^cStuart and Huggett. ¹⁹ ^dTL = PL × 1.198 + 52.4. ²⁰ ^eVerheyen. ²¹ ^fFrom specimens in the southern Benguela system. ^gPeterson *et al.* ²² ^hUsing the equation $\ln(\text{dry mass}) = 2.74\ln(\text{PL}) - 16.41$. ²³ ⁱFrom egg diameter (ED): $\ln(\text{dry mass}) = -3.381 + 0.0143 \times \text{ED}$. ²⁰

and growth in the northern Benguela system are only available for autumn and winter, our production estimate may be biased. Since there is perennial upwelling in the northern Benguela system,²⁷ however, extrapolation from autumn/winter data alone may still give a reasonable annual estimate of copepod production.

Results and discussion

Estimates of daily egg production and female growth rate of several dominant copepod species, as well as daily somatic growth rate of various copepodite stages, in the northern Benguela system are summarized in Table 2. A total of 348 egg production and 4 moulting rate experiments was performed. The minimum daily egg production rate for all species was 0 eggs per female d⁻¹.^{*} Maximum egg production per female varied considerably among the species examined, from 1.0 to 224.7 eggs d⁻¹, and showed no consistent relationship with body size. Mean daily egg production rates of most species (*Nannocalanus minor*, *Pleuromamma* spp., *Scolecithrix* spp., *Metridia lucens*, *Euchaeta* spp., *Undinula vulgaris*, *Calanoides carinatus*, *Eucalanus* spp., *Rhincalanus nasutus* and Pontellidae spp.) were low, <12 eggs d⁻¹. However, females of *Candacia armata* and *Eucalanus elongatus* produced on average >20 eggs d⁻¹, whereas daily egg production of *Centropages brachiatus*

averaged 62 eggs d⁻¹.

These are the first direct measurements of egg production and juvenile somatic growth of copepods in the northern Benguela system. Moreover, to our knowledge, female egg production and growth rates for *Candacia armata* (27.1 eggs d⁻¹, 0.085 d⁻¹), *Eucalanus elongatus* (22.4 eggs d⁻¹, 0.008 d⁻¹), *Pleuromamma* spp. (2.8 eggs d⁻¹, 0.039 d⁻¹) and *Scolecithrix* spp. (0.67 eggs d⁻¹, 0.017 d⁻¹) measured in this study are the first direct field estimates for these copepods.

Growth rates measured for other species in this study are generally similar to previous field estimates obtained on the same or related species in different regions. Mean egg production per female of *Metridia lucens* (2.1 eggs d⁻¹) was similar to estimates for the same species (means ranged from 0.3 to 3.4 eggs d⁻¹) in the North Sea,²⁸ and other *Metridia* spp. usually lay 1–10 eggs d⁻¹.²⁹ For *Euchaeta* spp., our estimates of mean egg production and growth rate (1.28 eggs d⁻¹, 0.038 d⁻¹) are comparable to those found for *Euchaeta marina* (3.4 eggs d⁻¹, 0.07 d⁻¹) in warm Jamaican waters.³⁰ For *Undinula vulgaris*, our estimates of 6.2 eggs d⁻¹ and 0.016 d⁻¹ are similar to those for the same species off Jamaica (~12.4 eggs d⁻¹, ~0.04–0.08 d⁻¹)³⁰ and Hawaii (6.4 eggs d⁻¹).³¹ Our estimates of 10.9 eggs d⁻¹ and 0.049 d⁻¹ for *Eucalanus* spp. are similar to those for *Eucalanus californicus* (25.2 eggs d⁻¹, ~0.045 d⁻¹) in the California Current upwelling region off Oregon.³² The estimates of mean egg production and growth rates of Pontellidae spp. (10.05 eggs d⁻¹, 0.005 d⁻¹) are comparable

*In this paper, egg production is quoted in eggs per female per day (eggs d⁻¹), and growth rate in units of d⁻¹.

