

A MODEL OF
COPEPOD POPULATION DYNAMICS
IN THE
SOUTHERN BENGUELA UPWELLING REGION

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Nature is complex. It is therefore sometimes mistakenly thought that models of nature must be equally complex. Einstein, who knew better, said that theories should be as simple as possible, but not too simple.

What is meant by 'simple' depends in part on current technology.

Clark (1993)

For my parents,
with thanks for their love and support

DECLARATION

This thesis reports the results of original research which I have carried out in the Marine Biology Research Institute, University of Cape Town, between 1992 and 1995. This work has not been submitted for a degree at any other university and any assistance I received is fully acknowledged. Most of the data that are presented were obtained from published studies, and are referenced as such.

Signed by candidate

Éva Elizabeth Plagányi

30/4/95

Date

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ABSTRACT. Plagányi, É.E. 1995. *A model of copepod population dynamics in the Southern Benguela upwelling region.* M.Sc thesis, University of Cape Town

A simple population dynamics model is constructed to simulate temporal variability in the biomass of a dominant copepod *Calanoides carinatus* (Copepoda: Calanoida) along the West Coast region of South Africa. *C. carinatus* is extensively preyed upon by the commercially important anchovy *Engraulis capensis* and 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 initialise 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 results obtained are consistent with data from field studies.

The model is robust with respect to most of its parameters because minor changes in their values result in predictable changes in model output. The effect on model predictions of errors in field estimates is quantified. The model showed greatest sensitivity to parameters which 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 attempts to simulate copepod population dynamics in the region.

The Southern Benguela system is patchy on a range of different space and time scales. The effect of fine-scale distributional heterogeneity on mesoscale patterns of copepod productivity was investigated by assuming that spatial patchiness affected the degree of overlap between zooplankton and phytoplankton populations. The effect of spatial patchiness is particularly prevalent under poor feeding conditions, and may result in predictions based on average feeding conditions underestimating zooplankton production by as much as 30% in some circumstances. Estimates of zooplankton production are sensitive to both the spatial arrangement and intensity of food patches in a heterogeneous environment. There is a need to isolate the essential mechanisms causing distributional heterogeneity and to quantify the effect of spatial patchiness on model predictions to permit the correct averaging of model results over broad horizontal areas.

Because of the model's sensitivity to the predator-induced mortality rate, a temporally and spatially integrated system is used to quantify this parameter as a function of varying patterns of predator and prey abundance. Shoals of anchovy recruits are explicitly modelled feeding on patches of *C. carinatus* prey, and the fish's performance is quantified through temporal and spatial integration of periods and patches of prey abundance and shortage. Constant high fish densities dampen the spatial variability in copepod abundance, whereas a pulsed predation pressure permits locally depleted copepod populations a short respite in which to recover some growth, thereby allowing the persistence of a few good prey patches which offer favourable energy returns for foraging fish.

The model suggested that at high densities of anchovy recruits, predicted growth rates are strongly density-dependent and predation rates may exceed copepod production rates. Absolute measures of prey availability are sometimes unable to predict anchovy feeding success as mechanisms permitting temporal and spatial segregation play a vital role in synchronizing the relationship between fish predation pressure and prey turnover rates. The model emulates observed variability in anchovy growth rates and analysis of the output indicates that the availability of high sustained abundances of food along the West Coast may be a critical "bottleneck" contributing to the strength of recruitment to the pelagic purse-seine fishery in South African waters.

Observed chlorophyll *a* concentration and sea surface temperature data in 1971 and 1972 were used as inputs into an annual version of the basic model, and model-predicted patterns of copepod biomass were compared with observed patterns of zooplankton biomass in the two years. The ability of the model to simulate major differences in the general features observed in the two years supports its use as a tool to describe net patterns of zooplankton productivity over large horizontal areas. The model identified the need to quantify the role of major size-class groups, such as the microzooplankton and macrozooplankton, in mediating the flow of energy from phytoplankton to fish.

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CHAPTER 1

INTRODUCTION

The Southern Benguela system (Fig. 1.1) is characterized by spatial and temporal variability in primary and secondary productivity. Coastal upwelling, being wind-driven, is episodic at temporal scales of days or weeks (Andrews & Hutchings 1980, Shannon *et al.* 1984a, Brown & Hutchings 1987). In conjunction with mesoscale oceanographic discontinuities (for example, oceanic fronts and storms) (Kjørboe 1991), this results in pulses of elevated primary productivity that are patchy in both time and space. A diverse spectrum of marine food chain models have been developed to explore ways in which these pulses of primary production are propagated (through grazing) up the food chain (or food web or trophic continuum) (eg. Sheldon *et al.* 1977, Silvert & Platt 1980, Cousins 1985, Denman *et al.* 1989, Rothschild 1991, Moloney & Field 1991, Anderson 1992, Moloney 1992, Painting *et al.* 1992, Polis & Holt 1992, Aksnes & Wassmann 1993). Of particular interest to fisheries managers is the way in which these pulses ultimately translate into harvestable fish biomass.

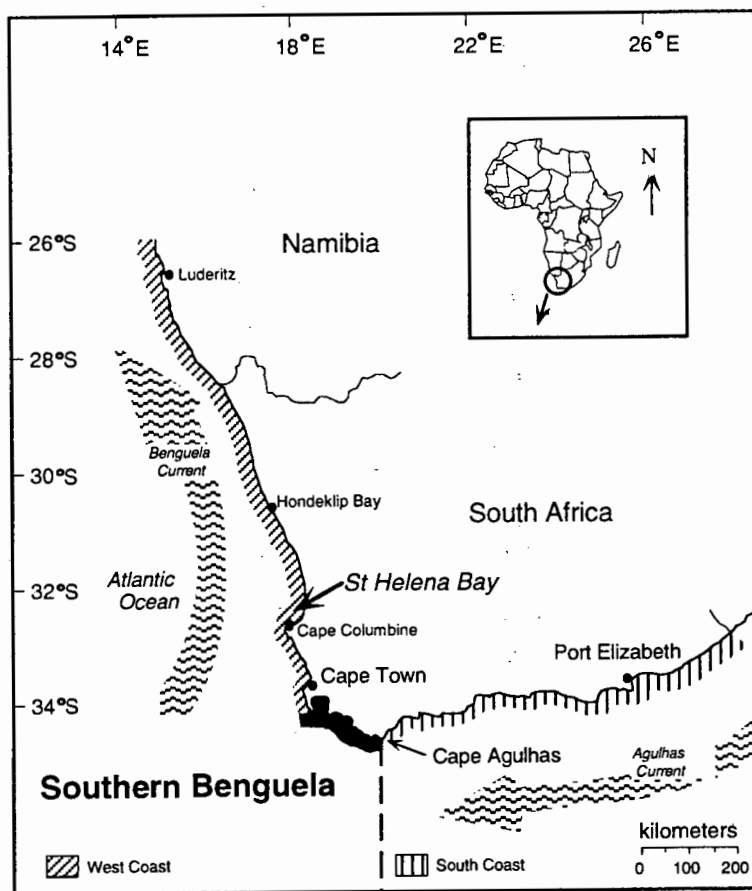


Fig. 1.1. Location of the model ecosystem off South Africa

In the upwelling region along the West Coast of South Africa, 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 and the larger heterotrophs. Most primary production in the form of small cells ($< 5\mu\text{m}$) is unavailable to copepod grazers (Bartram 1980, Paffenhofer 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 & Peterson 1991), rather than on the longer "microbial" pathways (picoplankton-flagellate-ciliate) in which primary production is consumed and remineralized by microorganisms before being transferred along the food web (Azam *et al.* 1983, Hobbie 1988, Pomeroy & Wiebe 1988).

Copepods often dominate zooplankton communities both in terms of numbers and biomass and it has been suggested that in pelagic ecosystems they collectively constitute the single most important prey source for planktivorous fish (Kjørboe 1991). In the Southern Benguela region calanoid copepods (Copepoda: Calanoida) form an important part of the diet of, *inter alia*, anchovy *Engraulis capensis*, round herring *Etrumeus whiteheadi*, lightfish *Maurollicus muelleri* and lanternfish *Lampanyctodes hectoris* (Armstrong *et al.* 1991a).

Along the West Coast region of the Southern Benguela system, the calanoid copepod *Calanoides carinatus* is the dominant copepod in terms of biomass, accounting for up to 67% of the biomass of the mesozooplankton community (Verheye 1991). Moreover, it is an important component of all of the African upwelling systems (Peterson & Painting 1990). In contrast, the Agulhas Bank is dominated by *Calanus agulhensis*, which comprises between 60 and 95% of the copepod biomass in this region (Verheye *et al.* 1992). To survive in fluctuating upwelling systems, it is hypothesized that zooplankton should have short generation times and be capable of withstanding prolonged periods of starvation (Dagg 1977). The copepod *C. carinatus* has generation times varying between 12 days at 19.5°C and 18.3 days at 15.5°C (Peterson & Painting 1990). Although *C. carinatus* develops more rapidly than any other copepod species studied to date, differences in development rates between small and large-sized copepods are generally small (Peterson & Painting 1990). Calanoid copepods are capable of food storage because the adults and older juveniles have a fat body or mid-gut oil sac (Holland 1978). Several workers (eg. Runge *et al.* 1985, Borchers & Hutchings 1986, Diel & Klein Breteler 1986, Attwood & Peterson 1989, Walker & Peterson 1991) have

concluded that copepod growth rates (calculated either as juvenile growth rates or female egg production rates) are often food-limited.

Calanoid copepods typically have a life cycle involving moults into six naupliar, five copepodite, and, finally, into an adult stage. Models describing the population dynamics of copepods need to consider the major life stages as separate variables because they have different rates of growth, fecundity and mortality. Estimates of total biomass are of little value in trying to assess the availability of food to size-selective fish predators such as anchovy.

One of the aims of the present study was to assist the Benguela Ecology Programme in its efforts to understand the variability of pelagic fish stocks in relation to the environment. The Southern Benguela system supports a purse seine fishery of considerable economic and social importance to the region (eg. Hutchings & Boyd 1992). The anchovy has dominated purse seine catches in the region since 1966 (Crawford *et al.* 1983, Crawford 1987), but at least four-fold differences in the recruitment success of this species occur between years: annual landings varying between 150 000 and 600 000 metric tonnes (Hutchings & Boyd 1992). The life history and migration patterns of anchovy are well documented (Crawford *et al.* 1983, Shelton 1986, Crawford 1987, Hampton 1987). Briefly, anchovy spawn serially from October to January on the Agulhas Bank, from where most eggs and larvae are transported northwards in a jet current. The larvae and juveniles then migrate from the outer shelf region to a narrow coastal belt along the West Coast, which acts as a nursery region before the recruits return south again to spawn on the Agulhas Bank the following spring/summer. The anchovy therefore recruit to the fishery in their first year, when they are between 8 and 9 centimetres in length (Waldron *et al.* 1992).

Predictive fish recruitment models are notoriously difficult to construct because of the plethora of interacting factors which may affect recruitment, coupled with the problems of interpreting the nonlinear system dynamics (Fogarty *et al.* 1991). A great deal of effort has been expended in attempting to isolate the central factors influencing recruitment strength in anchovy (Waldron *et al.* 1989, Cochrane & Starfield 1992, Hutchings 1992, Hutchings & Boyd 1992, Peterson *et al.* 1992, Cochrane & Hutchings 1995). One possible contributing factor is the abundance of food for anchovy in the nearshore West Coast shelf region. Because juvenile anchovies occupy a narrow coastal belt along this region over much of the year (Hampton 1987), and depletion of plankton stocks may adversely affect their food

consumption rates (Armstrong *et al.* 1991a), measures of potential food availability (in terms of zooplankton abundance) along the West Coast may assist in understanding, and perhaps even predicting, some of the variability in anchovy recruitment levels. A better understanding of the relations between hydrography, phytoplankton abundance and zooplankton production may thus facilitate management of fish stocks and ultimately assist in prediction of their production rates.

Scientists have repeatedly, and mostly unsuccessfully, attempted to establish significant correlations between fisheries production and primary production (eg. Lasker 1988), or between hydrographic parameters and copepod biomass (Hanson *et al.* 1986, Kiørboe & Johansen 1986, Kiørboe 1991). The failure of these models highlights the inadequacy of using an indirect approach. Forecasts based on broad-scale correlations should similarly be viewed with caution because they do not confirm cause and effect, and hence perturbation of an ecosystem by a major oceanographic or biological anomaly may lead to nonlinear feedback which cannot then be predicted. This results because variables such as temperature, which are easily measured and therefore commonly employed, may only be 'proxy' variables which are themselves correlated with a common causative process (Denman *et al.* 1989). In a similar vein, correlations between fish performance and ship-collected 'snapshot' estimates of copepod abundance, measured on widely separated spatial and temporal scales, are, at most, tenuous. The performance of the fish is likely to be a function of the variability, both spatially and temporally, of its food resource. Measures of intra-seasonal and spatial patterns of variability in zooplankton productivity are therefore necessary if any attempt is to be made to assess the relative importance of food availability in predicting anchovy recruitment success.

A large number of relatively complex models of marine trophic systems exist (eg. Walsh 1975, Andersen *et al.* 1987, Andersen & Nival 1989, 1991; Fasham *et al.* 1990, Cochrane *et al.* 1991, Moloney & 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.

Because of the large number of interactions involved in predicting the distribution and abundance of phytoplankton, which forms the basis of the pelagic food chain, 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, with a minimum area of resolution of approximately 1 km². The NASA Sea Viewing, Wide field-of-view Sensor (SeaWiFS) is due to be launched in October 1995 and will provide colour data around southern Africa for fisheries and other research (F. Shillington, pers. comm.) My copepod population dynamics model uses these estimates of phytoplankton abundance and thereby circumvents the need to estimate the phytoplankton component of the food chain as a function of a set of hydrographic parameters. This greatly reduces the number of linkages in the model, and, therefore, the loss of resolution in predicting the way in which disturbances (eg. upwelling cycles) are propagated up the food chain. The generation times of most predators are at least an order of magnitude longer than their prey (Kiørboe 1991). Predicting a change in predator biomass arising from an earlier change in some prey characteristic therefore requires spatial and temporal integration of periods and patches of prey abundance and shortage.

The primary aim of this study was therefore 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. Much of my work has centred on the problems of integrating the results of a local model both spatially and temporally, in an attempt to create a tractable model that describes net productivity patterns over large horizontal areas, while still retaining the critical features of the population's dynamics.

The thesis is divided into seven chapters. The second chapter describes the development of a general copepod population dynamics model and presents some simulation results. Model output is assessed by comparing results with empirical data collected at a fixed station in St Helena Bay for 27 consecutive days during March/April 1987 (Verheye 1991). Because the model is designed to be applicable to a general inshore area along the West Coast, no attempt is made to fine tune model parameters by fitting the model to the Anchor Station time-series. Forcing any model to mirror local anomalies is likely to result in biased parameter estimates when extending the model to other areas.

In chapter three, a standard simulation is used to serve as a basis for comparing output from a sensitivity analysis. The sensitivity analysis assesses to what degree model results depend on the parameter values and model assumptions. The model

may be initialized using data collected on cruises, and, because field estimates are inevitably imprecise, the real values often varying substantially in both time and space, a sensitivity analysis is critical to evaluate the model's predictions over a range of parameters (Gladstein 1991).

The fourth chapter explores the effect of patchiness or spatial heterogeneity on the trophic transfer process from phytoplankton to zooplankton. It is well known that both phytoplankton and zooplankton populations are patchy on a multitude of scales (Haury *et al.* 1978, Steele 1978, Verheye & Hutchings 1988, Davis *et al.* 1992). Technical difficulties generally preclude detailed field studies of micro-scale patchiness, although it is on this scale that interactions between phytoplankton and zooplankton occur. Rothschild (1992) has even suggested that the micro-scale distribution of prey may be important to the entire trophodynamics in the ocean. Simulations conducted in this chapter therefore attempt to quantify the effect of patchiness in the distribution of phytoplankton on the net performance of zooplankton, when averaged over large spatial scales. The importance of this work is that it provides a first and rough means of estimating the scale of, or attempting to correct, errors in spatial averaging which occur because of variable couplings between zooplankton and phytoplankton populations. Quantification of the relationships between hydrographic parameters (eg. wind and sea surface temperature) and water stability (including eg. the vertical structure of turbulence and its effect on patterns of plankton patchiness) are needed before the results of this preliminary study can be extrapolated to the field.

The fifth chapter describes a model which explicitly simulates shoals of anchovy feeding on spatially resolved populations of copepods. The aim of the model is to explore the best form of the predator mortality function to be used under varying patterns of predator and prey abundance, and to gain insight into the way in which local structure varies over large spatial scales.

In chapter six, the basic model of chapter one is integrated temporally by accounting for the seasonal variation in the biomass of fish present in the area. This is achieved using the spatially averaged mortality rates calculated in chapter five. Unfortunately delays in the launch of the SeaWiFs sensor have meant that formal validation of the model, as was envisaged to have taken place during the course of this study, is not possible at present and alternative forms of validation have therefore been sought. To test whether or not the model is in fact capable of predicting, with a reasonable degree of accuracy, different secondary production

patterns in different years, chlorophyll *a* concentration and sea surface temperature data from 1971 and 1972 (Andrews & Hutchings 1980) are used as inputs into the model and the output is compared with the mean observed zooplankton standing stocks in each year.

A brief summary follows (Chapter 7) of some model results and of some of the additional factors which may need to be considered in future modifications of the model. Uncertainties associated with the estimation of critical model parameters and inconsistencies between field and model results are highlighted to guide future field and experimental studies, and hence to mediate the development of new (or improvement of existing) models in parallel with new results.

CHAPTER 2

DEVELOPMENT OF A SIMPLE COPEPOD POPULATION DYNAMICS MODEL

INTRODUCTION

A large body of field and experimental data has been collected to test the importance of a range of factors in influencing both physiological and population growth rates of marine plankton. For example, studies have focused on food selection by copepods (Poulet & Marsot 1980, Paffenhofers & Van Sant 1985, Cowles *et al.* 1988, Turner *et al.* 1993); the effects of food quality, food concentration and temperature on rates of zooplankton ingestion and production (Ambler 1986, Houde & Roman 1987, Kjørboe 1989, White & Roman 1992); the importance of feeding history on rates of egg production (Dagg 1977, Attwood & Peterson 1989, Tester & Turner 1990) and survival (Borchers & Hutchings 1986); the estimation of secondary productivity from rates of egg production (Berggreen *et al.* 1988, Peterson *et al.* 1991); and, the effects of food availability (Borchers & Hutchings 1986, Huntley *et al.* 1987, Green *et al.* 1991) and temperature (Huntley & Lopez 1992) on rates of development. Furthermore, studies have focused not only on the direct numerical effects of predation on copepod dynamics, but also on the indirect effects (Kerfoot & DeAngelis 1989); the role of predation in determining zooplankton distribution and species composition (Kimmerer & McKinnon 1989, Soto & Hurlbert 1991); and the effect of increased predation on the behavioural response of the zooplankton (Fancett & Kimmerer 1985, Ohman 1988, Bollens & Frost 1989, 1991a,b, Bollens & Stearns 1992).

A variety of models have been constructed to investigate the dynamics of plankton populations. These range from simple mathematical models (eg. Bossicart & Mommaerts 1979), to more complex models (Andersen & Nival 1989), and include *inter alia*: models based on age and stage categories (Carlotti & Sciandra 1989, Fransz *et al.* 1991); size classes (Moloney & Field 1991); biomass dynamics (Steele & Frost 1977, Fasham *et al.* 1990); those incorporating the effect of predators (Davis 1984); those simulating shifts in copepod species dominance (Gaedke & 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 & DeAngelis 1989, Holling 1992, Rastetter *et al.* 1992, Lawton & Jones 1993). The reduction in complexity of an aggregated model, and therefore the limit to the number of interactions which should be included in a model, must be balanced against the loss of precision which results from errors in parameter estimation associated with a large number of separate model compartments (Lawton & Jones 1993). Furthermore, when averaged over longer time or larger spatial scales, different signals from local effects may either average out (Lawton & Jones 1993) or propagate out. The task of modelling copepod population dynamics over large horizontal areas therefore 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.

This chapter describes the development of a population dynamics model to simulate the time scale and nature of a copepod population's response to changes in its environment. The population dynamics of copepods are determined by rates of recruitment, death, diffusion, advection and behavioural migration (Hutchings *et al.* 1993). These rates are in turn influenced by factors such as feeding rates, growth and reproductive capability. The model developed here focuses primarily on the essential mechanisms driving copepod population dynamics, and a progressive assessment is then made of the need to add additional detail. 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.

BACKGROUND TO THE MODEL

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). The present model assumes that these are also the key variables operating in the field. To maintain the model's objectivity, wherever possible, mathematical formulations are based on known parameters or functional

relationships. The exception is the rate of mortality due to predation, which is extremely difficult to quantify in the field.

The model developed here simulates the dynamics of the 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 to April (Brown & 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 over this period. The model focuses on *C. carinatus* for a number of reasons:

- i) It is the dominant copepod (in terms of biomass) in the West Coast shelf region;
- ii) Comprehensive field and laboratory studies on its biology and ecology have been conducted (Borchers & Hutchings 1986, Verheye 1989);
- iii) Extensive feeding studies (James 1987, Armstrong *et al.* 1991a) have shown that mesozooplankton, and in particular the large calanoid copepods (eg. *C. carinatus*), form a major component of the diet of anchovy; and
- iv) 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.

MODEL DESCRIPTION

The model is a one-dimensional depth-independent model of a time-dependent zooplankton population in an horizontally homogeneous volume of water. The effect of reducing the system's dimensionality and of assuming a horizontally homogeneous distribution of both phyto- and zooplankton is investigated in later sections.

Division into lumped stage-classes: In copepods, growth and mortality are both age- and stage-related processes, whereas fecundity is age- and sex-related. A degree of aggregation of life stages was chosen using the principle that age- and stage-classes should be lumped wherever possible for simplicity, while still retaining a sufficiently high degree of resolution to ensure that individuals within a model category do not differ dramatically in any of the life history characteristics. A minimum division of the copepod population into seven distinct classes was deemed necessary: Eggs; Naupliar stages N1 - NVI; Copepodite stages CI - CIV; Copepodite stage CV; Adult

Males; Unripe Females and Ripe Females (assuming females take 3 days to lay eggs (Borchers & Hutchings 1986). The model classes are in actuality lumped stage classes but for simplicity are broadly referred to as age classes in the text.

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 one day is used to update changes in standing stocks. Because the model presupposes uniformity over a large horizontal area, losses due to horizontal advection into adjacent areas are assumed equal to horizontal diffusive gains. Furthermore, 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 & Field 1992). The exception to the above arises when individuals of copepodite stage CV, which overwinter in deep water, emerge from diapause and restock inshore populations (Verheye 1991). This process was not modelled in the present version which focuses on summer conditions: although animals could well emerge from diapause in spring and recolonise throughout the upwelling season, the model may be initialised from cruise data collected in November, and hence this factor does not warrant inclusion in the model.

Zooplankton, including the near-shore calanoid copepods, undertake vertical migrations (Pillar 1984a, Hutchings 1985, Forward 1988, Verheye & Hutchings 1988, Longhurst & Harrison 1989). Evidence suggests that these movements are primarily mediated by changes in food availability, light and predator abundance (see eg. Pearre 1979, Huntley & Brooks 1982, Bollens & Frost 1989, Arinardi 1991, Bollens & Stearns 1992, Verheye & Field 1992, Bollens *et al.* 1993) The effects of the behavioural migration patterns of *C. carinatus* on its population dynamics are explored in the sensitivity analysis in chapter three.

Driving variables: The model is driven by satellite-derived images of sea surface temperature (SST) and chlorophyll *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 biannual research cruises.

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

DEFINING FOOD AVAILABILITY FOR COPEPODS

The Grazing Threshold

Marine ecosystem models generally require a critical phytoplankton abundance value (- the grazing threshold) below which organisms become food-limited (Steele 1974, Walsh 1975). Determination of the grazing threshold (F_{crit}) is especially important in pulsed food environments such as the Benguela ecosystem where it is hypothesized that secondary production is constrained by food availability (Borchers & Hutchings 1986, Attwood & Peterson 1989). Indeed, the greater patchiness in coastal upwelling systems is responsible for the order of magnitude larger F_{crit} values required in models of upwelled systems relative to those of non-upwelled systems (Walsh 1976).

Net-chlorophyll as an index of food quality: Calanoid copepods exhibit active choice in food selection and both the size and quality of food particles are important in models of copepod feeding (Paffenhofer & Van Sant 1985, DeMott 1990, Kerfoot & Kirk 1991). Because most primary production in the form of small cells ($< 5\mu\text{m}$) is unavailable to mesozooplankton grazers (Paffenhofer 1986, Vanderploeg *et al.* 1990), food availability to copepods is better defined as a function of the chlorophyll content of the $>10\mu\text{m}$ fraction (net-chlorophyll) (Runge 1985, Peterson & Bellantoni 1987, Kjørboe *et al.* 1990, Armstrong *et al.* 1991b, Peterson *et al.* 1991, Walker & Peterson 1991, Mitchell-Innes & Pitcher 1992). The model therefore uses measures of net-chlorophyll *a* concentration as an index of food quality for copepods.

The only instance in which this assumption will obviously be erroneous is if food concentrations are high, but the phytoplankton is dominated by toxic dinoflagellates (net-phytoplankton) (Sykes & Huntley 1987, Nielsen *et al.* 1990). The occurrence of toxic dinoflagellate blooms in the Southern Benguela is rare (Shannon & Pillar 1986), and the effect on zooplankton not quantified, so no further consideration is given to this matter here, although it should be noted that when such blooms occur the model will overestimate productivity rates.

Estimating net-chlorophyll biomass from measures of total chlorophyll: 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 & Pitcher 1992, Kjørboe 1993).

Following Mitchell-Innes & Pitcher (1992), the biomass of the $>10\mu\text{m}$ chlorophyll fraction ($B_{>10}$) is therefore calculated as a linearly increasing function of total chlorophyll (CHL), i.e.

$$B_{>10} = 0.98 \times \text{CHL} - 1.2 \quad (2.1)$$

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 (Cushing 1989, Probyn 1985, Brown & Hutchings 1987, Mitchell-Innes & Walker 1991, Mitchell-Innes & Pitcher 1992). Regression analyses indicate that phytoplankton populations with chlorophyll concentrations below a critical limit of *ca.* 3 mg.m^{-3} are composed predominantly of small cells, $< 5\mu\text{m}$ in diameter (Mitchell-Innes & Pitcher 1992), and the grazing threshold is therefore taken as 3 mg.Chla.m^{-3} . From (2.1) it can be seen that the grazing threshold corresponds to a net-chlorophyll content of 1.74 mg.m^{-3} , which is similar to the chlorophyll concentration below which growth rates of small copepods become food-limited under laboratory conditions (Peterson *et al.* 1991).

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 & Pitcher 1992). Flagellates are effectively $< 10 \mu\text{m}$ in diameter and it is therefore assumed that this shift in community composition also results in food-limitation of *C. carinatus*.

Age-independence of F_{crit} : The same grazing threshold is assumed to operate for juvenile and adult copepods, the rationale being that adults are primarily constrained by the reduced availability of suitably sized food particles, and juveniles are limited by the low biomass of food available. 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 utilising small cells (Mensah 1974, Verheye 1989) which predominate at low phytoplankton concentrations. Competition between young and adult copepods is minimized by the differential exploitation of different phytoplankton size classes (Nival & Nival 1976, Tranter & Abraham 1971), lending support to the above. Furthermore, Walker and Peterson (1991) demonstrated that small copepods, including juvenile *C. carinatus* individuals, are less dependent on the availability of large-sized food particles than larger or older individuals; small copepods showed little or no difference in growth rate in diatom-dominated (large-cell) and flagellate-dominated (small-cell) water.

But, small and juvenile copepods both have high daily food requirements relative to their body weight.

Although large copepods generally have high individual ingestion rates, small copepods (Bautista & Harris 1992) and young stages such as copepod nauplii (Turner & Tester 1992, Morales *et al.* 1993) have higher 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 high biomass (White & Roman 1992). Thus, in the present model, starvation commences simultaneously in all stage classes when chlorophyll concentrations fall below the grazing threshold. However, the way in which different categories respond to the length of the starvation period differs dramatically.

Can a single depth-independent and satellite-derived estimate of chlorophyll *a* concentration adequately describe a copepod's food environment?

A central premise of the model is that the production of our representative animal, *C. carinatus*, is controlled largely by variability in its food supply. Predicting *in situ* patterns of secondary productivity for copepods distributed within a certain area of ocean therefore requires reasonably accurate estimates of the amount of food available to copepods at that point.

