

A review of the biology and ecology of *Calanus agulhensis* off South Africa

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Calanus agulhensis is the dominant large copepod on South Africa's Agulhas Bank, and is an important food item for pelagic fish. This paper reviews current knowledge and understanding of its biology and ecology and includes comparisons with other *Calanus* species. Its distribution is influenced by the prevailing hydrography, being advected from the eastern to the western Agulhas Bank and then north along the edge of the west coast shelf. Highest biomass of *C. agulhensis* is on the central Agulhas Bank in the vicinity of a cool ridge of upwelled water that is thought to enhance local retention. Daily vertical migration on the Agulhas Bank is linked to food concentration, with a strong correlation between the extent of migration of large stages (C4-female) and food abundance in the chlorophyll-rich layer. A diel feeding rhythm has been observed, independent of whether or not animals are migrating vertically. Females offered natural assemblages show a preference for the larger particles of the dominant size classes. Development time from egg to adult (20.3 d at 15.5°C) is fast compared with other *Calanus* species. The long N3 stage duration suggests that it is the first feeding stage. Isochronal growth is approximated, but the equiproportional rule is not adhered to. In the field, growth rate is influenced more by food than by temperature, particularly larger stages that are more frequently food-limited. This is probably because the small phytoplankton cells that dominate at warm temperatures are generally at low concentrations (<2 mg chlorophyll *a* m⁻³), insufficient for fast growth of large stages. Egg production following short periods (1–3 d) of starvation returns quickly to normal on the reintroduction of food, an adaptation that may be beneficial in the relatively stable food environment of the Agulhas Bank. Following long periods (9 d) without food, however, many females are unable to regain normal levels of egg production. At present, there is no information on the extent of omnivory in *C. agulhensis*, and little on the ecology of the naupliar and young copepodite stages. These may be fruitful areas for future research.

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Introduction

The species now known as *Calanus agulhensis* was first recorded in South African waters by Cleve (1904), who identified it as *Calanus finmarchicus*. This name persisted for many years, and was used by De Decker (1964) in a comprehensive report on the marine Copepoda of South Africa. He subsequently referred to the copepod as *C. finmarchicus sensu lato*, to designate a form of uncertain taxonomic status (De Decker, 1973, 1984).

Hutchings (1985) referred to it as *C. finmarchicus* var. *australis*, whereas in more recent papers the name *Calanus australis* has been used (Attwood and Peterson, 1989; Peterson *et al.*, 1990). *C. agulhensis* sp. nov. was finally described in 1991 (De Decker *et al.*, 1991).

C. agulhensis belongs to the *Calanus helgolandicus* species group and is closely related to other southern hemisphere calanids, such as *C. australis* (De Decker *et al.*, 1991). However, it is most similar morphologically to *Calanus pacificus*, an exclusively northern hemisphere

species. *C. agulhensis* is one of the smaller species in the *C. helgolandicus* group, with a mean body length of 2.72 mm for females (range 2.15–3.2 mm) and 2.61 mm for males (range 2.08–3.13 mm; Table 1).

There have been two broad areas of research in South Africa concerning *C. agulhensis*. The first is an applied approach, relating the spawning and recruitment of the dominant pelagic fish species in the region, Cape anchovy (*Engraulis capensis*), to the availability of *C. agulhensis*, its primary food source on the Agulhas Bank (Peterson *et al.*, 1992; Hutchings *et al.*, 1995; Richardson *et al.*, 1998). The Agulhas Bank is a roughly triangular extension of the continental shelf off southernmost Africa, extending eastwards from Cape Point. There is a strong inverse relationship between the abundance of adult anchovy and that of copepods on the Agulhas Bank, implying density-dependent regulation of the anchovy spawning stock (Peterson *et al.*, 1992; Richardson, 1998). This approach differs from most other regions, where the emphasis has been on *Calanus* nauplii and young copepodites as food for fish larvae.

The second approach has endeavoured to explain the population dynamics and life history of *C. agulhensis*. The copepod inhabits the warm and relatively stable waters of the Agulhas Bank and the outer shelf along South Africa's west coast. This contrasts with the distribution of *Calanoides carinatus*, which dominates the cool and dynamic coastal upwelling region off the west coast. The different distributions of the two species, despite their apparent similarity, has stimulated comparative studies on their diet, their response to a fluctuating food environment, their production rates and their vertical migratory behaviour.

Relatively little has been published on the life history and population dynamics of *C. agulhensis*. In this paper, we review what we consider to be the key factors that control its population dynamics off South Africa, using published and recent unpublished work, and provide comparisons with sibling species and suggestions for future research. In so doing, we hope that the information will add new perspectives on the biology and ecology of *Calanus* in general.

Distribution, abundance, and population structure

Early investigations identified the Agulhas Bank as the centre of distribution of *C. agulhensis* (Cleve, 1904; De Decker, 1964), although it is also found off the west and east coasts of South Africa (De Decker, 1984). The most extensive information on the distribution and abundance of *C. agulhensis* has been collected by Marine & Coastal Management (formerly the Sea Fisheries Research Institute) during biannual, hydroacoustic pelagic fish stock assessment surveys since 1988. Data

from 16 cruises, eight each during winter (May/June) and summer (November/December), show that *C. agulhensis* is abundant over the entire Agulhas Bank, as illustrated by the distribution of females in Figure 1. Animals are also found off South Africa's west coast, but there they are less abundant, although densities are sometimes high beyond the shelf edge (Figure 1), particularly during summer.

C. agulhensis accounts for 53–82% of the copepod biomass on the Agulhas Bank (Verheye *et al.*, 1994). Biomass of *C. agulhensis* is highest over the midshelf of the central bank and declines towards the east and west (Figure 2). Between 1988 and 1993, the proportion of early juvenile stages (C1–C3) was generally higher east of Cape Agulhas than farther west (Hutchings *et al.*, 1995). Animals are found all year round on the Agulhas Bank (De Decker *et al.*, 1991), reproducing continuously and with no evidence of diapause. Highest densities of *C. agulhensis* during summer are often associated with a quasi-permanent ridge of cool, upwelled water south of Mossel Bay [Figure 3(a), (b); Peterson *et al.*, 1992; Boyd and Shillington, 1994; Peterson and Hutchings, 1995]. Although cyclonic circulation around the ridge is thought to enhance local retention of *C. agulhensis* (Peterson *et al.*, 1992), it has been hypothesized that there is a net westward advection of various stages across the Agulhas Bank (Largier *et al.*, 1992). Several observations support this hypothesis. First, there is a general movement of fish eggs and larvae westwards across the bank (Shelton and Hutchings, 1982; Huggett *et al.*, 1998). This advection continues north around Cape Point and onto the west coast, where *C. agulhensis* lives in warm water along the shelf break (Figure 1). Second, the largest densities of copepods on the western Agulhas Bank are generally found midshelf (Pillar, 1986; Richardson *et al.*, 1998), spatially disassociated from the inshore chlorophyll *a* maximum (Brown, 1992; Mitchell-Innes *et al.*, 1999). This is thought to be a consequence of advective input from the adjacent eastern Agulhas Bank, rather than *in situ* growth (Largier *et al.*, 1992; Peterson *et al.*, 1992). Last, the distribution of stages N6–C3 is usually centred on the cool upwelling ridge, whereas that of older stages C4–C6 is offset towards the west [Figure 3(b); Largier *et al.*, 1992; Peterson and Hutchings, 1995]. Moreover, when the ridge is absent, as it was in November 1990, the centre of distribution of *C. agulhensis* is displaced westwards (Hutchings *et al.*, 1995).