Table 2. Egg production (eggs per female per day, mean \pm standard error), growth rate (d^{-1} , mean \pm s.e.) and number of samples (n) for all copepod species and developmental stages in this study. Data for species from the northern Benguela (NB) were collected during the 1997 and 1999 BENEFIT cruises. Data for species from the southern Benguela (SB) were published previously^{6,7}, except for *Paracalanus parvus*, *Pleuromamma* spp. and *Candacia armata*. Species/taxa are in ascending order of body size.

Species/taxon	Stage	Region	Egg production		Growth rate (mean \pm s.e.)	n
			Mean \pm s.e.	Maximum		
<i>Calanus agulhensis</i>	N6	SB	–	–	0.550 \pm 0.017	39
<i>Calanoides carinatus</i>	N6	SB	–	–	0.584	1
<i>Calanus agulhensis</i>	C1	SB	–	–	0.517 \pm 0.021	96
<i>Calanoides carinatus</i>	C1	SB	–	–	0.464 \pm 0.030	4
<i>Calanus agulhensis</i>	C2	SB	–	–	0.422 \pm 0.018	117
<i>Paracalanus parvus</i>	Fem	SB	34.0 \pm 10.8	140.3	0.382 \pm 0.099	14
<i>Calanoides carinatus</i>	C2	SB	–	–	0.443 \pm 0.080	11
<i>Calanoides carinatus</i>	C3	SB	–	–	0.180 \pm 0.028	8
<i>Calanoides carinatus</i>	C3	NB	–	–	0.235	1
<i>Calanus agulhensis</i>	C3	SB	–	–	0.278 \pm 0.014	131
<i>Calanoides carinatus</i>	C4	SB	–	–	0.189 \pm 0.023	8
<i>Calanoides carinatus</i>	C4	NB	–	–	0.131 \pm 0.043	3
<i>Calanus agulhensis</i>	C4	SB	–	–	0.240 \pm 0.013	157
<i>Centropages brachiatus</i>	Fem	SB	83.6 \pm 4.7	278.7	0.276 \pm 0.014	158
	Fem	NB	62.0 \pm 2.0	224.7	0.232 \pm 0.041	33
<i>Nannocalanus minor</i>	Fem	SB	26.1 \pm 2.9	96.2	0.134 \pm 0.014	82
	Fem	NB	9.4 \pm 2.4	50.5	0.037 \pm 0.009	36
<i>Calanoides carinatus</i>	C5	SB	–	–	0.052 \pm 0.013	17
<i>Pleuromamma</i> spp.	Fem	SB	3.6 \pm 1.6	14.0	0.032 \pm 0.014	11
	Fem	NB	2.8 \pm 1.0	10.3	0.039 \pm 0.014	11
<i>Scolecithrix</i> spp.	Fem	NB	0.7 \pm 0.3	1.0	0.017 \pm 0.009	3
<i>Metridia lucens</i>	Fem	NB	2.1 \pm 0.9	28.0	0.016 \pm 0.006	33
<i>Calanus agulhensis</i>	C5	SB	–	–	0.092 \pm 0.007	151
<i>Candacia armata</i>	Fem	SB	19.6 \pm 4.8	66.2	0.092 \pm 0.022	14
	Fem	NB	27.1 \pm 26.8	80.7	0.085 \pm 0.084	3
<i>Euchaeta</i> spp.	Fem	NB	1.3 \pm 0.4	5.2	0.038 \pm 0.013	12
<i>Undinula vulgaris</i>	Fem	NB	6.2 \pm 2.1	48.8	0.016 \pm 0.005	43
<i>Calanoides carinatus</i>	Fem	SB	24.0 \pm 1.6	143.5	0.053 \pm 0.003	352
	Fem	NB	11.1 \pm 1.3	68.0	0.047 \pm 0.005	112
<i>Calanus agulhensis</i>	Fem	SB	19.2 \pm 0.6	130.8	0.033 \pm 0.001	1496
<i>Eucalanus</i> spp.	Fem	NB	10.9 \pm 1.9	31.3	0.049 \pm 0.008	26
<i>Neocalanus tonsus</i>	Fem	SB	16.1 \pm 4.3	98.2	0.019 \pm 0.005	33
<i>Rhincalanus nasutus</i>	Fem	SB	26.1 \pm 4.2	61.2	0.037 \pm 0.006	19
	Fem	NB	6.3 \pm 2.7	18.4	0.009 \pm 0.004	9
Pontellidae spp.	Fem	NB	10.1 \pm 2.1	23.7	0.005 \pm 0.001	14
<i>Eucalanus elongatus</i>	Fem	NB	22.4 \pm 5.0	63.5	0.008 \pm 0.002	18