The ability of marine zooplankton to either migrate to (Bainbridge 1953, Bird & 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 & 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 optimal aggregations of food as they occur in the vertical dimension (Verheye & 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 are generally highest (Verheye & Field 1992) (Fig. 2.1).

Although satellite imagery only measures chlorophyll 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 chlorophyll *a* (C_o) are almost identical to measures of the mean concentration throughout the euphotic zone (C_e) (Shannon *et al.* 1984b, Brown & Henry 1985). Furthermore, because phytoplankton blooms initially develop near the surface following an upwelling event, satellite-derived colour images are generally able to correctly estimate maximum chlorophyll levels (Fig. 2.1). The tendency of the chlorophyll *a* maximum to be situated at or near the sea surface is also observed during winter, when occasional stabilization of the water column permits vertical differences in chlorophyll concentration to develop (Brown & Henry 1985).

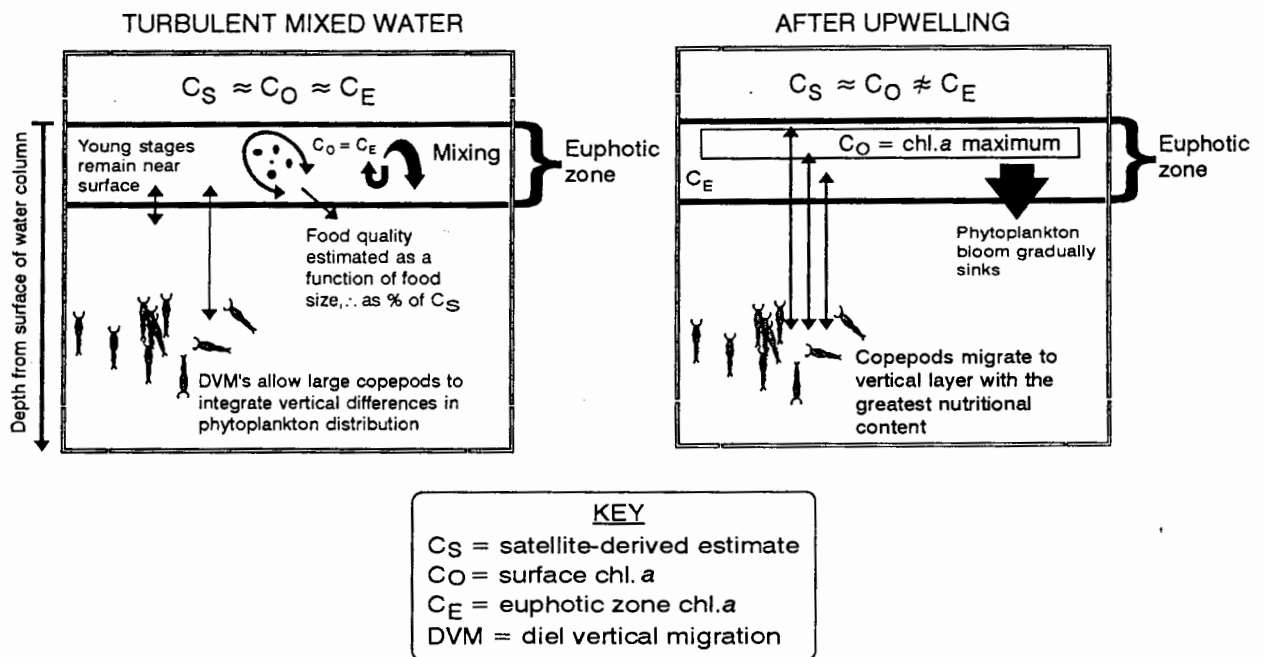


Fig. 2.1. A conceptual diagram illustrating the hypothesis that a single satellite-derived and depth-independent estimate of chlorophyll *a* concentration (C_s) provides an adequate description of food availability to copepods distributed in a hypothetical water column along the West Coast.

Subsurface chlorophyll maxima: The above arguments highlight the limitations of extending the model to areas such as the Agulhas Bank, which is strongly stratified in summer, and so has a well developed chlorophyll maximum situated at the thermocline (Carter *et al.* 1987). Subsurface chlorophyll maxima are not detected by

satellites (Shannon *et al.* 1984b). They may also occasionally develop in West Coast waters, and in these instances the model will underestimate production.

Do density-dependent effects limit individual intake when chlorophyll levels exceed F_{crit} ? Mesozooplankton are generally unable to control population sizes of the net-phytoplankton because of their lagged numerical response to phytoplankton blooms (Kiørboe 1993). Moreover, Verheye *et al.* (1992) estimated that copepods in the Southern Benguela are able to graze no more than 25 per cent of the phytoplankton biomass. The fact that net-phytoplankton blooms are largely unutilized by mesozooplankton grazers (Kiørboe 1993) therefore suggests that maximum measures of net-chlorophyll adequately describe food availability to individual copepods, irrespective of copepod numerical density. Depth-integrated measures of chlorophyll are therefore considered unnecessary because in the model copepods become food-limited when chlorophyll *a* concentrations fall below the grazing threshold F_{crit} (when density-dependent effects are likely to be at their strongest). Furthermore, when chlorophyll levels exceed F_{crit} , the cumulative amount of food in the euphotic zone divided by the number of copepods is assumed to be greater than the *per capita* requirement.

FECUNDITY ESTIMATES

Copepod fecundity is determined by both the quality and quantity of available food (Checkley 1980a,b, Runge 1984,1985, Peterson & Bellantoni 1987, Peterson 1988, Peterson *et al.* 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 (Durbin *et al.* 1983, Frost 1985, Runge 1985, Beckman & Peterson 1986, Kiørboe & Johansen 1986, Walker & Peterson 1991). Phytoplankton size and biomass are both included as predictors of copepod productivity in the model. Egg production rates of copepods do not respond instantaneously to changes in environmental conditions, but are instead an integrated response to recent feeding history (Stearns *et al.* 1989). When chlorophyll 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 ($B_{>10}$) $>10\mu\text{m}$ phytoplankton size fraction, according to the equation of Armstrong *et al.* (1991b):

$$\ln F = 0.430 \times \ln[B_{>10}] + 0.447 \times \ln[B_{>10(-1)}] - 1.278 \quad (2.2)$$

A one-day time lag between ingestion and egg laying is used (Armstrong *et al.* 1991b). Egg production in large calanoid copepods is typically initiated at chlorophyll *a* concentrations of 2-3 mg.m⁻³ and rates plateau at 5-10 mg.m⁻³ (Peterson & Bellantoni 1987, Verheye 1989, Armstrong *et al.* 1991b). In the model, egg production is initiated at a chlorophyll *a* concentration of 1 mg.m⁻³ and set at 1 egg.female⁻¹.day⁻¹ for concentrations in the range 1-2 mg.chla.m⁻³, and 5 eggs.female⁻¹.day⁻¹ for concentrations in the range 2-3 mg.chla.m⁻³ (averages calculated from Hutchings (1992)). Above a concentration of 10 mg.chla.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 Fig. 2.2. The values of *F* are the maximum daily rates when food is not limiting; otherwise, they are modified as a function of feeding history.

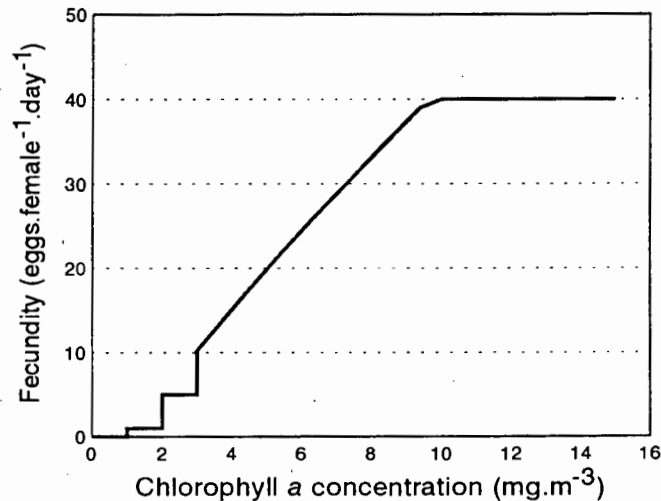


Fig. 2.2. The basic fecundity-chlorophyll *a* concentration relationship used in the model. For chlorophyll *a* concentrations > 3 mg.m⁻³, values of *F* shown assume that females have not starved recently. Also, values in the model are based on both the previous and present day's chlorophyll *a* concentration (equation 2.2).

The effect of feeding history on fecundity: In a pulsed, patchy food environment, copepod fecundity is influenced by not only the amount of food available at any one time, but also by the frequency of 'food events' (Kjørboe 1991). Feeding history is probably the dominant factor controlling the production of calanoid eggs in the Southern Benguela (Attwood & Peterson 1989). Starvation is known to terminate egg production in copepods (Checkley 1980b, Borchers & Hutchings 1986, Attwood & Peterson 1989), while the cumulative number of eggs produced during five days of feeding is reduced as a function of the length of the preceding starvation period (Attwood & Peterson 1989). A recovery period of approximately five days elapses before egg production is restored to the average in both *C. carinatus* and *C. australis*

(Borchers & Hutchings 1986, Attwood & Peterson 1989). The effect of feeding history on fecundity is modelled using a modified form of the power curve derived by Attwood & Peterson (1989) for *C. australis* - the intercept is adjusted to reflect the higher average fecundity of *C. carinatus*. Thus,

$$F_S = F_N e^{-0.176s} \quad (2.3)$$

where F_S is the total number of eggs produced during five 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.

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

$$F_d = (d-1)/6 \times (F_S - (F_N/5)) \quad (2.4)$$

where F_d is the number of eggs produced by *C. carinatus* per day, for days (d) one to four 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). Attwood and Peterson (1989) found an exponential pattern of increase for *C. australis* but a linear functional response is preferred for mathematical simplicity.

Total daily egg production rates: Egg abundance is computed as the product of the fecundity and the density of ripe females (F_r - defined here as egg-laying individuals). The interval between moulting to the adult female stage and laying eggs is assumed to be three days (Borchers & Hutchings 1986).

DEVELOPMENT TIME

Are development times food-limited? In a recent review, Huntley and Lopez (1992) demonstrated that temperature alone explains more than 90 per cent 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 nonlinear function of temperature (McLaren 1978, Corkett & McLaren 1970, McLaren & Corkett 1981, Peterson & Painting 1990), the extent to which development times in the field are affected by food

availability is more of a contentious subject. Evidence abounds that development rates in the laboratory are influenced by food availability (eg. Vidal 1980b, Huntley & Boyd 1984, Huntley *et al.* 1987, Borchers & Hutchings 1986, 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 & Nival 1992a). 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 chlorophyll *a* concentration and particle size. Food limitation of growth rates is therefore assumed to occur at chlorophyll concentrations below the grazing threshold F_{crit} .

Calculating total development time D_t : *C. carinatus* eggs take one day to hatch (Borchers & Hutchings 1986) and subsequent development times are modified depending on whether the animals feed continuously or intermittently. Intermittent feeding is defined as occurring when chlorophyll concentrations fall below F_{crit} for three 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 & Painting 1990). This gives:

$$D_t = 1469.2 \times (T - 1.5)^{-1.665} \quad (2.5)$$

where D_t is the total development time (in days) at ambient temperature T (°C). For animals feeding intermittently, development times are doubled. The relationship between D_t and temperature when food is not limiting is illustrated graphically in Fig. 2.3.

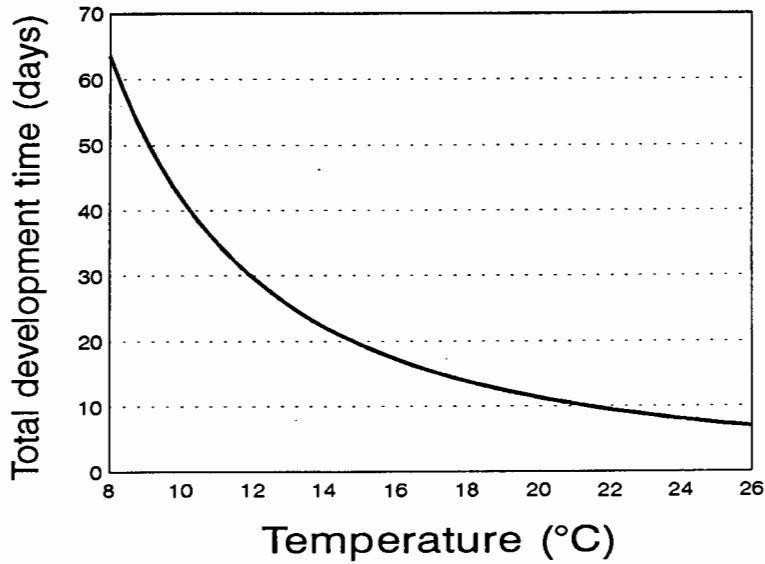


Fig. 2.3. The relationship between total development time D_t and temperature used in the model. D_t is doubled for animals feeding intermittently.

Calculating growth transfers between model groups: *C. carinatus* conforms to the 'rule' of equiproportional development (Peterson & 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.* 1984, 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 & 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 proportion of individuals in model group i which moult into the next age group $i+1$ during time t , is given by:

$$dev_{i,t} = s / (p_i \times D_t) \quad (2.7)$$

where s is the time step in days. Given that daily changes in recruitment into the various age classes are modelled, s is simply set as one. Similarly, the loss of individuals from an age group due to growth processes is $(1-dev_{i,t})$ times the number of individuals at time t in that group.

MORTALITY ESTIMATES

The mathematical form of the mortality function and the values given to the parameters in plankton models have very marked effects on the overall response (Steele & Henderson 1992). 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.

M_{egg}

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 & Peterson 1986, Kjørboe *et al.* 1988) and a high density-dependent egg mortality rate (M_{egg}) of 0.90 day^{-1} is assumed in the model. The egg mortality rate is assumed to include implicitly all losses in the rate of recruitment to the naupliar stage, such as those attributable to the production of nonviable eggs (*see* Ianora & Poulet 1993).

M_{pred}

Predators are not modelled explicitly, rather their effects are simulated by the mortality coefficient M_{pred} . An initial approximation of M_{pred} was obtained 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 in the 1987 anchor station study (Verheye 1991). If P_t represents total copepodite population size (number.m^{-3}), we

can calculate an average daily rate of egg production as the product of the number of ripe females ($0.0384 \times P_t$) and the average fecundity of *C. carinatus*, measured as $F_{ave} = 28 \text{ eggs.female}^{-1}.\text{day}^{-1}$ (from Armstrong *et al.* 1991b). Assuming the model egg mortality rate ($M_{egg} = 0.90$), this gives an average daily rate of reproduction of $0.0384 (1-M_{egg}) P_t F_{ave} = 0.1075 P_t \text{ eggs.m}^{-3}.\text{day}^{-1}$. To satisfy the requirement for equal rates of mortality and reproduction, we therefore require a mortality rate of 0.1075. For mathematical simplicity, a base-case value of 0.10 was chosen for M_{pred} . Sensitivity analyses to test the effect of variation in this mortality coefficient on the model's output are presented in the next section.

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 select large copepods at high concentrations, and medium and large copepods at low concentrations (Schmitt 1986, James & Findlay 1989). The proportion of large individuals (CIV, CV and adults) which succumb daily to predators over the period May to August, when anchovy are particularly abundant along the West Coast, may be very much greater than this. This facet is dealt with further in chapter five.

Invertebrate predators: The impact of invertebrate predators on copepod populations in the Southern Benguela is equally variable but in general their combined impact is probably less than that of vertebrate predators. Gibbons *et al.* (1992) estimate that groups of carnivorous zooplankton such as ctenophores, cnidarians, chaetognaths and hyperiid amphipods, together remove at least 5.7 per cent of copepods per day. Swarms of gelatinous zooplankton or amphipods may result in total depletion of zooplankton patches (Gibbons *et al.* 1992), but because they occur rarely, they are excluded from the analysis below. Omnivorous zooplankton such as euphausiids also form swarms and can remove up to 60 per cent of the copepod biomass per day, whereas at non-swarving densities they are thought to remove between 2 and 7 per cent of copepods per day (Stuart & Pillar 1990, Pillar & Stuart 1988, Pillar *et al.* 1992). A crude estimate of the minimum and maximum impact of invertebrate predators on copepod populations is therefore 7.7 - 65.7 per cent per day. On average, *C. carinatus* comprises 23% of the total copepod biomass (Verheye 1989), and thus assuming the different copepod species are impacted equally, this suggests that between 1.8 and 15.1 per cent of *C. carinatus* biomass is removed daily by invertebrate predators: a range which encompasses the value of M_{pred} assumed in the model.

M_{food}

The mortality coefficient M_{food} , which depicts mortality due to starvation, is modelled as an age-dependent process. Most copepod mortality occurs during the naupliar stages when animals are most vulnerable to starvation (Mullin & Brooks 1970, Paffenhofers 1976, Borchers & Hutchings 1986). The adults and copepodite stage CV of *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 & Hutchings 1986). In addition, adults may benefit from carnivory (Borchers & Hutchings 1986). Most starvation mortality is therefore modelled as due to the naupliar stages NI-NVI and the early copepodite stages CI-CIV. *C. carinatus* individuals start feeding immediately after hatching (Borchers & 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 & Hutchings 1986). This suggests that lipid reserves accumulate in a linear fashion in *C. carinatus* and hence the starvation tolerance of the copepodite stages is modelled as twice that of the naupliar stages.

The starvation tolerance of juvenile *C. carinatus* depends on the length of the previous feeding period (Borchers & Hutchings 1986) and the various feeding cycles which the juveniles can tolerate are calculated from the matrix presented in Borchers & 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 two days with no food. Because body reserves are used up more rapidly at high temperatures, starvation tolerance is inversely related to temperature (Borchers & Hutchings 1986). The mortality coefficient M_{food} is calculated as:

$$M_{\text{di}} = T_{\text{ave}}/18 \times M_{ij}/100 \quad (2.8)$$

where T_{ave} is the average temperature (°C) over the starvation period. An example of starvation mortalities calculated for naupliar and copepodite CI-CIV stages experiencing different ambient temperature conditions and with different feeding histories is shown in Fig. 2.4. Individuals which survive a starvation period are assumed to have found sufficiently high local concentrations of food over this period;

and therefore their feeding histories are reset before moving into the next starvation period.

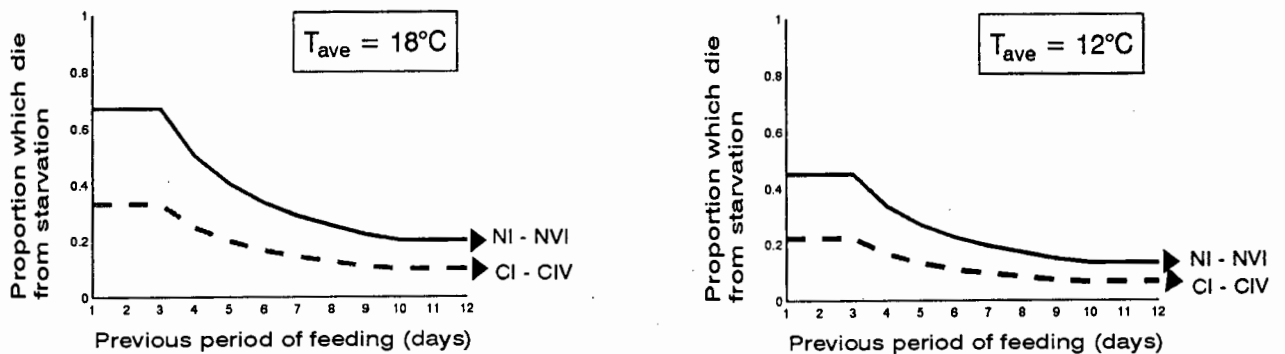
The adult starvation tolerance level M_{50}

The starvation tolerance of adults, while inversely related to temperature, is not related to feeding history as is the case for juveniles (Borchers & Hutchings 1986). A 50% starvation tolerance level (M_{50}) is calculated for adults and CV stage copepodites from Borchers and Hutchings (1986: Fig.4) as:

$$M_{50} = 18/T_{ave} \times 12 \quad (2.9)$$

and represents the number of days of starvation required to induce 50% adult mortality.

After 4 days starvation



After 8 days starvation

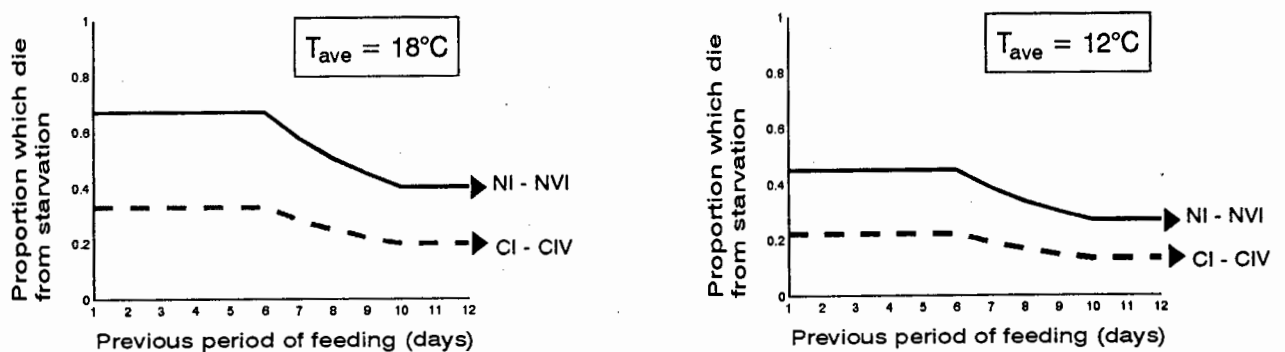


Fig. 2.4. Four examples of the proportion of individuals in the model groups NI-NVI and CI-CIV, which starve to death under various temperature and feeding cycles (adapted from Borchers & Hutchings 1986).

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:

$$\begin{aligned}
 \text{NAUP}_{t+1} &= \text{REC}_{t+1} + [(1-\text{dev}_{1,t}) - M_{\text{pred}} - M_{\text{food}}] * \text{NAUP}_t \\
 &\quad \text{where } \text{REC}_{t+1} = (1-M_{\text{egg}}) \cdot F_t \cdot F_{r_t} \\
 \text{COP1}_{t+1} &= \text{dev}_{1,t} \text{NAUP}_t + [(1-\text{dev}_{2,t}) - M_{\text{pred}} - M_{\text{food}}] * \text{COP1}_t \\
 \text{COP2}_{t+1} &= \text{dev}_{2,t} \text{COP1}_t + [(1-\text{dev}_{3,t}) - M_{\text{pred}} - \text{MOR}_{\text{food}}] * \text{COP2}_t \\
 \text{AD}_{t+1} &= \text{dev}_{3,t} \text{COP2}_t + [1 - M_{\text{pred}} - \text{MOR}_{\text{food}}] * \text{AD}_t \quad \dots\dots\dots (2.10)
 \end{aligned}$$

where $M_{\text{food}} = 0$ for values of the starvation index (SI) < 1 and $\text{MOR}_{\text{food}} = 0.50$ when $\text{SI} > M_{50}$.

The number of males and females are simply calculated using the population sex ratio, while the number of ripe females F_r at time t is the number of females which attained adulthood more than three days previously. A schematic illustration of the model's structure and the major processes driving the population's dynamics is shown in Fig. 2.5.

MODEL INITIALIZATION

Initial Abundance Estimate N_1

An initial estimate of the average number of adults and copepodites per m^{-3} is obtained from *in situ* shipboard measurements. The model is initialized by scaling this value upwards to account for the number of naupliar stage individuals, assuming a stable age structure. This yields an initial estimate of average standing stock (N_1).

Population Sex Ratio

The ratio of the number of females to males (F:M sex ratio) in the model system is based either on 'snapshot' field estimates of this parameter, or on average values obtained for an entire season or region. Pending further insight into the way in which this parameter varies with time, sex ratios are held constant throughout a season in the model.

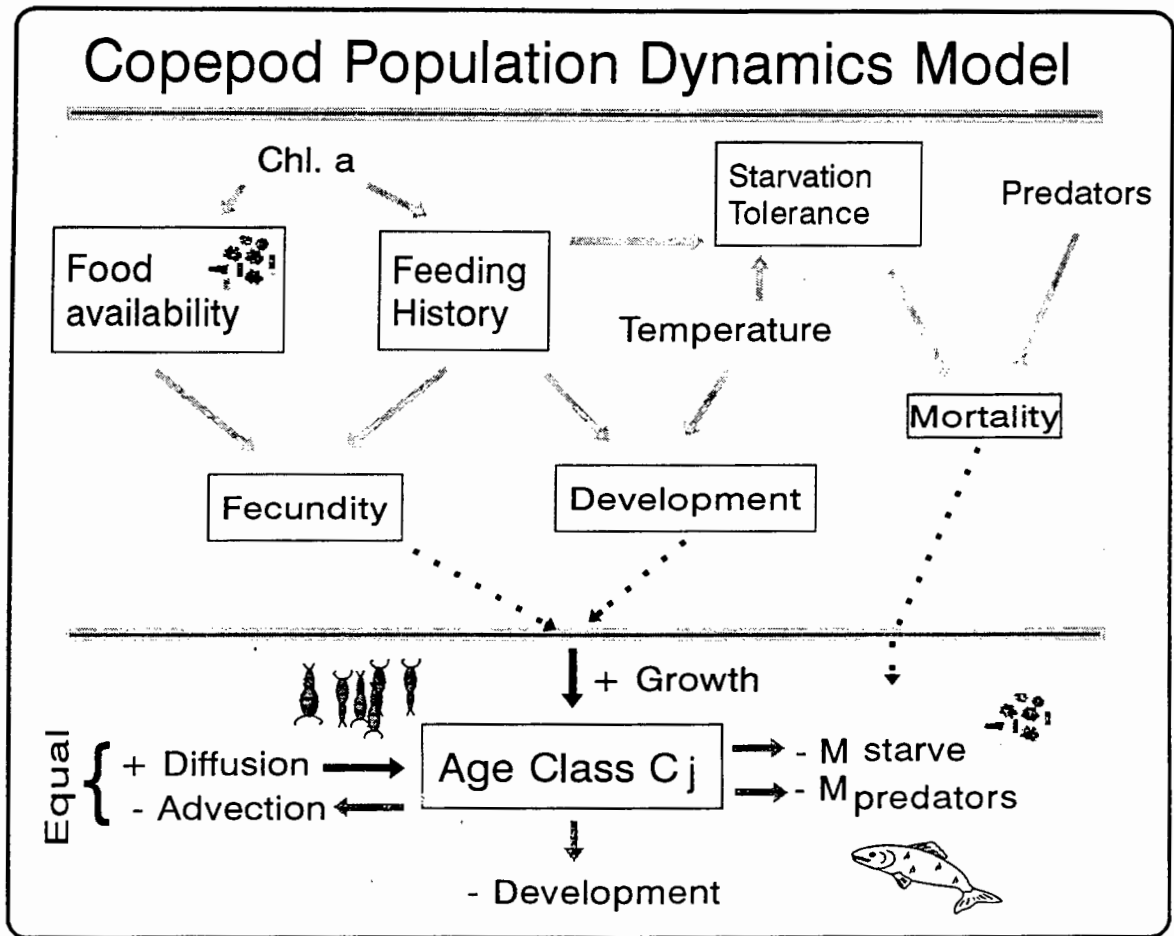


Fig. 2.5. Summary of the way in which the major physical and biological factors affect the calculation of biological functions in the model, and the way in which these in turn determine the changes in standing stock in each of the model 'age classes' C_j .

Population Age Structure

To initiate the model, the population age structure may be based on either direct estimates of the stage-specific abundances ($\text{number} \cdot \text{m}^{-3}$), or a mean population composition. In the latter case, mean population values used are those observed by Verheye (1991) during a 27-day anchor station time-series study in March to April 1987 in the Southern Benguela upwelling region. Combining the individual stage-specific abundances of the early copepodite stages into a single estimate yields a mean population composition of 63% CI-CIV, 19% CV and 18% adults. The naupliar stages are not retained by the $200\mu\text{m}$ 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 & 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 30.5% NI-NVI, 44% CI-CIV, 13% CV and 12.5% 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 3.84%. A summary of the mean population age structure used in the model is presented in Fig. 2.6.

