

A model of copepod population dynamics in the southern Benguela upwelling region

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Abstract. A simple population dynamics model was constructed to simulate temporal variability in the biomass of a dominant copepod *Calanoides carinatus* (Copepoda: Calanoida) along the West Coast region of South Africa. *Calanoides carinatus* is extensively preyed upon by the commercially important anchovy *Engraulis capensis*, thus variability in zooplankton production may serve as a useful predictor of variability in anchovy recruitment levels. The model developed here circumvents the need to include a large number of parameters because it uses satellite-derived estimates of chlorophyll *a* concentration and sea surface temperature as primary inputs. Abundance estimates necessary to initialize the model are readily obtainable from biannual research cruises. The model successfully simulates observed features of a copepod population's response to pulses of upwelling and is robust with respect to most of its parameters because minor changes in their values result in predictable changes in model output. The model showed greatest sensitivity to parameters that are difficult to determine empirically, such as predator-induced mortality rates. Gaps in our present understanding of the nature and scale of processes affecting copepod egg abundance, survival and viability in the southern Benguela system were identified as the dominant impediment to simulating copepod population dynamics in the region.

Introduction

In the upwelling region along the West Coast of South Africa (Figure 1), food chains are generally short (Ryther, 1969; Cushing, 1989; Moloney *et al.*, 1991; Painting *et al.*, 1992) and copepods play a key role in linking primary producers to the larger heterotrophs. Most primary production in the form of small cells (<5 µm) is unavailable to copepod grazers (Bartram, 1980; Paffenhöfer, 1986; Vanderploeg *et al.*, 1990). Because copepods feed mainly on large phytoplankton cells, carbon fixed by these large cells is transferred directly to planktivorous fish. The present study focuses on this so-called 'copepod' pathway (Walker and Peterson, 1991), rather than on the longer 'microbial' pathways (picoplankton–flagellate–ciliate).

Because of the large number of interactions involved in predicting the distribution and abundance of phytoplankton, which forms the basis of pelagic food webs, attempts to link primary and secondary production levels or primary production and fish demographics, for example, have been greatly impeded. This limitation will be largely overcome in the near future with the advent of large-scale ocean colour satellite imagery, e.g. the NASA Sea Viewing, Wide field-of-view Sensor (SeaWiFS) has a minimum area of resolution of ~1 km². The copepod population dynamics model described here was developed to use these estimates of phytoplankton abundance and thereby circumvent the need to estimate the phytoplankton component of the food chain as a function of a set of

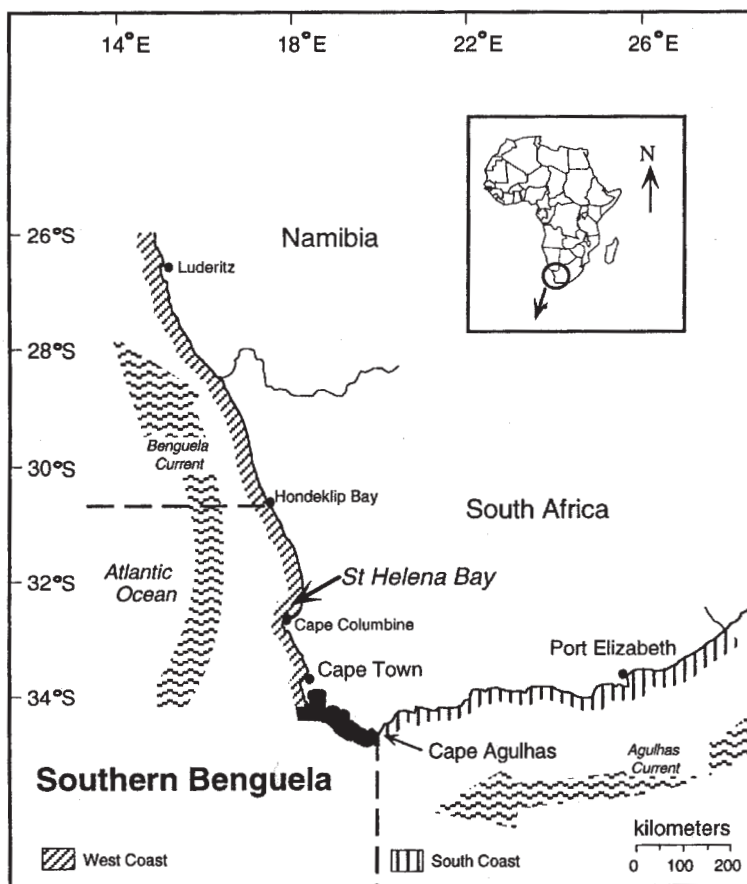


Fig. 1. Location of the model ecosystem off South Africa.

hydrographic parameters—the classic NPZ approach. This greatly reduces the number of linkages in the model and, therefore, the loss of resolution in predicting the way in which disturbances (e.g. upwelling pulses) are propagated through the food web.

Models to investigate the dynamics of plankton populations range from simple mathematical models (e.g. Bossicart and Mommaerts, 1979), to more complex models (Andersen and Nival, 1989), and include *inter alia*: models based on age and stage categories (Carlotti and Sciandra, 1989; Fransz *et al.*, 1991); size classes (Moloney and Field, 1991); biomass dynamics (Steele and Frost, 1977; Fasham *et al.*, 1990); those incorporating the effect of predators (Davis, 1984); those simulating shifts in copepod species dominance (Gaedke and Ebenhoh, 1991); and those designed to estimate production rates from food availability (Sciandra *et al.*, 1990). Models which explicitly describe the internal dynamics of systems or complex biological interactions generally have a fairly low level of aggregation.

One of the biggest challenges facing applied ecologists today is the problem of how to aggregate and simplify fine-scale knowledge or detailed, mechanistic models so that they may be applied to coarser scale phenomena such as ecosystem processes or net fluxes (Kerfoot and DeAngelis, 1989; Holling, 1992; Rastetter *et al.*, 1992; Lawton and Jones, 1993). The task of modelling copepod population dynamics over large horizontal areas requires separation of the critical mechanisms underlying the population's dynamics from those that merely account for details which may be averaged out over larger scales. An *a priori* criterion in model development was that the model should be simple enough to offer generality, but still retain sufficient complexity to ensure that it provides a reasonable description not only of the quantitative, but also of the qualitative, dynamics of the system. Simple mathematical models which do not explicitly simulate the underlying causal mechanisms driving variability are generally incapable of predicting a population's response to the full range of environmental conditions.

The primary aim of this study was to construct a simple and practical model, using only easily measured hydrographic parameters, in an attempt to simulate the dynamics of zooplankton populations in inshore areas along the West Coast of South Africa.

Model description

The model developed here simulates the dynamics of the calanoid copepod *Calanoides carinatus* (Copepoda: Calanoida) in inshore areas along the West Coast of South Africa. The main upwelling season in the southern Benguela region is September–April (Brown and Hutchings, 1987) and the model is directed at the dynamics of the 'active' component (non-diapausal nearshore component) (Verheye *et al.*, 1991) of the population during the austral summer. The model focuses on *C. carinatus* for a number of reasons.

1. It is the dominant copepod (in terms of biomass) in the West Coast shelf region.
2. Comprehensive field and laboratory studies on its biology and ecology have been conducted (Borchers and Hutchings, 1986; Verheye, 1989; Peterson and Painting, 1990; Peterson *et al.*, 1990).
3. Extensive feeding studies (James, 1987; Armstrong *et al.*, 1991b) have shown that mesozooplankton, and in particular the large calanoid copepods (e.g. *C. carinatus*), form a major component of the diet of the commercially important anchovy.
4. Because so many of the details of its life history are (qualitatively at least) analogous to those of other copepods, it may tentatively be used as an index of the status of a broad range of other copepod species.

The model is a one-dimensional, depth-independent model of a time-dependent zooplankton population in a horizontally homogeneous volume of water.

Division into lumped stage classes

A minimum division of the copepod population into seven distinct classes was deemed necessary: eggs; naupliar stages NI–NVI; copepodite stages CI–CIV; copepodite stage CV; adult males; unripe females; ripe females [assuming that females take 3 days to lay eggs (Borchers and Hutchings, 1986)].

Model processes

Rates of change of standing stocks in the various compartments are determined by rates of recruitment, growth and mortality for each compartment. A discrete time step of 1 day is used to update changes in standing stocks. Laboratory studies have shown that temperature and food supply are the chief variables controlling rates of somatic and reproductive growth in marine copepods (Peterson *et al.*, 1991). With one exception, it is not necessary to assume any major net transport losses or gains to or from the system as a whole, because the West Coast shelf region forms a semi-closed system; flow fields and the vertical migratory behaviour of *C.carinatus* both ensure that populations are maintained within this region (Verheye *et al.*, 1991, 1992; Verheye and Field, 1992). The diapause-restocking process was not modelled in the present version, which focuses on summer conditions; the model may be initialized from cruise data collected in November, and hence this factor does not warrant inclusion in the model.

Driving variables

The model is assumed to be driven by satellite-derived images of sea surface temperature (SST) and chlorophyll (Chl) *a* concentrations. The only additional input required is an initial estimate of biomass, population composition and the population sex ratio. This information is readily available from routine research cruises.

In what follows, the conceptual basis of the model is described in some detail, and a summary of model parameters and assumptions is then presented.

Defining food availability for copepods

Copepod growth rates (calculated either as juvenile somatic growth rates or female egg production rates) are often food limited (e.g. Runge *et al.*, 1985; Borchers and Hutchings, 1986; Diel and Klein Breteler, 1986; Attwood and Peterson, 1989; Walker and Peterson, 1991). Determination of the critical phytoplankton abundance value (the grazing threshold F_{crit}) below which organisms become food limited is especially important in pulsed food environments such as the southern Benguela ecosystem, where it is hypothesized that secondary production is constrained by food availability (Borchers and Hutchings, 1986; Attwood and Peterson, 1989).