to those of the Pontellid *Epilabidocera longipedata* (8.5 eggs d^{-1} , \sim 0.015 d^{-1}) off Oregon.³² Similar average egg production rates have also been reported for the Pontellid *Labidocera aestiva* (10–19 eggs d^{-1}) under varied food and light regimes in the laboratory.³³ For a comparison of rates of egg production and female growth of *Centropages brachiatus*, *Nannocalanus minor*, *Calanoides carinatus* and *Rhincalanus nasutus*, and for somatic growth of *Calanoides carinatus* between the Benguela and other systems, refer to Richardson and Verheye.⁶

Although there was no relationship between the number of eggs produced per female and female body size, growth rate decreased with body size. Small copepods (<1800 μ m: *C. carinatus* C3 and C4, and female *C. brachiatus*) grew rapidly, between 0.13 and 0.24 d^{-1} , compared with larger copepods (females of *Nannocalanus minor*, *Pleuromamma* spp., *Scolecithrix* spp., *Metridia lucens*, *Candacia armata*, *Euchaeta* spp., *Undinula vulgaris*, *Calanoides carinatus*, *Eucalanus* spp., *Rhincalanus nasutus*, Pontellidae spp. and *Eucalanus elongatus*), which grew at rates of <0.1 d^{-1} (Table 2).

To identify relationships between growth rate (g) and body mass (BM), log-transformed mean growth rates were plotted against log-transformed mean body mass (Fig. 1), giving the following regression equations: $\log g = -0.384 - 0.711 \times \log BM$ ($r^2 = 0.59$, $P < 0.001$, $n = 15$) for the northern Benguela system and $\log g = -0.185 - 0.624 \times \log BM$ ($r^2 = 0.79$, $P < 0.0001$, $n = 21$) for the southern Benguela. Although the slopes of the two regression lines were not significantly different (ANCOVA, P

> 0.05), the intercepts were different ($P < 0.01$), so the data were not combined to give one equation for the Benguela system.

The slope and intercept of the growth rate–body mass relationship in this study were substantially different from the global equation for growth rate of marine planktonic copepods at 10–25°C described by Hirst and Lampitt (Fig. 1).²⁴ In our study, the slopes (–0.71 for the northern Benguela system and –0.62 for the southern) were much steeper than that (–0.49) of the global equation. This is because of the faster growth rates of smaller species/younger stages and the slower rates of larger species/older stages in our study. This difference in rates is probably attributable to differences in food limitation, because small copepods in the Benguela grow at closer to their maximal rates and larger copepods are more food limited.⁷

It must be noted that the log-log model is a transformation of the original data and is thus only an approximation of the actual non-linear relationship. Prior to the advent of powerful desktop computers, it was difficult to use iterative methods to perform non-linear analyses. Logarithmic transformations were used to linearize the data so that conventional least-squares regression techniques could be used. With increased computing power and easy-to-use non-linear fitting tools, it is now possible to fit non-linear regressions directly without the need to transform the data. These methods provide the best approximation to the non-linear relationship and thus yield superior fits.