Vertical migration

Studies on vertical migration are essential to investigate hypotheses regarding plasticity of behaviour, such as the interplay between hunger and predation risk, and population retention mechanisms. Two studies on the diel

Table 1. Summary of *Calanus agulhensis* parameters. All data were collected from the field except for those marked with superscripts ^a, ^b, ^c, ^d, and ^h.

Parameter	Variable	Female	Male	C5	C4	C3	C2	C1	N6
Mass (μg dry weight)		202 ^a , 184.4 ^b	110 ^c	97 ^a	46 ^a	22 ^a	9 ^a	4 ^a	1 ^a
Total length (μm)		2760 ^d , 2730 ^e , 2717 ^f	2720 ^d , 2609 ^f	2300 ^d , 2310 ^f	1700 ^d , 1839 ^f	1350 ^d , 1413 ^f	950 ^d , 1055 ^f	780 ^d , 832 ^f	—
Prosome length (μm)		2130 ^d , 2173 ^f	1990 ^d , 1999 ^f	1780 ^d , 1833 ^f	1400 ^d , 1462 ^f	1090 ^d , 1136 ^f	800 ^d , 848 ^f	650 ^d , 674 ^f	—
Ingestion (ng chlorophyll <i>a</i> individual ⁻¹ d ⁻¹ ; % body C d ⁻¹)	Chl <i>a</i> <3 mg m ⁻³	72/167; 3.7/8.5 ^g	4; 0.4 ^h	40/141; 4.2/14.9 ^g	78/141; 17.4/31.4 ^g	—	—	—	—
Stage duration in laboratory (d) ^h	Chl <i>a</i> >3 mg m ⁻³	430/732; 21.8/37.1 ^g , 302–324; 15.3–16.4 ^a	—	—	144–160; 32.1–35.7 ^a	95; 44.3 ^a	—	—	—
Stage duration in field (d) ⁱ	15.5°C	—	—	3.0	2.1	1.7	2.0	1.5	1.6
Growth (d ⁻¹) ^j	19.5°C	—	—	2.5	2.4	1.4	1.3	1.1	1.2
Growth (d ⁻¹) vs. Chl <i>a</i> (mg m ⁻³) ^k	9–23°C	—	—	8.48	3.11	2.65	2.12	1.59	1.27
Growth (d ⁻¹) vs. cell size ^l	g_a	0.05/0.33	—	0.10/0.47	0.24/0.72	0.28/0.71	0.42/0.85	0.51/0.81	0.55/0.69
Lipid content (% dry weight)	k	0.180	—	0.144	0.396	0.400	0.551	0.612	0.550
	a	0.150	—	0.895	0.591	1.035	1.435	1.970	4.827
	b	0.322	—	0.028	0.105	0.161	0.304	0.417	0.514
		36.814	—	0.133	0.318	0.257	0.367	0.278	0.094
		16.7 ^o	—	—	—	—	—	—	—

^aPeterson *et al.* (1990).^bAttwood and Peterson (1989).^cMarine & Coastal Management, unpublished data.^dStuart and Huggett (1992).^eDe Decker *et al.* (1991).^fJAH, unpublished data.^gMean/maximum ingestion rate (JAH, unpublished data).^hFood-satiated stage duration (Peterson and Paiming, 1990).ⁱGeometric mean of stage duration (Richardson and Verheye, 1999).^jMean/maximum growth rate (Richardson and Verheye, 1999).^k $g = g_a(1 - e^{-kx})$; g =growth rate, g_a =asymptotic growth, k =rate at which g approaches g_a , c =chlorophyll *a* (Richardson and Verheye, 1999).^l $y = a + bx$; y =growth rate and x =the proportion of cells >10 μm in size (Richardson and Verheye, 1998).

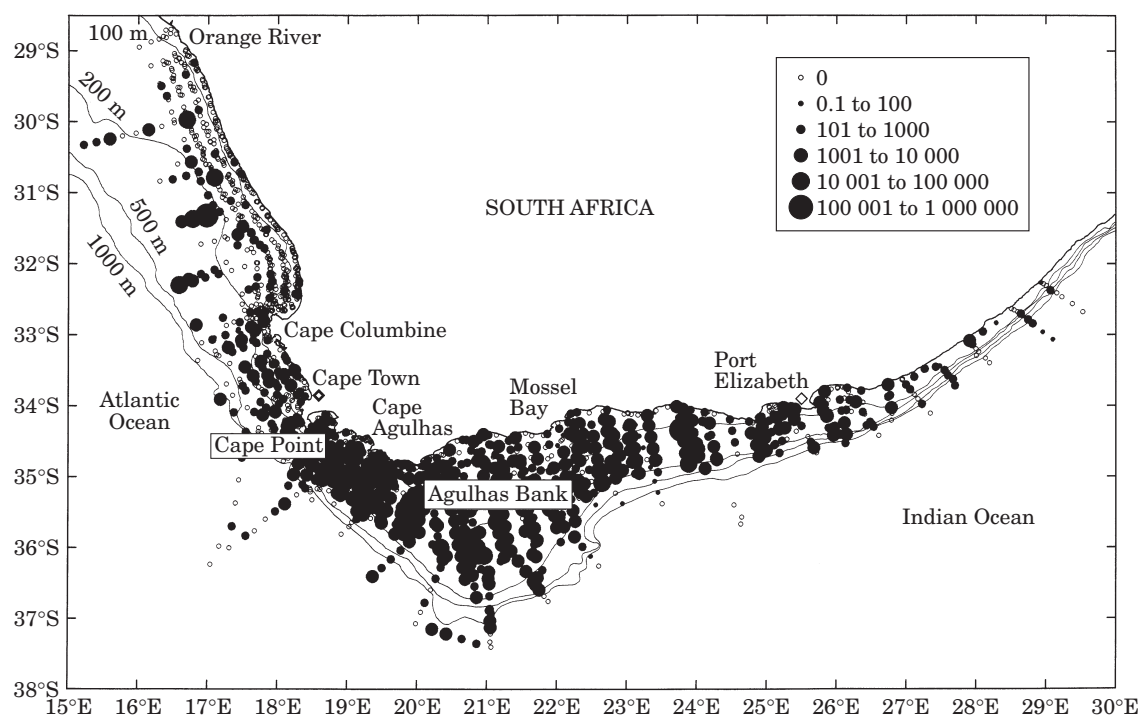


Figure 1. Composite map of distribution (m^{-2}) of *C. agulhensis* females from 16 cruises (winter and summer data pooled) around the coast of South Africa between 1990 and 1996.

vertical migration (DVM) of *C. agulhensis* have been undertaken, one off the west coast and one on the Agulhas Bank.

Off the west coast, Peterson *et al.* (1990) investigated vertical migration of *C. agulhensis* along a cross-shelf transect. Chlorophyll *a* concentrations in the upper 20 m ranged from high (17.2 mg m^{-3}) inshore to moderate (3.8 mg m^{-3}) offshore, indicating that food was unlikely

to be limiting. Normal DVM was apparent for C4, C5, and female *C. agulhensis* near the shelf edge (190 m deep), but younger copepodites showed similar daytime and night-time abundances in the upper water column. Stage C5 and female *C. agulhensis* were scarce inshore (80 m deep), but the younger copepodites again seemed to remain in the upper water column by day and night.

A more comprehensive study of diel vertical migration by *C. agulhensis* was made at three stations on the Agulhas Bank during March 1994 (JAH, unpublished data). The first station (100 m deep) was characterized by persistently high concentrations of chlorophyll *a* ($\sim 5 \text{ mg m}^{-3}$) in the upper mixed layer [Figure 4(a)]. There, *C. agulhensis* exhibited typical DVM, ascending to the food-rich, upper layers at night, and descending before sunrise. By mid-morning, the entire population, except for the C1s, had returned to deeper water. Ontogenetic layering was evident during the day, with older stages found progressively deeper.