Calanoid copepods exhibit active choice in food selection and both the size and quality of food particles are important in models of copepod feeding (Paffenhöfer

and Van Sant, 1985; DeMott, 1990; Kerfoot and Kirk, 1991). Because most primary production in the form of small cells ($<5\ \mu\text{m}$) is unavailable to mesozooplankton grazers (Paffenhöfer, 1986; Vanderploeg *et al.*, 1990), food availability to copepods is better defined as a function of the Chl content of the $>10\ \mu\text{m}$ fraction (net-Chl) (Runge, 1985; Peterson and Bellantoni, 1987; Kiørboe *et al.*, 1990; Armstrong *et al.*, 1991a; Peterson *et al.*, 1991; Walker and Peterson, 1991; Mitchell-Innes and Pitcher, 1992). The model therefore uses measures of net-Chl *a* concentration as an index of food quality for copepods.

Chlorophyll concentrations in the sea are usually positively correlated with mean phytoplankton cell size because, while the concentrations of small phytoplankton remain relatively stable, net-phytoplankton blooms develop periodically in turbulent environments, with high concentrations of nutrients (Mitchell-Innes and Pitcher, 1992; Kiørboe, 1993). Following Mitchell-Innes and Pitcher (1992), the net-Chl *a* fraction (mg m^{-3}) is therefore calculated as a linearly increasing function of total Chl.

Implicit in this approach is the assumption that a classic succession of phytoplankton occurs following an upwelling event: from small to larger diatom species and subsequently to flagellates (Probyn, 1985; Brown and Hutchings, 1987; Cushing, 1989; Mitchell-Innes and Walker, 1991; Mitchell-Innes and Pitcher, 1992). Regression analyses indicate that phytoplankton populations with Chl concentrations below a critical limit of $\sim 3\ \text{mg m}^{-3}$ are composed predominantly of small cells, $<5\ \mu\text{m}$ in diameter (Mitchell-Innes and Pitcher, 1992), and the grazing threshold F_{crit} is therefore taken as $3\ \text{mg Chl } a\ \text{m}^{-3}$. At temperatures above 15°C , there is an abrupt shift from a diatom- to a flagellate-dominated community in the southern Benguela system (Mitchell-Innes and Pitcher, 1992). Flagellates are effectively $<10\ \mu\text{m}$ in diameter and it is therefore assumed that this shift in community composition similarly results in food limitation of *C. carinatus*.

The same grazing threshold is assumed to operate for juvenile and adult copepods. Although adults have the advantage of integrating their food supply over a much larger volume of water (due to their mobility), juveniles (by virtue of their smaller size) are more efficient at utilizing small cells (Mensah, 1974; Verheye, 1989; Walker and Peterson, 1991) which predominate at low phytoplankton concentrations. Large copepods generally have fast individual ingestion rates, whereas small copepods (Bautista and Harris, 1992) and young stages such as copepod nauplii (Turner and Tester, 1992; Morales *et al.*, 1993) have greater overall grazing requirements because of their numerical dominance. In the mesohaline Chesapeake Bay, nauplii of the calanoid copepods *Acartia* spp. have higher carbon-specific ingestion rates than adults and consume a substantial proportion of the available phytoplankton because of their large biomass (White and Roman, 1992). Thus, in the present model, starvation commences simultaneously in all stage classes when Chl concentrations fall below the grazing threshold. However, the way in which different categories respond to the length of the starvation period differs.

A central premise of the model is that the production of the copepod *C. carinatus* is controlled largely by variability in its food supply in the temperate waters of the Benguela upwelling system. The ability of marine zooplankton to either

migrate to (Bainbridge, 1953; Bird and Kitting, 1982) or to remain in (Tiselius, 1992; Saiz *et al.*, 1993) patches of high food availability is well documented. Laboratory experiments using the calanoid copepod *Centropages typicus* suggest that it can integrate daily fluctuations in its food supply if patches are on the same scale as are manifest in the field (Davis and Alatalo, 1992). The diel vertical migratory behaviour (DVMs) of *C. carinatus*, and therefore its ability to regulate its position in the water column, allows it to exploit aggregations of food optimally as they occur in the vertical dimension (Verheye and Field, 1992). Because of their ability to integrate vertical differences in the spatial arrangement of food concentration, food quality or food composition, the use of depth-independent estimates of food availability is considered a plausible simplification. Of course, an environment which appears fine grained to an adult may appear coarse grained to a juvenile because of its reduced motility. This problem is partly circumvented in *C. carinatus* because the younger stages undertake less extensive diel migrations than the older stages and are concentrated in the surface layers where food concentrations and production are generally highest (Verheye and Field, 1992) (Figure 2).

Although satellite imagery only measures Chl concentrations in the uppermost layers of the ocean (C_s), along the West Coast, which typically has a well-mixed euphotic zone, measures of sea surface Chl *a* (C_o) are almost identical to measures of the mean concentration throughout the euphotic zone (C_e) (Shannon *et al.*, 1984; Brown and Henry, 1985). Furthermore, because phytoplankton blooms initially develop near the surface following an upwelling event, satellite-derived colour images are generally able to estimate maximum Chl levels correctly (Figure 2).

Mesozooplankton are generally unable to control population sizes of the net-phytoplankton after upwelling or mixing events because of their lagged response to phytoplankton blooms (Verheye *et al.*, 1992; Kiørboe, 1993). Maximum measures of net-Chl therefore adequately describe food availability to individual copepods, irrespective of copepod density.

Fecundity estimates

Copepod fecundity is determined by both the quality and quantity of available food (Checkley, 1980; Runge, 1984, 1985; Peterson and Bellantoni, 1987; Peterson, 1988). The pulsed availability of food in the southern Benguela system results in spatial and temporal variation in copepod productivity, and egg production is food limited for much of the time (Walker and Peterson, 1991). When Chl concentrations exceed F_{crit} in the model, fecundity estimates (F) of *C. carinatus* are calculated as a function of the biomass of the lagged [$B_{>10(-1)}$] and non-lagged ($B_{>10}$) $>10 \mu m$ phytoplankton size fraction, according to the equation of Armstrong *et al.* (1991a):

$$\ln F = 0.430 \times \ln[B_{>10}] + 0.477 \times \ln[B_{>10(-1)}] - 1.278 \quad (1)$$

A 1 day time lag between ingestion and egg laying is used (Armstrong *et al.*, 1991a). Egg production in large calanoid copepods is typically initiated at Chl *a*

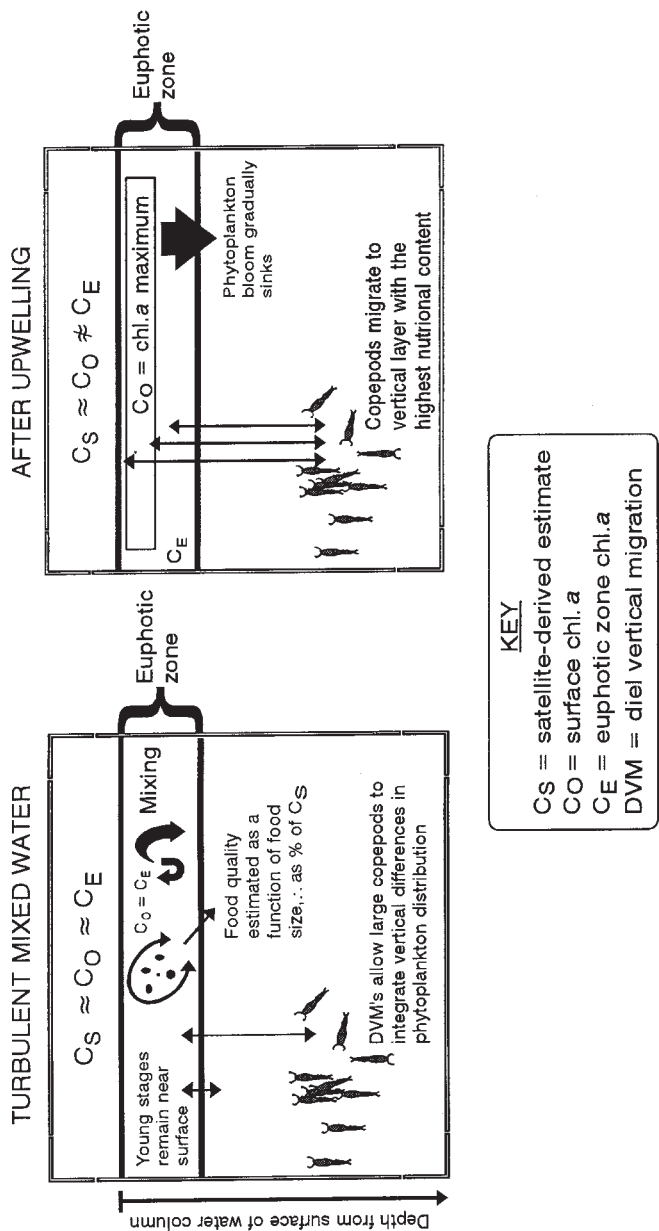


Fig. 2. A conceptual diagram illustrating the hypothesis that a single satellite-derived and depth-independent estimate of Chl *a* concentration (C_s) provides an adequate description of food availability to copepods distributed in a hypothetical water column along the West Coast.

concentrations of 2–3 mg m⁻³ and rates plateau at 5–10 mg m⁻³ (Armstrong *et al.*, 1991a). In the model, egg production is initiated at a Chl *a* concentration of 1 mg m⁻³ and set at 1 egg female⁻¹ day⁻¹ for concentrations in the range 1–2 mg Chl *a* m⁻³ and 5 eggs female⁻¹ day⁻¹ for concentrations in the range 2–3 mg Chl *a* m⁻³ [averages calculated from Hutchings (1992)]. Above a concentration of 10 mg Chl *a* m⁻³, there is no further increase in egg production. A simplified representation of the fecundity–food concentration relationship used in the model is shown in Figure 3. The values of F are the maximum daily rates when food is not limiting; otherwise, they are modified as a function of feeding history.