We fitted a non-linear model to the growth rate–body mass data using the quasi-Newton method, to compare with the

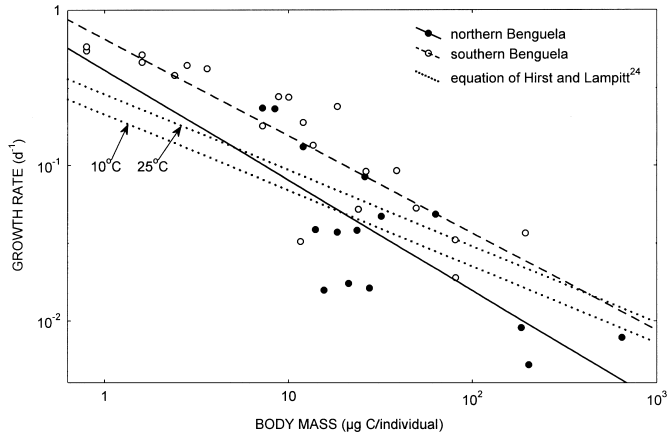


Fig. 1. Log-log plot of mean growth rate (d^{-1}) against mean body mass ($\mu\text{g C}$ per individual). The fitted equation for the northern Benguela system is $\log g = -0.384 - 0.711 \times \log \text{BM}$ ($r^2 = 0.59$, $P < 0.001$, $n = 15$) and for the southern Benguela system is $\log g = -0.185 - 0.624 \times \log \text{BM}$ ($r^2 = 0.79$, $P < 0.0001$, $n = 21$). Also shown is a global equation of copepod growth against body mass at 10°C and 25°C (from ref. 24).

log-log model. This yielded the following relationships (Fig. 2a): $g = 0.866 \times 10^{-0.075\text{BM}}$ ($r^2 = 0.81$, $n = 15$) for the northern Benguela, and $g = 0.572 \times 10^{-0.042\text{BM}}$ ($r^2 = 0.89$, $n = 21$) for the southern Benguela system. The proportion of variance explained by each of these relationships is substantially larger (81% and 89%) than that for the log-log model (59% and 79%), indicating a better model fit. As it may be useful to estimate growth rate from size data collected using the optical plankton counter or from size-differentiated biomass from net samples, equations relating growth rate to total copepod length (TL) in the northern Benguela ($g = 1.926 \times 10^{-0.0007\text{TL}}$, $r^2 = 0.77$) and southern Benguela ($g = 1.104 \times 10^{-0.0005\text{TL}}$, $r^2 = 0.93$) systems are also shown (Fig. 2b).

To compare the predictive capability of the non-linear and log-log models of copepod growth, we plotted the predicted growth rate from the two models against the observed growth rate. For the northern Benguela system (Fig. 3a), the log-log model severely underestimates the growth rate by 46–60% at fast growth rates ($\sim 0.24 d^{-1}$). Moreover, there is a strong bias in predicted growth rates for observed growth rates above $0.04 d^{-1}$; predicted values are all below the 1:1 line. Predictions from the non-linear model are relatively unbiased, occurring on both sides of, and close to, the 1:1 line.

For the southern Benguela system, the log-log model has a very poor fit at fast growth rates (Fig. 3b), here overestimating the growth rate by $\sim 35\%$. The log-log model, however, probably does slightly better than the non-linear model at estimating slow growth rates. The log-log model also generally underestimates growth rates between $0.1 d^{-1}$ and $0.45 d^{-1}$. Predictions from the non-linear model are close to, and are randomly distributed on both sides of, the 1:1 line.

In summary, the non-linear model is substantially better than the log-log model at faster growth rates (smaller copepods), whereas the log-log model is slightly better at predicting slow growth rates (larger copepods). Advantages of the log-transformed model include that it is possible to calculate a significance level, it is possible to test whether two equations have the same slopes and intercepts, and it is easily compared with previous studies that have used log-log models. In the current study, however, it is desirable to have precise estimates of growth of smaller individuals because they are numerically (and by mass) more abundant, and they also grow quickly, so that they contribute more to production. Thus, errors in their estimation have a large impact on production estimates. Therefore, we suggest