At the second station (140 m deep), chlorophyll *a* levels in the upper mixed layer were initially low ($\sim 1 \text{ mg m}^{-3}$), but they increased to $\sim 5 \text{ mg m}^{-3}$ during the afternoon [Figure 4(b)]. The near-surface presence of animals at the start of sampling, before sunset, suggested either an early ascent or lack of descent the previous day, enabling the animals to maximize their food intake near the surface. As food levels increased, the copepods resumed migratory behaviour,

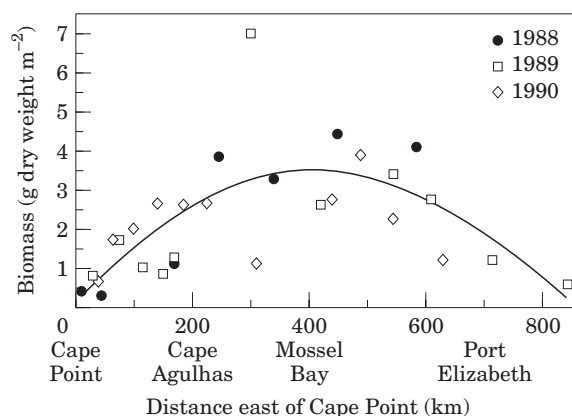


Figure 2. Biomass of *C. agulhensis* across the Agulhas Bank during 1988, 1989, and 1990. Each data point is the mean of a cross-shelf transect. Note that the greatest biomass is off Mossel Bay (redrawn from Verheye *et al.*, 1994). The curve was fitted using the distance-weighted least squares procedure.

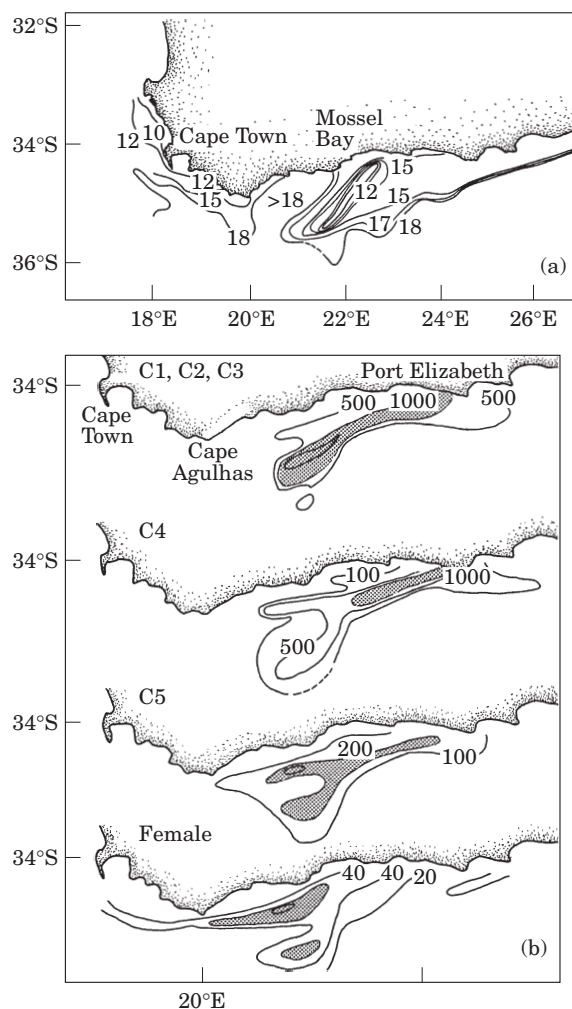


Figure 3. (a) Temperature ($^{\circ}\text{C}$) at 30 m over the Agulhas Bank during November 1989, indicating the "ridge" of cool upwelled water south of Mossel Bay (from Peterson *et al.*, 1992). (b) Distribution (m^{-2}) of *C. agulhensis* developmental stages over the Agulhas Bank during November 1989 (after Largier *et al.*, 1992).

with younger stages (C1–C3) responding later than older ones (C4–C6). Daytime ontogenetic layering was again evident, with a relatively deeper distribution during conditions of abundant food.

At the third station (80 m deep), very low subsurface chlorophyll *a* ($<1 \text{ mg m}^{-3}$) was associated with a strong thermocline, which formed the upper limit of the copepods' nocturnal distribution [Figure 4(c)]. Subsequent daytime weighted mean depths were similar to those of the previous night, with the animals apparently remaining to feed on what low levels of phytoplankton existed in order to reach satiation.

DVM of young *C. agulhensis* stages (C1–C3) was variable during this study. At the first station vertical

migration appeared to be related to food availability, but at the second station there was no relationship. The extent of DVM of the large stages (C4–female), however, was significantly correlated with food abundance in the chlorophyll maximum layer at all stations (Figure 5), indicating that vertical migratory behaviour was directly linked to food availability. Large stages of *C. agulhensis* therefore spent more time near the surface under poor food conditions than under conditions of good food, apparently in order to achieve satiation prior to descending to relative safety from predators in deeper water. Off the west coast, juvenile and adult *Calanoides carinatus* migrate extensively when chlorophyll *a* is plentiful near the surface, but display suppressed DVM when surface chlorophyll *a* is low (Verheye and Field, 1992). Similar behaviour was noted for *C. pacificus* during a mesocosm study (Huntley and Brooks, 1982). *C. pacificus* copepodites performed high-amplitude migrations when phytoplankton was abundant, and individual ingestion rates were high. As food availability declined, migration amplitudes decreased and eventually ceased, such that copepodites remained in the relatively food-rich surface waters at all times.

Ontogenetic layering has been observed for many *Calanus* species, including *C. finmarchicus* (Tande, 1988a; Unstad and Tande, 1991), *C. glacialis* (Hansen *et al.*, 1990; Unstad and Tande, 1991), *C. helgolandicus* (Williams and Conway, 1980), *C. pacificus* (Huntley and Brooks, 1982; Osgood and Frost, 1994), and *C. sinicus* (Uye *et al.*, 1990). This is thought to be a consequence of stage-specific feeding behaviour and swimming ability, as well as size-related susceptibility to predation, and may be important in reducing competition between different life stages (Tande, 1988a). Ontogenetic layering may be more pronounced under conditions of strong thermal stratification (Huang *et al.*, 1992), and has been suggested as a mechanism for population retention in regions subject to strong advection such as upwelling areas (Verheye *et al.*, 1991; Peterson, 1998).