In a pulsed, patchy food environment, copepod fecundity is influenced by the amount and frequency of ‘food events’ (Kiørboe, 1991). Feeding history is probably the dominant factor controlling the production of calanoid eggs in the southern Benguela (Attwood and Peterson, 1989). Starvation is known to terminate egg production in copepods, whereas the cumulative number of eggs produced during 5 days of feeding is reduced as a function of the length of the preceding starvation period (Attwood and Peterson, 1989). A recovery period of ~5 days elapses before egg production is restored to the average in both *C. carinatus* and *Calanus australis* (Borchers and Hutchings, 1986; Attwood and Peterson, 1989). The effect of feeding history on fecundity is modelled using a modified form of the power curve derived by Attwood and Peterson (1989) for *C. australis*—the intercept is adjusted to reflect the higher average fecundity of *C. carinatus*. Thus:

$$F_S = F_N e^{-0.176s} \quad (2)$$

where F_S is the total number of eggs produced during 5 days of feeding and following a starvation period of s days. F_N represents the total number of eggs produced over the same period for a copepod fed continuously.

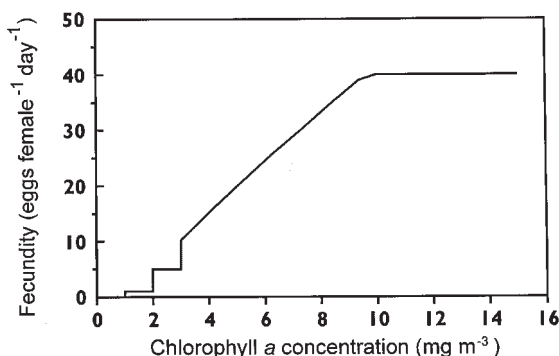


Fig. 3. The basic fecundity–Chl *a* concentration relationship used in the model. For Chl *a* concentrations > 3 mg m⁻³, values of F shown assume that females have not starved recently. Also, values in the model are based on both the previous and present day's Chl *a* concentration [equation (2)].

Following starvation, the recovery of egg production is modelled as a linear function, with no eggs produced for the first 24 h and egg production rising rapidly thereafter to the average level by the fifth day. Thus:

$$F_d = \frac{d-1}{6} \left(F_S - \frac{F_N}{5} \right) \quad (3)$$

where F_d is the number of eggs produced by *C. carinatus* per day, for days (d) 1–4 after the resumption of feeding. This approach corresponds well to the near-linear increase in egg production following starvation, demonstrated for *C. carinatus* by Borchers and Hutchings (1986). Egg abundance is computed as the product of the fecundity and the density of ripe females (F_r ; defined here as egg-laying individuals).

Development time

Huntley and Lopez (1992) demonstrated that temperature alone explains >90% of the variance in the growth rate of 33 species of marine copepods. Whilst it is generally accepted that development times of copepods are a non-linear function of temperature (McLaren and Corkett, 1981; Peterson and Painting, 1990), the extent to which development times in the field are affected by food availability is a more contentious subject. Evidence abounds that development rates in the laboratory are influenced by food availability (e.g. Vidal, 1980b; Huntley and Boyd, 1984; Borchers and Hutchings, 1986; Huntley *et al.*, 1987; Berggreen *et al.*, 1988), but it is argued that the order of magnitude higher mortality rates in the field ensure that net or cohort development rates remain maximal (Lopez, 1991). This is because food-limited individuals develop more slowly and have a greater probability of death, so that if a sufficiently large proportion of them die, only the fastest growing individuals will survive (Lopez, 1991; Carlotti and Nival, P., 1992). The complete absence of food will obviously still retard the rate at which copepods moult: Vidal (1980a) demonstrated that growth is negative below a critical level of food concentration.

For *C. carinatus*, support in favour of the hypothesis that growth rates are food limited stems from the work of Borchers and Hutchings (1986) who demonstrated that laboratory development times were prolonged when food was limiting, while Walker and Peterson (1991) demonstrated *in situ* that the rate at which copepodite stages CII–CV moult, and their associated development times, depends upon both Chl *a* concentration and particle size. Food limitation of growth rates is therefore assumed to occur at Chl concentrations below the grazing threshold F_{crit} .

Calanoides carinatus eggs take 1 day to hatch (Borchers and Hutchings, 1986) and subsequent development times are modified depending on whether the animals feed continuously or intermittently. Intermittent feeding is defined as occurring when Chl concentrations fall below F_{crit} for 3 days or more.

For continuous feeding, total development times are calculated using the power curve of Borchers and Hutchings (1986). Following Verheye (1991), a

1.5°C temperature lag is invoked for reasons of consistency with development times calculated elsewhere (Hirche, 1980; Peterson and Painting, 1990). This gives:

$$D_t = 1469.2(T - 1.5)^{-1.665} \quad (4)$$

where D_t is the total development time (in days) at ambient temperature T (°C). For animals feeding intermittently, development times are doubled (Borchers and Hutchings, 1986).

Calculating growth transfers between model groups

Calanoides carinatus conforms to the ‘rule’ of equiproportional development (Peterson and Painting, 1990), such that the relative proportion of the total development time spent in each developmental stage is the same regardless of temperature (Corkett *et al.*, 1986; McLaren *et al.*, 1988). Median development times for the three groups, NI–NVI, CI–CIV and CV, are thus modelled as a constant proportion (p) of the total development time (D_t). The proportions p are calculated using the median development times and stage durations derived for *C.carinatus* by Peterson and Painting (1990). For each of the three groups above, p is calculated as the sum of the stage durations of all of the component copepod stages comprising a group, as a fraction of the median development time from an egg to an adult. It follows that $dev_{i,t}$, the daily proportion of individuals in model group i which moult into the next age group $i + 1$ during time t , is given by:

$$dev_{i,t} = \frac{1}{p_i \cdot D_t} \quad (5)$$

Mortality estimates

Accurate estimates of copepod mortality are difficult to obtain and are virtually non-existent in the literature. For analytical convenience, the mortality factor in the present model is divided into two components: mortality (M_{pred}) due to biotic factors such as predation and cannibalism; and mortality (M_{food}) due to the effect of food abundance on the animals’ survival. In addition, the mortality rate of eggs (M_{egg}) is accounted for separately.

Mortality rate of eggs. Although no quantitative estimates exist, Verheye *et al.* (1992) deduced that rates of predation on copepod eggs in the southern Benguela may be severe. Predators cited include some of the dominant copepods such as *Centropages brachiatus* and *Metridia lucens*, as well as the dinoflagellate *Noctiluca miliaris*, which can be present in extremely high numbers during frequent blooms in the southern Benguela system. Other likely sources of mortality of eggs include cannibalism (Verheye *et al.*, 1992), physiological processes and losses due to transport processes. Daily egg mortality in broadcast spawning copepods can exceed

90% (Beckman and Peterson, 1986; Kiørboe *et al.*, 1988) and a high density-dependent egg mortality rate (M_{egg}) of 0.90 day^{-1} is assumed in the model.

Mortality rate M_{pred} . Predators are not modelled explicitly, instead their effects are simulated by the mortality coefficient M_{pred} . A base-case value of 0.10 day^{-1} was chosen for M_{pred} by assuming a steady state for *C. carinatus* population dynamics under saturated feeding conditions, implying equal rates of mortality and reproduction. This was shown to be the case during the first of two upwelling cycles observed during a 27 day anchor station time series study in March–April 1987 in the southern Benguela upwelling region (Verheye, 1991). M_{pred} is assumed equal over all age classes because although the small size of the younger age classes makes them vulnerable to a wider spectrum of predators, the late larvae and adults of large predators, such as the anchovy (with large metabolic requirements), tend to feed selectively on large copepods (Schmitt, 1986; James and Findlay, 1989).

Mortality rate M_{food} . The mortality coefficient M_{food} , which depicts mortality due to starvation, is modelled as a stage-dependent process. Most copepod mortality occurs during the naupliar stages when animals are most vulnerable to starvation (Mullin and Brooks, 1970; Paffenhöfer, 1976; Borchers and Hutchings, 1986). The adults and copepodite stage CV in *C. carinatus* have a large lipid sac which allows them to survive longer periods of adverse feeding conditions than can the younger age classes (Borchers and Hutchings, 1986). In addition, adults may benefit from carnivory (Borchers and Hutchings, 1986). Most starvation mortality is therefore modelled as due to the naupliar stages NI–NVI and the early copepodite stages CI–CIV. *Calanoides carinatus* individuals start feeding immediately after hatching (Borchers and Hutchings, 1986) and thus it is not necessary to consider separate survival times for newly hatched nauplii. Survival times of *C. carinatus* individuals starved in the laboratory increase linearly with increasing age (Borchers and Hutchings, 1986). This suggests that lipid reserves accumulate in a linear fashion in *C. carinatus* and hence it is assumed that the starvation tolerance of the copepodite stages is twice that of the naupliar stages.

The starvation tolerance of juvenile *C. carinatus* depends on the length of the previous feeding period (Borchers and Hutchings, 1986) and the various feeding cycles which the juveniles can tolerate are calculated from the matrix presented in Borchers and Hutchings (1986: Table V). Matrix entries M_{ij} are the percentage offspring starving to death at 18°C after a starvation period of j days, preceded by i days of feeding. All juveniles can survive for at least 2 days with no food. Because body reserves are used up more rapidly at high temperatures, starvation tolerance is inversely related to temperature (Borchers and Hutchings, 1986). The mortality coefficient M_{food} is calculated as:

$$M_{\text{food}} = \frac{T_{\text{ave}}}{18} \times \frac{M_{i,j}}{100} \quad (6)$$

where T_{ave} is the average temperature ($^\circ\text{C}$) over the starvation period.