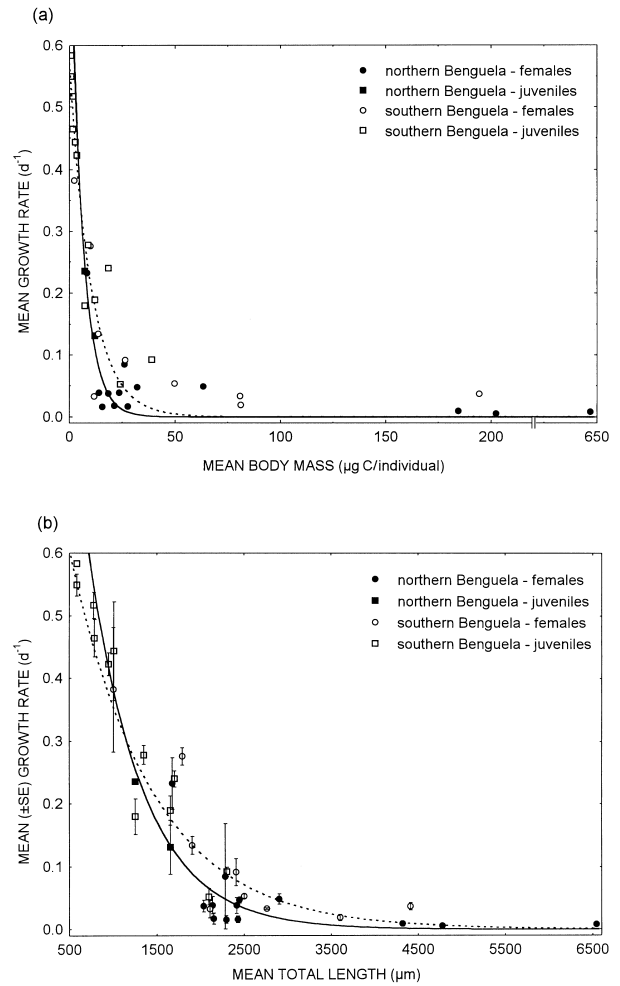


Fig. 2. a, Mean growth rate (g, d^{-1}) against mean body mass (BM, $\mu\text{g C}$ per individual) for the northern (solid line) and southern Benguela (dotted line) systems. The fitted equation for the northern Benguela system is $g = 0.866 \times 10^{-0.075\text{BM}}$ ($r^2 = 0.81$, $n = 15$) and for the southern Benguela system is $g = 0.572 \times 10^{-0.042\text{BM}}$ ($r^2 = 0.89$, $n = 21$). Note the scale break in the x-axis at 250 $\mu\text{g C}$. For ease of interpretation, standard errors are not shown; **b,** mean growth rate (d^{-1}) against mean total length (TL, μm): the fitted equation for the northern Benguela system is $g = 1.9256 \times 10^{-0.0007\text{TL}}$ ($r^2 = 0.77$) and for the southern Benguela system is $g = 1.1035 \times 10^{-0.0005\text{TL}}$ ($r^2 = 0.93$).

that for the estimation of production over a broad size range of copepods, a non-linear model gives more precise estimates.

Using the non-linear model, the estimated copepod production for the northern Benguela system is $39 \text{ g C m}^{-2} \text{ yr}^{-1}$ and for the southern Benguela system is $99 \text{ g C m}^{-2} \text{ yr}^{-1}$. (Note that the log-log model substantially underestimates production, giving an annual copepod production of only $18 \text{ g C m}^{-2} \text{ yr}^{-1}$ in the northern Benguela (46% of the estimate from the non-linear model), and $80 \text{ g C m}^{-2} \text{ yr}^{-1}$ (80% of the estimate from the non-linear model) in the southern Benguela.