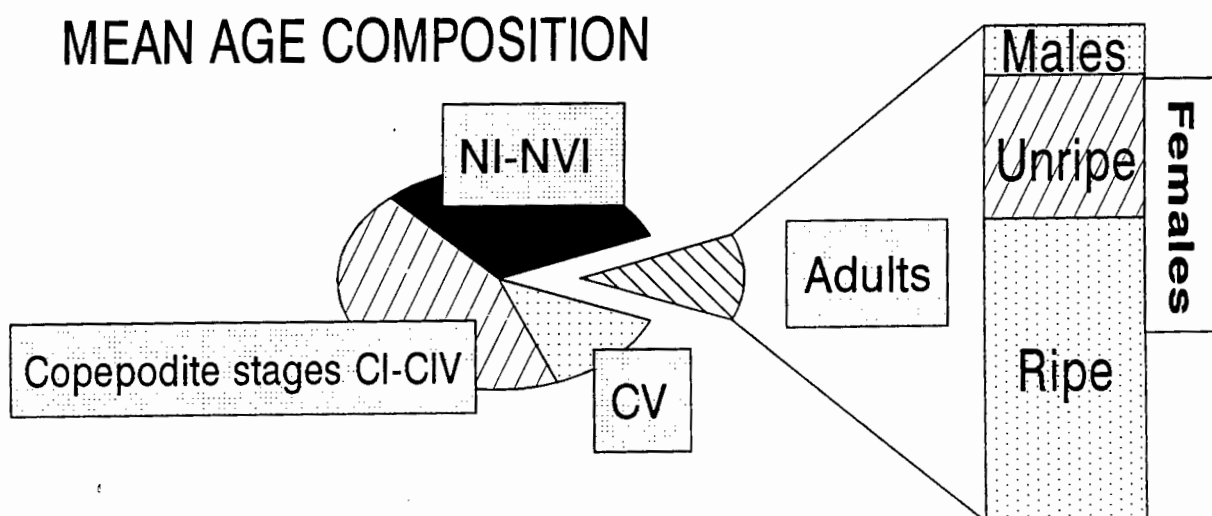


Fig. 2.6. Diagram illustrating the mean population age composition assumed in the model. Population composition estimates are based on data in Verheye (1991), but are adjusted to account for the naupliar stage individuals which are not retained by the sampling nets used in his study.

BIOMASS ESTIMATES T_{biom}

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 (μgC). The mean body weight of copepodite stage CI-CIV individuals, copepodite stage CV individuals and male and female adults were calculated from published (Verheye 1991) weight and carbon content measurements (see Table 2.1).

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 study. Note that the value of T_{biom} does not include the biomass of the naupliar stages. A summary of notation used to describe model variables is presented in Table 2.2a.

Table 2.1. Mean body weights (μgC) of *C. carinatus* life cycle stages (from Verheye 1991).

CI-CIV	8.97*
CV	31.57
Adult Male	35.72
Adult Female	56.81

* determined as the arithmetic mean of the summed products of the percentage abundance of each life cycle stage and the individual body weight (μgC) of that stage.

MODEL EXECUTION

A listing of the computer program used to simulate the model system, as well as instructions for its use, is presented in Appendix I to the thesis. The model is written in Turbo Pascal 6 for use on IBM compatible computers (PCs). The program is divided into a number of separate procedures and the structure is such that the value of parameters or model assumptions can easily be altered to test the effect on model output. Daily chlorophyll *a* concentration and SST values are read into the model from external files. Briefly, the user is required to initialize standing stocks in the various model compartments and the results of model executions are written to external files in a comma-delimited form, to enable them to be imported into spreadsheet programs such as LOTUS 1-2-3.

When repeating model runs, as becomes necessary when introducing random components to the model, a second program is run in sequence to calculate the mean and standard deviations of, for example, T_{biom} values from n runs and for each of t days.

STANDARD UPWELLING SERIES

To determine the magnitude and time scale of a copepod population's response to a phytoplankton bloom, characteristic chlorophyll *a* and SST changes over a 12-day upwelling cycle (Brown & Hutchings (1987)) are used as inputs into the model (Fig. 2.7). The data (P. Brown, pers. comm.) were obtained by superimposing the peaks in bloom development observed for 5 different bloom development cycles, which were

tracked during the course of 5 cruises conducted in the Southern Benguela region (Brown & Hutchings 1987).

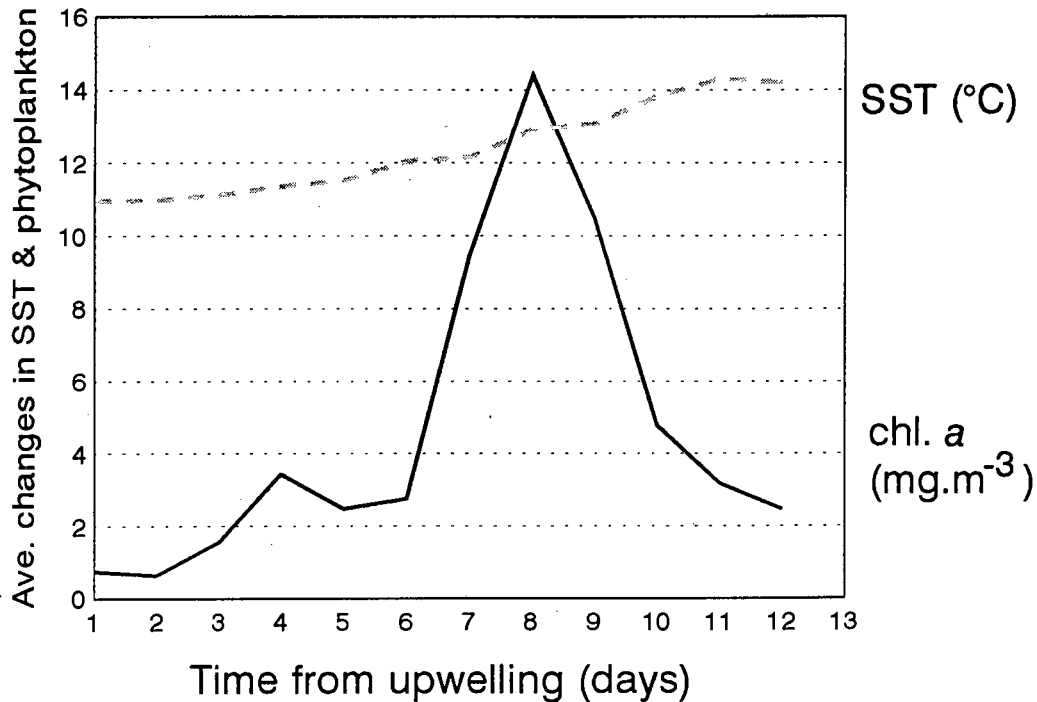


Fig. 2.7. Plots of the average observed changes in chlorophyll *a* concentration and sea surface temperature (SST) in newly upwelled water (after Brown & Hutchings 1987). Data represent the mean pattern of changes observed on five different drogue cruises subsequent to an upwelling event (Brown & Hutchings 1987).

To test the effect of alternating upwelling cycles and quiescent periods, chlorophyll *a* data was interpolated between the 12-day upwelling cycles by assuming that chlorophyll *a* concentrations decreased to 1.86 mg.m^{-3} on day 13 and then remained at 1 mg.m^{-3} throughout quiescent periods. Sea surface temperature data was interpolated by assuming that heat flux into the surface waters caused temperatures to increase by 0.5°C per day, up to a maximum of 18°C . Daily heat flux into the sea warm the upper 10m mixed layer in the Southern Benguela system by as much as 0.65°C per day (Guastella 1992).

A second, shorter upwelling series, based on data in Brown & Hutchings (1987), was also used in model executions (Fig. 2.8).

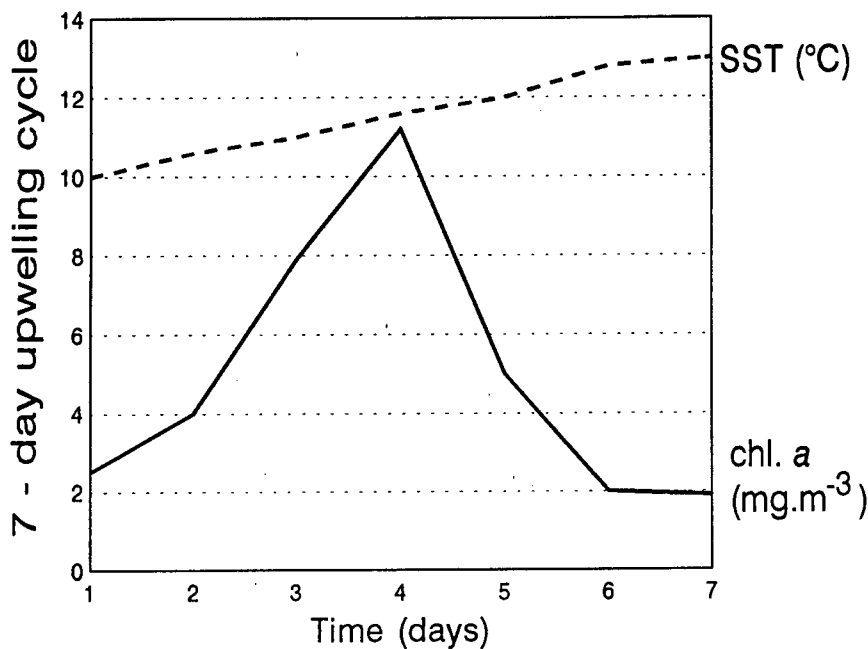


Fig. 2.8. Plots of changes in chlorophyll *a* concentration and sea surface temperature used to simulate a 7-day upwelling cycle.

MODEL ASSESSMENT

The performance of the model was assessed using chlorophyll *a* and SST data collected during the 27-day anchor station study (Mitchell-Innes & Walker 1991) as inputs (Fig. 2.9), 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: some of the biological functions (eg. the basic fecundity relationship (Fig. 2.2)) used in the model were based on data collected during the anchor station study.

To initiate the run, N_1 was set at 402 individuals, which is the abundance estimate observed on day 1 of the anchor station series plus the expected number of naupliar individuals which were not retained by the sampling net. The starting population age structure used in the simulation was the average composition observed over the full 27 day period, whereas the F:M sex ratio was that observed on day 1 of the series. 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 2.2b. Table 2.2c lists the model's major assumptions.

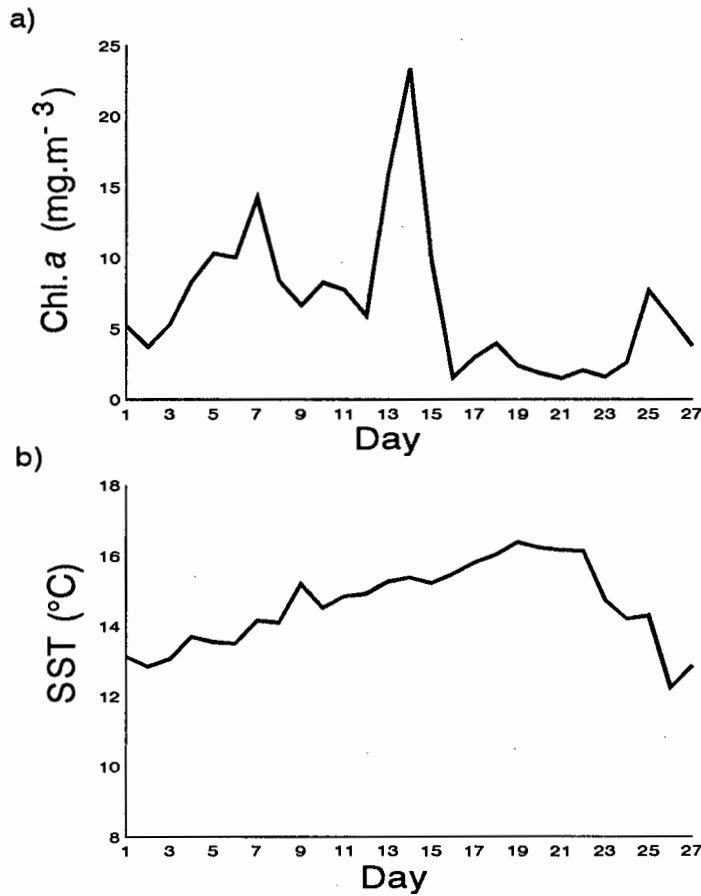


Fig. 2.9. Time series of a) mean euphotic zone chlorophyll *a* concentration and b) sea surface temperature observed during a 27-day fixed station study conducted in St Helena Bay in 1987 (Mitchell-Innes & Walker (1991)).

MODEL OUTPUT

Changes in Standing Stocks following an Upwelling Event

The succession of developmental stages following an upwelling event is presented in Fig. 2.10. There is a two 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 one day interval between ingestion and spawning, and eggs take a further one 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 the stage class's 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 (Fig. 2.11). The time scale of the population's response is determined in part by temperature, because it controls how fast individuals develop.

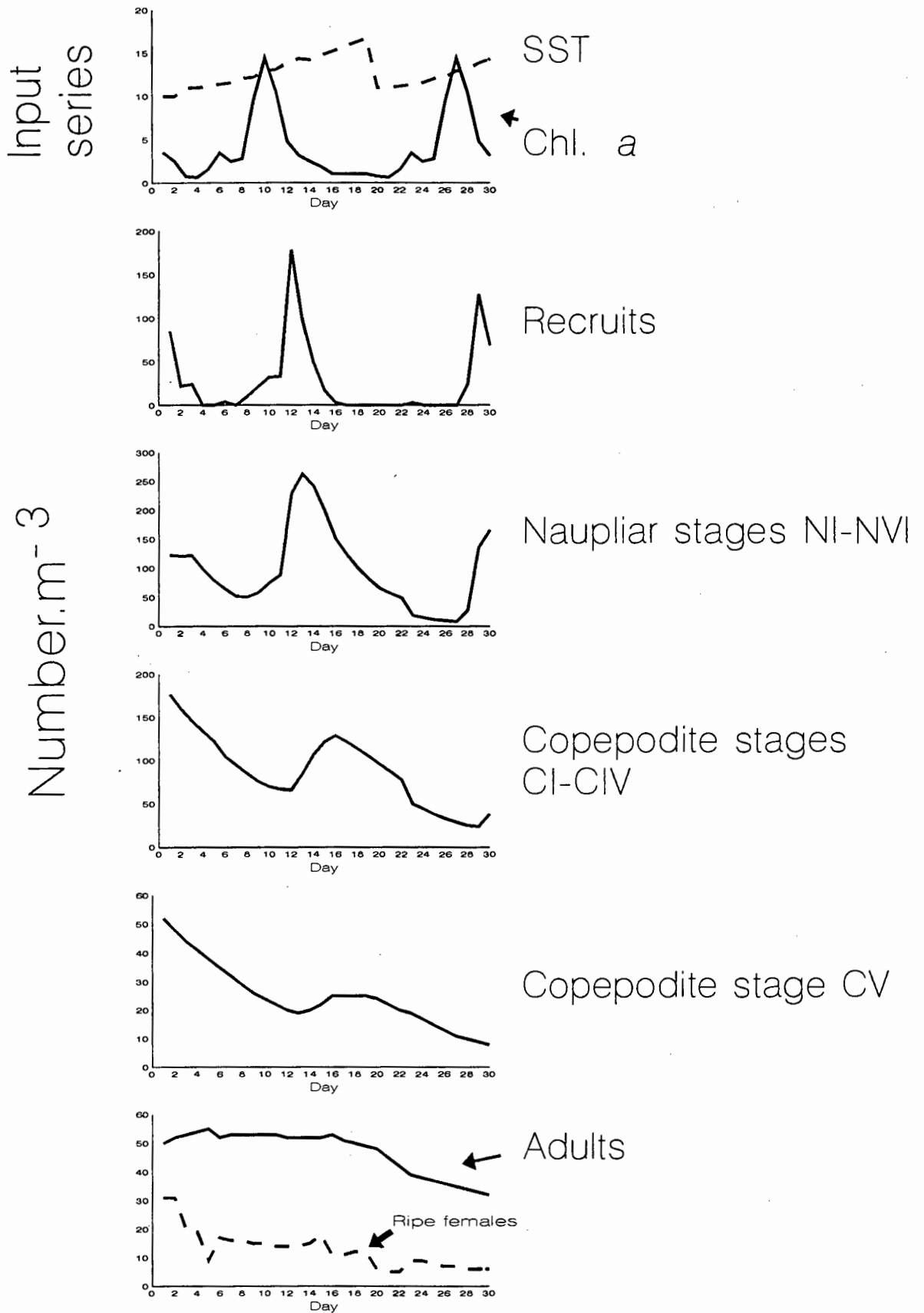


Fig. 2.10. Temporal changes in the abundances of the various developmental stages following a characteristic 12-day upwelling cycle. For comparative purposes, the number of individuals recruiting to the population (- newly hatched nauplii) is shown separately from the curve depicting the predicted changes in the standing stocks of the naupliar stages.

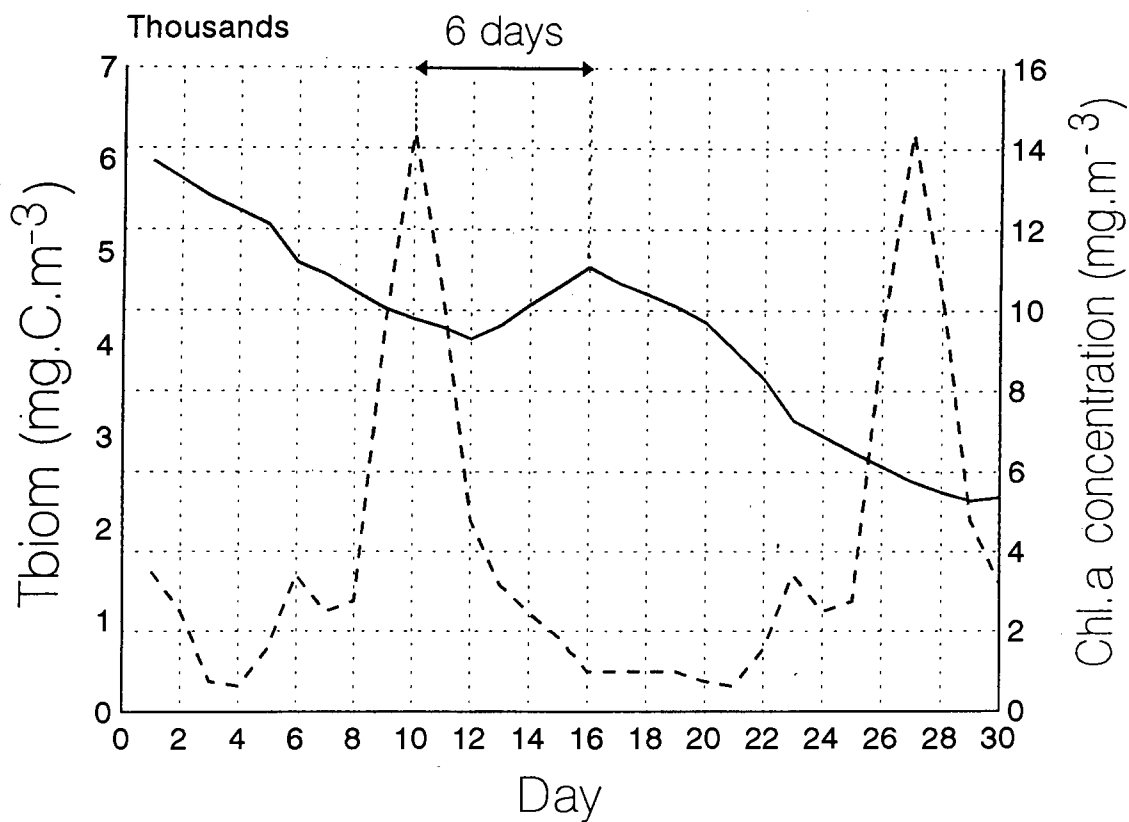


Fig. 2.11. The time course for a peak in the biomass of the copepodite and adult stages to manifest itself following a perturbation in the primary production level.

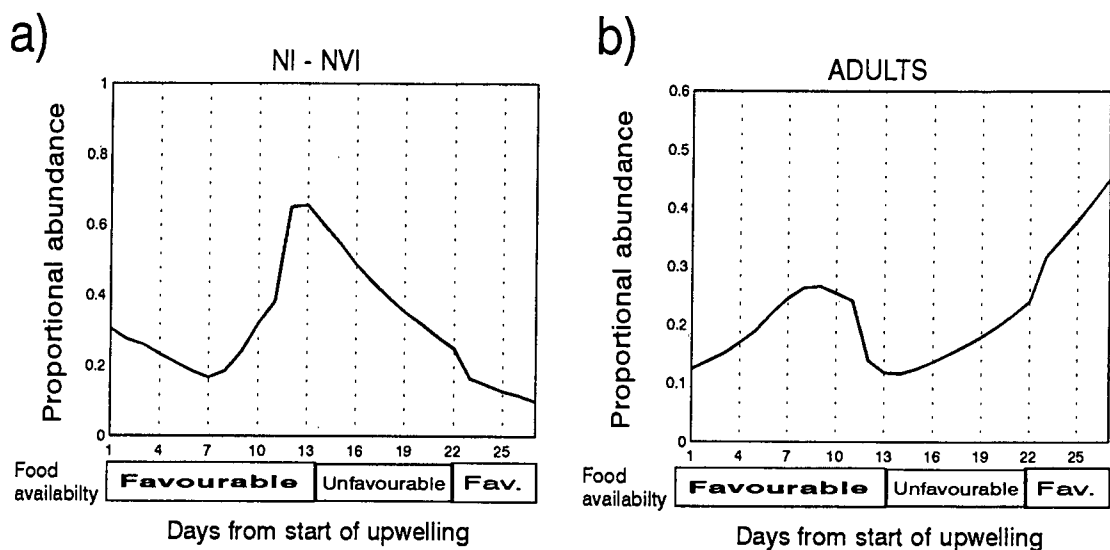


Fig. 2.12. A comparison between the relative abundance of the naupliar stages and the adults under favourable and unfavourable conditions.

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 (see Appendix 2.1).

In simulations run over longer time periods, if chlorophyll 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 significantly affect the T_{biom} trend.

Comparison of the proportional abundances of the naupliar stages and adults under favourable and unfavourable conditions (Fig. 2.12) highlights the disproportionately 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.

Assessing the Model's Fit to the Anchor Station Series

The model provided a reasonably good fit to both the observed number (Fig. 2.13a), and biomass (Fig. 2.13c), of copepodites and adults. 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 requires 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. This facet is investigated further in chapter six.

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 (Fig. 2.13b).

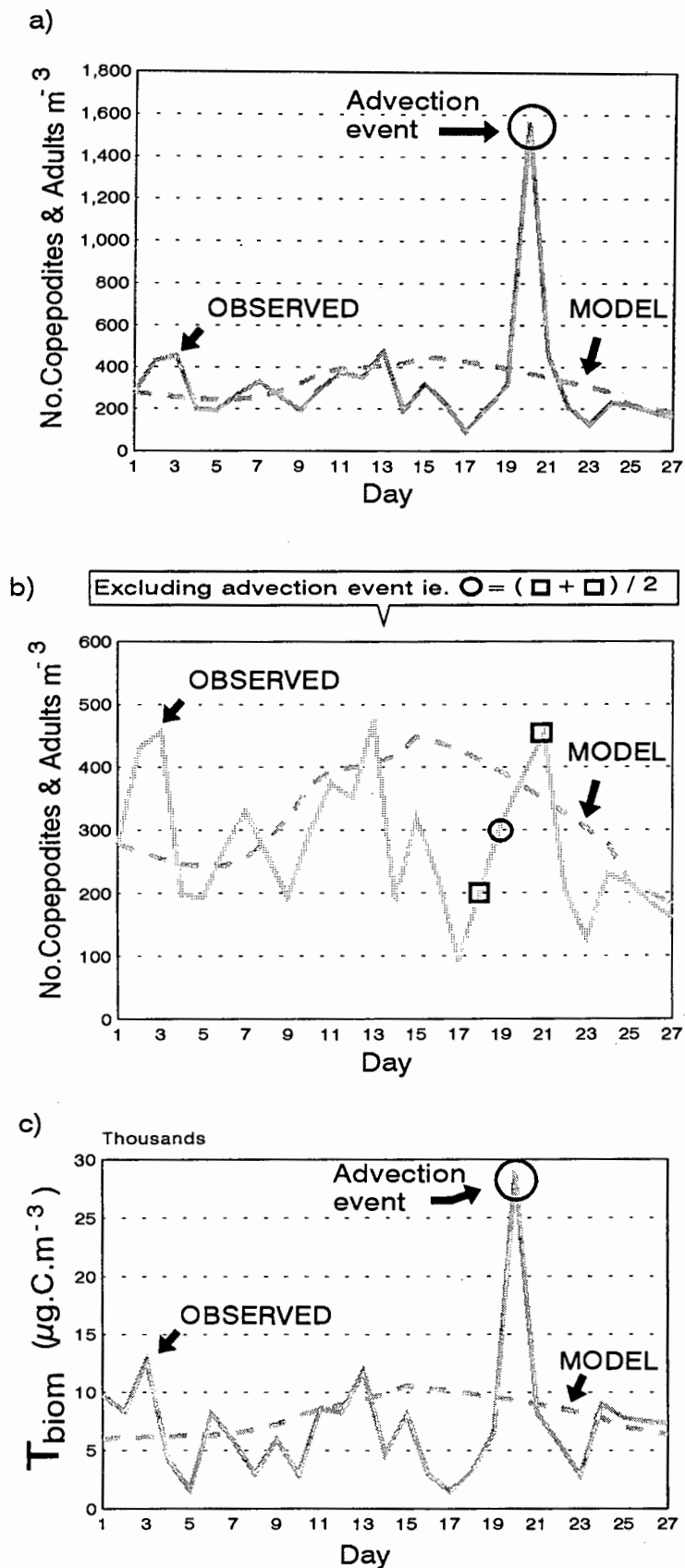


Fig. 2.13. Comparisons between model-predicted population trends and those observed during the 27-day anchor station study (Verheye 1991). The peak on day 20 in figures a and c is due to the advection of copepodite stage CIV and CV individuals into the area, and has been excluded from the observed trend in figure b. Observed and model starting values in figure b differ because although the total number of individuals present on day 1 is the same, the model uses a different (mean) starting age composition. The model-predicted T_{biom} trend in figure c is used as a base-case in simulations conducted in section 2, to test to what extent the model's predictions depend on its assumptions and the value of its parameters.

Egg production rates: The close coupling between levels of primary productivity and copepod fecundity is illustrated in Fig. 2.14. Observed values in Fig. 2.14b were estimated using the Egg Ratio Method (Armstrong *et al.* 1991b). Following Armstrong *et al.* (1991b), an anomalously high value observed on the sixth day has been omitted.

The additional constraints and assumptions applied in calculating egg production rates in the model result in only minor differences between the observed and model-predicted pattern of copepod fecundity. The close correlation between chlorophyll concentrations and simulated egg production rates (Fig. 2.14 a vs b) highlights a central premise underlying the model's construction, namely that *C. carinatus* females are well adapted to survive in an unpredictable environment because of their ability to respond rapidly to short-term increases in food availability (Armstrong *et al.* 1991b).

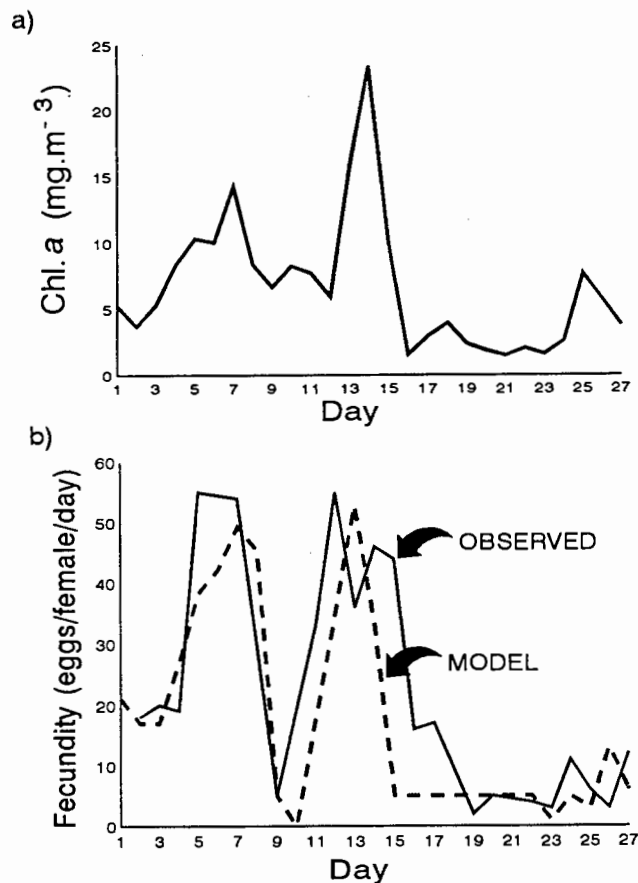


Fig. 2.14. Temporal changes in a) chlorophyll *a* concentrations and b) observed and model-predicted patterns of copepod fecundity.