Inverse ontogenetic layering, with youngest stages deeper than older ones, has been observed for *C. helgolandicus* (Williams and Conway, 1980) and *C. glacialis* (Unstad and Tande, 1991), the latter when co-occurring with *C. finmarchicus* in the Barents Sea. Williams and Conway (1980) suggested that different ontogenetic behaviour by congeneric species serves to minimize interspecific competition where the species have sympatric distributions. Different migratory behaviour has also been found for co-occurring *C. pacificus* and *Metridia lucens*, with *M. lucens* copepodites sometimes performing reverse migrations (Osgood and Frost, 1994). Those authors suggest that *M. lucens* may be more susceptible to invertebrate predation, or may simply be capable of a wider range of migratory behaviours during development than *C. pacificus*. As each species integrates factors such as predation risk and

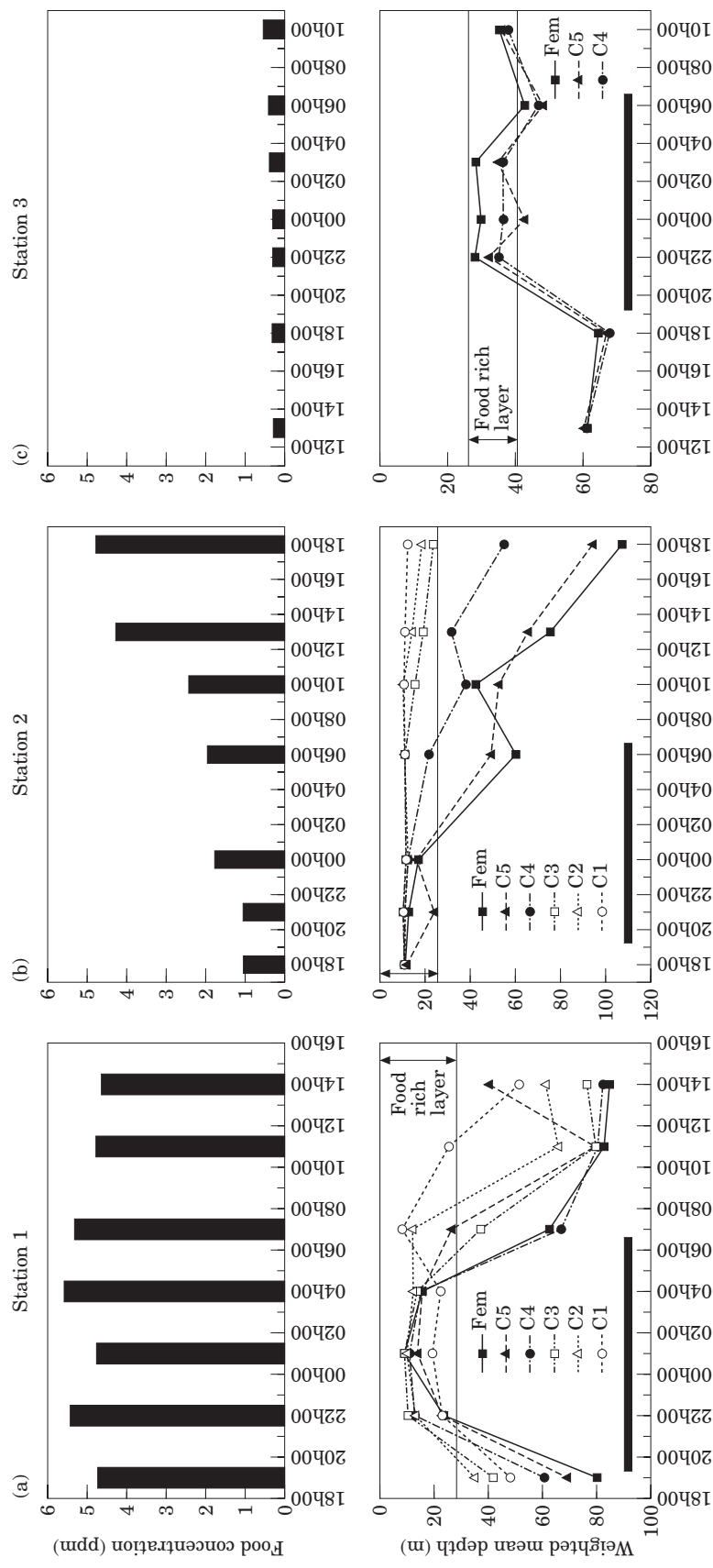


Figure 4. Mean food concentration in the upper mixed layer, and weighted mean depth (m) of *C. agulhensis* stages at Sins (a) 1, (b) 2, and (c) 3 on the Agulhas Bank during March 1994. Horizontal bars indicate hours of darkness.

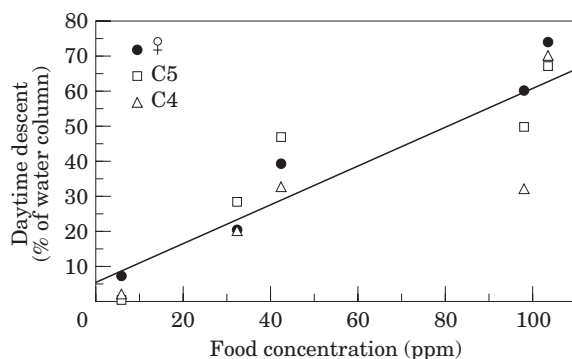


Figure 5. Positive linear relationship ($R^2=0.72$, $n=15$, $p<0.0001$) between the maximum diel vertical migration of C4, C5, and female *C. agulhensis* and food concentration at the depth of maximum fluorescence.

energetic gains from food in a unique way, interspecific differences in diel migratory behaviour are to be expected even under identical conditions (Dagg *et al.*, 1998).

Feeding ecology

Compared with the highly dynamic west coast upwelling regime (Shannon, 1985), the Agulhas Bank provides a relatively stable food environment, with a seasonal structure typical of temperate continental shelf systems (Probyn *et al.*, 1994) such as the Georges Bank (Hutchings, 1994). Although higher concentrations of chlorophyll *a* are associated with inshore coastal upwelling ($\sim 3 \text{ mg m}^{-3}$) and dynamic upwelling along the eastern shelf edge ($>2 \text{ mg m}^{-3}$), mean concentrations over most of the south coast shelf are moderately low ($1\text{--}2 \text{ mg m}^{-3}$; Brown *et al.*, 1991; Brown, 1992).

There are few studies on ingestion rates of *C. agulhensis* in the field, but they do show that individuals are often food-limited. Maximum ingestion rates of *C. agulhensis* females increased from $167 \text{ ng chlorophyll } a \text{ individual}^{-1} \text{ d}^{-1}$ (mean=72) under low concentrations of chlorophyll *a* ($<3 \text{ mg m}^{-3}$) to $732 \text{ ng chlorophyll } a \text{ individual}^{-1} \text{ d}^{-1}$ (mean=430) at high concentrations ($>3 \text{ mg m}^{-3}$; Table 1). Ingestion rates as a percentage of body C d^{-1} (Table 1) were calculated by assuming that water low in chlorophyll *a* is flagellate-dominated (Mitchell-Innes and Pitcher, 1992), with a C:chlorophyll ratio of 41 (Cochrane *et al.*, 1991), and water high in chlorophyll *a* to be diatom-dominated, with a C:chlorophyll ratio of 30. Faster ingestion rates by large juveniles (C4 and C5) were also observed under high compared to low chlorophyll *a* conditions. The high concentrations of chlorophyll *a* often observed on the west coast (Brown *et al.*, 1991; Brown, 1992) therefore support faster rates of ingestion than the