The adult starvation tolerance level M_{50} . A 50% starvation tolerance level (M_{50}) is calculated for adults and CV stage copepodites from Borchers and Hutchings (1986: Figure 4) as:

$$M_{50} = 18/T_{\text{ave}} \times 12 \quad (7)$$

and represents the number of days of starvation required to induce 50% adult mortality. The starvation index (SI) records the total number of consecutive days that Chl a concentrations fall below the grazing threshold F_{crit} .

Model equations

In summary, the population growth equations for the model classes naupliar stages NI–NVI ($NAUP$), recruits to the naupliar stage (REC), copepodite stages CI–CIV ($COP1$), copepodite stage CV ($COP2$) and adults (AD) are:

$$\begin{aligned} REC_{t+1} &= (1 - M_{\text{egg}}) \cdot F_t \cdot Fr_t \\ NAUP_{t+1} &= REC_{t+1} + [(1 - dev_{1,t}) - M_{\text{pred}} - M_{\text{food}}] \cdot NAUP_t \\ COP1_{t+1} &= dev_{1,t} NAUP_t + [(1 - dev_{2,t}) - M_{\text{pred}} - MOR_{\text{food}}] \cdot COP1_t \\ COP2_{t+1} &= dev_{2,t} COP1_t + [(1 - dev_{3,t}) - M_{\text{pred}} - MOR_{\text{food}}] \cdot COP2_t \\ AD_{t+1} &= dev_{3,t} COP2_t + [1 - M_{\text{pred}} - MOR_{\text{food}}] \cdot AD_t \end{aligned} \quad (8)$$

where $MOR_{\text{food}} = 0.50$ when $SI > M_{50}$.

A schematic illustration of the model's structure and the major processes driving the population's dynamics is shown in Figure 4.

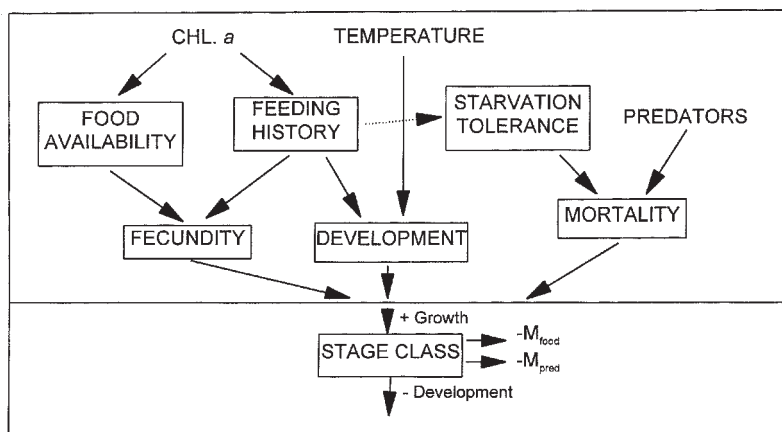


Fig. 4. Summary of the way in which the major physical and biological factors affect the calculation of biological functions in the model, and the way in which these in turn determine the changes in abundance in each of the model 'stage classes'.

Model initialization

To initiate the model, the population age structure was based on the mean population composition (number m^{-3}) observed by Verheye (1991) during the 1987 anchor station study. Combining the individual stage-specific abundances of the early copepodite stages into a single estimate yields a mean population composition of 59% CI–CIV, 19% CV and 22% adults. The naupliar stages are not retained by the 200 μm sampling net used and hence no direct estimate of their abundance is available. An estimate of the relative naupliar abundance was calculated as follows. The proportion of *C. carinatus* development time spent in the naupliar stages is 0.35 (Peterson and Painting, 1990) or, equivalently, 0.54 of the time spent in the copepodite stages. Thus, assuming a stable age structure, the expected total population composition becomes 30% NI–NVI, 42% CI–CIV, 13% CV and 15% adults. From the population composition estimates above and the mean abundance (number m^{-3}) of ripe females given in Verheye (1991: Table 5), a feasible initial abundance of ripe females is calculated to be 3.8%.

Biomass estimates

Biomass estimates of copepodite and adult *C. carinatus* were calculated as the product of the daily stage abundance (number m^{-3}) and mean individual body weight ($\mu\text{g C}$) (Table I). Total biomass estimates T_{biom} for each day are calculated as the sum of the biomasses of the adult and copepodite stage individuals, and are used as an index of population growth throughout this paper. Note that the value of T_{biom} does not include the biomass of the naupliar stages. A summary of the notation used to describe model variables is presented in Table IIa.

Standard upwelling series

To determine the magnitude and time scale of a copepod population's response to a phytoplankton bloom, characteristic Chl *a* and SST changes over a 12 day upwelling cycle (Brown and Hutchings, 1987) are used as inputs into the model (Figure 5). The data were obtained by superimposing the peaks in bloom development observed for five different bloom development cycles, which were tracked during the course of five cruises conducted in the southern Benguela region (Brown and Hutchings, 1987).

Table I. Mean body weights ($\mu\text{g C}$) of *C. carinatus* life cycle stages (from Verheye, 1991)

Stage	Body weight
Copepodite stages CI–CIV	8.97 ^a
Copepodite stage CV	31.57
Adult male	34.26
Adult female	56.81

^aDetermined as the arithmetic mean of the summed products of the percentage abundance of each life cycle stage and the individual body weight ($\mu\text{g C}$) of that stage.

Table II. Summary of (a) variable names and their associated units, (b) base-case parameter values and (c) model assumptions

(a)

Description of variables	Notation	Units
Stage classes NI–NVI	<i>NAUP</i>	no. m ⁻³
CI–CIV	<i>COPI</i>	no. m ⁻³
CV	<i>COP2</i>	no. m ⁻³
Adults	<i>AD</i>	no. m ⁻³
Ripe females	<i>F_r</i>	no. m ⁻³
Unripe females	<i>F_u</i>	no. m ⁻³
Biomass of copepodite stages CI–CVI	<i>T_{biom}</i>	µg C m ⁻³
Sea surface temperature	<i>SST (T)</i>	°C
Average temperature over starvation period	<i>T_{ave}</i>	°C
Chlorophyll <i>a</i> concentration	<i>CHL</i>	mg m ⁻³
Net-chlorophyll (>10 µm)	<i>B_{>10}</i>	mg m ⁻³
... lagged net-chlorophyll concentration	<i>B_{>10(-1)}</i>	mg m ⁻³
Recent feeding history (days fed)	<i>FH</i>	days
Starvation index (days starved)	<i>SI</i>	days
Total development time	<i>D_t</i>	days

(b)

Parameter/model function	Notation	Units	Base-case value
<i>Initial values</i>			
Initial abundance estimate	<i>N₁</i>	no. m ⁻³	402
Population sex ratio	F:M ratio		9:1
Population age composition:	Prop. NI–NVI		0.30
	CI–CVI		0.42
	CV		0.13
	ADULTS		0.15
<i>Model parameters/functions</i>			
Grazing threshold	<i>F_{crit}</i>	mg Chl <i>a</i> m ⁻³	3
Net-chlorophyll fraction	<i>B_{>10}</i>	mg (Chl <i>a</i> > 10 µm) m ⁻³	<i>f</i> (Chl <i>a</i>) ^a
Egg mortality rate	<i>M_{egg}</i>	day ⁻¹	0.9
Predator-induced mortality rate	<i>M_{pred}</i>	day ⁻¹	0.1
Starvation mortality (NI–NVI, CI–CIV)	<i>M_{food}</i>	day ⁻¹	<i>f</i> (age, <i>T</i> , <i>FH</i> , <i>SI</i>) ^a
Adult and CV starvation tolerance	<i>M₅₀</i>	days	<i>f</i> (<i>T</i>) ^a
Fecundity	<i>F_i</i>	eggs female ⁻¹ day ⁻¹	<i>f</i> (<i>B_{>10(1,-1)}</i> , <i>SI</i>) ^a
Total development time	<i>D_t</i>	days	<i>f</i> (<i>T</i> , <i>SI</i>) ^a
Proportion of individuals moulting per time step	<i>dev_{i,t}</i>	day ⁻¹	<i>f</i> (<i>D_t</i> , age) ^a

^aCalculated as a function of the variables in parentheses, as described in the text.

(c) Major assumptions. The evidence in support of the various assumptions is indicated by the symbols in parentheses as follows: (–) poor; (+) fair and (++) good

1. Horizontal losses = horizontal gains (+)
2. The use of single depth-independent estimates of Chl *a* and *SST* provides an adequate description of ambient conditions experienced by copepods (+)
3. Development rates are food limited (++)
4. Individual egg production is independent of copepod numerical density (–)
5. The same grazing threshold operates for all ages (+)