Comparisons of the fit to the abundance of the various stage classes: The model's predictions are in no instance widely different from observed values and the model provides a reasonable description of the average changes in standing stocks of the various developmental stages observed during the anchor station study (Fig. 2.15). As in the previous simulations, there is a close coupling between the peaks in primary production and in naupliar stage abundance (Fig. 2.15a). No field data are available to compare the predicted patterns of naupliar growth with observed trends. The response of the adult and copepodite stage individuals to the increase in primary production is more lagged (Fig. 2.15 b,c&d). It takes 8 days for the pulse in primary production which peaks on day 7 to propagate through the various developmental stages and manifest itself as a peak in T_{biom} .

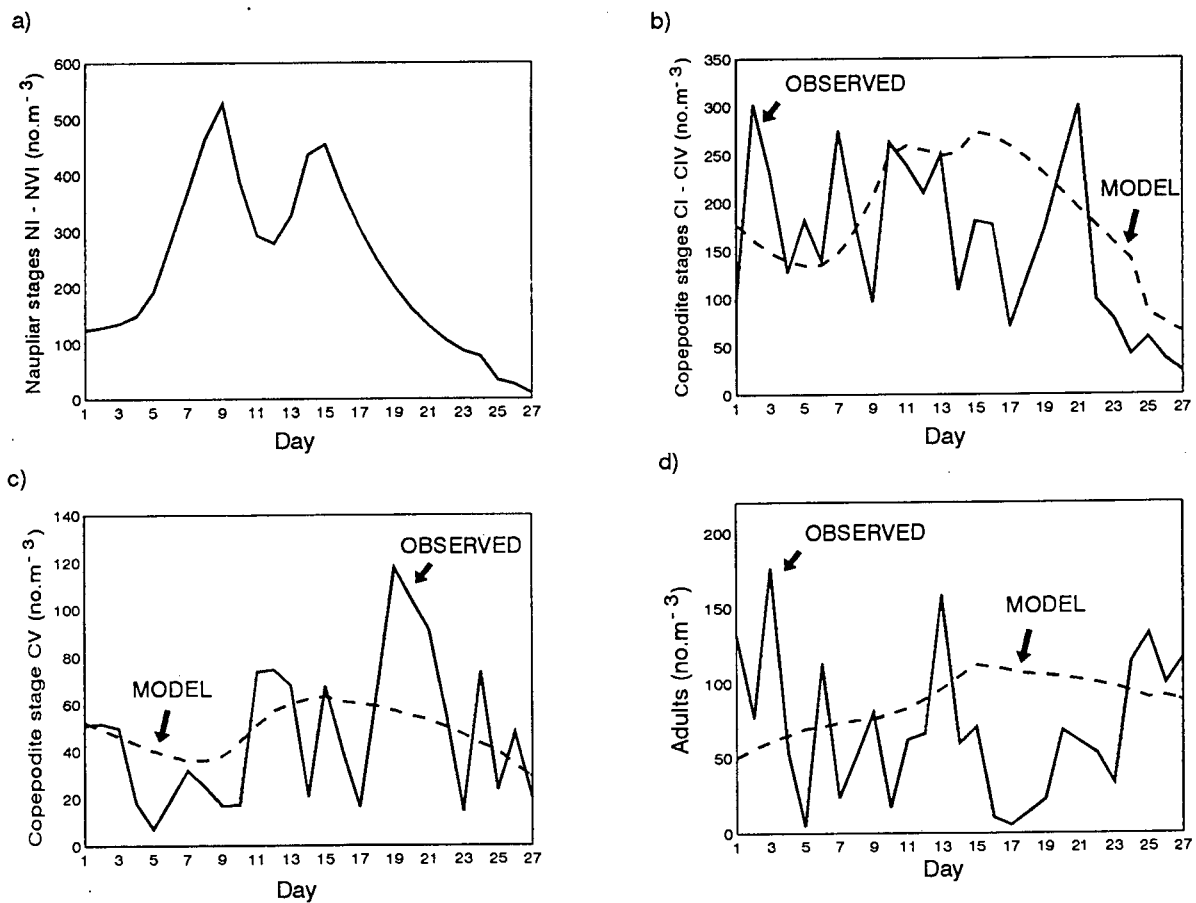


Fig. 2.15. Temporal changes in a) the model-predicted abundance of the naupliar stages; and in both the observed and model-predicted abundances of b) copepodites CI-CIV; c) copepodite stage CV; and d) adult *C. carinatus* individuals.

In Fig. 2.16, changes in standing stocks 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 & ADULTS) fluctuate less. This highlights the difficulty in trying to establish correlations between food availability for fishes (the older stage biomass) and *in situ* measures of phytoplankton abundance.

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

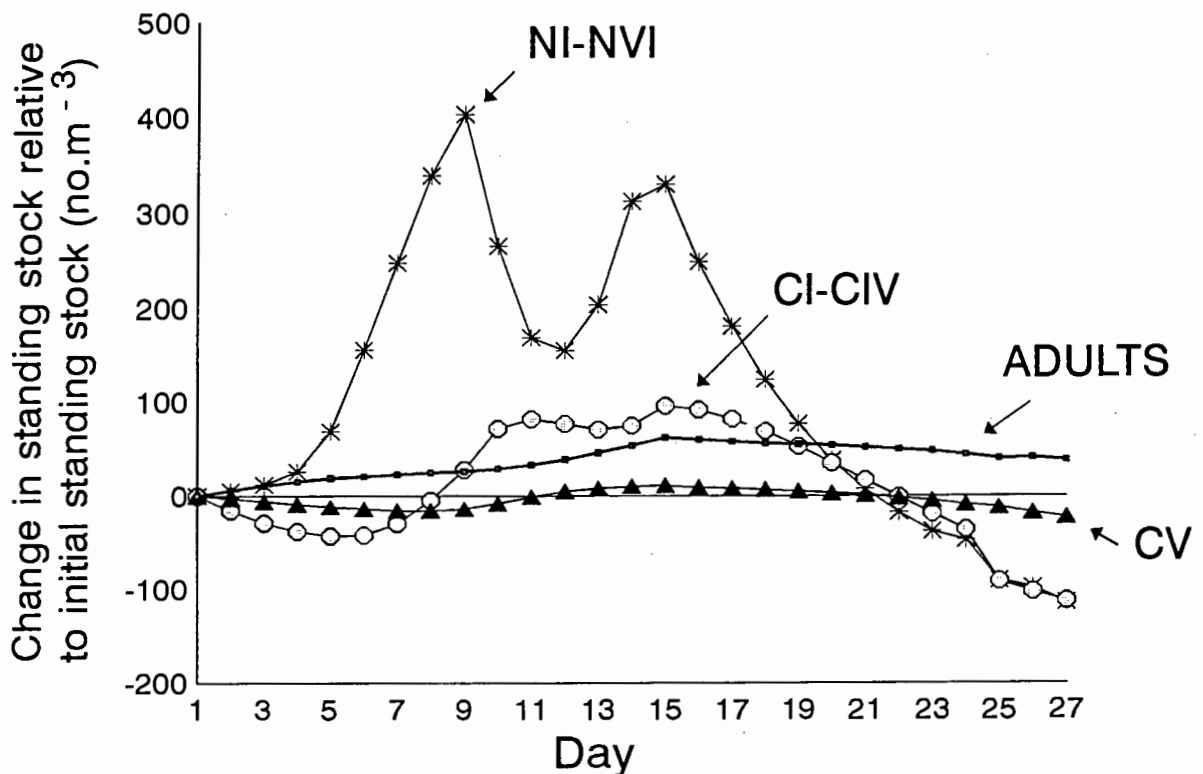


Fig. 2.16. Plots of model-predicted changes in the standing stocks of the various developmental stages relative to their initial values. Note the differences in both the magnitude and time scale of the response of the different developmental stages to an earlier change in primary production.

Comparison of model-predicted and observed age compositions: To provide further insight as to the 'goodness of fit' of the model, predicted age compositions just before the advection event and on the final day were compared with the field estimates. As no field data on naupliar abundances are available, only the relative abundances of copepodites and adults are shown (Fig. 2.17).

Despite different starting age compositions, the model adequately describes the large proportion of the younger stages which manifest themselves over the first half of the

series. The development of two phytoplankton blooms over this period results in a 'boom' of recruits and a consequent high proportional abundance of the younger stages (CI-CIV). The model underestimates the relative abundance of copepodite stage CV on day 19, suggesting either a) that *in situ* densities observed were partly due to external sources, or b) that CV individuals developed too rapidly in the model.

The reduced intensity of upwelling in the latter half of the series is reflected in the accumulation of adult numbers and the increase in their model-predicted relative abundance on day 27. The model is obviously unable to simulate the extremely high observed proportional abundance of adults which is in part a consequence of the earlier advection event having displaced younger stages offshore (Verheye 1991).

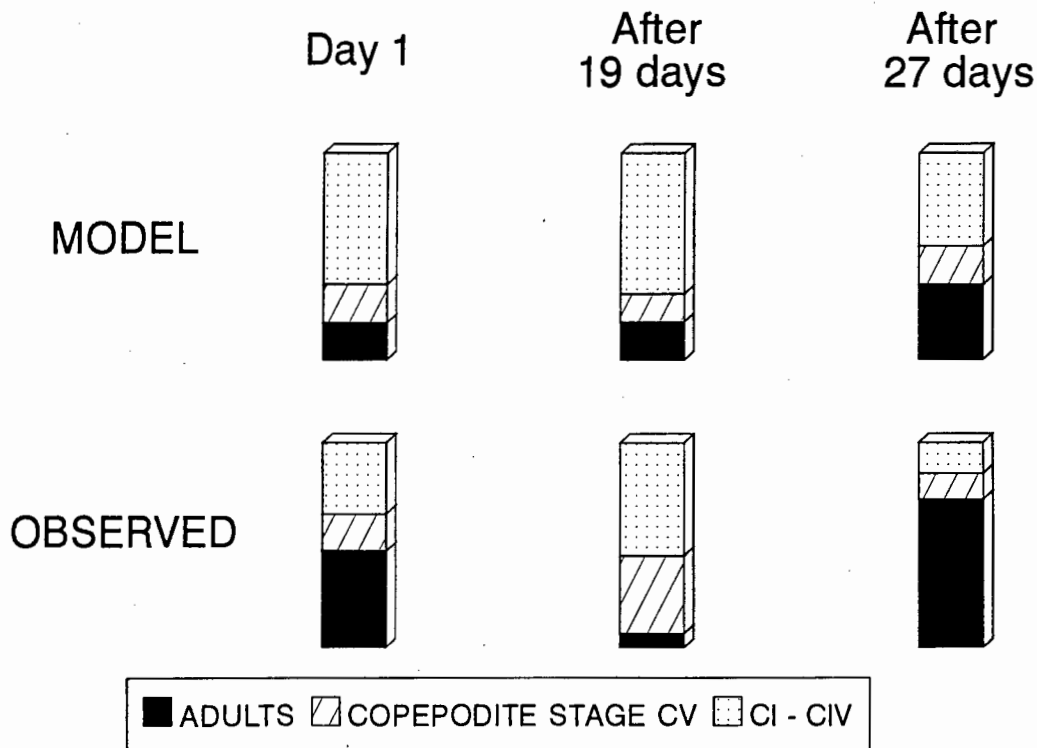


Fig. 2.17. A comparison between model-predicted and observed *C. carinatus* population age composition just prior to the advection event on day 20 and on the final day. Starting population compositions are different because the model was initialized assuming a mean population composition. Observed values are from Verheye (1991).

CONCLUSIONS

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. There is a close coupling between peaks in chlorophyll

concentration and the abundance of young life-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 about 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 and of different physical regimes 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-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. The model accurately captured the major features of the patterns of growth. Although a mathematically better fit, or an equally good fit based on a different set of parameters, could theoretically be obtained, the present model is preferred because it was built from first principles and is based on empirically-derived relationships. Models based on realistic assumptions about the underlying ecological processes are generally superior to those derived more subjectively (Berryman 1992a). 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. The model-predicted pattern of growth in the biomass of the copepodites and adults (T_{biom}), obtained using the anchor station input series is used as a base-case in comparing output from the sensitivity analysis in the next chapter.

An advantage of this model is that it is not fine-tuned to a particular local area and hence it can be generally applied to model the dynamics of calanoid copepods throughout most of the Southern Benguela. 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.

Table 2.2. 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	NAUP	no.m ⁻³
CI-CIV	COP1	no.m ⁻³
CV	COP2	no.m ⁻³
ADULTS	AD	no.m ⁻³
Ripe Females	Fr	no.m ⁻³
Unripe Females	Fu	no.m ⁻³
Biomass of copepodite stages CI-CVI	T _{biom}	µg.C.m ⁻³
Sea surface temperature	SST (T)	°C
Ave. temperature over starvation period	T _{ave}	°C
Chlorophyll <i>a</i> concentration	CHL	mg.m ⁻³
Net-chlorophyll (>10µm)	B _{>10}	mg.m ⁻³
.... lagged net-chlorophyll concentration	B _{>10(-1)}	mg.m ⁻³
Recent feeding history (days fed)	FH	days
Starvation index (days starved)	SI	days

b) PARAMETER / MODEL FUNCTION	NOTATION	UNITS	BASE-CASE VALUE
INITIAL VALUES			
Initial Abundance Estimate	N_1	no.m^{-3}	402
Population Sex Ratio	F:M ratio		9:1
Population Age Composition	Prop. NI_NVI		0.305
	CI-CIV		0.440
	CV		0.130
	ADULTS		0.125
MODEL PARAMETERS / FUNCTIONS			
Grazing Threshold	F_{crit}	mg.chla.m^{-3}	3
Net-chlorophyll fraction	$B_{>10}$	$\text{mg.(chla > 10}\mu\text{m).m}^{-3}$	$f(\text{CHL})$
Egg Mortality Rate	M_{egg}	day^{-1}	0.9
Predator-induced Mortality Rate	M_{pred}	day^{-1}	0.1
Starvation Mortality(NI-NVI,CI-CIV)	M_{food}	day^{-1}	$f(\text{age}, T, \text{FH}, \text{SI})$
Adult & CV Starvation Tolerance	M_{50}	days	$f(T)$
Fecundity	F_t	$\text{eggs.female}^{-1}.\text{day}^{-1}$	$f(B > 10(1,-1), \text{SI})$
Total Development Time	D_t	days	$f(T, \text{SI})$
Prop. of individuals moulting per time step	$dev_{i,t}$	day^{-1}	$f(D_t, \text{age})$

c) MAJOR ASSUMPTIONS	EVIDENCE IN SUPPORT OF
ASSUMPTION (- poor; + fair; ++ good)	
Rates of advection = rates of diffusion	+
The use of single depth-independent estimates of chl. <i>a</i> and SST provide an adequate description of ambient conditions experienced by copepods	+
Development rates are food-limited	++
Individual egg production is independent of copepod numerical density	-
The same grazing threshold operates for all ages	+

APPENDIX 2.1. The Problem of Forward Diffusion

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). The present model was constructed to be as simple as possible and life stages with similar life history characteristics were therefore lumped together, yielding a division of the copepod population into seven distinct classes. In particular, the naupliar stage individuals are all lumped together into one model category. One problem associated with the lumping of age- or stage-classes is the so-called "forward diffusion problem" (John Klinck, pers. comm.): 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 (Fig. A2.1.1).

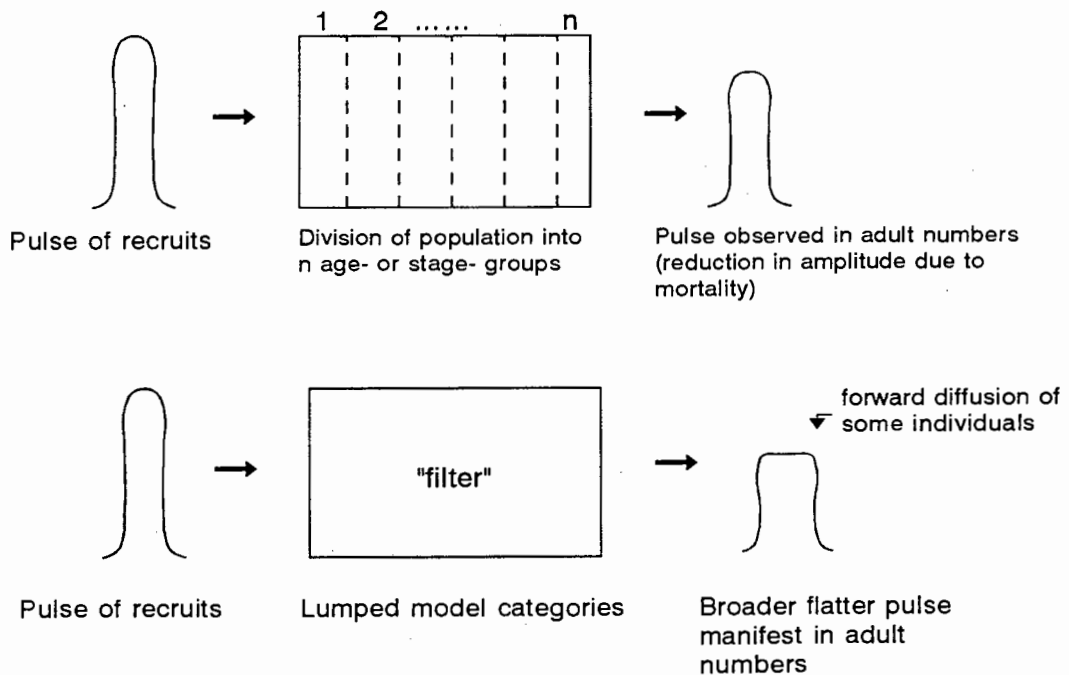


Fig. A2.1.1. Schematic diagram illustrating the effect of lumping model categories on the magnitude and pattern of the adult population size predicted by a model. Note that in the example above the period of the lump is greater than the period of the input pulse. The lumped model categories permit some individuals to diffuse through the population growth chain at a faster than normal rate, as well as acting as a "filter" by spreading out the input pulse.

A simple simulation model (see Appendix 2.2) was constructed to investigate the effect on model predictions of 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. The model (Appendix 2.2) simulates the basic population dynamics of *Calanoides carinatus*, but is simpler than the model described in chapter two. However, the model predicts growth patterns using both lumped stage-classes (NI-NVI, CI-CIII, CIV, CV, ADULT) and twelve discrete stage-classes. As before, a time step of one day is used. Total development time is varied from 13 to 36 days and the proportion of individuals in each model group which moult into the next group each day is calculated as before (equation 2.7), using the median development times given in Peterson and Painting (1990).

A mortality rate of 0.1 d^{-1} is used for all model categories, except the naupliar stages. The mortality rate increases linearly from 0.1 d^{-1} for naupliar stage six individuals to 0.2 d^{-1} for naupliar stage one individuals. An average mortality rate of 0.15 d^{-1} is used for the lumped naupliar stage category. The model is initialized assuming an initial abundance of 100 adult individuals. An even sex ratio is assumed. Fecundity is modelled as a function of chlorophyll *a* concentration (Armstrong *et al.* 1991b) using the relation shown in Fig. A2.1.2.

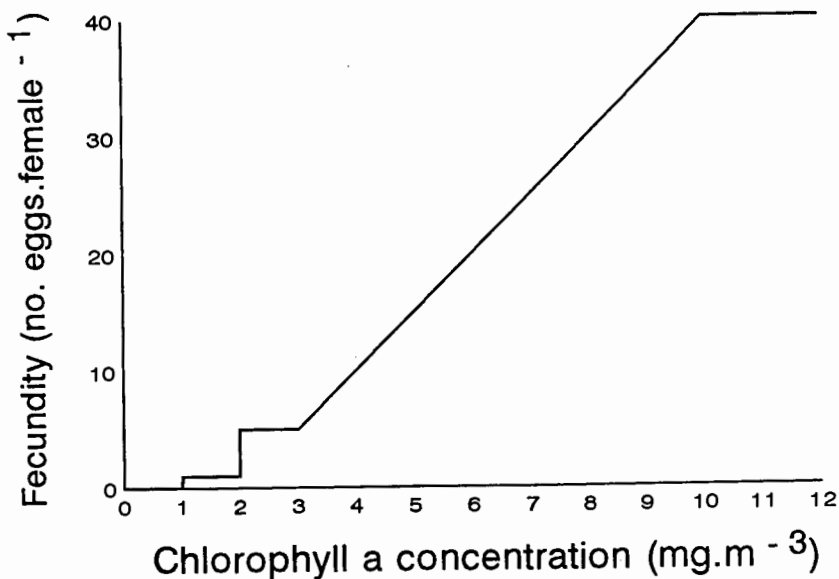


Fig. A2.1.2. The relationship between copepod fecundity and chlorophyll *a* concentration used in the forward diffusion model.

Because fecundity is calculated using chlorophyll *a* concentration, the latter variable essentially drives the model. Chlorophyll *a* concentration ($\text{mg}\cdot\text{m}^{-3}$) for each day x is calculated using the relation:

$$\text{CHL}(x) = 6.5 \sin(2\pi/p (x - p/4)) + 7.5 \quad \text{A2.1.1}$$

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

For each p value, the ratio of copepodite abundance (lumped) : copepodite abundance (nonlumped) was plotted (Fig. A2.1.3) as a function of the development time of the naupliar stages. This permitted testing of the hypothesis that the effect on model predictions of lumping depends critically on the relationship between the period of an input pulse and the temporal scale of a lump in the model. The major lump in the basic population dynamics model described in this thesis is the lumping of all six naupliar stages into a single category, and hence the total development time spent in the naupliar stages is used as the period of the model lump.

Median development times calculated in the laboratory for *C. carinatus* suggest that, on average, individuals spend 6.6 and 3.2 days in the naupliar stages at 15.5 and 19.5°C respectively (Peterson & 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 to 8 days (Brown & Hutchings 1987). However, because upwelling pulses are part of cycles lasting between 3 and 10 days (Nelson & Hutchings 1983, Hutchings & Nelson 1985), high chlorophyll *a* concentrations may persist for as many as 10 to 16 days after the start of an upwelling cycle (Brown & 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 chlorophyll-rich water. Frequent spatial overlaps are likely because *C. carinatus* possess well adapted differential migration strategies which facilitate the optimal utilisation of patchy food resources (Verheye & Field 1992). Rather than pulses of primary production, the true input pulse driving a copepod population's dynamics is the number of newly hatched naupliar stage NI

individuals recruiting to the population. It should therefore be borne in mind that the amplitude of a reproductive pulse is less than that of a primary production pulse, because egg production rates plateau at high chlorophyll *a* concentrations (Armstrong *et al.* 1991).

As phytoplankton blooms develop, mean sea surface temperatures increase from approximately 11°C to 15°C, due to mixing and solar heating processes (Brown & 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 or on the same time scale as the period of input pulses in the region.

Results of the present simulation exercise suggested that the effect of lumping on model predictions is not critical provided the length of the lump is shorter than the period of the input pulse (Fig. A2.1.3). The level of aggregation of model compartments used in this study is therefore not a drastic oversimplification, but the problem of forward diffusion needs to be considered in future modelling efforts. Over the range of feasible development rates considered, model results become increasingly sensitive to the effect of lumping as the period of an input pulse is decreased (Fig. A2.1.3). In the lumped scenario, input pulses with a short period result in approximately a 50% overestimate of copepodite abundance predicted after three months. This is chiefly because some individuals attain adulthood faster than in the nonlumped case, and so contribute to cumulative egg production rates. The implication is that the choice of an appropriate level of aggregation in a model should be based on consideration of the scale of environmental variability characterising the environment.

An additional point in support of the belief that model predictions in this study are not overly biased by the problem of forward diffusion, concerns the fact that spatial and temporal variability are not synonymous at the scale over which model predictions are integrated. The finest scale of resolution of ocean colour satellite images, and therefore the minimum area over which model results are to be averaged, is 1 km². Because of spatial patchiness, a temporal primary production pulse, for example, is not simultaneously or even universally experienced by all copepod aggregations occupying an area of 1 km² or larger. Spatial patchiness therefore results in much higher growth rates in some areas than in others, so that when

averaged over a large spatial scale, the temporal manifestation of a spatially patchy but temporally distinct input pulse becomes blurred. The existence of a "filter" in a population dynamics model may therefore inadvertently improve the accuracy of average patterns of productivity in a spatially heterogeneous environment.

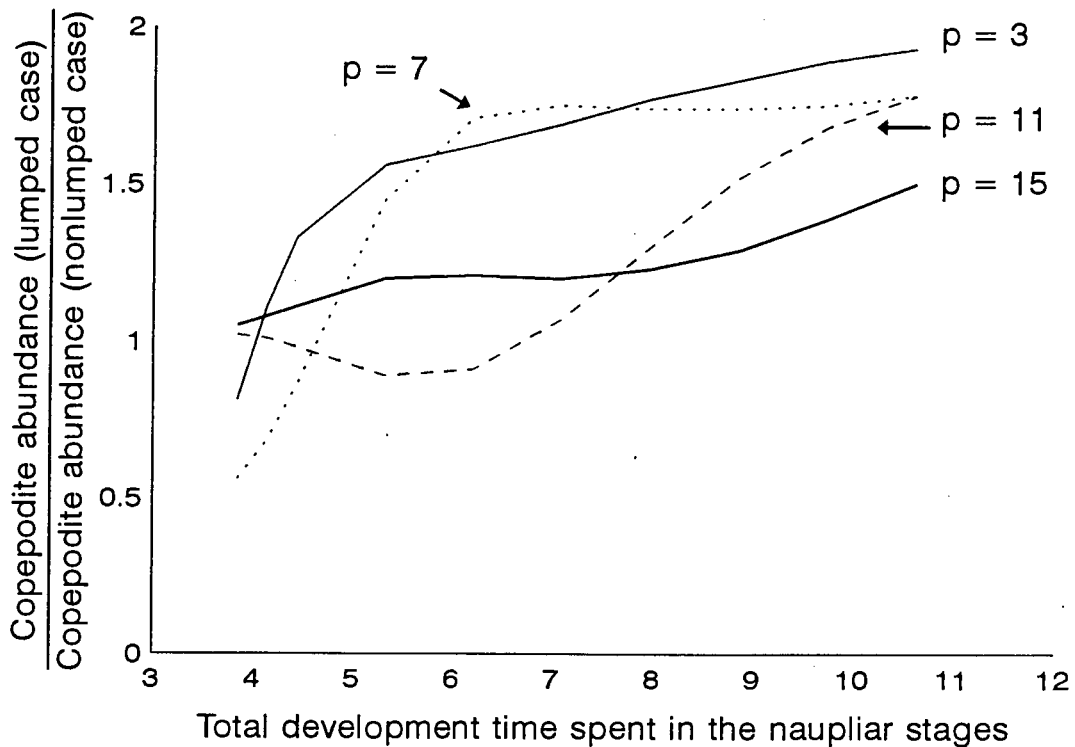


Fig. A2.1.3. A tentative analysis of the effect on model predictions of the relationship between the period p of an input pulse and the period of a lump in a model. The major lumping of model categories in the basic model presented in this thesis occurs because the naupliar stages are treated as a single entity. The effect on model predictions of lumping is therefore assessed as a function of the average length of time individuals spend in the naupliar stages.

APPENDIX 2.2. LISTING OF FORWARD DIFFUSION MODEL

The program listed is used to explore the relationship between the period of an input pulse and the level of aggregation in a model and is written in True BASIC version 3.04, for use on IBM compatible computers (PCs). The period p of an input pulse and the total development time DEV are both input into the model by the user. For present purposes, p was varied in the range 3 to 21 days, and DEV in the range 13 to 36 days. The model computes the average predicted copepodite abundance (month three) for the model cases:

- (a) nonlumped (12 separate model compartments), and
- (b) lumped (5 separate model compartments, with all six naupliar stages lumped into a single model category).