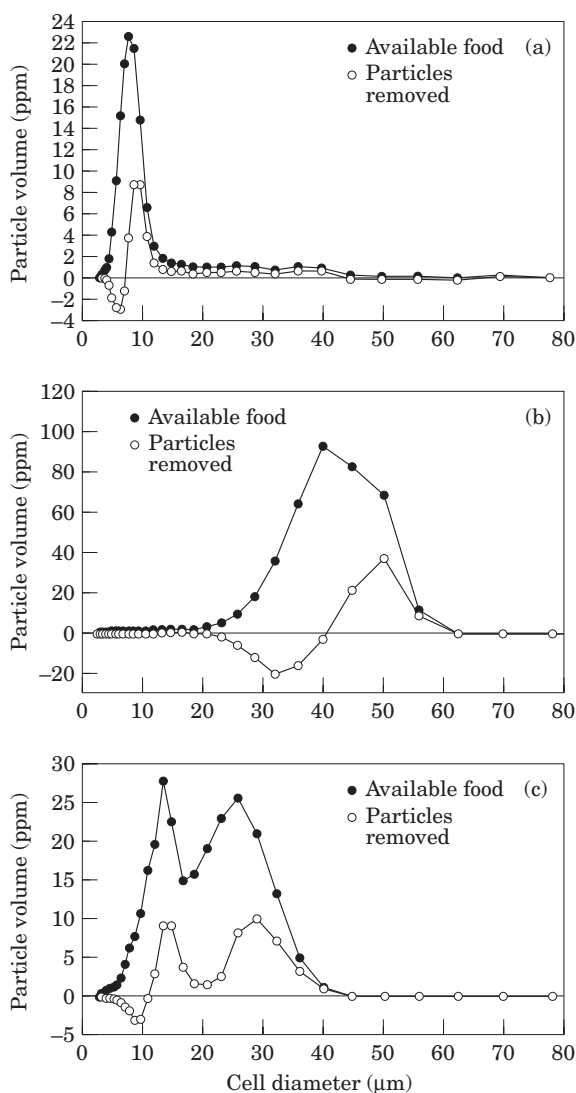


Figure 6. Feeding (indicated by distribution of removed particles) by female *C. agulhensis* on (a) small, (b) large, and (c) bimodal-sized ambient food distributions.

generally low concentrations characteristic of the Agulhas Bank.

Calanus spp. are generally considered to prefer large phytoplankton cells (Frost, 1972; Peterson and Bellantoni, 1987; Walker and Peterson, 1991), although *C. finmarchicus* is able to utilize small ($<10 \mu\text{m}$) cells (Huntley, 1981; Nejstgaard *et al.*, 1997; Båmstedt *et al.*, 1999) if they are sufficiently abundant. During ship-board experiments off South Africa, the distributions of particles removed by female *C. agulhensis* incubated in natural food assemblages suggest a preference for the larger particles of the dominant size classes (JAH, unpublished data; Figure 6). Most particles ingested were similar to, or slightly larger than, peak ambient

size, whether food size was small [$\sim 8 \mu\text{m}$; Figure 6(a)], large [$\sim 45 \mu\text{m}$; Figure 6(b)] or bimodal [12 and $25 \mu\text{m}$; Figure 6(c)]. A similar feeding pattern was exhibited by *C. chilensis* females, which, at high concentrations of food, selectively ingested particles with the greatest relative abundance, or particles slightly larger than those with greatest relative abundance (Cowles, 1979). Disproportionate ingestion, or “preference” (Turner and Tester, 1989), of large particles from natural assemblages has been observed for *C. pacificus* (Richman and Rogers, 1969; Harris, 1982) as well as for *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* (Barthel, 1988). Nevertheless, it has been proposed that this may be because *Calanus* handles large cells more efficiently than small cells (Frost, 1977).

Other studies have documented non-selective feeding behaviour by *Calanus* spp. Huntley (1981) found that, under non-saturated feeding conditions, *C. finmarchicus*, *C. glacialis*, and *C. hyperboreus* removed particles in direct proportion to their abundance, with no apparent size-selective ingestion. Turner and Tester (1989) proposed that copepods are primarily non-selective when suspension-feeding on natural phytoplankton assemblages. These differences in feeding behaviour may be related to differences in food availability. Cowles (1979) found that selectivity decreased with declining food abundance, as would be expected from optimal foraging theory. However, Barthel (1988) found that selectivity was independent of food abundance. Factors such as food quality, experimental methodology, and the often unknown extent of omnivory further complicate the interpretation of feeding studies, and the issue of food selectivity is likely to be debated for some time to come.

Diel feeding patterns appear to be less enigmatic. *C. agulhensis* exhibited a diel feeding rhythm off the west coast, independent of whether or not they were vertically migrating (Peterson et al., 1990). Gut pigment content was low during daylight and increased rapidly one hour before sunset. Gut fullness then declined 2–3 h after sunset, levelling off at up to six times higher than mean daytime values. Stages C3–C5 ingested 20% of their daily ration during daylight, whereas females ingested approximately 15% during the day.

Diel feeding rhythms have been noted for many other *Calanus* species, including *C. chilensis* (Castro et al., 1991), *C. finmarchicus* (Daro, 1985), *C. helgolandicus* (Harris and Malej, 1986; Harris, 1988), *C. pacificus* (Dagg et al., 1989; Landry et al., 1994; Dagg et al., 1998), the boreal species *C. cristatus* and *C. plumchrus* (Ishii, 1990), and the subantarctic species *C. propinquus* and *C. similimus* (Atkinson et al., 1992a, b, 1996). These feeding rhythms are sometimes bimodal (Ishii, 1990) and seem to be independent of vertical migration. Dagg et al. (1989) observed that, although some *C. pacificus* appeared in the surface layer up to 2.5 h before sunset, feeding increased substantially only well after sunset.

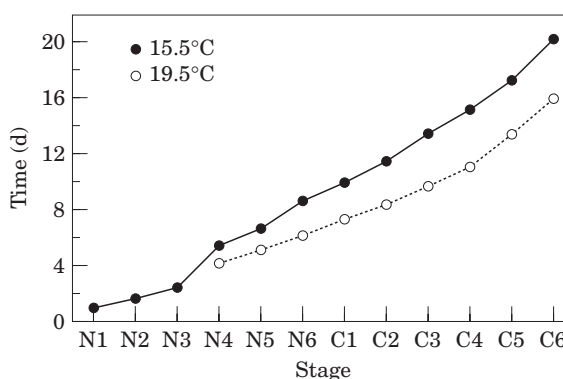


Figure 7. Cumulative median development time for *C. agulhensis* at 15.5 and 19.5°C (after Peterson and Painting, 1990).

This is thought to be linked to predator avoidance, because the food-packed guts of copepods feeding during daylight may attract visual predators (Stearns, 1986; Dagg et al., 1989; Bollens and Stearns, 1992).

Development and growth

Development rate

The maximum rate of development of *C. agulhensis* was investigated by feeding individuals excess quantities of a mixture of the diatom *Thalassiosira weissflogii* and the flagellate *Tetraselmis suecica* in the laboratory (Peterson and Painting, 1990). *C. agulhensis* developed from egg to adult in 20.3 d at 15.5°C and in 16.0 d at 19.5°C. Egg hatching time was 21 h at 15.5°C. Stages N1 and N2 moulted quickly to N3 (<1 d per moult), but the N3s had a relatively long stage duration (~ 3 d at 15.5°C) before moulting to N4 (Figure 7). The range between first and last appearance of a stage was 4–7 d from N3 to C5. Most of the variability was evident at the N3 stage, with some added variability at the C5 stage. Isochronal development (Miller et al., 1977) was approximated from N4 to C5 at 15.5°C and from N4 to C4 at 19.5°C.

C. agulhensis conforms to the common developmental pattern summarized by Landry (1983), whereby: (i) the first (non-feeding) naupliar stages have a short duration; (ii) the first-feeding naupliar stage (in this case N3) is prolonged; (iii) the remaining naupliar stages and most of the copepodite stages develop at the same rate; and (iv) the fifth copepodite stage is prolonged. However, growth of *C. agulhensis* does not adhere strictly to either the isochronal or the equiproportional rule (Corkett, 1984).