Our estimate of copepod production of $39 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the northern Benguela system is below the range of the only previous (indirect) estimate of $52\text{--}69 \text{ g C m}^{-2} \text{ yr}^{-1}$ (calculated from Cushing,⁹ assuming perennial production; Table 3). The estimate for the northern Benguela system may be underestimated because information from the warm Angola-Benguela Front region was combined with data from the northern Benguela proper, because of the paucity of growth rate data. Moreover, few data on species/size-differentiated copepod biomass in the northern Benguela necessitated the assumption that the size distribution of copepod biomass in this system is similar to that

Table 3. Estimates of annual copepod production ($\text{g C m}^{-2} \text{ yr}^{-1}$) in the northern and southern Benguela systems.

Region	Production ($\text{g C m}^{-2} \text{ yr}^{-1}$)	Source
Northern Benguela	39	This study
	52–69	Calculated from Cushing ⁹ assuming perennial production
Southern Benguela	99	This study
	25–33	Calculated from Cushing ⁹ assuming perennial production
	11	Hutchings ³⁵
	20–30	Borchers and Hutchings ³⁶
	40–60	Borchers and Hutchings ³⁶
	79	Verheye ²¹
	65.6–74.5	Walker and Peterson ³⁷
	18.6 (1988)	Peterson <i>et al.</i> ³
	27.2 (1989)	Peterson <i>et al.</i> ³
	17–120 ^a	Calculated from Fig. 14 in Hutchings <i>et al.</i> ⁴
53.0 (1993/94)	Richardson ⁸	
89.8 (1994/95)	Richardson ⁸	

^aIncorrectly given as $150 \text{ g C m}^{-2} \text{ yr}^{-1}$ in their paper.

in the southern Benguela. This assumption makes estimates of copepod production in the northern Benguela system rather speculative. As biomass is the component of the production equation that is least predictable,^{24,34} more estimates of biomass in the northern Benguela system are needed. Only with improved biomass estimates can copepod production be more reliably calculated.

The value of $99 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the southern Benguela system is at the upper limit of previous estimates of copepod production

in the region, ranging from 11 to $120 \text{ g C m}^{-2} \text{ yr}^{-1}$ (Table 3), depending on the method used (see ref. 4). The large amount of data (~ 3000 growth rate measurements and ~ 2500 samples of species/size-differentiated biomass), together with standard methods for collection of copepod biomass and measurement of growth rate, should make the present estimate of copepod production in this region more accurate than previous ones. The empirical growth–size relationship reported in this study covers a broad size range of copepods and is a useful tool for estimating secondary production in the Benguela system, based on broad-scale surveys of copepod biomass and detailed analyses of species and size composition.

We thank the masters, officers and crew of the RV *Petr Kottsov* and the FRS *Africana*, as well as the Branch: Marine and Coastal Management Coordination of the Department of Environmental Affairs and Tourism for logistical support and research facilities. Funding was provided by the BENEFIT Programme, the Deutsche Gesellschaft für Technische Zusammenarbeit (Germany), and the European Union-sponsored ENVIFISH Programme (contract number: IC18-CT98-0329). We also thank Jenny Huggett, Rob Leslie, Delphine Thibault and an anonymous reviewer for their constructive comments on the manuscript.