Results obtained for the nonlumped and lumped categories are compared, and the ratio of these two values plotted (using a separate spreadsheet package) as a function of p .

```
! FORWARD DIFFUSION PROBLEM
CLEAR
DIM NAUP(100)
DIM COP1(100),COP2(100),COP3(100),AD(100)
DIM N1(100),N2(100),N3(100),N4(100),N5(100),N6(100)
DIM C1(100),C2(100),C3(100),C4(100),C5(100),C6(100)
DIM CHL(100)

INPUT PROMPT "Enter the period of the input pulse... ":p
INPUT PROMPT "Enter total copepod development time... ":DEV

FOR k = 1 TO 99
  LET CHL(k) = 6.5*SIN(2*PI/P*(k-P/4)) + 7.5
NEXT k

FOR DAY = 1 TO 99

  IF DAY < 80 THEN
    IF (MOD(DAY,P) = 0) AND (MOD(DAY,2) = 1) THEN
      FOR i = (DAY+1) TO (DAY+P)
        LET CHL(i) = 0.5

      NEXT i
    END IF
  END IF

  LET FEC = 5*CHL(DAY)-10
  IF FEC > 40 THEN LET FEC = 40
  IF CHL(DAY) <= 2 THEN LET FEC = 1
  IF CHL(DAY) < 1 THEN LET FEC = 0
  IF CHL(DAY) <= 3 THEN LET FEC = 5

  LET D1 = 1 / (.0765*DEV)
  LET D2 = 1 / (.0437*DEV)
  LET D3 = 1 / (.0437*DEV)
  LET D4 = 1 / (.06*DEV)
  LET D5 = 1 / (.0765*DEV)
  LET D6 = 1 / (.0492*DEV)
  LET D7 = 1 / (.087*DEV)
  LET D8 = 1 / (.082*DEV)
  LET D9 = 1 / (.104*DEV)
  LET D10 = 1 / (.0874*DEV)
  LET D11 = 1 / (.12*DEV)
  LET D12 = 1 / (.169*DEV)
```

```

LET AD(1) = 100
LET REC = 0.1 * (AD(DAY)/2 * FEC)
LET C6(1) = 100
LET REC2 = 0.1 * (C6(DAY)/2 * FEC)

LET N1(DAY+1) = 0.8*((1-D1)*N1(DAY) + REC2)
LET N2(DAY+1) = 0.82*((1-D2)*N2(DAY) + D1*N1(DAY))
LET N3(DAY+1) = 0.84*((1-D3)*N3(DAY) + D2*N2(DAY))
LET N4(DAY+1) = 0.86*((1-D4)*N4(DAY) + D3*N3(DAY))
LET N5(DAY+1) = 0.88*((1-D5)*N5(DAY) + D4*N4(DAY))
LET N6(DAY+1) = 0.9*((1-D6)*N6(DAY) + D5*N5(DAY))
LET C1(DAY+1) = 0.9*((1-D7)*C1(DAY) + D6*N6(DAY))
LET C2(DAY+1) = 0.9*((1-D8)*C2(DAY) + D7*C1(DAY))
LET C3(DAY+1) = 0.9*((1-D9)*C3(DAY) + D8*C2(DAY))
LET C4(DAY+1) = 0.9*((1-D10)*C4(DAY) + D9*C3(DAY))
LET C5(DAY+1) = 0.9*((1-D11)*C5(DAY) + D10*C4(DAY))
LET C6(DAY+1) = 0.9*(C6(DAY) + D11*C5(DAY))

LET DEV1 = 1 / (.295*DEV)
LET DEV2 = 1 / (.361 * DEV)
LET DEV3 = 1 / (.12 * DEV)
LET DEV4 = 1 / (.169 * DEV)

LET NAUP(DAY+1) = 0.85*((1-DEV1)*NAUP(DAY) + REC)
LET COP1(DAY+1) = 0.9*((1-DEV2)*COP1(DAY) + DEV1*NAUP(DAY))
LET COP2(DAY+1) = 0.9*((1-DEV3)*COP2(DAY) + DEV2*COP1(DAY))
LET COP3(DAY+1) = 0.9*((1-DEV4)*COP3(DAY) + DEV3*COP2(DAY))
LET AD(DAY+1) = 0.9*(AD(DAY) + DEV4*COP3(DAY))

NEXT DAY

LET DAY = 100
LET TOT= COP1(DAY)+COP2(DAY)+COP3(DAY)+AD(DAY)
LET TOT2= C1(DAY)+C2(DAY)+C3(DAY)+C4(DAY)+C5(DAY)+C6(DAY)
PRINT P,tot/tot2
CLEAR

SET WINDOW 1,90,0,20
FOR DAY = 1 TO 90
  PLOT DAY,CHL(DAY);
NEXT DAY
CLEAR

SET WINDOW 1,90,0,1000
FOR DAY = 60 TO 90
  LET TOT= COP1(DAY)+COP2(DAY)+COP3(DAY)+AD(DAY)
  LET TOT2= C1(DAY)+C2(DAY)+C3(DAY)+C4(DAY)+C5(DAY)+C6(DAY)
  PLOT DAY,TOT;
  LET TOTLUMP = TOTLUMP + TOT
  LET TOTALL = TOTALL + TOT2
NEXT DAY
PRINT "P - TOTLUMP/30 - TOTALL/30 - LUMP/ALL "
PRINT P,TOTLUMP/30,TOTALL/30,(TOTLUMP/30)/(TOTALL/30)

END

```

CHAPTER 3

SENSITIVITY ANALYSIS

INTRODUCTION

Two important criteria for accepting a model are that it does not make impossible predictions and that its underlying assumptions and derivations are logical (Berryman 1992a). Our imperfect knowledge of systems and the difficulties of obtaining precise estimates of field parameters highlight the importance of evaluating a model's predictions over a range of parameter values (Gladstein 1991).

A fundamental aim of this model is to provide an index of zooplankton productivity on a scale that is large enough to permit evaluation of model results in terms of the potential impact on fish populations. For example, anchovy are capable of migrating up to about 15 kilometres per day (L. Hutchings, pers. comm.), and therefore the minimum area over which model results need to be integrated is *ca.* 15 x 15 km². In view of this, estimates of the average effect on model predictions of applying various sensitivity tests are deemed more meaningful than a single estimate based on 'local' conditions only. Consideration of average effects thus guards against, for example, underestimating the importance of a particular parameter/assumption whose effect is only dramatic under a narrow range of environmental conditions, or overestimating the importance of a particular parameter/assumption whose effect is averaged over larger scales.

The aims of this chapter are as follows:

- a) to explore further the conceptual basis of the model developed in chapter two;
- b) to check whether changes in model parameters or assumptions result in predictable changes in model output;
- c) to quantify the effect on model predictions of errors in field estimates used to initialize the model;
- d) to assess to which parameter the model is most sensitive; and
- e) to determine whether the model is more sensitive to empirical data or to its assumptions.

Furthermore, because the model was designed to be as simple as possible, the effect on model predictions of having stripped some of the detail is quantified by modifying model functions so that they depict more finely the hypothesized underlying structure of the population. An attempt is also made to assess the importance of assumptions which, because of controversy surrounding their validity, were made subjectively.

METHODS

The sensitivity of the model was tested with respect to: i) sensitivity to initial values; ii) sensitivity to parameters; iii) sensitivity to functional form and iv) sensitivity to model structure (Platt *et al.* 1981). 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 each of the following was evaluated:

- a) The total biomass (mg.C.m^{-3}) of copepodites and adults (T_{biom}) (unless otherwise specified, hereafter 'total biomass' refers to the value of T_{biom});
- b) The relative abundance of each age category of copepods (NI-NVI, CI-CIV, CV & ADULTS); and
- c) The mean egg production (no. eggs / day), as well as the average production rate (no. eggs / female / day).

Graphical or other displays are presented for tests which yielded results that are either surprising or substantial.

To assess to which of the parameters 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. The value of T_{biom} was specifically chosen as an index for comparative purposes because it is the value which has the most direct relevance to the management objectives of the model. To test if changes in any of the model parameters produced a better fit to the *C. carinatus* copepodite biomass trend observed during the anchor station, the sum of the squared differences between daily model-predicted and observed copepodite biomass estimates was computed in each instance.

Because the anchor station series spans a relatively short period of time, the longer-term qualitative and quantitative effects of the various tests on model output were investigated by running simulations for a further four months. The present model simulates the dynamics of *C. carinatus* during the summer upwelling season (November to March) and, because no suitable continuous input series are available for simulations over an entire upwelling season, a base-case input series was derived as follows:

- i) A single near-surface chlorophyll and sea surface temperature (SST) estimate was obtained for each of the months January to April, using ocean colour and thermal imagery maps (Shannon *et al.* 1985). The maps are based on *Nimbus-7* CZCS imagery for January through April 1979, and average chl.*a*

and SST values were calculated for a representative $\frac{1}{4}^{\circ} \times \frac{1}{4}^{\circ}$ inshore area situated just north-west of Cape Columbine on the West Coast.

- ii) Gaussian random numbers were generated for each month, with a mean equal to the values calculated in (i) and a standard deviation equal to a characteristic value for an upwelling season. The standard deviation used to generate the chl.*a* input series (STD=5.6) is based on the observed value associated with mean summer measurements of chl.*a*, both at the sea surface and in the euphotic zone, and averaged over the period 1977-1980 (Brown & Henry 1985). A standard deviation of 2°C was used to generate the SST input and a minimum of 8°C allowed. Andrews & Hutchings (1980) defined upwelling water as having a temperature between 8°C and 10°C.
- iii) The input data were structured such that a random number of upwelling cycles (range: 1-3) occurred each month, still ensuring that mean monthly values approximated those calculated in (i). Upwelling cycles were simulated using a characteristic 7-day cycle, which is simply the peak extracted from the 12-day upwelling cycle used in the previous section (Brown & Hutchings 1987) (Fig. 3.1).

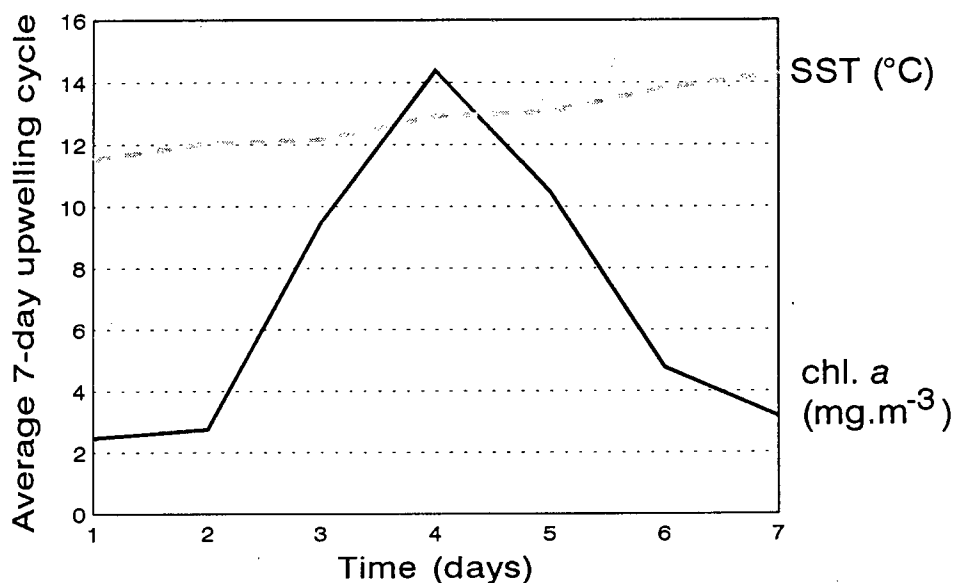


Fig. 3.1. Plot of the chl. *a* and SST values used to simulate average 7-day upwelling cycles to generate input series for the sensitivity runs. The values are based on means of *in situ* measurements (from Brown & Hutchings (1987)).

- iv) Successive runs produce two probability distributions of input values that represent the most probable mean pattern of chl.*a* and SST respectively, based on the constraints outlined above. Provided the number of runs is large enough, one may then predict the mean expected pattern of zooplankton

abundance over an upwelling season characterised by the above features. This approach allows the model's **average** response to a particular sensitivity test to be assessed, and is therefore relatively independent of the particular input series used. Sensitivity results are thus not biased by, for example, the increased importance of a parameter under a specific set of environmental conditions.

As the number of runs is increased, the coefficient of variation (CV) associated with the mean T_{biom} value, predicted after both one month and five months, first decreases and then plateaus shortly after 100 runs (Fig. 3.2). It was therefore assumed that results obtained from 100 simulations were adequately representative of all possible combinations. All results obtained using base-case input data are therefore the means of 100 runs. Since the standard deviations associated with model estimates were similar throughout, for ease of viewing they are only shown in the base-case.

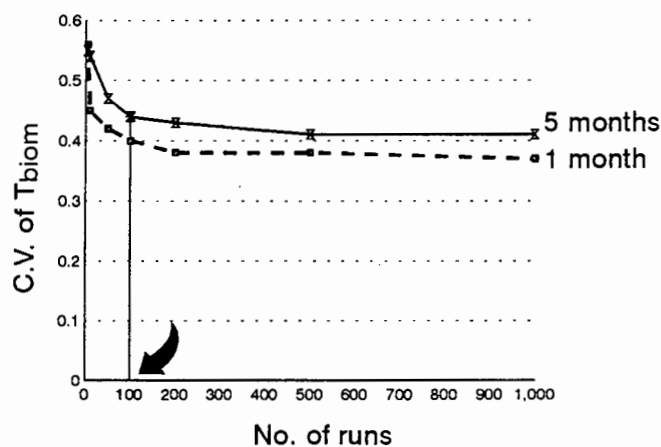


Fig. 3.2. Plot of the coefficient of variation associated with mean $T_{\text{biom}}(30)$ and $T_{\text{biom}}(150)$ values versus the number of runs used to calculate the means.

Both the mean and standard deviations of the base-case input series and the base-case T_{biom} , or output series, used for comparative purposes are presented in Figure 3.3. An example of a single run is also shown. To summarize this approach: for each run result, averages are calculated from individual simulations run using the same average environmental conditions, but with slight differences in the timing and magnitude of primary production (or other) events. Results can therefore be envisaged as representing either the mean pattern of zooplankton productivity corresponding to an average set of environmental conditions, or as a spatially integrated value which is averaged over a number of discrete 'subpopulations', each subject to local differences in the forcing functions. It should also be borne in mind that in what follows, 'average' refers to the average of 100 simulations.

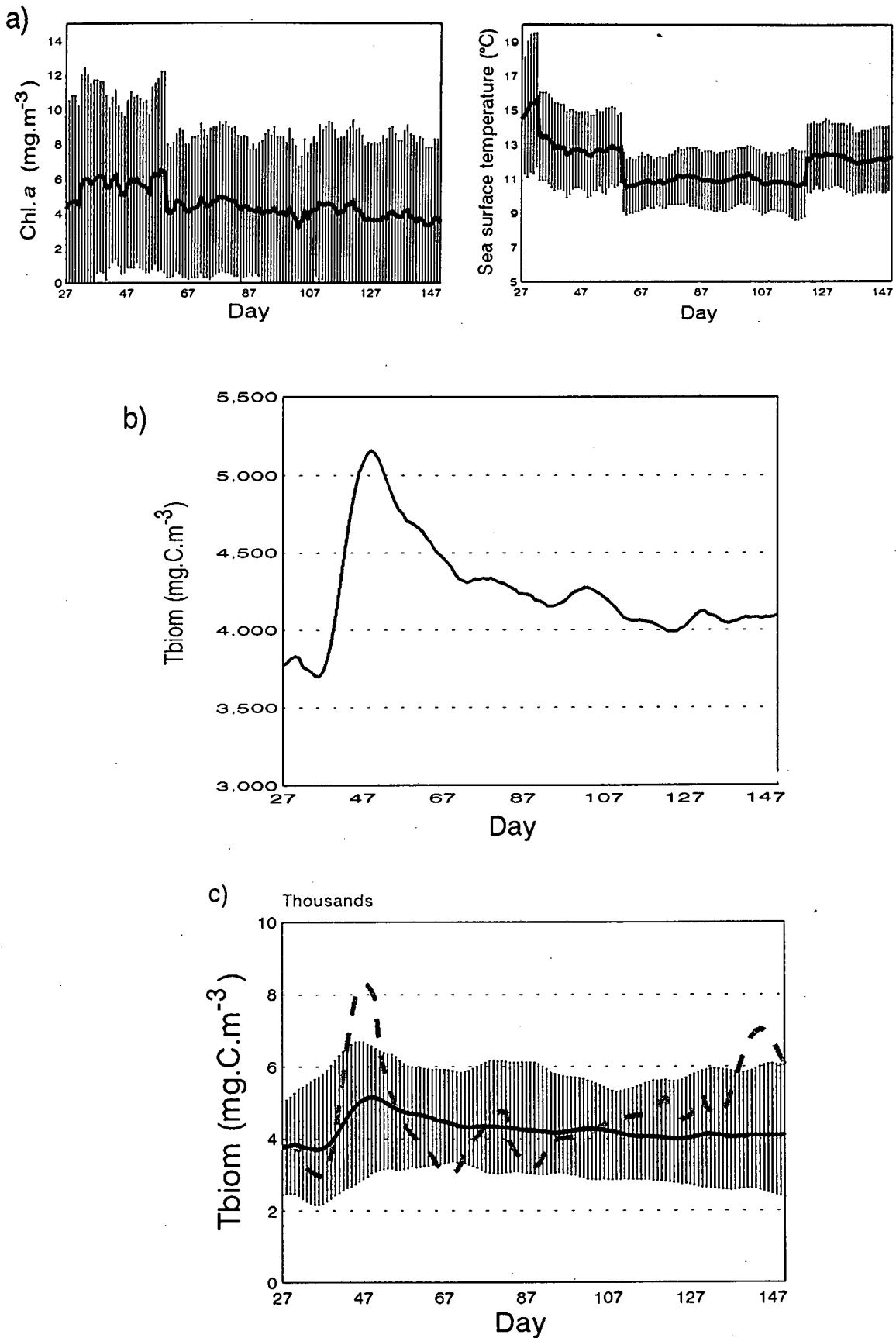


Fig. 3.3. The means (100 runs) and associated standard deviation of the base-case input series used in the sensitivity analysis is shown in (a), while (b) shows the resulting mean (100 runs) base-case T_{biom} series. An example of a single run (dashed line) as compared to the base-case T_{biom} trend and its associated standard deviation is shown in (c). Note that the peak in T_{biom} during the first month corresponds to higher average chl.a and SST values. For ease of viewing, the vertical scales in (b) and (c) are different.

RESULTS AND DISCUSSION

i) Sensitivity to Initial Values

The present model was designed to predict within-season variability in secondary productivity and the starting biomass in each population age class is initialised using data collected on sampling cruises. It is therefore important to assess to what degree model-predicted results depend on the initial 'snapshot' values used. To test this, a number of simulations were executed in which the following were altered: the initial *C. carinatus* abundance estimate N_1 ; the sex ratio and the initial age composition.

Initial Abundance Estimate N_1

Changes in the initial abundance estimate resulted in quantitative changes in the abundance of all age classes, but the general qualitative trend remained unchanged. As expected, quantitative changes in biomass were proportional to the change in the initial abundance estimate (Fig. 3.4). This suggests that the model should be initialised with a sufficient degree of accuracy to ensure that predicted patterns of population growth are simulated on roughly the right scale.

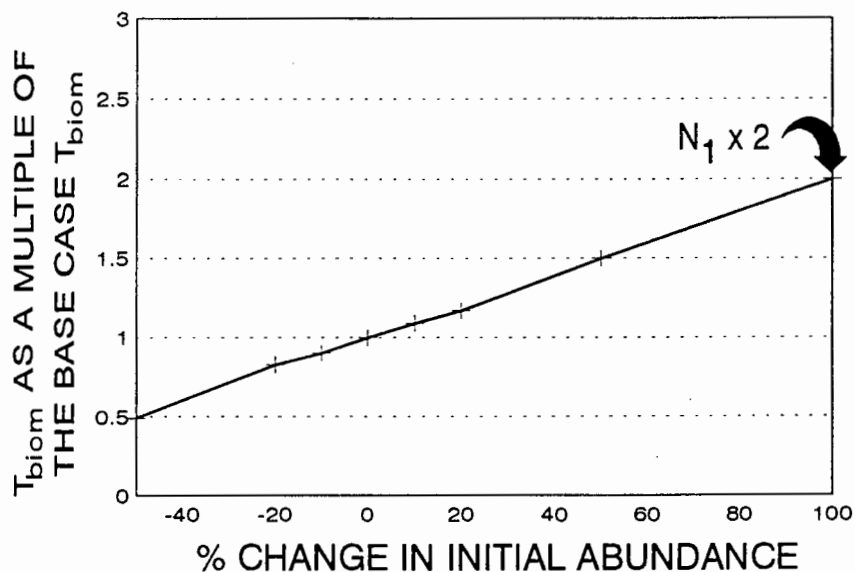


Fig. 3.4. The effect on the predicted biomass of copepodites and adults after 27 days of changing N_1 at intervals as shown.

The Sex Ratio

The relative proportions of females and males (F:M sex ratio) in a population is important in controlling the population's dynamics because it affects the rate of reproduction. Observed sex ratios in *C. carinatus* vary widely in both time and space (Verheye 1991). An evaluation of the model's sensitivity to variations in the sex ratio revealed that changes in the proportional abundance of females result in slightly less than proportional changes in $T_{\text{biom}}(27)$ (Fig. 3.5a).

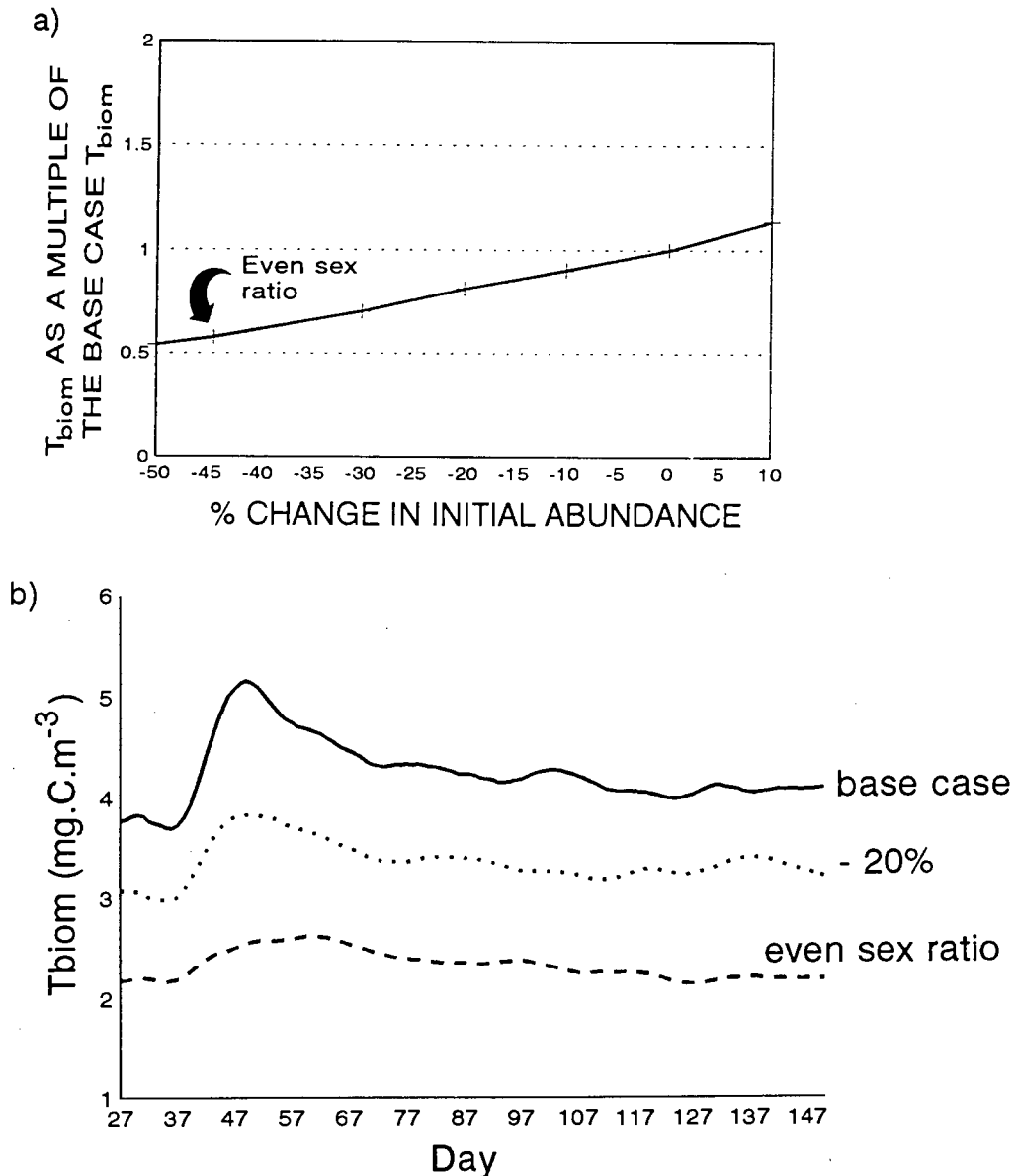


Fig. 3.5. (a) The effect on $T_{\text{biom}}(27)$ of changing the relative abundances of males and females at intervals as shown. The base-case assumes the same sex ratio (F:M = 9:1) as that observed on day 1 of the anchor station series. (b). The average effect (mean of 100 runs) of changes in the population sex ratio on the predicted pattern of T_{biom} . Simulations are run for 4 months using as starting points the value of $T_{\text{biom}}(27)$ obtained using the anchor station input series.

Increasing the sex ratio (F:M) actually improved the fit of the model to the anchor station series (Table 3.1), while decreasing the proportional abundance of females by more than about 50% caused the population to start declining. The model response highlights one of the simplifying assumptions implicit in the model, namely, that under equivalent environmental conditions, the rate of reproduction is a linear function of the number of fertile females. Very high or very low adult densities are therefore not modelled as limiting egg production. The effect of a nonlinear relationship between egg production and female density on the predicted population growth rate is investigated in a later section.

Although it may be possible to initialize a model with reasonably good field estimates of the sex ratio, there is a paucity of data describing the within season variability in sex ratio. There is a similar gap in our understanding of which causal mechanisms may be important influences on this parameter. Model simulations suggest that an error of 10% in our initial field estimate of sex ratio results in an equivalent error in the final biomass estimate. To test whether or not this difference would increase exponentially in time, model-predicted values on day 27 were used as the starting points in a 4 month simulation run, using the standard upwelling series described earlier. The effect of both a 20% and a 44% (F:M = 1:1) error in the initial sex ratio remains stable with time (Fig. 3.5b), but decreases in the abundance of reproductive females substantially dampen the amplitude of population fluctuations. It follows that large population fluctuations will be induced by increasing the survival rates of the eggs produced.

Errors in field estimates of the population sex ratio will be more marked if this parameter varies seasonally or if the availability of males at high female:male sex ratios can limit a copepod's potential fecundity. There are some indications that sex ratio may be related to food availability. For example, Verheye (1991) found that the relative abundance of females, as a proportion of the total number of adults, ranged between 0.67 and 0.78 during the upwelling season, but increased to 0.86 during winter. A better understanding of sources of variability in this parameter could assist in fine-tuning model predictions.

Age Structure

The model can be initialised using either field estimates of the observed population age composition or by assuming a mean age composition. The latter approach, or one which uses average values for a shelf region, was preferred because it guards

against results which are biased by local differences in population age structure. The local differences arise because of differential transport rates of the various developmental stages across the shelf (Verheye *et al.* 1991), which in turn makes it difficult to determine if co-occurring individuals belong to the same population.

The model was found to be relatively insensitive to initial age composition. A 50% increase or decrease in the initial proportional abundance of each of the age classes resulted in at most a 24% change in $T_{\text{biom}}(27)$.

The observed population age composition on day one of the anchor station series differs markedly from the base-case mean population composition (Fig. 3.6), and was used to explore the effect on model predictions of initialising the model with widely different starting age structures. Because no field data on the proportional abundance of the naupliar stages were available, the same initial proportional abundance of naupliars was assumed as that calculated for the base-case.

The 2.6 fold difference in the initial proportional abundance of adults resulted in a 1.8 fold increase in the value of $T_{\text{biom}}(27)$, but differences soon converge. Only minute differences in the predicted age compositions remain after 27 days, and these are completely absent after two months (Fig. 3.6).