Equiproportional development was observed for *C. sinicus* by Uye (1988) and for *Calanoides carinatus* by Peterson and Painting (1990), but not for *C. marshallae* (Peterson, 1986), which demonstrated a sigmoidal pattern of development. Contrasting patterns of

development have been described for *C. finmarchicus* in different areas. Equiproportional development was reported off eastern Canada by Corkett *et al.* (1986), but not in studies in the North Sea (Thompson, 1982) or off northern Norway (Tande, 1988b). Although experimental variability may contribute to these differences, variation in relative developmental rates in different regions could also be indicative of different ecotypes among *C. finmarchicus* populations (Tande, 1988b).

C. agulhensis egg hatching time and total development time from egg to adult is generally faster than that of other *Calanus* spp. at similar temperatures (Table 2). Fastest development (19 d) was observed for *C. pacificus* reared on the dinoflagellate *Gymnodinium splendens* (Paffenhöfer, 1970). Animals developed more slowly when reared on other phytoplankton species, so highlighting the importance of food quality as well as food concentration.

Effect of temperature on growth and egg production

C. agulhensis egg and egg-to-adult development time decreased with increasing temperature, with a corresponding decline in stage duration (Table 1; Peterson and Painting, 1990). Under excess food conditions in the laboratory, egg production increased linearly from 27.3 eggs female⁻¹ d⁻¹ at 9°C to 75.3 eggs female⁻¹ d⁻¹ at 21°C (JAH, unpublished data; Figure 8). Maximum rates of egg production of *C. finmarchicus* and *C. pacificus* also increased with temperature (Runge 1984; Hirche, 1996; Runge and Plourde, 1996; Hirche *et al.*, 1997), with exponential and linear regressions fitting the data equally well (Hirche *et al.*, 1997).

A large number of moulting rate (~700) and egg production (~3000) experiments for *C. agulhensis* have been collected off the South African coast. This represents one of the largest data sets of copepod growth rates from the field anywhere in the world and has provided new perspectives on the debate about the relative importance of food and temperature to copepod growth rates (see Huntley and Lopez, 1992; Kleppel *et al.*, 1996).

Female growth rate, measured by egg production, suggests a dome-shaped relationship with temperature in the field, with growth rates of 0.2 d⁻¹ (60 eggs female⁻¹ d⁻¹) for temperatures <13°C and >18°C, and up to 0.4 d⁻¹ (120 eggs female⁻¹ d⁻¹) between 13 and 18°C [Figure 9(a)]. A similar relationship was found between somatic growth and temperature for the larger copepodite stages (C3–C5), with slower growth for temperatures <13°C and >18°C, and faster growth between 13 and 18°C (Richardson and Verheye, 1998). These relationships are probably a consequence of the dome-shaped relationship between chlorophyll *a* and temperature (Mitchell-Innes and Pitcher, 1992; Pitcher

et al., 1996; Richardson and Verheye, 1998); low concentrations of chlorophyll *a* are associated with both cool (<13°C) and warm (>18°C) temperatures [Figure 9(b)], whereas water of 13–18°C has higher concentrations of chlorophyll *a*. Growth rates of smaller stages did not show this dome-shaped relationship with temperature. These results emphasize that temperature-specific growth rates measured under food-satiated conditions in the laboratory cannot necessarily be extrapolated to the field.

Effect of food concentration and particle size on growth and egg production

There is considerable evidence to suggest that larger *C. agulhensis* stages are increasingly food-limited (Hutchings *et al.*, 1995; Peterson and Hutchings, 1995; Richardson and Verheye, 1999). First, mean growth rate decreased by an order of magnitude from 0.55 d⁻¹ for N6 to 0.05 d⁻¹ for females (Table 1; Figure 10), whereas maximum growth rate only showed a twofold decrease, from 0.69 d⁻¹ for N6 to 0.33 d⁻¹ for females. The decrease in maximum growth rate is probably a consequence of allometry, whereas the decrease in mean growth rate implies that an environmental factor may be acting differentially on the growth rate of different stages. Second, large stages required more food to reach food-saturated growth rates than smaller stages (Figure 11). Third, large copepods were only rarely growing maximally, whereas small stages were mostly growing at near-maximal rates (Figure 5 of Richardson and Verheye, 1999). Finally, the optimal size of food particles is related to copepod size (Berggreen *et al.*, 1988; Mauchline, 1998), larger copepods preferring larger phytoplankton cells. Large cells, such as diatoms, are only periodically abundant (usually at times of relaxation in upwelling), whereas small cells, such as flagellates, are ubiquitous (Richardson and Verheye, 1999). Collectively, these findings suggest that the ambient food environment limits the growth rate of large *C. agulhensis* stages, with stage duration in the field increasing significantly for older stages. By contrast, small *C. agulhensis* stages are always growing at near-optimal rates. Similarly, Vidal (1980) found that sub-optimal food concentration only slightly retarded the growth of young copepod stages, whereas older stages were more seriously affected. A consequence of progressive food limitation of *C. agulhensis* with increasing body size is that juvenile growth is unrelated to female growth (Hutchings *et al.*, 1995; Richardson and Verheye, 1999).

Field studies have also shown that *C. agulhensis* egg production and somatic growth rates are related to phytoplankton cell size. The somatic growth rates of all copepodites are positively related to the proportion of cells >10 µm (Richardson and Verheye, 1998).

Table 2. Egg hatching time, development time and first feeding stage of *Calanus* spp. at 15°C.

Species	Region	Egg hatching time (h)	Egg to adult (d)	N1 to adult (d)	N1 to C1 (d)	First feeding stage	Reference
<i>C. agulhensis</i>	Southern Benguela	21	20.3	19.4	9.1	N3	Peterson and Painting (1990)
<i>C. chilensis</i>	Northern Chile	28.6 ^a	38.1	36.9	7.4	—	Escribano <i>et al.</i> (1998)
<i>C. finmarchicus</i>	UK and Norway	20–26	—	—	—	—	Marshall and Orr (1955)
<i>C. finmarchicus</i>	Tromsø, Norway	26.9 ^a	—	—	—	—	McLaren <i>et al.</i> (1969)
<i>C. finmarchicus</i>	Nova Scotia, Canada	21.5 ^a	—	22.7 ^a	8.3 ^a	—	Corkett <i>et al.</i> (1986)
<i>C. finmarchicus</i>	Clyde Sea area, UK	—	27	—	—	—	Nicholls (1933)
<i>C. finmarchicus/helgolandicus</i> ^b	Southern North Sea	33.1 (30.9 ^{a,c})	27.6	26.2	8.4 (8.9 ^{a,d})	N3	Thompson (1982)
<i>C. glacialis</i>	Frobisher Bay, NWT, Canada	34.7 ^a	—	—	—	—	McLaren <i>et al.</i> (1969)
<i>C. glacialis</i>	Nova Scotia, Canada	25.2 ^a	—	—	9.6 ^a	—	Corkett <i>et al.</i> (1986)
<i>C. glacialis</i>	Nova Scotia, Canada	27.7 ^a	—	—	9.6 ^a	—	McLaren <i>et al.</i> (1988)
<i>C. helgolandicus</i>	English Channel	29.6 ^a	—	—	—	—	Corkett (1972)
<i>C. hyperboreus</i>	Nova Scotia, Canada	36.9 ^a	—	—	13.2 ^a	—	Corkett <i>et al.</i> (1986)
<i>C. hyperboreus</i>	—	—	—	—	—	N5	Mauchline (1998)
<i>C. marshallae</i>	Washington, USA	25.1 ^a	—	—	11.8 ^a	—	McLaren <i>et al.</i> (1988)
<i>C. marshallae</i>	Oregon, USA	<24	35.8	~34.8	~7.6	N3	Peterson (1986)
<i>C. pacificus</i>	Washington, USA	24.9 ^a	—	—	6.5 ^a	—	McLaren <i>et al.</i> (1988)
<i>C. pacificus</i>	Southern California, USA	—	—	23	—	—	Mullin and Brooks (1970)
<i>C. pacificus</i>	Southern California, USA	24	19–34	18–33	—	—	Paffenhöfer (1970)
<i>C. pacificus</i>	Southern California, USA	25.8	19.8	18.8	6.5	N3	Landry (1983)
<i>C. sinicus</i>	Inland Sea of Japan	24 (26.2 ^a)	24.7	23.7	—	N3	Uye (1988)

^aCalculated from Bélehrádek's temperature functions, assuming equiproportional development.^bProbably *C. helgolandicus* (Corkett *et al.*, 1986).^cCorkett *et al.* (1986).^dMcLaren *et al.* (1988).