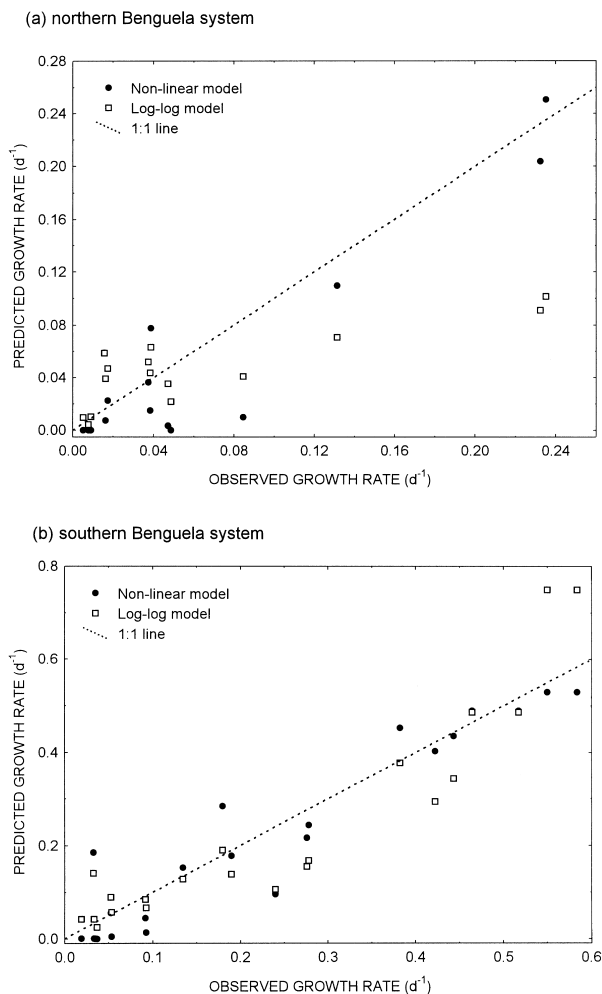


Fig. 3. Growth rate (d^{-1}) predicted from the non-linear and log-log models against observed growth rate (d^{-1}) for (a) the northern Benguela and (b) southern Benguela systems. The 1:1 line is also shown.

- Humes A.G. (1994). How many copepods? *Hydrobiologia* **292/293**, 1–7.
- Schmitt W.L. (1965). *Crustaceans*. University of Michigan Press, Ann Arbor.
- Peterson W.T., Hutchings L., Huggett J.A. and Largier J.L. (1992). Anchovy spawning in relation to the biomass and the replenishment rate of their copepod prey on the western Agulhas Bank. In *Benguela Trophic Functioning*, eds A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn. *S. Afr. J. mar. Sci.* **12**, 487–500.
- Hutchings L., Verheye H.M., Mitchell-Innes B.A., Huggett J.A. and Painting S.J. (1995). Copepod production in the southern Benguela system. *ICES J. mar. Sci.* **52**, 439–455.
- Peterson W.T. and Hutchings L. (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. Plank. Res.* **17**, 2275–2294.
- Richardson A.J. and Verheye H.M. (1998). The relative importance of food and temperature to copepod egg production and somatic growth in the southern Benguela upwelling system. *J. Plank. Res.* **20**, 2379–2399.
- Richardson A.J. and Verheye H.M. (1999). Growth rates of copepods in the southern Benguela upwelling system: the interplay between body size and food. *Limnol. Oceanogr.* **44**, 382–392.
- Richardson (1998). *Within-season variability of copepod abundance and growth in the southern Benguela upwelling system and implications for the spawning of the Cape anchovy*. Ph.D. thesis, University of Cape Town.
- Cushing D.H. (1971). Upwelling and the production of fish. *Adv. Mar. Biol.* **9**, 255–334.
- Frost B.W. (1977). Feeding behavior of *Calanus pacificus* in mixture of food particles. *Limnol. Oceanogr.* **22**, 472–491.
- Berggreen U., Hansen B. and Kiørboe T. (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.
- Mitchell-Innes B.A. and Pitcher G.C. (1992). Hydrographic parameters as indicators of the suitability of phytoplankton populations as food for herbivorous copepods. In *Benguela Trophic Functioning*, eds A.I.L. Payne, K.H. Brink, K.H. Mann and R. Hilborn. *S. Afr. J. mar. Sci.* **12**, 355–365.