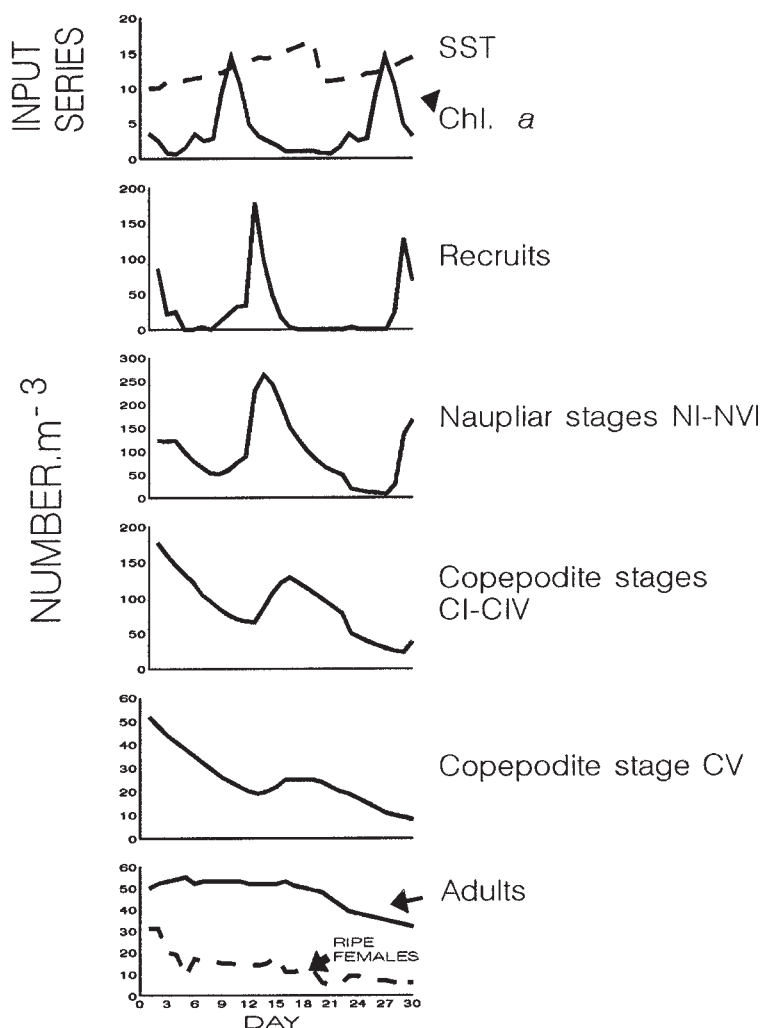


Fig. 5. Temporal changes in the abundances of the various developmental stages following a characteristic 12 day upwelling cycle. For comparative purposes, the number of individuals recruiting to the population (newly hatched nauplii) is shown separately from the curve depicting the predicted changes in the standing stocks of the naupliar stages.

To construct a representative time series with alternating upwelling cycles and quiescent periods, Chl *a* data were interpolated between the 12 day upwelling cycles by assuming that Chl *a* remained at 1 mg m^{-3} throughout quiescent periods. Sea surface temperature data were interpolated by assuming that heat flux into the surface waters caused temperatures to increase by $0.5^\circ\text{C day}^{-1}$, up to a maximum of 18°C (Figure 5). Daily heat flux into the sea warms the upper 10 m mixed layer in the southern Benguela system by as much as $0.65^\circ\text{C day}^{-1}$ (Guastella, 1992).

Model assessment

The performance of the model was assessed using Chl *a* and SST data collected during the 27 day anchor station study (Mitchell-Innes and Walker, 1991) as inputs, and comparing output with observed changes in *C. carinatus* biomass over this period (Verheye, 1991). The purpose of this exercise was to assess and not validate model results. This is because the model was not constructed completely independently of empirical observations made during the anchor station study.

Results obtained from this simulation exercise were used as a base case for comparative purposes in the sensitivity analysis. A summary of the values used to initialize the model as well as the base-case values assigned to parameters is presented in Table IIb. Table IIc lists the major assumptions.

Results

Changes in standing stocks following an upwelling event

The simulated succession of developmental stages following an upwelling event is presented in Figure 5. There is a 2 day lag between the peak in primary production which occurs on day 10 and the peak in the number of new recruits to the population. Recruits are newly hatched nauplii and the lag occurs because there is a 1 day interval between ingestion and spawning, and eggs take a further 1 day to hatch. As a pulse of new production moves up through the various developmental stages, there is a successive increase in the time taken for a peak to develop in a particular stage class, as well as a successive dampening of a class response to the earlier perturbation. The biomass of the naupliar stages peaks 3 days after the peak in primary production, while the biomass of the copepodite and adult stages peaks 6 days after the primary production peak, or 10 days after the initial increase in primary productivity. The time scale of the population's response is determined in part by temperature, because it controls how fast individuals develop. Model-predicted temporal scales describing the movement of an 'input pulse' through the various *C. carinatus* stage classes may be slightly faster than normal due to the problem of forward diffusion discussed in a later section.

In simulations run over longer periods, if Chl *a* concentrations fall below the critical grazing threshold level for 16 or more successive days in the quiescent periods between upwelling cycles, a peak in T_{biom} does not develop. The younger stage individuals either perish from starvation or develop too slowly to affect the T_{biom} trend significantly.

Comparison of the proportional abundances of the naupliar stages and adults under favourable and unfavourable conditions (Figure 6) highlights the greater susceptibility of the younger stages to periods of starvation as well as the reduced rates of production over these adverse periods. The relative abundance of the naupliar stage individuals declines sharply when conditions are poor while the relative abundance of adults increases. Calbet and Alcaraz (1997) recently demonstrated experimentally that survival time to starvation increases linearly with age for the calanoid copepod *Acartia grani*.

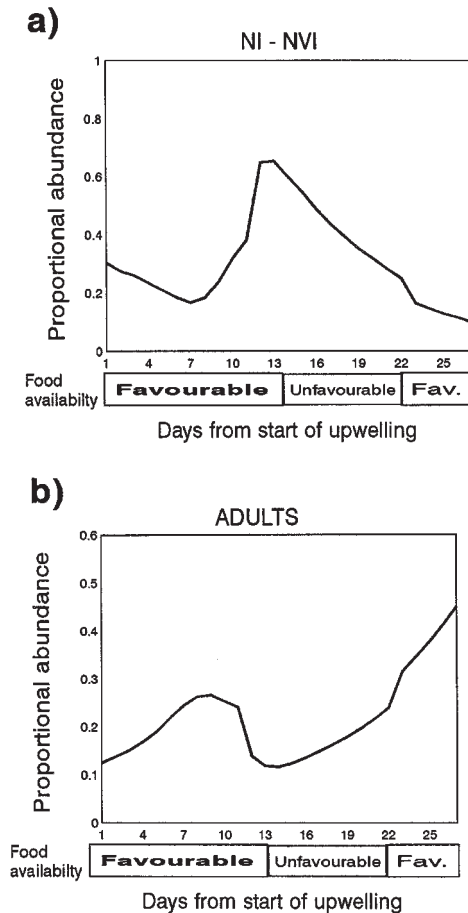


Fig. 6. A comparison between the relative abundance of the naupliar stages (**a**) and the adults (**b**) under favourable and unfavourable conditions.

Assessing the model's fit to the anchor station series

Running the model with the anchor station input series (Figure 7a) resulted in a simulated copepodite and adult abundance trend on approximately the same scale as that observed during the 27 day period (Figure 7b). The extremely high peak on day 20 of the series is due to the advection of a discrete water mass containing high densities of copepodite stage CIV and CV individuals (Verheye, 1991). Forcing any model to mirror such an anomalous event would result in biased parameter estimates. Attempts to simulate major advective gains or losses to or from a population require consideration of physical transport processes, behavioural migration patterns and the spatial scale over which results are averaged. Quantification of the resultant change in local population structure is probably best simulated using a random factor.

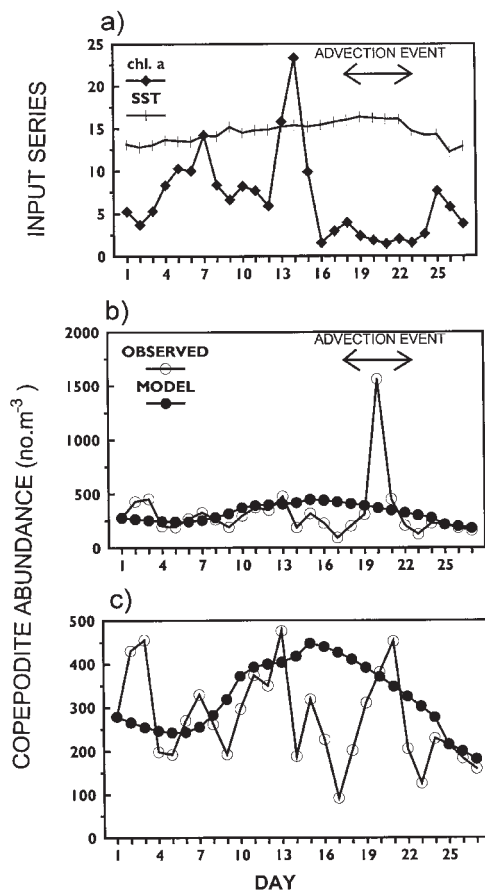


Fig. 7. Time series of (a) mean euphotic zone Chl *a* concentration and sea surface temperature (SST) observed during a 27 day fixed station study conducted in St Helena Bay in 1987 (Mitchell-Innes and Walker, 1991) and (b) comparisons between model-predicted population trends and those observed during the anchor station study (Verheye, 1991). The peak on day 20 in (b) is predominantly due to the advection of copepodite stage CV individuals into the area, and has been excluded from the observed trend shown in (c).

In model comparisons, it is assumed that co-occurring individuals belong to the same population, with the exception of the individuals advected into the area on day 20. To facilitate comparison of the model-predicted and observed trends, the advection event is therefore excluded and a population abundance estimate for day 20 calculated as the average of that observed on days 19 and 21 (Figure 7c).

To quantify the relationship between model estimates and data, the former were plotted against the latter and the goodness of fit assessed separately for each of the classes CI–CIV, CV and adults (Table III). No field data are available to compare the predicted patterns of naupliar growth with observed trends. Whereas significant positive correlations exist between the model and data for the categories CI–CIV and CV, there was no significant linear trend between

model and observed adult numbers (Table III). On average, the model overestimates adult numbers, possibly due to the problem of forward diffusion.

As a further test of the model's ability to replicate the major features of the population trends observed during the anchor station study, the model and observed age structure were compared (Figure 8). As before, the advection event

Table III. Summary of least squares regressions applied to analyse the degree of linear relatedness between model-predicted estimates y and observed values of copepodite abundance x

Model 'stage class'	m	c	d.f.	r	P
CI-CIV	0.54	56.9	25	0.402	<0.05
CV	1.37	-21.2	24 ^a	0.479	<0.05
Adult	-0.9	148	25	0.336	(ns)

^aExcluding outlier on day 20 (see the text for details).