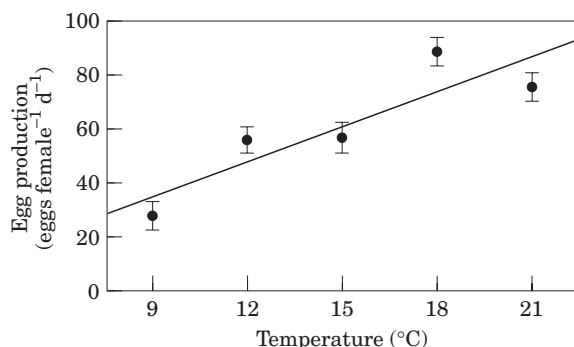


Figure 8. Mean egg production ($EP \pm \text{s.e.}$) of female *C. agulhensis* in relation to temperature (T) in the laboratory. The fitted line is $EP = -2.283 + 4.2448T$, $R^2 = 0.385$, $n = 77$, $p < 0.001$.

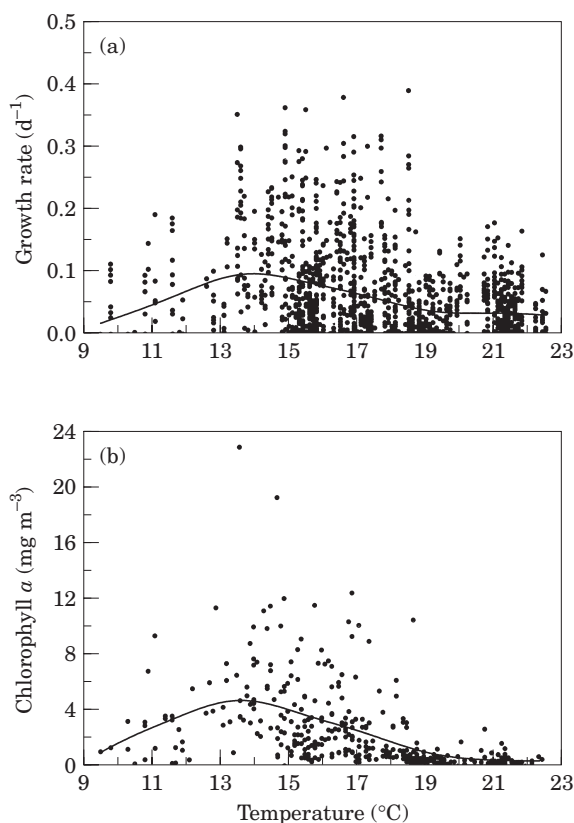


Figure 9. The dome-shaped relationship (from field observations) between (a) female growth rate and temperature, and (b) chlorophyll a concentration and temperature. The curves were fitted using the distance-weighted least squares procedure (after Richardson and Verheye, 1998).

Moreover, Walker and Peterson (1991) observed an almost sevenfold improvement in daily egg production in areas dominated by large cells over areas dominated by small cells. Off the west coast of South Africa, chlorophyll a concentration is positively related to cell

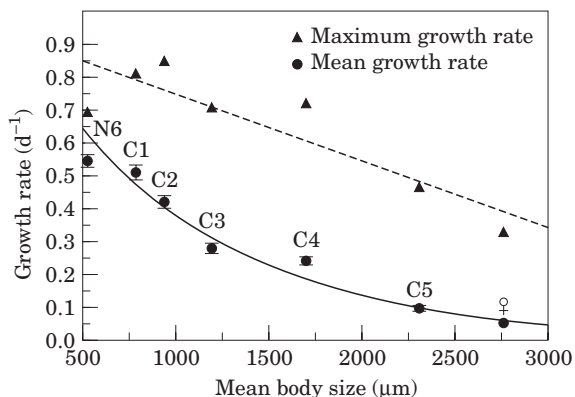


Figure 10. Mean ($\pm \text{s.e.}$) and maximum *C. agulhensis* growth rate in relation to mean body size. The equation fitted to mean growth rates is $y = 1.085641 e^{-0.001047x}$, $R^2 = 0.97$, $n = 7$, $p < 0.0001$. The equation fitted to maximum growth rates is $y = 0.94436 - 0.0002x$, $R^2 = 0.77$, $n = 7$, $p < 0.001$ (after Richardson and Verheye, 1999).

size (Mitchell-Innes and Pitcher, 1992), so the effect of cell size on growth is confounded with the effect of cell concentration. Richardson and Verheye (1998) concluded that, when small phytoplankton cells dominate the phytoplankton assemblage, growth of *C. agulhensis* in the field may not be limited by cell size *per se*, but by the typical concentrations of these cells ($\leq 2 \text{ mg chlorophyll } a \text{ m}^{-3}$, equivalent to $\leq 82 \text{ mg C m}^{-3}$). Båmstedt *et al.* (1999) found that *C. finmarchicus* was able to attain maximum rates of egg production when feeding on high concentrations ($> 800 \text{ mg C m}^{-3}$) of algae as small as $4\text{--}8 \mu\text{m}$.

Effect of starvation on egg production

C. agulhensis appears to be better adapted to the more stable food environment characteristic of the Agulhas Bank than *Calanoides carinatus*, which is adapted to upwelling environments (Thiriot, 1978; Borchers and Hutchings, 1986). Females of both species acclimated to excess *Thalassiosira weissflogii* were subjected to varying periods of starvation, then returned to the excess food medium and their egg production monitored (JAH, unpublished data). *C. agulhensis* recovered more rapidly from short (1–3 d) periods of starvation, although recovery following longer periods of starvation (5–9 d) was slower than that of *C. carinatus* females (Figure 12). Moreover, many *C. agulhensis* females did not regain normal, unstarved rates of egg production after 9 d without food. The time required for post-starvation egg production to return to normal levels was proportional to the starvation period, up to a limit of 7 d starvation for *C. agulhensis*.