13. Webber M.K. and Roff J.C. (1995). Annual biomass and production of the oceanic copepod community off Discovery Bay, Jamaica. *Mar. Biol.* **123**, 481–495.
14. Hocutt C.H. and Verheye H.M. (2001). BENEFIT marine science in the Benguela Current region during 1999: Introduction. *S. Afr. J. Sci.* **97**, 195–198.
15. Runge J.A. and Roff J.C. (2000). The measurement of growth and reproductive rates. In *ICES Zooplankton Methodology Manual*, eds R.P. Harris, P.H. Wiebe, J. Lenz, H.R. Skjoldal and M. Huntley, pp. 401–454. Academic Press, New York.
16. Peterson W.T., Tiselius P. and Kjørboe T. (1991). Copepod egg production, moulting and growth rates, and secondary production, in the Skagerrak in August 1988. *J. Plank. Res.* **13**, 131–154.
17. Kimmerer W.J. and McKinnon A.D. (1987). Growth, mortality and secondary production of the copepod *Acartia tranteri* in Westernport Bay, Australia. *Limnol. Oceanogr.* **32**, 14–28.
18. Paffenhöfer G-A. (1994). Variability due to feeding activity of individual copepods. *J. Plank. Res.* **16**, 617–626.
19. Stuart V. and Huggett J.A. (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.
20. Van der Lingen C.D. (2000). *The feeding ecology of, and carbon and nitrogen budgets for, sardine Sardinops sagax in the southern Benguela upwelling ecosystem*. Ph.D. thesis, University of Cape Town.
21. 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.
22. Peterson W.T., Painting S.J. and Hutchings L. (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. Plank. Res.* **12**, 259–281.
23. Chisholm L.A. and Roff J.C. (1990). Size–weight relationships and biomass of tropical neritic copepods off Kingston, Jamaica. *Mar. Biol.* **106**, 71–77.
24. Hirst A.G. and Lampitt R.S. (1998). Towards a global model of in situ weight-specific growth in marine planktonic copepods. *Mar. Biol.* **132**, 247–257.
25. Barangé M. (1989). Zooplankton size structure off Namibia in July 1983 and 1984. *Colln scient. Pnp. int. Commn SE. Atl. Fish.* **16**, 31–41.
26. Hutchings L., Pillar S.C. and Verheye H.M. (1991). Estimates of standing stock, production and consumption of meso- and macrozooplankton in the Benguela ecosystem. *S. Afr. J. mar. Sci.* **11**, 499–512.
27. Shannon L.V. (1985). The Benguela ecosystem: Part I. Evolution of the Benguela, physical features and processes. *Oceanogr. Mar. Biol. Ann. Rev.* **23**, 105–182.
28. Nielsen T.G. and Richardson K. (1989). Food chain structure of the North Sea plankton communities: seasonal variation of the role of the microbial loop. *Mar. Ecol. Prog. Ser.* **56**, 75–87.
29. Batchelder H.P. and Williams R. (1995). Individual-based modelling of the population dynamics of *Metridia lucens* in the North Atlantic. *ICES J. mar. Sci.*, **52**, 469–482.
30. Hopcroft R.R. and Roff J.C. (1998). Zooplankton growth rates: the influence of female size and resources on egg production of tropical marine copepods. *Mar. Biol.* **132**, 79–86.
31. Park C. and Landry M.R. (1993). Egg production by the subtropical copepod *Undinula vulgaris*. *Mar. Biol.* **117**, 415–421.
32. Gómez-Gutiérrez J. and Peterson W.T. (1999). Egg production rates of eight calanoid copepod species during summer 1997 off Newport, Oregon, USA. *J. Plank. Res.* **21**, 637–659.
33. Marcus N.H. (1988). Photoperiodic conditions, food patchiness and fecundity. *Bull. mar. Sci.* **43**, 641–649.
34. Huntley M.E. and Lopez M.D.G. (1992). Temperature-dependent production of marine copepods: a global synthesis. *Am. Nat.* **140**, 201–242.
35. Hutchings L. (1979). *Zooplankton of the Cape Peninsula upwelling region*. Ph.D. thesis, University of Cape Town.
36. Borchers P. and Hutchings L. (1986). Starvation tolerance, development time and egg production of *Calanoides carinatus* in the southern Benguela Current. *J. Plank. Res.* **8**, 855–874.
37. Walker D.R. and Peterson W.T. (1991). Relationships between hydrography, phytoplankton production, biomass, cell size and species composition, and copepod production in the southern Benguela upwelling system in April 1988. *S. Afr. J. mar. Sci.* **11**, 289–305.