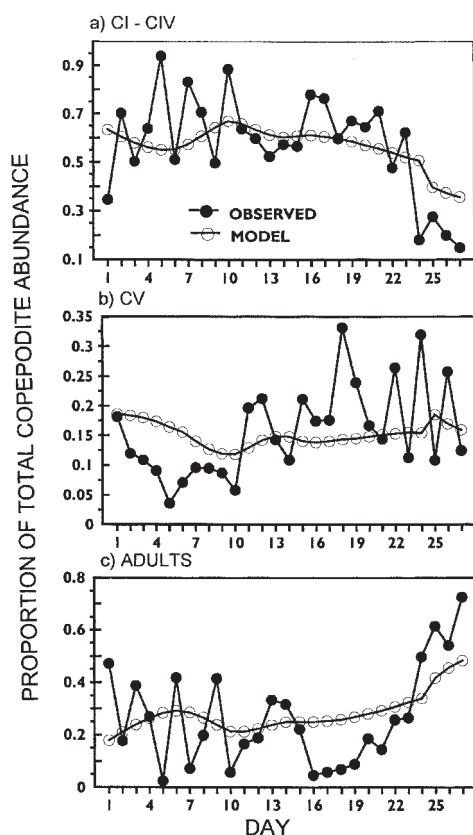


Fig. 8. Temporal changes in both the observed and model-predicted proportional abundances of (a) copepodites CI-CIV, (b) copepodite stage CV and (c) adult *C.carinatus* individuals. As explained in the text, copepodite stage CV abundance on day 20 was calculated as the average of that recorded on days 19 and 21 so as to exclude the advection event from the analysis.

on day 20 was ignored in the analysis. In comparing model estimates and data, it should be borne in mind that a single closed population is unlikely to show fluctuations in age composition of the scale indicated by the data—the fluctuations in the data are to some extent an artefact of sampling error as well as the difficulties of tracking a single population in the field. On average, the model's predictions were in no instance widely different from observed values, and the model provided a reasonable description of the changes in proportional abundance, simulating the decrease in the relative abundance of the CI–CIV stages and the concomitant increase in the relative abundance of adult copepods observed towards the end of the time series (Figure 8).

In Figure 9, changes in abundance of the various developmental stages are plotted on the same scale and such that they show changes relative to the initial value in each class. Whilst the dramatic fluctuations in the numbers of the younger stage individuals (NI–NVI, CI–CIV) are obvious, numbers of the older stage individuals (CV and ADULTS) fluctuate less. This highlights the difficulty of trying to establish correlations between food availability for fish (the older stage biomass) and *in situ* measures of phytoplankton abundance.

The abundances of both the nauplii and copepodites decrease to below their initial values towards the end of the series, concomitant with the reduced level of food availability that prevails following the initial two advection events.

Sensitivity analysis

The base-case simulation using the anchor station input series was used for comparative purposes. Model parameters were varied one at a time or in concert and the effect, relative to the base run, on the total biomass (mg C m^{-3}) of copepodites and adults (T_{biom}) was evaluated. To assess to which of the parameters

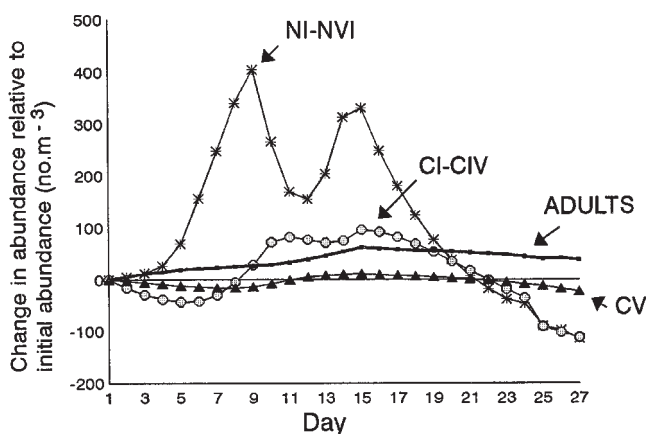


Fig. 9. Plots of model-predicted changes in the abundances of the various developmental stages relative to their initial values. Note the differences in both the magnitude and the time scale of the response of the different developmental stages to an earlier change in primary production.

the model is most sensitive, the ratio of the T_{biom} value predicted after 27 days (the time period of the anchor station series), $T_{\text{biom}}(27)$, to the T_{biom} value of the base run was used.

Graphical or other displays are only presented for tests which yielded results that are either surprising or substantial. The model was found to be relatively insensitive to parameters which can easily be determined empirically, such as the initial abundance estimates, age compositions and sex ratios.

Mortality rates are notoriously difficult to determine empirically and the choice of an appropriate mortality rate may be further complicated by age-dependent or sex-related differences in mortality. For example, ovigerous females of several copepod species are thought to frequent deep water as a means of reducing predation risk [see Bollens and Frost (1991) for a review of the trade-offs]. Because of the model's sensitivity to this parameter and the uncertainty regarding the best value to use, the effect on $T_{\text{biom}}(27)$ was assessed by (i) changing estimates of M_{pred} one at a time over the full range of plausible values and (ii) varying $M_{\text{pred}}(\text{CV\&ADULTS})$ and $M_{\text{pred}}(\text{NI-NVI,CI-CIV})$ in concert (Figure 10). Increasing M_{pred} resulted in an approximately exponential decrease in the value of $T_{\text{biom}}(27)$ and could potentially result in an order of magnitude error in model predictions (Figure 10a). However, when averaged over large areas, mortality rates are unlikely to be so great or populations would be unable to sustain

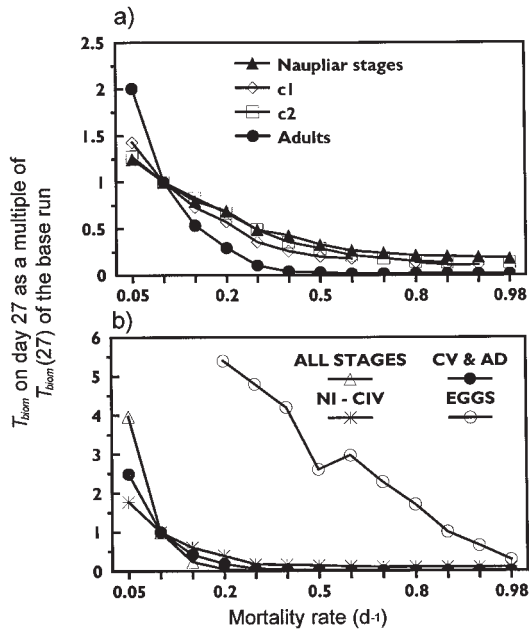


Fig. 10. The effect on the value of T_{biom} predicted on day 27 (using the anchor station input series) of (a) changing estimates of M_{pred} one at a time to the value indicated, and (b) varying $M_{\text{pred}}(\text{CV\&ADULTS})$ and $M_{\text{pred}}(\text{NI-NVI,CI-CIV})$ in concert. The effect of changing the egg mortality rate M_{egg} to the values indicated is shown in (b).

themselves. Decreasing M_{pred} of all the stages in concert results in at most a 4-fold increase in $T_{\text{biom}}(27)$ (Figure 10b). The model was more sensitive to changes in the mortality rates of the older stages (CV and adults) than the younger stages (nauplii, CI–CIV) (Figure 10b).

The model is very sensitive to changes in the value of the egg mortality rate M_{egg} , demonstrating a near-linear relationship between the value of $T_{\text{biom}}(27)$ and M_{egg} (Figure 10b). Decreasing M_{egg} by 20% resulted in more than a doubling in the value of $T_{\text{biom}}(27)$, while a 50% decrease in M_{egg} caused a 4-fold increase in $T_{\text{biom}}(27)$. The fact that M_{egg} is critical in determining the magnitude of the model predictions suggests that quantification of the egg mortality rate is a major limiting factor in constructing models of copepod population dynamics. The high fecundities of copepods, coupled with, *inter alia*, the broad spectrum of predators which may exploit copepod eggs, as well as their vulnerability to physiological processes and their immobility (which permits losses due to transport processes), all combine to render this an extremely difficult parameter to quantify *in situ*. Laboratory studies can assist in part by quantifying the role of food composition, for example, on hatching success and egg viability (Ianora, 1992; Ianora and Poulet, 1993; Head and Harris, 1994), although care should be taken in extrapolating results obtained using much denser food concentrations than occur in the ocean.

An interesting problem might arise if egg mortality rates were inversely density dependent. This could result because, following an upwelling cycle, egg production rates are high in response to increased food availability. Because copepod eggs are of similar size to some phytoplankton (5–20 μm), the concomitant increase in both eggs and phytoplankton might result in reduced rates of predation on copepod eggs simply because of the availability of alternative prey to consumers. However, if decreased predatory pressures on eggs are balanced by increased losses due to transport processes such as advection, then using a constant large M_{egg} value would be justified.

Decreasing the starvation mortality rate M_{food} results in less ‘steep’ population peaks because more individuals survive and grow to adulthood following a decrease in food concentrations. Increasing M_{food} by 50% results in an average error of 12% in predicted standing stocks (Figure 11). This scenario crudely tests the effect of assuming that physiological mortality rates are under- or overestimated in the model when food concentrations are limiting. This is important in light of the ‘critical moulting weight hypothesis’ of Carlotti and Nival, P. (1992): unless both small (Carlotti and Nival, S., 1992) and large (Carlotti *et al.*, 1993) copepod individuals ingest sufficient food to attain a critical weight, they are unable to moult to the next stage. The probability of moulting decreases with increased time spent in a stage, as does the probability of death. The present model does not explicitly account for this additional source of mortality, which is presumably most important during periods of reduced food availability. This does not necessarily mean that M_{food} is underestimated in the model because the individuals that succumb first to starvation mortality must intuitively be those that have ingested the least food. This suggests (i) that it is unnecessary to differentiate between different age classes within each stage in models of copepod growth

and development (Carlotti and Nival, P., 1992), and (ii) that it is unnecessary to account separately for enhanced mortalities of ‘slow developers’ when food is limiting. During optimal food conditions, however, spatial patchiness of phytoplankton might mean that some individuals are still food limited, and therefore this mechanism might result in an additional physiological source of mortality that has hitherto received little attention. More work needs to be done regarding this mechanism before it can explicitly be included in models as, for example, a function of prey patchiness.