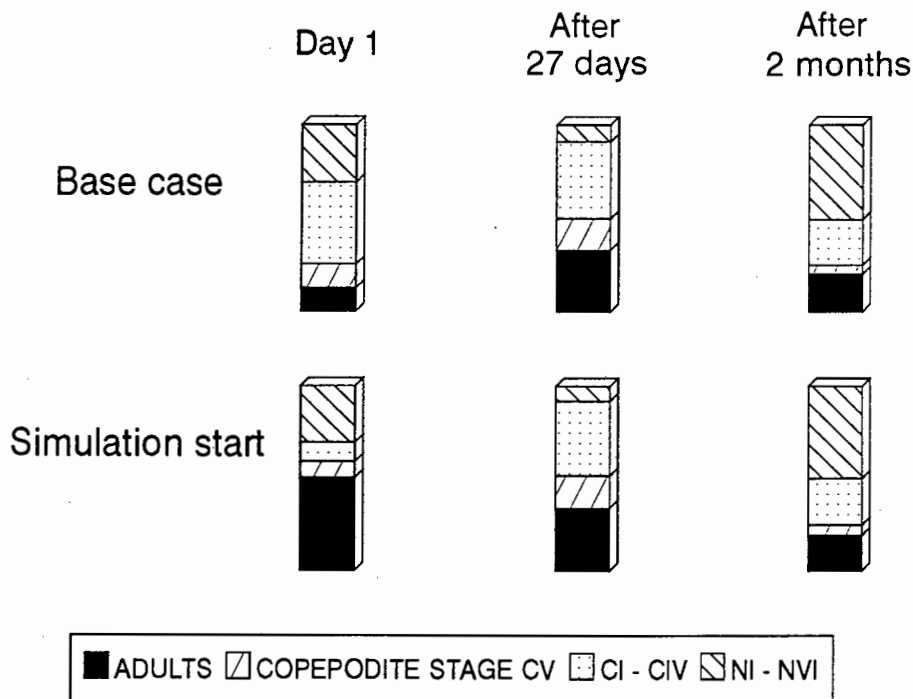


Fig. 3.6. The effect on population composition after 27 days, and the average effect after 2 months, of starting the model with a completely different age structure. The base-case is initialized using a mean population composition while the simulation run starts with the same population composition as that observed on day 1 of the anchor station series.

A poorer fit to the anchor station series is obtained using the observed, rather than the mean, initial age composition, while a marginally better fit is obtained by increasing the initial proportional abundance of copepodite stage CV (Table 3.1).

Age structure itself is most dramatically affected by juvenile mortality rates, as is demonstrated below.

ii) Sensitivity to Parameters

The Grazing Threshold (F_{crit})

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 $mg.chla.m^{-3}$ to 2 $mg.chla.m^{-3}$ or even 1 $mg.chla.m^{-3}$ (Fig. 3.7). There are two main reasons for this: i) chlorophyll concentrations less than 3 $mg.chla.m^{-3}$ 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, and ii) during the quiescent periods between upwelling pulses, chlorophyll concentrations are mostly well below 3 $mg.chla.m^{-3}$ anyway, so in the model food is limiting for individuals for roughly 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. Decreasing its value to as little as 0.5 $mg.chla.m^{-3}$ for example, assumes that individuals can tolerate a much lower feeding threshold level and results in a significant reduction in the proportion of juveniles which die from starvation. Because individuals are food-limited for less of the time, average development rates are also increased and the overall effect after 27 days is to cause a 36% increase in $T_{biom}(27)$. Conversely, increasing F_{crit} to 4 $mg.chla.m^{-3}$ results in a 20% increase in both mean egg production rates and the value of $T_{biom}(27)$. Whilst it is reasonable to assume that the correct value of F_{crit} lies somewhere in the

range $0.5 < F_{crit} < 3$, it is unlikely that F_{crit} is in actuality much larger or smaller than this, because in the former case the high chlorophyll concentrations are almost certainly due to a bloom of net-phytoplankton (the preferred food of copepods), while in the latter case it is unlikely that net-phytoplankton is present at all (see Kiørboe 1993).

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 (Fig. 3.7). This result does not indicate any need to change the value of F_{crit} : models derived from realistic assumptions about the underlying ecological processes are generally considered more credible theoretical constructs than models derived from unknown or unreasonable assumptions (Berryman 1992a). Further motivation for assuming that use of the base-case F_{crit} value results in the best approximation to the true qualitative dynamics of the population comes from the fact that the base-case value produced the best fit to the observed anchor station time series (Table 3.1). It is therefore concluded that the model is relatively insensitive to the exact value of F_{crit} and it is not recommended that further effort be expended in trying to obtain better estimates of this parameter.

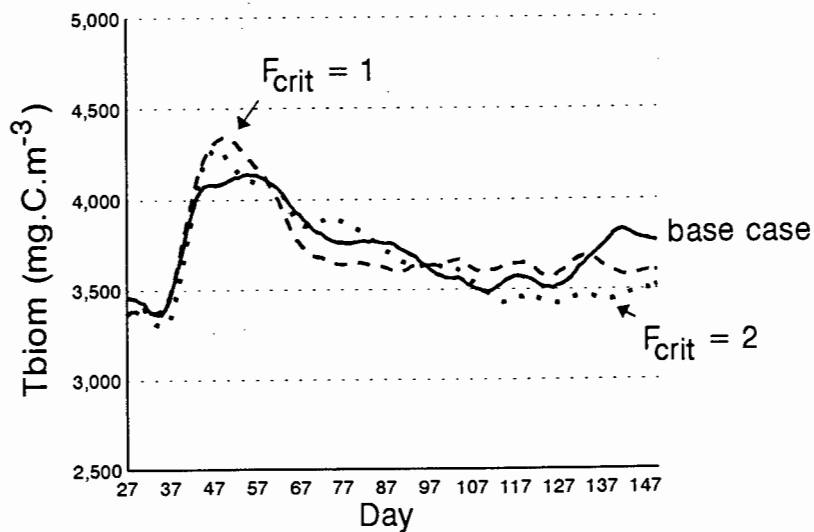


Fig. 3.7. The average effect of assuming that copepod individuals become food-limited at a lower grazing threshold level (F_{crit}). The base-case has F_{crit} set at 3 mg.chla.m^{-3} .

It should be borne in mind that any grazing threshold level adopted in a model is likely to be an over-simplification 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. This facet is explored more fully in chapter four.

The Mortality Rate M_{pred}

M_{pred} describes the proportion of individuals removed each day by predators or other biotic factors. The model is quantitatively most sensitive to changes in the adult mortality rate and least sensitive to changes in the naupliar mortality rate (Fig. 3.8).

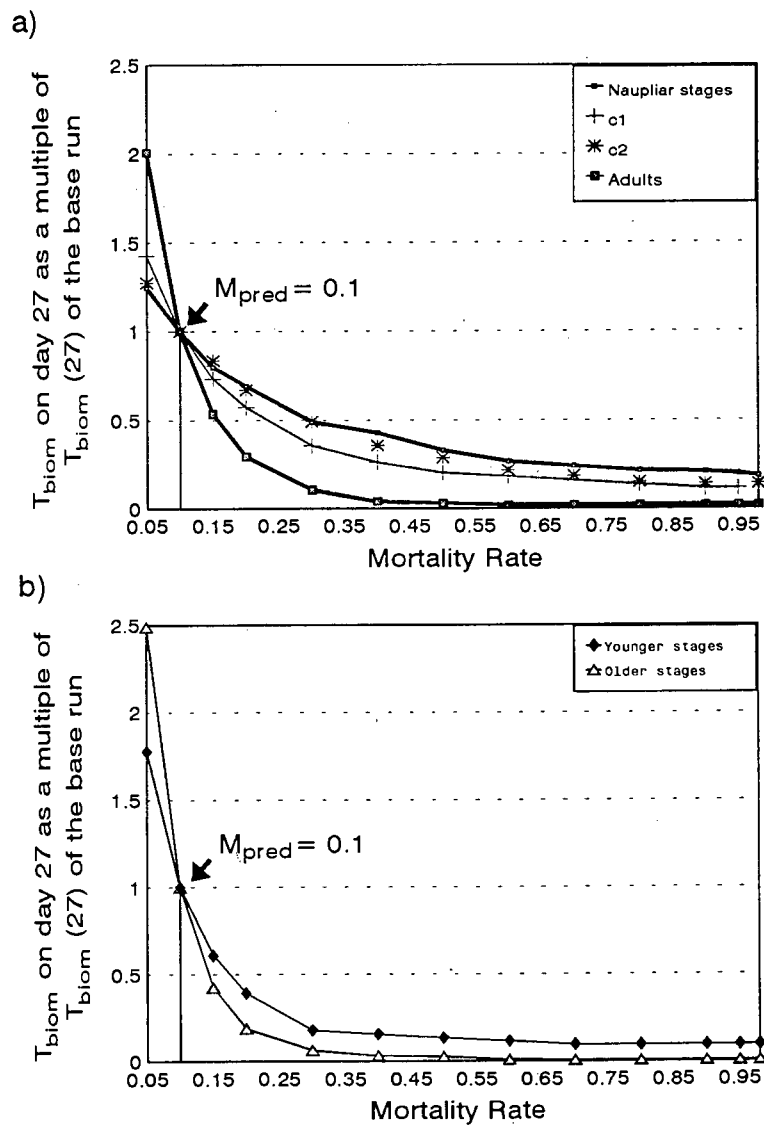


Fig. 3.8. The effect on T_{biom} after 27 days of a) changing estimates of M_{pred} one at a time to the value indicated, and b) varying $M_{pred}(CV\&ADULTS)$ and $M_{pred}(NI-NVI,CI-CIV)$ in concert.

Doubling and halving the $M_{\text{pred}}(\text{adults})$ rate resulted respectively in a two-fold decrease and increase in the total predicted biomass after 27 days. The most obvious effect of changing the adult mortality rate is that it changes the net egg production: a 50% decrease in $M_{\text{pred}}(\text{adults})$ resulted in a 44% decrease in the mean number of eggs produced while a 50% increase in $M_{\text{pred}}(\text{adults})$ resulted in a 30% increase in the mean number of eggs produced during the first 27 days.

Mortality rates were varied in combination and one by one, up to a factor of nine times, and in all but one instance ($M_{\text{pred}}(\text{naupliars}) = 0.05$), the base-case provided the best fit to the anchor station series (Table 3.1). The model was more sensitive to combined changes in the mortality rates of the older stages (CV and ADULTS) than the younger stages (NAUPLIARS, CI-CIV) (Fig. 3.8).

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. A detailed analysis of the effects of spatial and temporal variability in the mortality rates of the older stages on model-predicted biomass trends is presented in chapter five. The effects of changes in the juvenile mortality rates on T_{biom} are shown in Fig. 3.9.

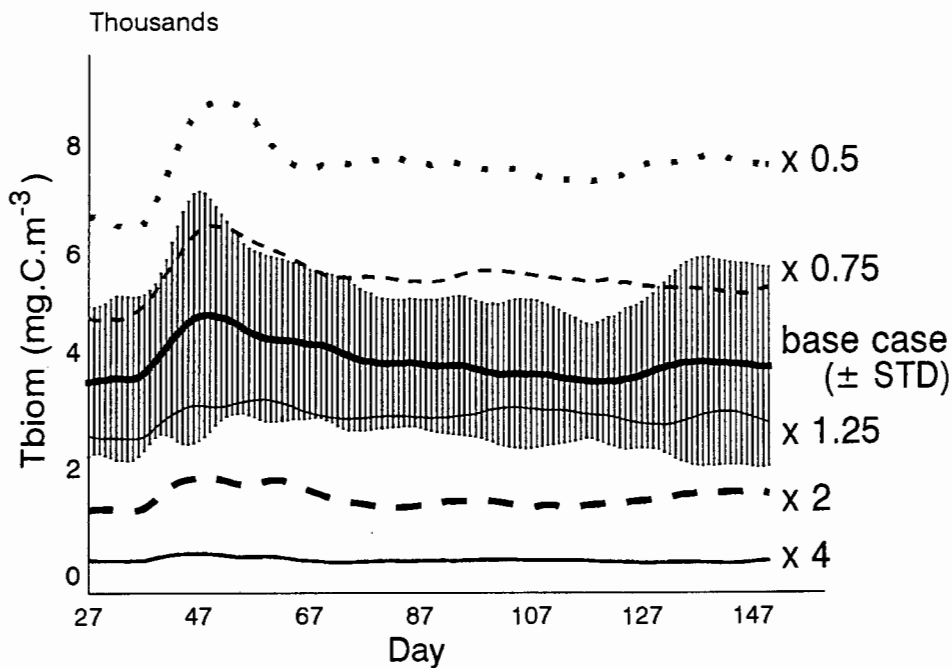


Fig. 3.9. The average effect of changing the proportion of the young stages (NI-NVI & CI-CIV) killed by predators by the factor indicated.

Although changes in $M_{pred}(NI-NVI,CI-CIV)$ result in substantial changes in the magnitude of T_{biom} , differences relative to the base-case remain consistent for simulations run over a further four months. For mortality rates greater than about four times the base-case value, the population stabilizes at a level approximately 20% that of the base-case level.

The Egg Mortality Rate M_{egg}

The model is very sensitive to changes in the value of the egg mortality rate. Decreasing M_{egg} by 20% resulted in more than a doubling in the value of $T_{biom}(27)$, while a 50% decrease in M_{egg} caused a four-fold increase in $T_{biom}(27)$ (Fig. 3.10).

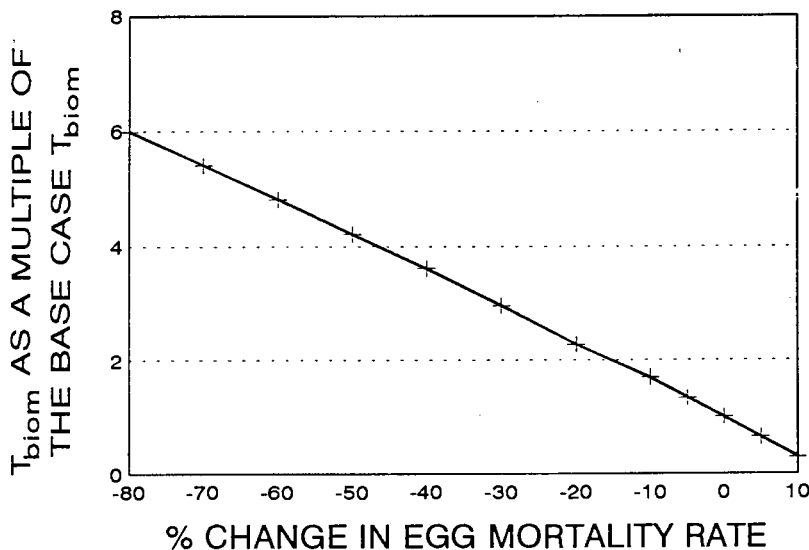


Fig. 3.10. The effect on T_{biom} after 27 days of changing M_{egg} at intervals as shown.

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 & Poulet 1993).

In light of the many factors which may decrease the survival rates of eggs, the notion of a high egg mortality rate seems intuitively correct. Nonetheless, if egg mortality rates are in actuality much lower than this, the model will substantially underestimate zooplankton production rates (Fig. 3.11).

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. However, 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. 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.

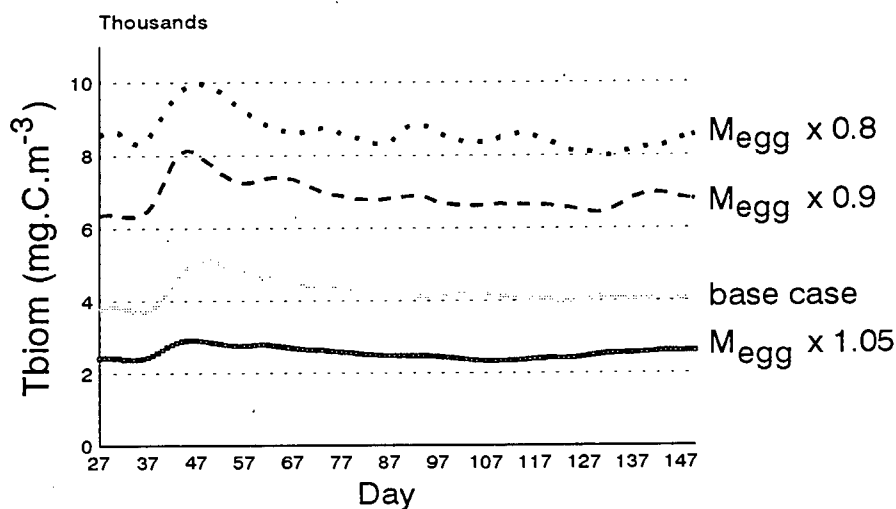


Fig. 3.11. The effect of changes in the egg mortality rate (M_{egg}) on the magnitude of T_{biom} .

The Rate of Mortality due to Starvation

Starvation tolerance, and therefore the rate at which individuals die due to sub-threshold feeding conditions, is modelled as a function of feeding history, temperature and age. Although calculations of rates of mortality due to starvation are as objective as possible because they are based on empirical observations, spatial patchiness in the distribution of phytoplankton makes this a difficult parameter to quantify accurately. The model assumes implicitly that individuals which survive periods of low food availability were able to locate sufficient patches of food to survive.

M_{food} - the proportion of NI-NVI and CI-CIV individuals starving to death: Decreasing M_{food} results in less 'steep' population peaks because more individuals survive and grow to adulthood following a drop in food concentrations (Fig. 3.12). Small increases in M_{food} cause fairly minor changes in predator standing stocks, while increasing rates of mortality by 50% results in an average error of 12% in predicted standing stocks (Fig. 3.12). Further increases cause standing stocks to start declining, a trend only reversed by sufficiently frequent pulses of food availability. Successively larger increases in M_{food} do not produce successively larger changes in predicted standing stocks because starvation tolerances are reduced to such a degree that all juveniles die when food is limiting.

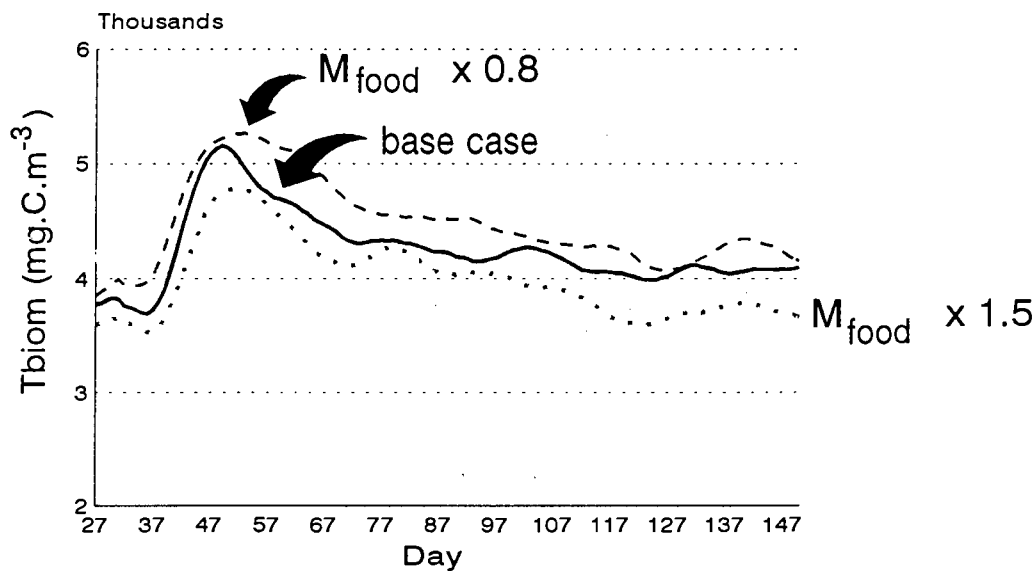


Fig. 3.12. The average effect of assuming that the proportion of NI-NVI and CI-CIV individuals which die from starvation is increased and decreased by the factor indicated.

The above scenario 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 lieu of the recently proposed 'critical moulting weight hypothesis' of Carlotti & P. Nival (1992): unless both small (Carlotti & S. Nival 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 a) that it is unnecessary to differentiate between different age classes within each stage in models of copepod growth and development (Carlotti & P. Nival 1992), and b) 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 the model as, for example, a function of prey patchiness.

M₅₀ - the average starvation tolerance (days) of adult and CV stage individuals:

Although food concentrations fell below the grazing threshold in the anchor station series, thus constraining female egg production rates, starvation intervals were not long enough to result in the death of adults or CV individuals. However, reducing the starvation tolerance of adults and CVs by half results on average in a 12% decrease in the value of T_{biom} predicted after four months (Fig. 3.13). This difference will be far greater in periods of less upwelling, when the relatively high starvation tolerance levels of the older stages are particularly critical in ensuring the survival of populations. Increased susceptibility of adults to starvation affects cumulative egg production rates and hence the shape of the population growth curve.

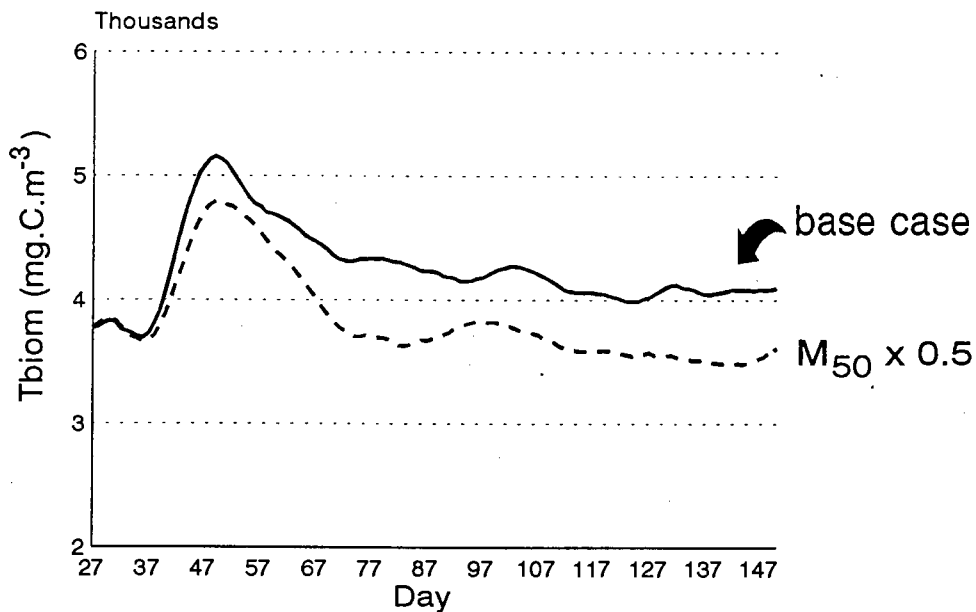


Fig. 3.13. The average effect of assuming that the starvation tolerance of adult and CV stage individuals is reduced by half.

iii) Sensitivity to Functional Form

Density-dependent Egg Production

As mentioned earlier, one of the simplifying assumptions implicit in the model is that egg production is a linear function of the number of fertile females. Because egg production rates are directly linked to food availability, and feeding rates can be inhibited at sufficiently high numerical densities of conspecifics or competing heterospecifics (Hargrave & Geen 1970, Wong 1988), this assumption may be faulty. To provide a rough indication of the error incurred in the model if egg production rates in the field are density-dependent, a sensitivity test was devised as outlined below.

In a study describing intra-annual variations in *C. carinatus* abundance across the West Coast shelf, Verheye (1989) recorded the lowest female *C. carinatus* densities in June (average = 11 females.m⁻³) and the highest densities in March (ca. 106 females.m⁻³). For present purposes it was therefore assumed that female densities greater than 10 females.m⁻³ were limiting to egg production, while female densities greater than 100 females.m⁻³ were all assumed to exert the same constant inhibitory effect on egg production rates. For female densities > 10 females.m⁻³, fecundity rates were first calculated as usual and the value of E_u , the *per capita* number of eggs produced under non-limiting conditions, then modified as a linearly decreasing function of the number of females (Fig. 3.14).

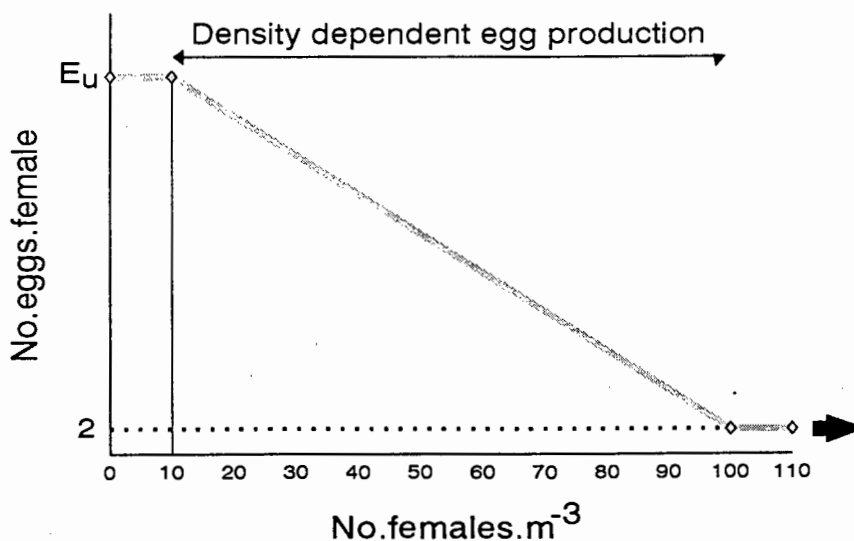


Fig. 3.14. Model function describing the relationship between *per capita* fecundity rates and female *C. carinatus* abundance. E_u , calculated on the basis of past and present feeding history, is the number of eggs produced when female densities are not limiting.

Density-dependent effects were not assumed to result in a total cessation of egg production (as occurs in the model when food is limiting), and a minimum egg production rate was set at 2 eggs per female per day.

Although the model function described above has no empirical basis, it nonetheless provides an idea of the importance of the assumption that egg production rates are density-independent. Density-dependent limitation of egg production rates resulted in a 34% decrease in the average egg production rate and a 33% decrease, relative to the base-case, in the value of $T_{\text{biom}}(27)$. This difference expanded to an average difference of 38% after a further four-month simulation run (Fig. 3.15). The additional non-linear effects introduced into the model resulted in slight qualitative differences in the predicted biomass trend. If similar density-dependent effects are manifest in real zooplankton populations, then these results suggest that they would significantly dampen the peak in egg production (and hence the amplitude of population fluctuations) which usually follows a peak in primary production. As there is no empirical support for this, and no clear evidence demonstrating density-dependence in plankton populations, the use of a linear function is justified on the grounds of simplicity.

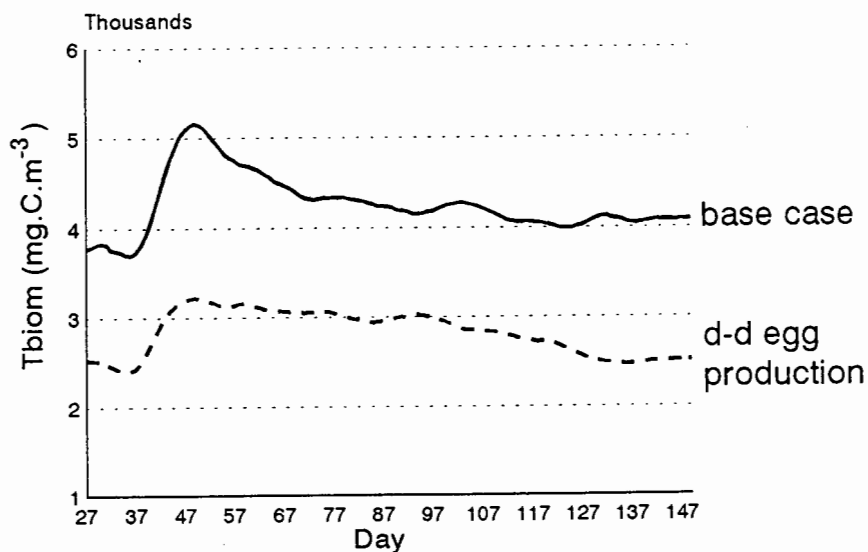


Fig. 3.15. The effect on T_{biom} of assuming that egg production rates are density dependent.

Stochastic vs Deterministic Predator Mortality Rates

On a local scale, mortality is likely to vary temporally in a stochastic rather than a deterministic manner because of the patchy distributions of both predator and prey. As the scale of observations is increased, however, it is hypothesized that localized

stochastic effects become averaged and so are both less dramatic and less important in influencing the net signal. Because the present model is designed to average processes over large horizontal areas, mortality rates used in its initial formulation were deterministic. The demographic consequences of assuming that mortality rate varies in a stochastic rather than a deterministic manner were investigated by allowing the predator-induced mortality rate (M_{pred}) to vary randomly from day to day within a specified range.