Somewhat contradictory results were reported by Attwood and Peterson (1989). They found that

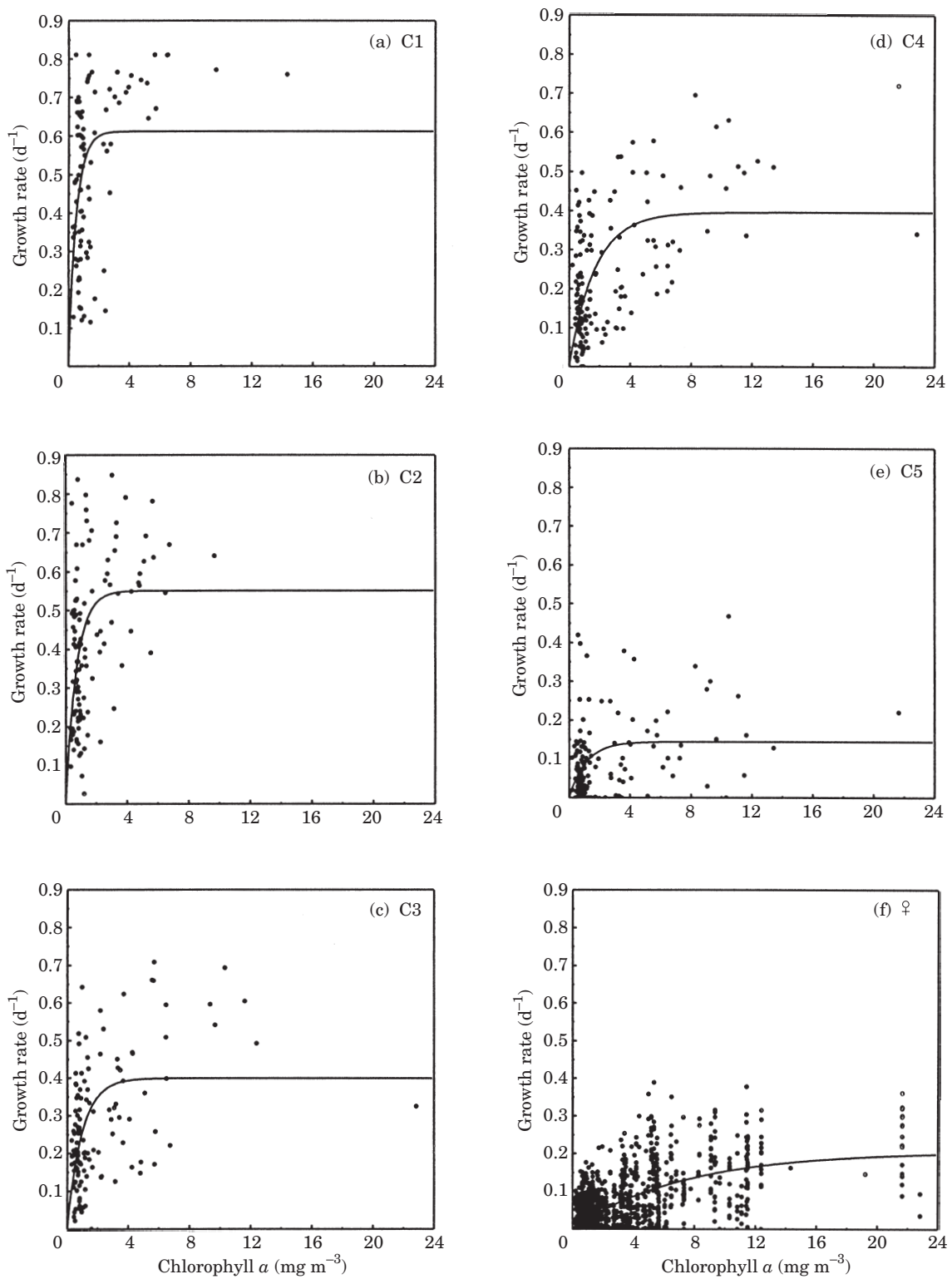


Figure 11. Mean growth rate in relation to chlorophyll *a* concentration for C1 to female *C. agulhensis*, where $g = g_a(1 - e^{-kc})$. Parameters g_a and k are given in Table 1 (after Richardson and Verheye, 1999).

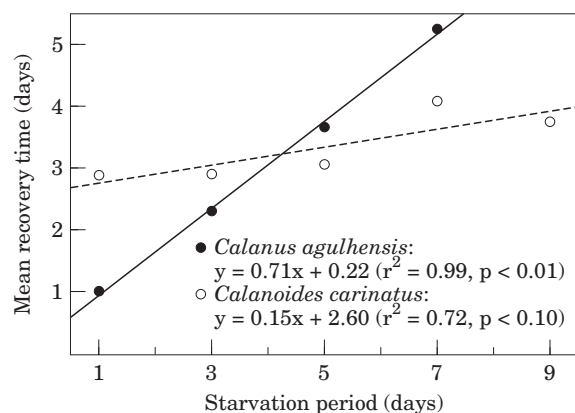


Figure 12. Mean time for egg production by *Calanus agulhensis* and *Calanoides carinatus* to return to normal following various periods of starvation.

C. agulhensis only regained normal egg production approximately 5 d after 1–5 d without food, compared to a recovery time of 1–4 d found by the current authors (JAH, unpublished data; Figure 12). Furthermore, the maximum egg production of *C. agulhensis* under food-satiated conditions reported in their study was only 40 eggs female⁻¹ d⁻¹ at 15°C, substantially lower than in other laboratory studies at the same temperature (87–99 eggs female⁻¹ d⁻¹; JAH, unpublished data) and field studies (130 eggs female⁻¹ d⁻¹; Richardson and Verheye, 1998). As the latter experiments were conducted during summer, the different findings of Attwood and Peterson (1989) could be because their study was conducted during winter, when females may have had a poor feeding history (females used in both laboratory studies were collected from the field, and not raised in the laboratory).

Regarding termination of egg production, *C. agulhensis* did not immediately stop producing eggs when placed in filtered seawater, but continued to lay eggs for at least 3 d (JAH, unpublished data). Delayed termination of egg production following starvation has been observed for other *Calanus* species. *C. glacialis* laid eggs for a further 3–6 d when starved (Hirche and Bohrer, 1987), whereas egg production by starved *C. finmarchicus* continued for up to 20 d, although at very slow rates (Hirche, 1990; Hirche et al., 1997). In contrast, termination of egg production within 24 h of starvation was observed for *C. marshallae* (Peterson, 1988) and *Calanoides carinatus* (Borchers and Hutchings, 1986), two species from upwelling areas. Continued (but slower) egg production during starvation may be an effective strategy in a relatively constant, but low chlorophyll *a* environment such as the Agulhas Bank, where interruptions in food availability tend to be brief. Hassett and Landry (1983) proposed that it might be energetically optimal for copepods experiencing short-term food

patchiness to maintain higher levels of digestive enzymes at low food concentrations in order to exploit higher concentrations of food when encountered. Similarly, it may be energetically more efficient to maintain egg production, albeit at a slower rate, rather than to stop and then restart egg production within a short period of time if the absence of food is likely to be short-lived. By contrast, if animals inhabit an environment where food deprivation is often prolonged, it might be energetically more efficient to cease egg production immediately and wait for better conditions. This may be the strategy used by the upwelling species *C. marshallae* and *Calanoides carinatus*.

Future directions

Much remains to be discovered about *C. agulhensis*. Research to date has only partially explained the dominance of *C. agulhensis* on the Agulhas Bank. A limitation of the fieldwork on growth, ingestion rates, and daily vertical migration is that *C. agulhensis* has been assumed to be entirely herbivorous, but the extent of omnivory in this species is unknown. Omnivory could be particularly important on the Agulhas Bank, where concentrations of chlorophyll *a* are generally low. We also know little about the lipid reserves of females, and nothing about those of juveniles. Laboratory experiments investigating food preference and growth in response to food concentration and starvation have all been conducted on female *C. agulhensis*. The effect of these factors on juvenile stages also needs to be investigated.

To improve our understanding of the population dynamics of *C. agulhensis*, a number of parameters still need to be investigated, such as the effects of starvation and predation on egg viability and mortality. Moreover, we need to know more about how *C. agulhensis* populations are maintained by processes such as vertical migration and advection. The hypothesis that *C. agulhensis* is advected from the eastern to the western Agulhas Bank could be verified by modelling the life-history parameters of *C. agulhensis*, in combination with current measurements and information on predation by pelagic fish. The vertical migratory behaviour of *C. agulhensis* should be explored not only in terms of the ambient food conditions, but also in terms of predation pressure. These studies are currently underway.

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