In the present model, the grazing threshold is a central parameter in that it affects the fecundity rate, development rates and the proportion of individuals which die due to starvation. Simulation results revealed that changes in the grazing threshold have the most pronounced effect on the younger age classes. For example, a 33% increase in the value of F_{crit} resulted in a 37% decrease in the model-predicted NI–NVI abundance on day 27, but only a 3% decrease in the predicted biomass of copepodites and adults [$T_{biom}(27)$]. The model was relatively insensitive to decreases in the value of F_{crit} from 3 to 2 mg Chl $a\ m^{-3}$ or even 1 mg Chl $a\ m^{-3}$ (Figure 11). There are two main reasons for this: (i) Chl concentrations $< 3\ mg\ Chl\ a\ m^{-3}$ result in generally low, or even zero, egg production rates, and hence changes in F_{crit} have only a small effect on mean egg production rates; (ii) towards the end of quiescent periods between upwelling pulses, Chl concentrations are mostly well below 3 mg Chl $a\ m^{-3}$ anyway, so in the model food is limiting for individuals for the same length of time irrespective of the exact value of F_{crit} . Nonetheless, the grazing threshold is a crucial determinant of predicted patterns of productivity in the model, and its complete removal would result in fairly large changes in model output. Changes in F_{crit} do result in slight qualitative differences in the predicted biomass trend, but the major features of the pattern are still captured. Any grazing threshold level adopted in a model is likely to be an oversimplification because an individual grazer’s performance is determined by not only the absolute magnitude of primary production, but also the proportion that is actually available for consumption. One of the major factors influencing the latter relationship is the spatial variability in primary production and this facet warrants further investigation.

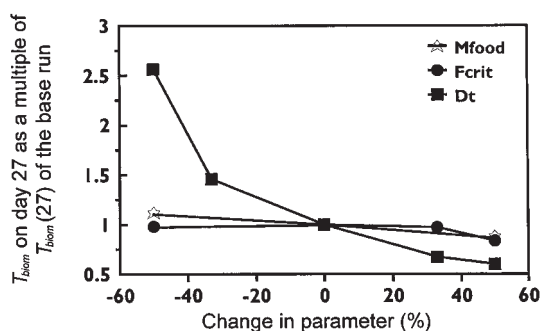


Fig. 11. Comparison of the model sensitivity to different parameters. The curves show the effect on $T_{biom}(27)$ when parameters were changed one at a time.

The problem of forward diffusion

Life stages with similar life history characteristics were lumped together in our model, yielding a division of the copepod population into seven distinct classes. One problem associated with the lumping of age or stage classes is the so-called ‘forward diffusion problem’: if a single pulse of reproduction enters the population pool, for example, it instantaneously increases the number of individuals in the first lumped category. Individuals then ‘diffuse’ out of this category at an artificially faster rate because at each time step a certain proportion of individuals in that category is assumed to grow into the next category. The net result is that some individuals attain adulthood quicker than they should. The effect of lumping age or stage classes is therefore somewhat analogous to the effect of a filter—pulses of reproduction passing through the ‘filter’ are both damped and spread out.

A simulation exercise was constructed to test model sensitivity to different levels of aggregation of model compartments. It was hypothesized that the scale of errors in model predictions attributable to the forward diffusion problem is a function of the relationship between the period of an input pulse and the length of a lump in the model.

A simpler version of our model was used, except that growth patterns were simulated using both lumped stage classes (NI–NVI, CI–CIII, CIV, ADULT) and 12 discrete stage classes. A time step of 1 day was used. Total development time D_t was varied from 13 to 20 days and the proportion of individuals in each model group which moult into the next group each day was calculated as before [equation (5)]. A mortality rate of 0.1 day^{-1} was used for the copepodite stages. The mortality rate of the naupliar stage individuals increased linearly from 0.1 day^{-1} for stage six individuals to 0.2 day^{-1} for stage one individuals. An average mortality rate of 0.15 day^{-1} was used for the lumped naupliar stage category. The model was initialized assuming an initial abundance of 100 adult individuals. An even sex ratio was assumed. Fecundity was modelled as a function of Chl *a* concentration using the relationship shown in Figure 3. Chlorophyll *a* concentration (mg m^{-3}) for each day x was calculated using the relationship:

$$CHL(x) = 6.5 \times \sin \left(\frac{2\pi}{p} \left(x - \frac{p}{4} \right) \right) + 7.5 \quad (9)$$

where p is the period (days) of Chl *a* fluctuations. Chl *a* concentration therefore increased in a cyclic fashion from 1 to $14 \text{ mg Chl } a \text{ m}^{-3}$, but with the added proviso that Chl *a* concentrations stayed constant at 0.5 mg m^{-3} for every second period of p days. Simulations were run over a period of 3 months and average copepodite biomass in the third month calculated for the lumped and non-lumped scenarios. Simulations were repeated for a range of p values and total development times.

Figure 12 shows the ratio of total copepodite biomass (lumped):copepodite biomass (non-lumped) for selected p values as a function of total development time. Results support the hypothesis that the effect on model predictions of lumping depends on the relationship between the period of an input pulse and the temporal scale of a lump in the model. For example, if total development time

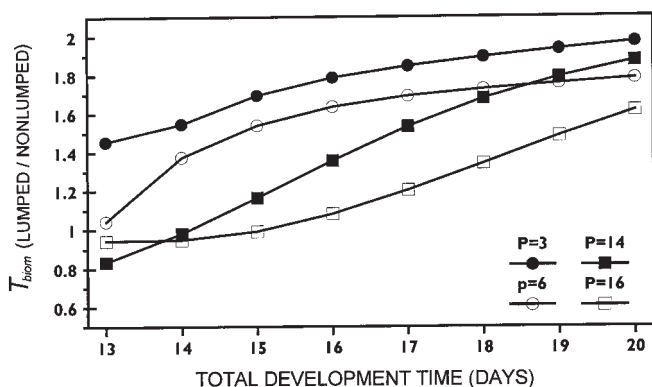


Fig. 12. The ratio of the total copepodite biomass T_{biom} predicted using a stage-aggregated approach to T_{biom} predicted using 12 unlumped stage classes, plotted as a function of the relationship between the period p of an input pulse and the period of a lump in the model. The time period of simulations was 3 months and T_{biom} represents the average value (in $\mu\text{g C m}^{-3}$) in the third month. The major lumping of model categories occurs because the six naupliar stages are treated as a single entity. The period of a lump in the model depends on the total development time D_t , where the average length of time spent in the naupliar stages is $0.35 \times D_t$. Input pulses of Chl a concentration have equal amplitudes but different periods p .

is fixed at 15 days (which corresponds to ~ 5 days spent in the naupliar stages), the effect of lumping the naupliar stages into a single category is to overestimate total copepodite abundance after 3 months by 16% and 54% for $p = 14$ and $p = 6$, respectively (Figure 12). Corresponding values using a longer total development time ($D_t = 20$ days; time in naupliar stages = 7 days) are 87 and 78%.

The major lump in our model described was the lumping of all six naupliar stages into a single category. Laboratory experiments suggest that, on average, *C. carinatus* individuals spend 6.6 and 3.2 days in the naupliar stages at 15.5 and 19.5°C, respectively (Peterson and Painting, 1990). In terms of the period of input pulses in nearshore areas along the West Coast, phytoplankton blooms have an average duration of 6–8 days (Brown and Hutchings, 1987). However, because upwelling pulses are part of cycles lasting between 3 and 10 days (Nelson and Hutchings, 1983), high Chl a concentrations may persist for as many as 10–16 days after the start of an upwelling cycle (Brown and Hutchings, 1987). The actual length of an ‘input’ pulse experienced by a local copepod aggregation will obviously depend on the degree of spatial coupling between the copepods and patches of Chl-rich water. Frequent spatial overlaps are likely because *C. carinatus* possess well-adapted differential migration strategies which facilitate the optimal utilization of patchy food resources (Verheye and Field, 1992). As phytoplankton blooms develop, mean sea surface temperatures increase from $\sim 11^\circ\text{C}$ to 15°C , due to mixing and solar heating processes (Brown and Hutchings, 1987). Copepod eggs which are produced in the vicinity of a developing bloom hatch and begin moulting from one naupliar stage to the next in surface waters which gradually increase in temperature, facilitating the rapid development of naupliar stage individuals. The average amount of time spent in the

naupliar stages is, therefore, generally less than the period of input pulses in the region, suggesting that errors incurred due to forward diffusion are not likely to be very large.

Discussion

A large number of relatively complex models of marine trophic systems exist (e.g. Walsh, 1975; Andersen *et al.*, 1987; Andersen and Nival, 1989, 1991; Cochrane *et al.*, 1991; Moloney and Field, 1991; Moloney *et al.*, 1991; Morel, 1991). These models are primarily mechanistic in nature and, whilst they have contributed to our understanding of the underlying dynamics driving these systems, there are few simpler models which can be used to predict potential secondary production in these ecosystems.