An example of the different responses of the model when a) M_{pred} for the older stages (CV & ADULTS) was varied stochastically and M_{pred} for the younger stages (NI-NVI & C1 - CIV) held constant and b) the reverse case applied, is presented in Fig. 3.16. In the latter case, the predicted T_{biom} trend was relatively flat because periodic large reductions in juvenile biomass dampened variability by preventing any major 'recruitments' of juvenile biomass into the older age classes. Patterns of production therefore remained even. In contrast, random variations in adult and CV mortality rates resulted in much larger fluctuations in the predicted T_{biom} trend. This is because changes in the number of individuals in the older stages represent far larger changes in calculated biomass values than an equivalent change in number of individuals in the younger stages. Also, stochastically-determined impacts on the survival of the older stages are quickly mirrored in cumulative egg production rates, thereby resulting in greater recruitment variability.

As a corollary to the above, it follows that higher average juvenile mortality rates should induce greater relative changes in population age structure than disproportionately high adult mortality rates. In the latter case, the population composition remains relatively even because when the older individuals die, proportional decreases occur in the abundance of the younger stages (Fig. 3.17). In contrast, the former case leads to a dramatically increased proportional abundance of adults because few of the younger stage individuals survive. Obviously the net effect is still to reduce the absolute abundance of adults because fewer instars moult into adulthood, but the important point is that the proportional abundance of adults is altered.

For case (a) in Fig. 3.16, the dramatic peak in T_{biom} during the first month is concomitant with the elevated primary production level over this period. This suggests that under favourable environmental conditions, the enhanced population growth rates (arising from the higher fecundities), are able to more than compensate for the periodic

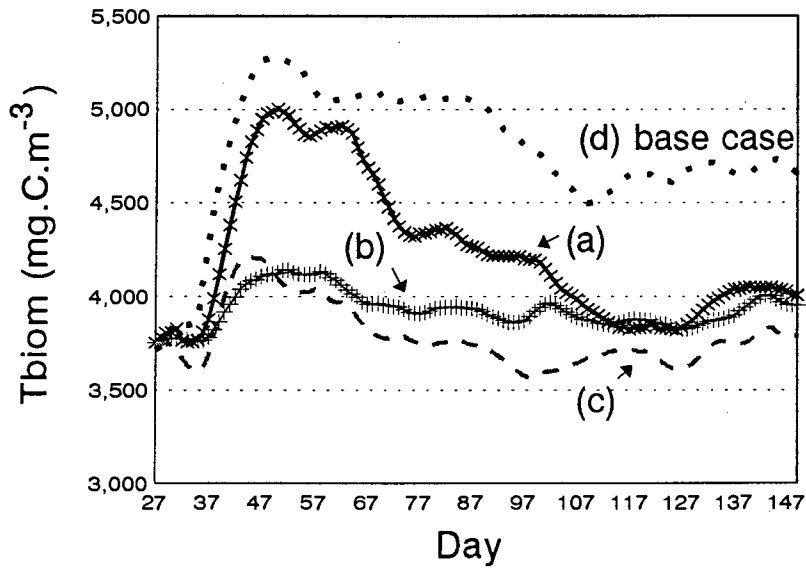


Fig. 3.16 The effect of a) stochastically varying M_{pred} (CV & ADULTS) and b) stochastically varying M_{pred} (NI-NVI & CI-CIV) in the range $0.1 < M_{pred} < 0.5$; c) varying both values of M_{pred} stochastically in the range $0.05 < M_{pred} < 0.40$; and d) setting $M_{pred} = 0.1$ for all stages (the base-case).

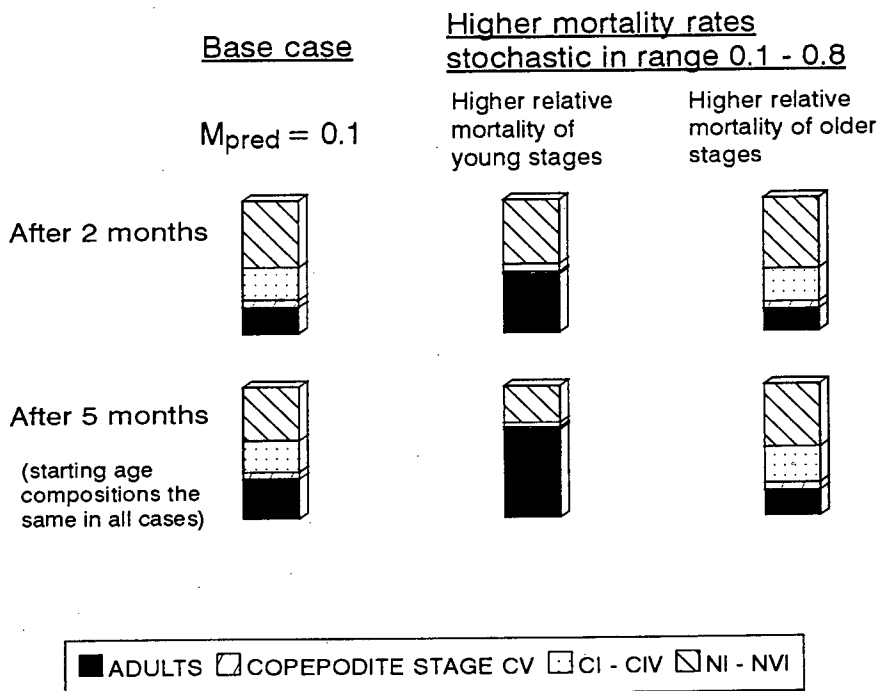


Fig. 3.17 The effect on population composition of higher relative mortality rates of a) the younger stages (NI-NVI & CI-CIV) and b) the older stages (CV & ADULTS).

loss of a large proportion of the adult biomass. However, with the subsequent drop in the level of primary production after the first month, T_{biom} for case (a) converges on T_{biom} for case (b) and both curves stabilize at a lower level, where the loss in CV and adult biomass is only just compensated by new recruitment.

As expected, the effect of simultaneously randomly varying M_{pred} for all stages always resulted in a lower level of T_{biom} than that obtained by varying rates one at a time. This, and the pattern of the predicted trend, results because, if M_{pred} values for the various stages are correlated (curves c&d vs a&b in Fig. 3.16), small or large changes in mortality will be compounded. This explains the similar qualitative trend in curves c and d.

Is the use of a mean mortality rate appropriate?

The simple simulation procedures described above were employed to test mathematically the hypothesis that deterministic mortality rates adequately describe patterns of population growth when averaged over the 'global' rather than the local scale. The results of a large number of individual runs, each assuming that M_{pred} varied stochastically, revealed distinct differences between the predicted patterns of copepod biomass and those derived using a mean M_{pred} value (calculated as the mean of the daily stochastic values). An example of an extreme difference observed in the two predicted patterns of copepod growth is shown in Fig. 3.18a. However, when the mean of 100 runs, each of which assumed that M_{pred} varied stochastically, was plotted, the magnitude of the predicted T_{biom} trend was not noticeably different from that predicted using the mean mortality rate (Fig. 3.18b). This result was consistent for several different stochastic mortality ranges and mean (or deterministic) mortality rates.

In this simulation exercise, the individual runs may be visualized as representing local populations subject to random fluctuations in the predation rate, whilst the mean run result represents the 'global' pattern of growth observed when averaged over a large number (100) of subpopulations, each subject to local differences in the value of M_{pred} . The results obtained therefore suggest that on a local scale, the growth of a copepod population subject to random fluctuations in mortality rate (as roving planktivorous predators cause periodic mass mortalities), cannot adequately be modelled using a mean value for the mortality rate. On a larger scale however, results suggest that dramatic local peaks and troughs in production are averaged out,

so that a mean mortality rate adequately describes the net pattern of population growth.

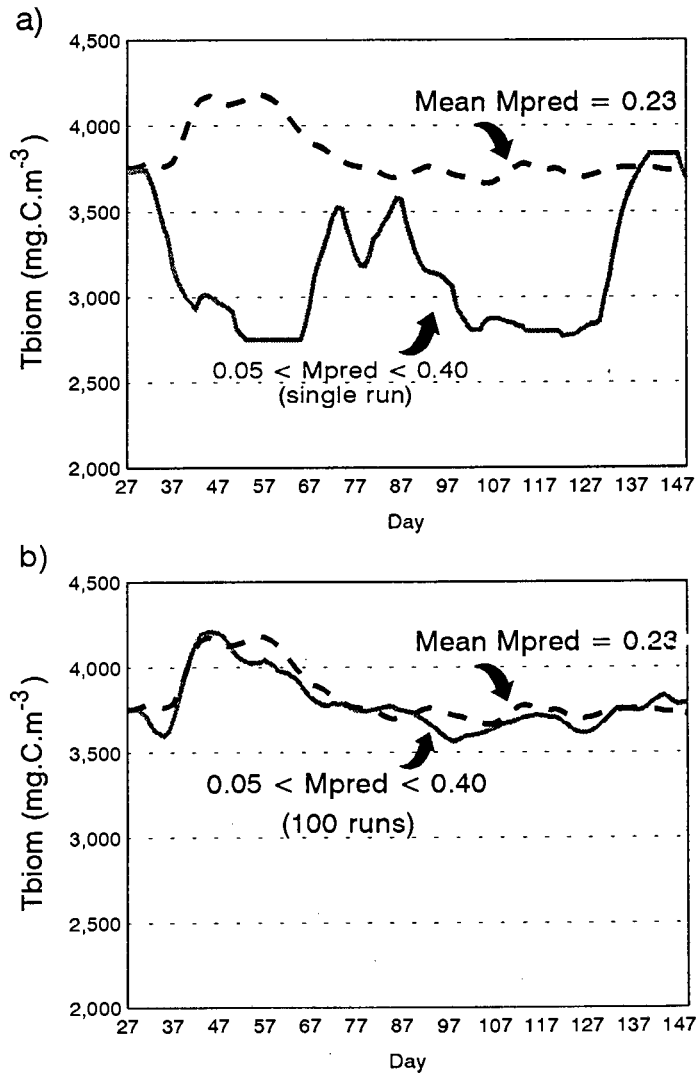


Fig. 3.18. A comparison between the predicted pattern of T_{biom} using a stochastically varying mortality rate versus a mean mortality rate. An example of an individual run is shown in a) while the solid line in b) represents the mean of 100 such runs. The dashed line depicts the mean pattern obtained using a constant mortality rate which is the mean of the stochastic values.

The result presented in Fig. 3.18 is of further interest because it contrasts with the results of studies on the effect of stochastic mortality rates on the dynamics of long-lived populations. Modelling exercises (eg. Tuljapurkar & Orzack 1980, Lande & Orzack 1988, Harwood & Hall 1990) generally predict that the most probable growth rate of populations subject to marked annual fluctuations in mortality rates is slower than the growth rate calculated using mean mortality rates. I ascribe the different

result obtained here to the short generation time of copepods, which allows them, under favourable conditions, to recover rapidly from depleted levels. Hutchings (1992) estimated that a local copepod population, severely impacted by predators, can double its biomass in as little as five days, provided it has access to a sufficiently high concentration of large cells on which to feed (*cf.* Peterson *et al.* 1990, 1992, Verheye 1991, Walker & Peterson 1991). Horizontal transport may also play a role in restocking areas subject to intense local predation (Verheye *et al.* 1991), suggesting that the 'metapopulation' structure of copepod populations allows their persistence.

Stochastic vs Deterministic Egg Mortality Rates

In the model a constant, high egg mortality rate is assumed. If mortality rates are allowed to fluctuate within a specified range and in a stochastic (ie. density-independent) manner, dramatic local population fluctuations result (example in Fig. 3.19). These are substantially dampened when averaged over many runs but population fluctuations are still greater than in the base-case (Fig. 3.19). The mean amplitude of fluctuations was positively correlated with the range within which M_{egg} was allowed to vary. Although the assumption that M_{egg} was density-independent allowed large population 'blooms' to develop, in no instance did the populations continue to increase unchecked because of other mechanisms in the model, such as starvation which causes periodic large reductions in the numbers of younger stage individuals in particular.

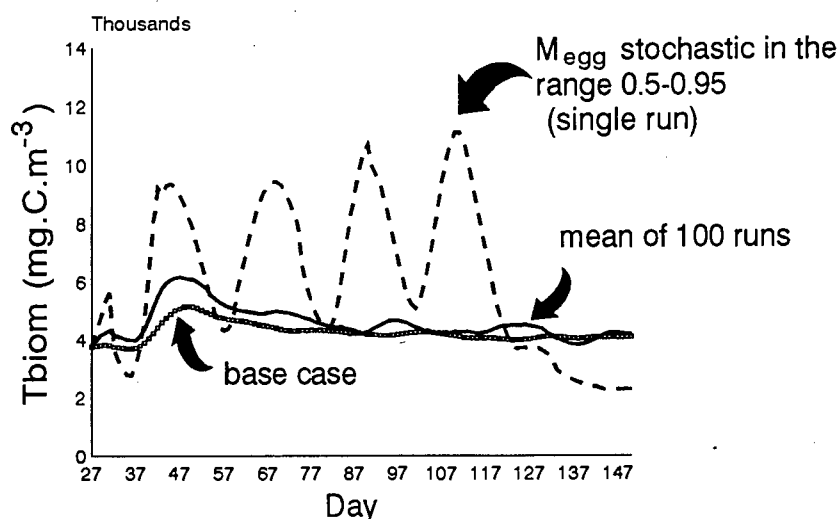


Fig. 3.19. The effect of allowing M_{egg} to vary stochastically within a prespecified range. An example of an individual run is shown as well as the mean of 100 such runs.

The Effect of Food Availability on Development Rates

The model assumes that development rates are retarded when food is limiting. This is an important assumption because its removal results in a 47% increase in the value of $T_{\text{biom}}(27)$ (Fig. 3.20). When feeding conditions deteriorate after the first upwelling cycle, early instars (which are less tolerant of starvation than the older stages) continue to develop at maximal rates in the simulation run and so 'escape' into the older stage classes. In the base-case scenario, the instars develop more slowly during the same unfavourable period and so, because they have lower starvation tolerances, more of them die.

The average effect of assuming that development rates do not depend on food availability is to reduce the interval between population "blooms" by two days and to prolong population peaks (Fig. 3.20). A greater proportion of individuals are able to attain adulthood before conditions become less favourable again.

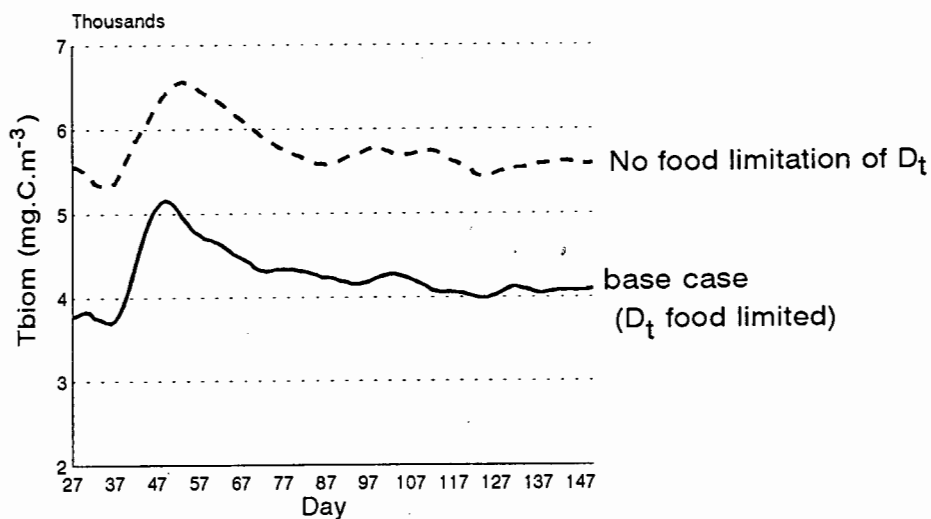


Fig. 3.20. The effect of assuming that total development time (D_t) is not prolonged when food is limiting.

Lopez (1991) hypothesized that "selective culling" of slow developers ensures that apparent development rates of copepod cohorts in the field remain maximal. If this is the case in West Coast mesozooplankton populations, the sensitivity analysis suggests that errors will occur in the model predictions of both the timing and magnitude of population 'blooms'. The arguments of Lopez (1991) raise an interesting question when extrapolated to the West Coast situation where there is a marked seasonal increase in the abundance of anchovy, a size-selective predator. The period in which these migratory fish are most abundant (April to September), also corresponds to

periods of reduced food availability. If the older mesozooplankton stages are disproportionately susceptible to predation over this period, then provided they are able to attain at least the critical weight needed to moult (Carlotti & P. Nival 1992), slow developers may be selected for in certain instances. The optimum growth rate (in terms of individual fitness) in local populations is likely to vary as a function of the timing of fish pulses moving through an area, a mechanism which could substantially increase rather than decrease variability in *in situ* growth rates. It would be interesting to compare cohort development times over the upwelling season and quiescent season to test the hypothesis that, even when food is limiting in the former case, the variability in total development time of cohorts is less than when anchovy are present in large numbers.

iv) Sensitivity to Model Structure

Input Data, Spatial Dimension & Depth Effects

The model is driven by satellite-derived input data which allow horizontal (on the order of 1 km²), but not vertical, resolution of chlorophyll *a* concentration and sea surface temperature patterns. The model does not therefore account for vertical differences in the properties of physical factors or distributions of planktonic animals. In actuality however, the depth structure of the ocean is continuously stratified and these variables may vary substantially at different depths in the water column (eg. Shannon *et al.* 1984a, Mullin *et al.* 1985, Armstrong *et al.* 1987, Verheye & Hutchings 1988). Motivation was presented in chapter two as to the validity of the assumption that vertical differences in chlorophyll *a* concentration do not drastically affect a grazer's performance (see Fig. 2.1). The discussion below addresses the possible effects on the average predicted pattern of zooplankton productivity of vertical differences in temperature and in the spatial distribution of *C. carinatus*.

Temperature: The chief effect of temperature in the model is to influence rates of development of the copepod stages. Vertical differences in temperature may therefore be important if they mediate development rates. Measures of sea surface temperature (SST) were considered reasonable estimators of the average ambient temperature experienced by the younger developmental stages because:

- a) the younger stages generally inhabit the surface layers of the water column, where the higher temperatures confer distinct metabolic advantages on individuals (Vidal 1980), and
- b) temperature variation is small in the upper mixed layer.

In the sensitivity analysis an attempt was made to estimate the maximum error which could be attributed to vertical temperature gradients.

Superimposing mean migration amplitudes for copepodite stages CI to CIV (Verheye & Field 1992) on vertical profiles of temperature variation (Mitchell-Innes & Walker 1991) suggests that individuals experience average changes in temperature of between 3 and 5°C as a consequence of their vertical migratory behaviour. Because thermoclines may limit the maximum depth penetrated by the young stages (Verheye 1989), and the naupliar stages occur close to the surface of the water, the vertical temperature gradient experienced on average by the young stages may be less than this. Also, the metabolic rates of copepods do not respond instantaneously to environmental conditions, but rather in a cumulative fashion (Huntley 1988), which implies that their growth rates must be a function of some average or integrated measure of the ambient environmental conditions experienced by an individual.

A worst case scenario was simulated, in which it was assumed that the physiological response of a copepod in the field is actually a function of temperatures T which are, on average, 5°C less than satellite-derived estimates of SST. This scenario almost certainly overestimates errors in production which could be attributed to the effect of vertical differences in temperature on development rates. A 5°C decrease in average temperature results in approximately a 50% increase in total development time D_t , and hence a relative reduction in $T_{\text{biom}}(27)$ of nearly 60%. Slower development rates result in a slower transfer of biomass from the younger to the older age groups and hence a shifting of age structure was observed, with greater relative abundance of the younger stages. This in turn affected the cumulative number of eggs produced: a 50% decrease in development rates over the 27-day model run resulted in an 8% decrease in the mean number of eggs produced. Assuming an error of anywhere between 1° and 5°C in calculating D_t did not in any instance improve the fit to the anchor station series (Table 3.1). A reasonable estimate of the decrease in temperature, relative to the satellite-derived SST estimate, that should be used to calculate development rates is thought to be 2°C. This results in a 30% decrease in $T_{\text{biom}}(27)$.

Differences in the value of $T_{\text{biom}}(27)$, relative to the base-case, remained stable over time (Fig. 3.21). The average trends revealed distinct differences in the time scale of the model's response - lower temperatures increase the gap between population peaks, while higher temperatures allow biomass to accumulate far quicker following a trough in production. Successively larger increases or decreases in T result in a

convergence of model predictions because temperature (and therefore D_T) is constrained within reasonable limits.

More work on the way in which vertical differences in temperature affect development rates needs to be done before this facet can be incorporated into the model in an objective fashion.

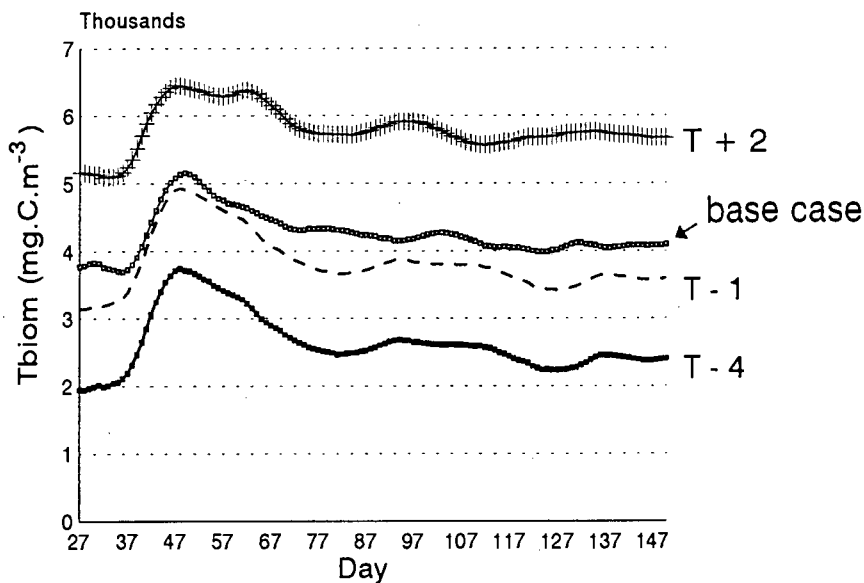


Fig. 3.21. Sensitivity analysis to test the hypothesis that vertical temperature differences affect development rates. The graph shows the average effect on T_{biom} of changing the value of T , the temperature which is used to calculate development rates in the model.

Diel Vertical Migrations (DVM): Ontogenetically-linked changes in the use of different depth strata by *C. carinatus* may be a form of population maintenance (Verheye & Field 1992). By altering rates of horizontal advection of the different developmental stages, DVMs result in differences in the cross-shelf distribution of developmental stages (Verheye & Field 1992).

Food limitation plays a fundamental role in regulating the DVMs of *C. carinatus* because at low food densities individuals need to spend longer periods of time feeding near the surface, despite the increased predation risk incurred (Verheye & Field 1992). To test the effects on model output of increased predation risk when food is limiting, the predator-induced mortality rate M_{pred} was increased by a factor of a) 20%, b) 50% and c) 100% whenever chlorophyll concentrations fell below the grazing threshold F_{crit} . No major quantitative effects were manifest: doubling predation risk when food was limiting resulted in no more than a 16% decrease in $T_{biom}(27)$ relative to the base-case. The increased number of individuals which

succumb to predators when food is limiting does not drastically affect model predictions because large mortalities due to starvation occur over these periods.

Analysis of the average effect on longer term trends suggested however that changes in the qualitative trend occur (Fig. 3.22). This results because increased mortalities under unfavourable environmental conditions retard the population's recovery rate when food is no longer limiting. Populations subject to more than about a five-fold increase in predation risk when food is limiting are unable to recover sufficiently after poor conditions to sustain numbers at a stable level.

An interesting twist arises from the work of Saiz *et al.* (1993) who demonstrated experimentally that the presence of a predator increased the rate of egg production by a calanoid copepod. Reasons cited included selective removal of individuals with lower fitness, and increased *per capita* food availability due to reduced grazing pressure. This has interesting implications for modelling population dynamics in the presence of predators.

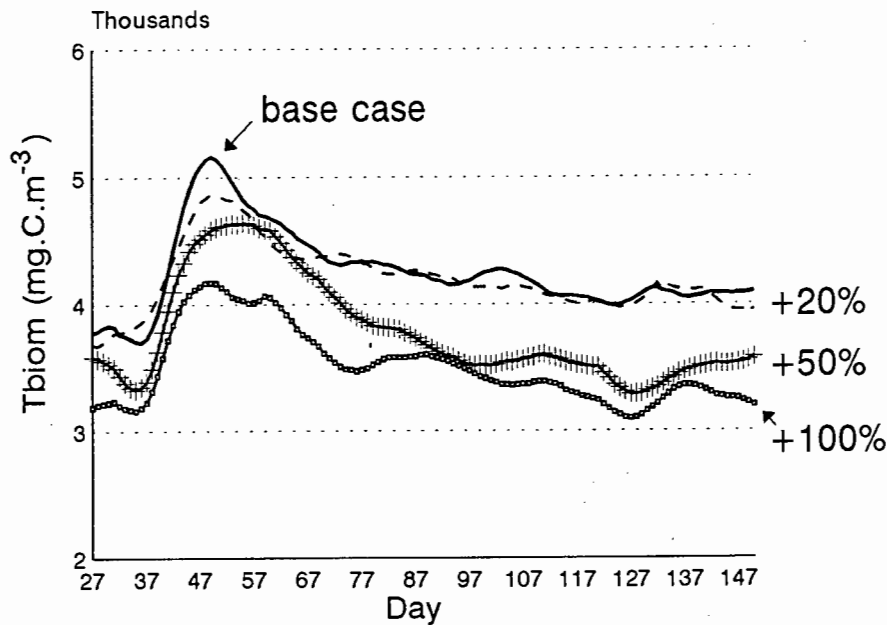


Fig. 3.22. The effect on T_{biom} of assuming that predation rates are increased by the factor indicated when food for copepods is limiting.

Use of Interpolation

Satellite-derived estimates of chl. *a* concentration and SST may not be available on a daily basis and the estimation of chlorophyll concentrations may be further complicated on any one day by factors such as cloud cover, fog or aeolian dust (Shannon 1985). Sensitivity tests were conducted to test the effect of gaps in the

input data series on model predictions, assuming that input data were updated every fourth day. For comparative purposes, two forms of interpolation were used: the first assumes a linear increase/decrease between data points while in the second case, the same value was retained for four days (constant interpolation) (Fig. 3.23a). The results, relative to the base-case which uses input data that are updated on a daily basis, revealed no major effects on model predictions (Fig. 3.23b): after 27 days T_{biom} is underestimated by only 3.4% using a constant form of interpolation and overestimated by 17.9% using a linearly increasing/decreasing interpolation technique.