A simple population dynamics model is constructed to simulate the timing and scale of patterns of growth of a dominant copepod in inshore areas along the West Coast of South Africa. The model simulates the way in which the effects of a pulse of primary production are successively dampened as it passes through the various developmental stages (Figure 5). There is a close coupling between peaks in Chl concentration and the abundance of young life cycle stages, but a 6–8 day lag before any change is manifest in the biomass of the older stages. If adverse food conditions are prolonged for more than ~16 days following an upwelling cycle, no peak in the biomass of the copepodites or adults occurs.

The model can be used as a basic tool to explore the effect of different patterns of primary productivity on copepod population dynamics. Its value as a basic tool is supported by its ability to reconstruct the major features of changes in the standing stocks of copepod life cycle stages which occur following an upwelling event, its provision of biologically realistic predictions and its minimal use of estimated parameters.

Model performance was assessed by comparing model output with copepod production patterns observed during a 27 day anchor station study in St Helena Bay (Figures 7 and 8, Table III). The fact that the model provides a reasonably good approximation to the observed dynamics of a copepod population suggests that, although the model is simplistic, the parameters critical for prediction have been incorporated. Ignoring advective losses is potentially a serious omission, but *C. carinatus* is well adapted to the Benguela upwelling circulation (Verheye *et al.*, 1991) and the population is mostly retained within the confines of the shelf. By virtue of its simplicity and the fact that it uses only easily measured hydrographic parameters, it is a first attempt at constructing a practical predictive model to simulate within-season changes in patterns of secondary productivity.

The point of departure in simulating a population dynamics framework is, of course, the establishment of the correct rates of reproduction and recruitment to fuel the population dynamics process. The rate of reproduction of, and the rate of recruitment to, a copepod population are linearly related in the present model, but it should be borne in mind that complex non-linear relationships may operate in the field if, for example, large temporal variability is evident in either the viability or mortality of copepod eggs (e.g. Ianora *et al.*, 1992).

Laboratory studies demonstrate a clear sigmoid-type functional relationship between food abundance and copepod fecundity, but, for most of the copepod species examined in the southern Benguela region, poor correlations exist between these variables when measured in the field (L.Hutchings, personal observation). A potential problem in the present model therefore exists in the relationship between food abundance and copepod fecundity (Figure 3). A plausible explanation for the failure to demonstrate a clear relationship in the field is that copepod fecundity is an integrated response to a spatially and temporally patchy feeding regime, which cannot be detected using standard sampling gear or techniques. If feeding history is an important factor controlling the production of calanoid eggs (Attwood and Peterson, 1989), then traditional shipboard egg production incubation methods may similarly yield inconsistent results. The hypothesis that locally dense and nutritious food patches are better correlates of zooplankton production than mean or integrated food abundance estimates needs to be tested in the field. *Calanoides carinatus* stages have been observed aggregating in areas with rapid phytoplankton growth rates (Verheye and Field, 1992). It has been proposed that phytoplankton growth rate more accurately describes nutritional value than absolute primary production or biomass measures (Napp *et al.*, 1988). The use of depth-integrated Chl *a* concentration data (as an index of food abundance) or consideration of vertical changes in Chl *a* concentration was considered superfluous in model construction because it is assumed that the vertical migratory behaviour of copepods allows them to exploit maximal, rather than average, regions of phytoplankton productivity in the water column (Figure 2). The reduced dimensionality of the model is therefore justified on the grounds that differences in the vertical dimension are not important if an animal can easily integrate them. It is, therefore, unlikely that increased resolution in the vertical dimension will improve the model or the strength of the fecundity–food relationship.

A potentially greater source of error which might obscure the fecundity–food relationship concerns the effect on copepod fecundity and viability of different species compositions in the diet of these highly selective omnivorous feeders (Ianora and Poulet, 1993; Ohman and Runge, 1994; Pond *et al.*, 1996). The present model estimates food ‘availability’ as a function of abundance and particle size only, but substantial changes in fecundity may result in response to, for example, different biochemical components of the diet (Stoecker and Capuzzo, 1990; Ianora and Poulet, 1993; Head and Harris, 1994). Furthermore, recent work demonstrating an inverse relationship between the size of eggs produced by copepods and food availability and fecundity (Guisande *et al.*, 1996; Pond *et al.*, 1996) suggests that more information is required to model zooplankton production and population dynamics accurately.

The model was robust with respect to most of its parameters because small changes in their values resulted in predictable and not widely divergent predictions. Quantitatively, the model was most sensitive to changes in the egg mortality rate (Figure 10); this suggests that more effort should be directed at trying to quantify this parameter. Day-to-day random variability in egg mortality rates could contribute significantly to population fluctuations and could be an

important determinant of patterns of population growth. *In situ* determination of critical factors affecting physiologically induced variability in egg viability may assist in future population dynamics studies.

As is often the problem with models, the model showed the greatest sensitivity to parameters which are difficult to determine empirically and about which the least is known (Figure 10). Whilst accurate field estimates of initial abundance levels are important in determining the quantitative characteristics of model predictions, accurate estimates of the actual population composition are less critical because extrinsic factors soon result in a common spread in population age structure.

The model suggested that the abundance of, and rates of survival of, the adult and CV stage individuals are more important in determining standing stocks than the equivalent juvenile rates (Figure 10) because changes in adult standing stocks are quickly mirrored as changes in rates of egg production. High adult mortality rates, therefore, maintain an even population age composition, whereas relatively higher juvenile mortality rates result in an increased proportional abundance of adults and hence have a marked effect on population composition (although less so on absolute standing stock). The sensitivity analysis highlighted the need to quantify predator-induced rates of mortality. Tracking a local copepod population will provide some insight into *in situ* copepod mortality rates, but sampling technology needs to be improved to measure the abundance of zooplankton populations and their predators on the same scale. Alternative methods for estimating mortality rates in copepod populations (e.g. Wood, 1994) should be explored. Large gaps exist in our knowledge of the effect on copepod populations of predation by invertebrate carnivores, such as gelatinous species (Gibbons *et al.*, 1992; Gibbons, 1997). More research is needed before models of the southern Benguela ecosystem can account for the effect on copepod mortality rates of carnivorous zooplankton groups, which sometimes occur in large swarms in response to dense food concentrations (Gibbons *et al.*, 1992).

In constructing models, a balance needs to be struck between the extent to which model compartments should be aggregated (which limits the number of interactions included) or treated as separate entities (which reduces the precision of results furnished due to the cumulative effect of errors in estimating a large number of parameters) (Rastetter *et al.*, 1992). Our model was constructed to be as simple as possible and hence life stages with similar life history characteristics were lumped together, yielding a division of the copepod population into seven distinct classes. We conducted a sensitivity analysis which suggested that in this instance forward diffusion could result in at most a 2-fold increase in model predictions relative to those expected using a model with no lumped stages. Model results became increasingly sensitive to the effect of lumping as the period of an input pulse was decreased (Figure 12). Based on estimates of the period of average upwelling cycles and the average length of time individuals spend in the naupliar stages, we concluded that although forward diffusion should be borne in mind as a possible source of error, the level of aggregation of model compartments used in our model was not a drastic oversimplification. It follows, however,

that the choice of an appropriate level of aggregation in a model should be based on consideration of the scale of environmental variability characterizing the environment.

A brief summary follows of which parameters or assumptions are most critical in determining the major population dynamics characteristics.

Average egg production rates (the average number of eggs produced per fertile female per day) are most affected by the value of the grazing threshold F_{crit} and, of course, by the assumption that egg production rates are independent of female density. Mean egg production rates (the average number of eggs produced per day) are directly influenced by scenarios which change either the absolute or relative abundance of fertile females, e.g. initial values and adult mortality rates. The effects of increased reproductive growth are cumulative as they lead to increased adult standing stocks.

The effects of increased rates of somatic growth are similarly cumulative because they shift population age structure to one dominated by adults. In this way, mean egg production rates are increased while juvenile mortality rates are simultaneously decreased: the faster individuals grow, the greater is their tolerance to starvation. The absolute magnitude of standing stocks is thus determined not only by the relative rates of recruitment and mortality, but also by changes in the development rate.

Following a pulse of primary production, the rate at which instars develop is more critical in determining final standing stocks than their starvation tolerances: if they develop quickly enough, they can 'escape' into the older stages before conditions deteriorate, but if they develop too slowly, minor differences in starvation tolerance are irrelevant as most die anyway.

Changes in the rate of growth and decay of population peaks, and therefore in the qualitative trend predicted, arise either directly from changes in development rates or indirectly from factors which affect the development rate, e.g. the assumption that development rates are food limited and, by association, the definition of the level at which individuals become food limited (F_{crit}). The model was relatively insensitive to reasonable changes in the value of F_{crit} .

The present study has contributed to attempts to develop a simple practical model to simulate secondary production, by demonstrating that a model driven essentially by input data derived from satellite observations of ocean colour and temperature can provide useful insights into zooplankton population dynamics. It was hypothesized that, on a broad scale, satellite-derived images of Chl *a* concentrations in the southern Benguela upwelling system may provide a useful index of food availability for copepods. The abundance and frequency of fluctuations in food availability are critical factors influencing the life history parameters of copepods, particularly in coastal and upwelling areas where phytoplankton are variable mainly at micro and fine scales (Calbet and Alcaraz, 1997). Simple simulation models can assist in improving our understanding of the ecological implications for zooplankton dynamics of different spatial and temporal overlaps between zooplankton and phytoplankton biomass and production, although more detailed information is required to predict reliably patterns of secondary production in a coastal upwelling system.

Acknowledgements

We thank Betty Mitchell-Innes, Grant Pitcher and Penny Brown for discussions and access to some of their data, and members of the Benguela Ecology Programme (BEP) for laying much of the groundwork upon which this study is based. Financial support for the senior author was provided by the Foundation for Research Development and by the Benguela Ecology Programme, and is gratefully acknowledged. Prof. J.H.Steele and an anonymous reviewer are thanked for their comments on an earlier version of the manuscript.

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Received on December 6, 1998; accepted on May 10, 1999