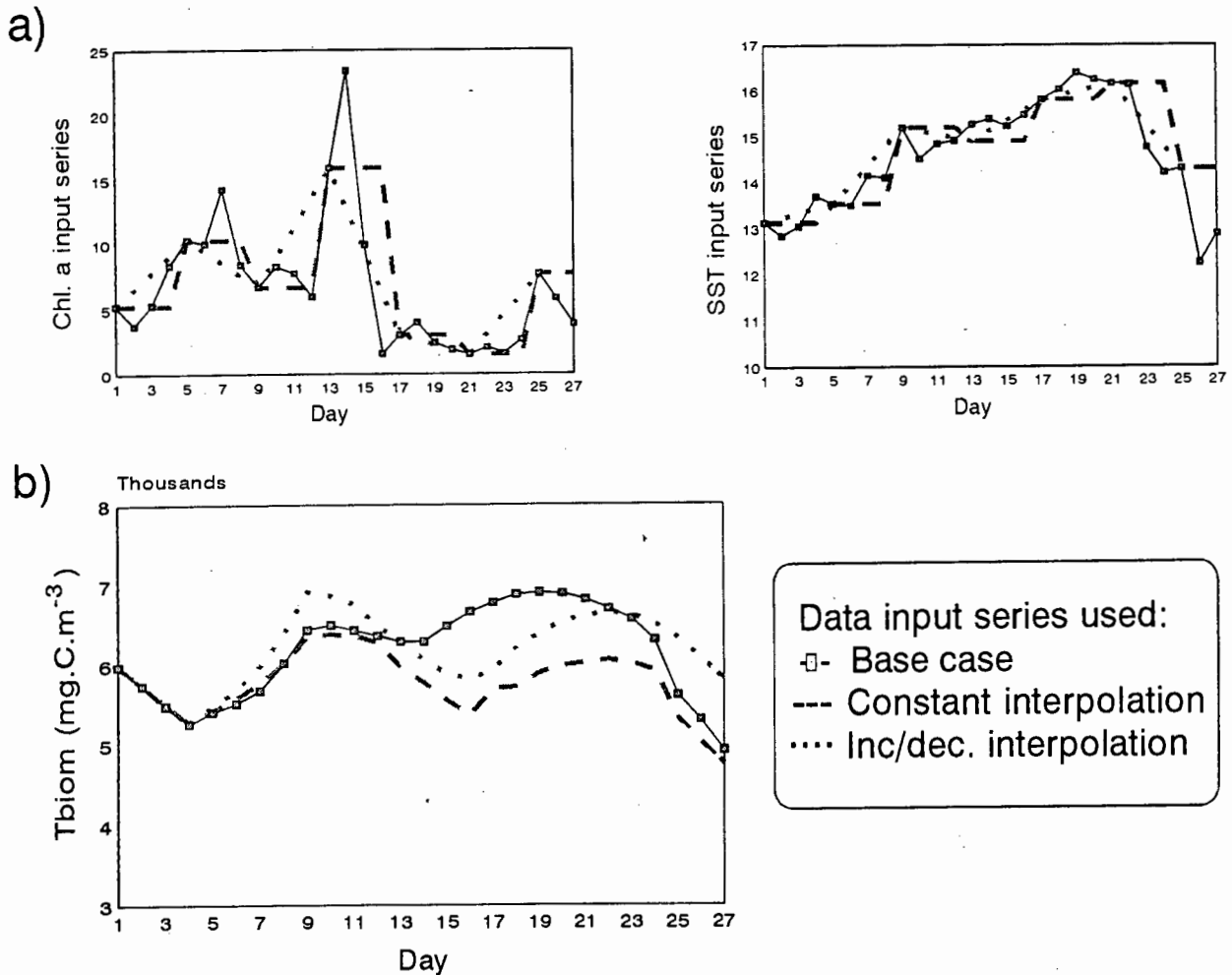


Fig. 3.23. The effect on model predictions of assuming that input data from the anchor station series was only available every fourth day. The curves in a) compare the structure of input data using a constant or linearly increasing/decreasing form of interpolation, while the curves in b) compare the effects on T_{biom} .

The latter form of interpolation is considered biologically more realistic and the effect of its use on model predictions was explored further by using six separate 5-month data series.

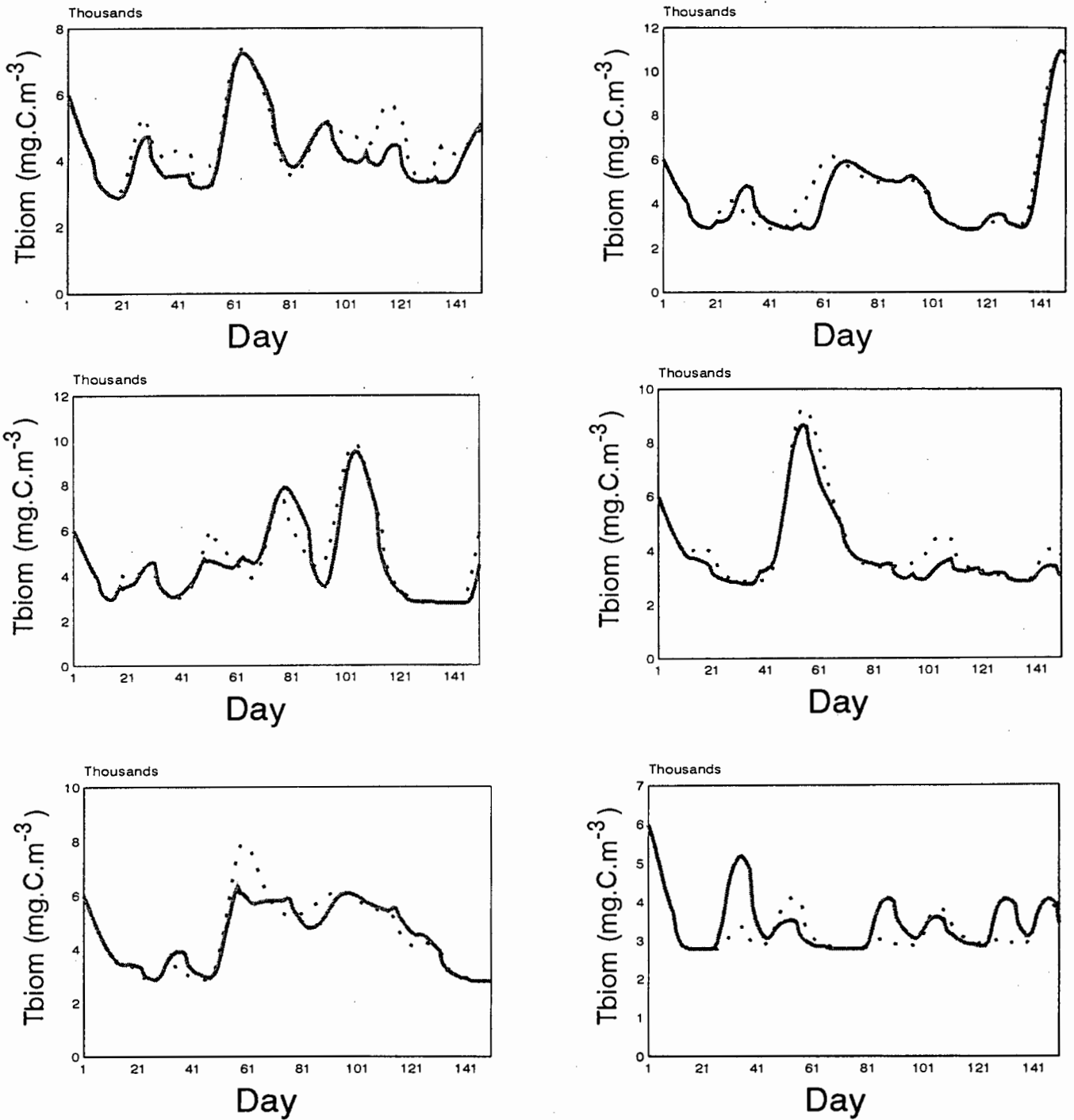


Fig. 3.24. Examples of the effect on T_{biom} of using a linearly increasing/decreasing form of interpolation between input data points. In each instance, the solid line shows the T_{biom} trend predicted using daily inputs of chl. a and SST, while the dotted line assumes that input data are updated every fourth day.

The predicted T_{biom} trend generated in each instance under the assumption that data points were only available every fourth day, was compared with predicted patterns of productivity generated using the continuous input series. Results obtained in all instances were of the same scale and suggested that the use of linear interpolation will not drastically affect model predictions (Fig. 3.24).

CONCLUSIONS

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: 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 greatest sensitivity to parameters which are difficult to determine empirically and about which the least is known (Fig. 3.25). 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 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).

There is a need to quantify rates of predator-induced mortality. While better quantification of rates of predation on the juvenile stages is beyond the scope of this thesis, an attempt will be made in chapter five to quantify seasonal differences in the rate of predation on the larger stages. Model results suggest tentatively that the use

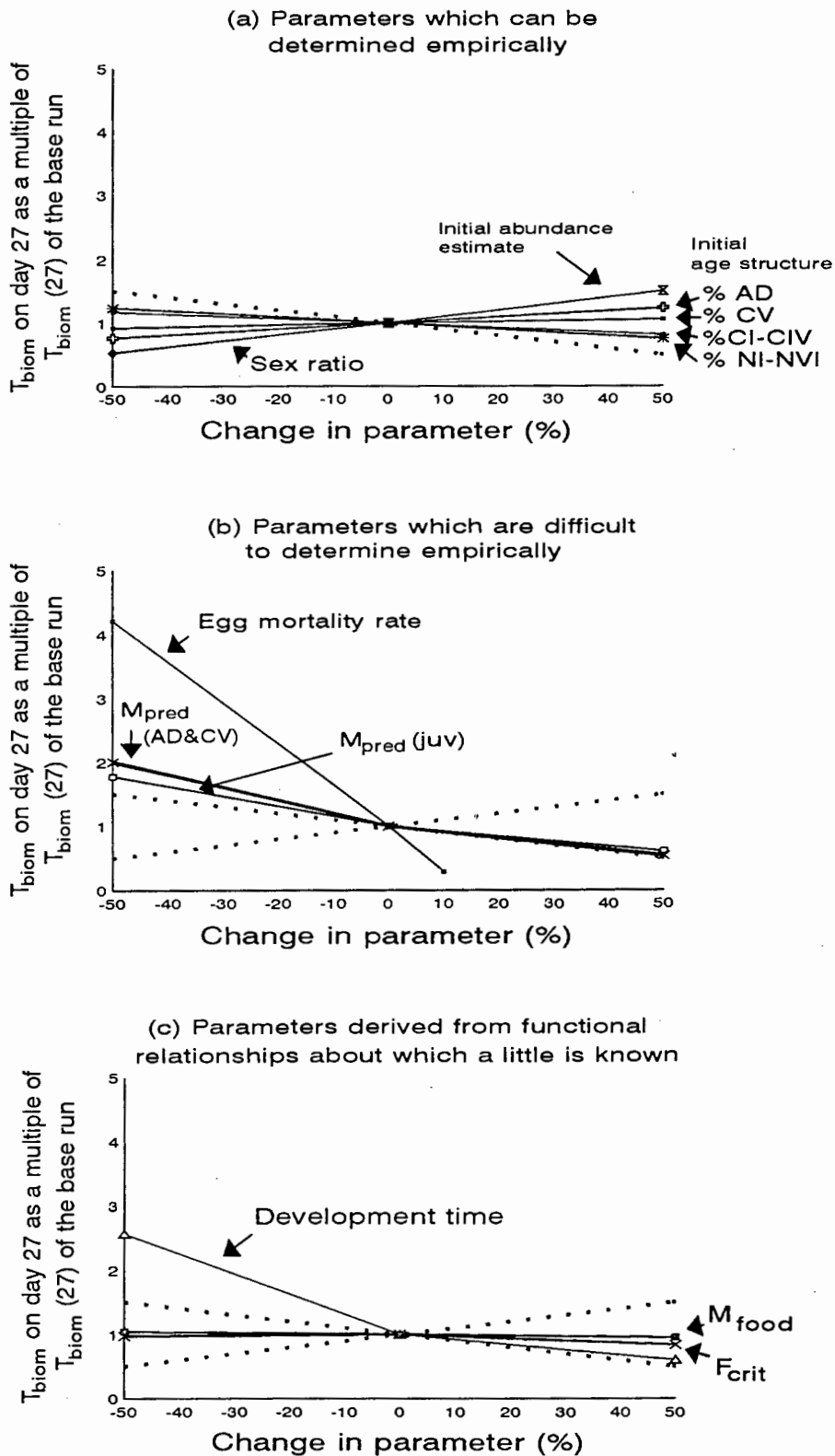


Fig. 3.25. Comparison of the model sensitivity to different parameters. The curves show the effect on the value of T_{biom} predicted on day 27 (using the anchor station input series), when parameters were changed one at a time. The dotted lines represent changes in parameters which result in changes on exactly the same scale in the model's response.

of an average mortality rate yields an adequate description of the net pattern of population growth when integrated over a large number of local populations, each subject to stochastic variations in the rate of mortality.

As expected, changes in development rates result in changes in the period of population fluctuations. The assumption that average *in situ* development rates are food-limited is an important one. Because development rates are an integrated response to ambient temperature, it was estimated that failure of the model to account for vertical differences in temperature gradients resulted on average in the model overestimating production rates by 30%. An interesting laboratory study to solve this dilemma requires containers of a sufficient height to permit estimation of maximal growth rates as a function of an integrated response to vertical temperature differences. The qualitative and quantitative sensitivity of the model to changes in development rate suggests that continued effort should be directed towards obtaining a greater understanding of both the nature of the variability associated with this parameter and the underlying causal mechanisms responsible for the observed variations.

It was hypothesized that, in general, satellite-derived data will provide an adequate description of the ambient food and temperature environment experienced by a copepod. Furthermore, neither the use of a depth-independent approach nor the need to interpolate between input data points were found to seriously affect model predictions.

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 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: for example, 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, for example, 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} .

Table 3.1. Sum of squared differences between daily *C. carinatus* copepodite biomass estimates measured during a 27-day Anchor Station study conducted in St Helena Bay in 1987 (Verheye 1991), and copepodite biomass predicted under various sensitivity test scenarios. Sum of squares measures are used as an index of the goodness of fit of various model versions, as compared with the fit obtained using the base-case model version. Sensitivity tests which resulted in an improved fit of the model to the observed time series are highlighted using an asterix *.

Sensitivity Test	Sum of Squares
Base-case	2600
<u>Sex ratio:</u>	
F:M (+10%)	2594*
F:M (-10%)	2639
F:M (-20%)	2709
F:M (-30%)	2851
<u>Initial proportional abundance of model group:</u>	
NI-NVI (+50%)	2842
NI-NVI (-50%)	2631
CI-CIV (+50%)	2885
CI-CIV (-50%)	2675
CV (+50%)	2568*
CV (-50%)	2656
ADULTS (+50%)	2678
ADULTS (-50%)	2897
<u>The grazing threshold Fcrit:</u>	
Fcrit = 0.5	2906
Fcrit = 1.0	2628
Fcrit = 2	2631
Fcrit = 4	2719
<u>Mortality rate Mpred:#</u>	
Mpred (NI-NVI) (-50%)	2596*
<u>Sea surface temperature (used to calculate D_t):</u>	
SST -1°C	2984
SST -2°C	2649
SST -3°C	2629
SST -4°C	2706
SST -5°C	2893

Due to the large number of different sensitivity tests conducted on mortality rates in the model, results of tests yielding sum of squared differences greater than the base-case value are not presented.

CHAPTER 4

Generation and Importance of Patchiness

Spatial patterns of patchiness in plankton distribution arise and persist because of the direct, indirect and combined effects of physical and biological processes (Steele 1978). The importance of, and the patterns of variability induced by, processes causing spatial patchiness is largely scale-dependent (Haury *et al.* 1978, Davis *et al.* 1991). For example, on the coarse and mesoscale, upwelling may be responsible for generating spatial heterogeneity, while on the fine-scale (meters to hundreds of meters) physical processes, such as local turbulence (Rothschild & Osborn 1988, Yamazaki *et al.* 1991, Haury *et al.* 1992), or biological processes, such as predation effects (Kerfoot & Sih 1987), may be important.

Patchiness occurs on local scales because organisms are affected by processes operating on the same scale as their population dynamics: for example, micro-organisms respond to micro-scale physics (Yamazaki & Osborn 1988). Davis *et al.* (1992) filmed actively swimming copepods in the field forming micro-scale colonies of the order of 10 cm. Starved copepods aggregate in the vicinity of a localised food source (Poulet & Marsot 1980, Poulet & Ouellet 1982). Patterns of patchiness in copepod populations are therefore reinforced to some extent by the patchiness of their food source, and relatedly, by their ability to detect dense food concentrations from afar (DeMott & Watson 1991). Spatial patterns of variability are also generated because of different species-specific responses to the physical structure of a water mass (Kjørboe 1993).

The importance and consequences of various patch attributes to the growth and survival of an organism needs to be considered on the same scale as an ecologically important ambit of the organism (Haury *et al.* 1978). The term ambit describes the sphere of action or influence of individuals during the course of movement through their environment (Haury *et al.* 1978). The ambit of a copepod is on the order of meters per day and therefore the fine-scale patchiness is the scale relevant to their foraging movements and the scale on which individual interactions between zooplankton take place. Studies which have been designed to look quantitatively at fine-scale aggregations have shown that pronounced variations in the numerical abundance of zooplankton species occur over small distances.

Small fluctuations in biomass at short time and space scales may substantially affect the average trophodynamic patterns observed over larger scales, so that the importance of processes operating, for example, on the micro-scale, should not be

underestimated (Rothschild 1992). Patchy prey distributions mediate to varying degrees the flow of energy through food webs by increasing the variance of the predator-prey encounter rate (Rothschild *et al.* 1989). Several studies (eg. Rothschild & Osborn 1988, Schneider & Bajdik 1992) have recently emphasized the fact that failure to consider the effect of small-scale turbulence on predator-prey encounter rate may result in incorrect estimates of zooplankton feeding rates. Because turbulence partly determines the degree of spatial patchiness in a habitat, the present study may provide some insight into the way in which the transfer of primary to secondary productivity is damped or propagated in response to different turbulence characteristics of the environment. Although low levels of turbulence increase encounter velocities in the plankton, higher levels tend to increase the degree of dispersion of phytoplankton populations in water masses (Lasker 1975, Haury *et al.* 1990, Davis *et al.* 1991).

Background to the Model

A central premise of the model is that the major ecological effect of introducing spatial patchiness into a system is to influence the relative distributions of grazers and their prey, and hence the patterns and consequences of coupling and decoupling between zooplankton and phytoplankton populations. It is in this light that the effect of spatial patchiness on community structure is therefore modelled.

In the discussion which follows, the degree of patchiness refers to the number of distinct prey aggregations or patches in the model area, while patch intensity refers to the intra-patch prey concentration. A summary of the model structure is presented in Fig. 4.1. As before, the model is tuned to simulate the population dynamics of the copepod *Calanoides carinatus* along the West Coast, and prey availability is expressed in terms of net-chlorophyll (>10 μ m fraction) concentration. Different species composition of patches is therefore not modelled explicitly.

The model area (which can be set to any desirable size) is divided into 50x50 cells, each measuring 10m X 10m. The dynamics of a copepod population within an individual cell is described by a local population equation. This does not imply however that the organisms are restricted to a particular cell. Instead, each local population has access to any other cell within the scale of its daily ambit and the division is merely to estimate the performance of each local aggregation as a function of potential prey availability. Prey availability is thus not constant throughout the environment, but exhibits different levels of spatial variability. The program

(APPENDIX III to thesis) used for model simulations is therefore almost identical to that used in chapter two, except that the spatial area is divided into a number of separate cells, with phytoplankton prey availability within each cell being generated as described in the text. Model output therefore represents an overall average integrated over 50x50 discrete cells.

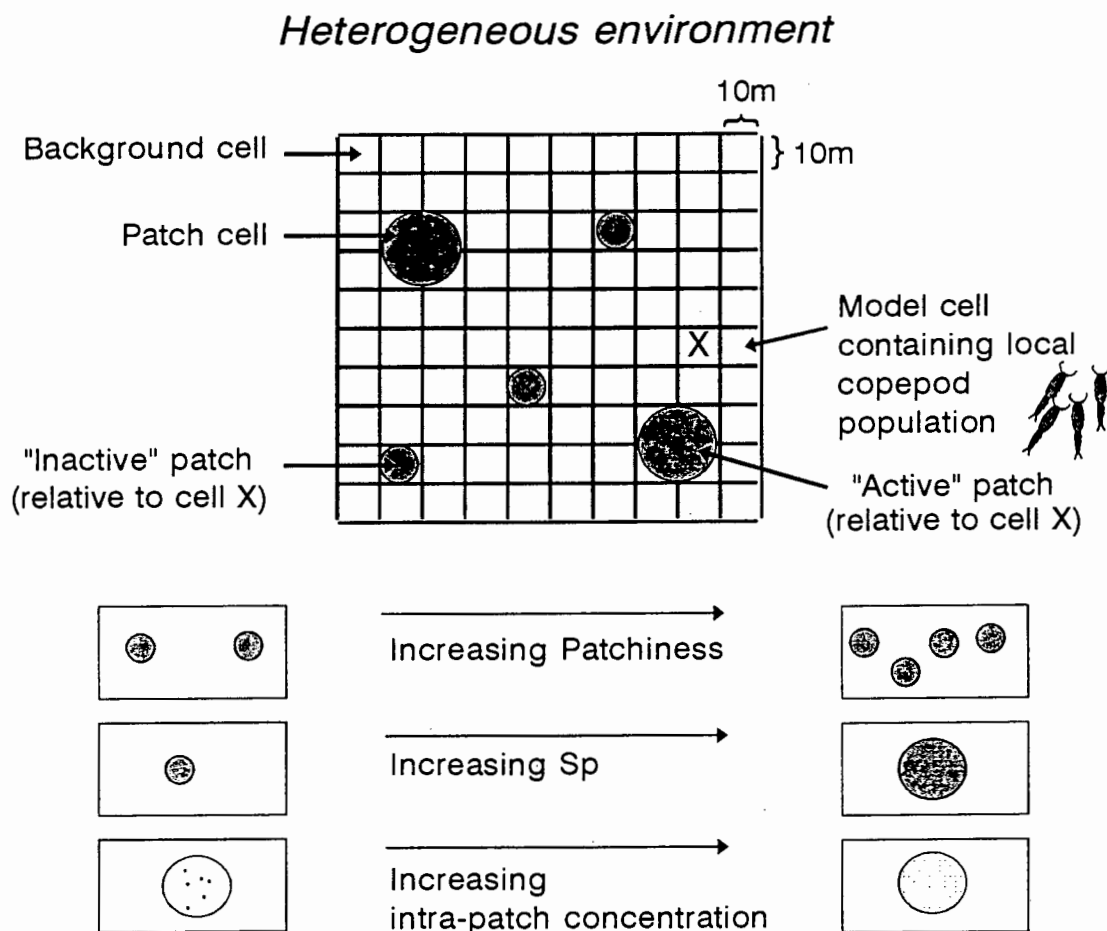


Fig. 4.1. Summary of the basic model structure and definitions. The spatial area is divided into a number of cells which represent the position of local copepod aggregations (subpopulations) relative to food patches of varying size and intensity. Subpopulations only potentially have access to food patches (termed "active" patches) closer than a minimum distance MD defined in the text. In the model the level of patchiness is increased by increasing the number of patches, the size of individual patches is altered by changing the spatial dimension coefficient S_p , and intra-patch chlorophyll *a* concentration is increased by increasing the patch intensity coefficient INT_p .

A basic assumption of the model is that the phytoplankton available to a copepod in any cell is a function of the surrounding degree of patchiness, patch intensity and the

mean distance to an aggregation of food organisms. For each cell, prey patches closer than a maximum distance MD are referred to as 'active' patches as they are potentially available to the cell's local copepod population. MD is calculated as twice the distance of the nearest patch to a cell - this is because the animals have a greater probability of locating prey patches closest to their present spatial position. For copepods in the vicinity of food patches, MD is thus not calculated absolutely in terms of the maximum active swimming speed a copepod can maintain while foraging: rather, the maximum scale of a copepod's daily ambit is modelled implicitly by assuming that the probability of reaching a patch on a particular day is inversely proportional to the distance to that patch. Copepods are assumed unable to reach prey patches five or more model cells distant from their present position. For copepods already in a patch, prey availability is synonymous with intra-patch prey concentration.

Modelling Different Patch Attributes

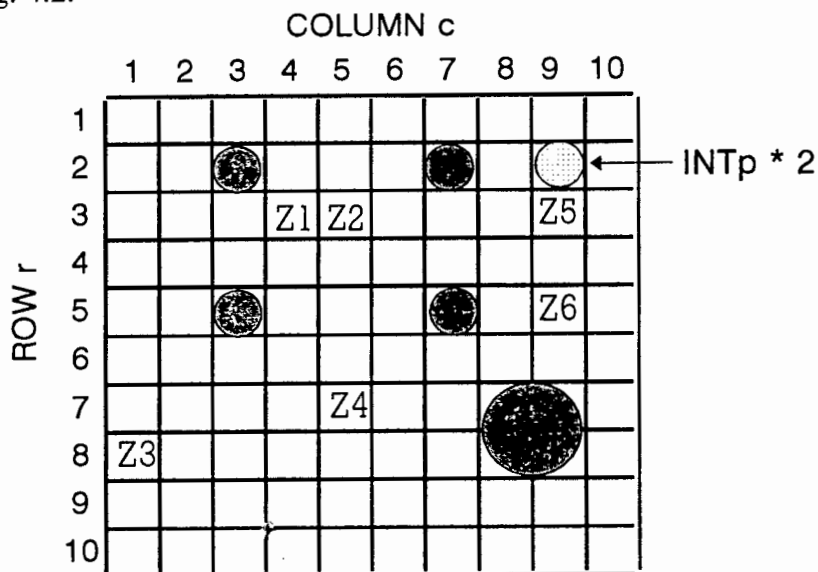
The degree of patchiness in the model area is depicted by the number of patches p and simulations are performed for a range of p values. The position of each of the p patch centres is generated randomly, along with a spatial dimension coefficient S_p which determines the size of each patch. A standard intra-patch chlorophyll concentration (PCHL) is input into the model each day and patch intensity may be varied by changing a patch intensity coefficient INT_p . The base-case has INT_p set at one for all patches and represents a model area with a constant intra-patch prey concentration. Prey availability (PA) in each of the background cells b is then calculated as a function of the surrounding degree of patchiness using the relation:

$$PA_b = \left(\sum_{i=1}^a \left(\frac{\sqrt{S_i} \times INT_i}{d_{ib}} \right)^a \right)^{\frac{1}{a}} \times PCHL \quad (4.1)$$

where a is the number of 'active' patches calculated for each cell b , and d_{ib} is the shortest distance between background cell b and the i th 'active' patch centre.

The exponentiation process in equation (4.1) ensures that the most distant food patches contribute relatively less to a copepod population's probability of finding food. The equation uses the square root of S_p because, as a copepod moves through a body of water, the probability of finding a food patch is assumed proportional to the linear dimensions of the patch. For a circular patch, the linear dimension is proportional to the square root of the surface area of the patch.

The distance d_{ij} is calculated in units of model cells so that it is effectively independent of the exact dimensions of a model cell. The advantage of this method is that zooplankton production can be quantified as a function of different degrees of patchiness, without knowledge of the exact scale of a copepod's daily ambit. To illustrate how equation (1) works, values of PA_i are calculated for six different zooplankton aggregations as a function of their proximity to the various food patches shown in Fig. 4.2.



Examples of Prey Availability calculated for zooplankton aggregations Z1 - Z6:			
Zooplankton aggregation	No. of active patches	Distance	PA_i
Z1	2	$d_{11}=1.41,$ $d_{12}=2.2$	3.37
Z2	4	$d_{21},d_{22}=2.2$ $d_{23},d_{24}=2.82$	2.34
Z3	1	$d_{31}=3.6$	1.11
Z4	3	$d_{41},d_{42}=2.82$ $d_{43}=3$	2.91
Z5	1	$d_{51}=1$	4
Z6	4	$d_{61},d_{62}=2$ $d_{63}=3,d_{64}=3.6$	4.24

Fig. 4.2. A schematic diagram and accompanying table to illustrate the method used to calculate potential prey availability for each subpopulation in the model. Shown are six local zooplankton aggregations, distributed differently with respect to six food patches in the model area. The standard intra-patch chlorophyll a concentration is set at 4 mg.m^{-3} in this example, and INT_p is one for all patches except patch(2,9), which is twice as dense as the other patches. The spatial dimension coefficient S_p is one except for a single patch with $S_p=4$. The table shows values of PA_i , calculated as a function (Equation 4.1) of each subpopulations proximity to food patches (termed "active" patches) closer than a minimum distance. Trivially, for subpopulations already in a food patch, PA_i is equal to the intra-patch chlorophyll a concentration.

The major patch attributes considered in the model are therefore the number of patches, patch intensity and the spatial dimensions of the patches. The ecological consequence of patchiness also depends on the temporal persistence of the pattern (Haury *et al.* 1978). Patch longevity is not modelled directly here but different patterns of patch persistence will arise as a consequence of the daily updates of prey abundance and the random generation of patch centres (ie. there is no limit imposed on the temporal persistence of a patch).

Estimating the Effect of Spatial Heterogeneity

In averaging local dynamics over a large horizontal area, the basic model developed in chapter two may be thought of as an homogeneous analog of the present model since it assumes an average density of zooplankton grazing on an average phytoplankton density. The effect of different patterns of spatial variability on zooplankton-phytoplankton interactions is quantified by comparing total zooplankton biomass (copepodites only) predicted using a patchy environment ($BIOM_p$) with that predicted using an homogeneous analog ($BIOM_h$). In both instances the integrated prey availability for the whole model area is the same, but its distribution varies.

The Base-Case

The model was initialized using an initial abundance estimate of $N_1=402$ individuals. m^{-3} and by assuming a stable age structure (see chapter 2). Base-case values for PCHL were obtained using the input series presented in Figure 4.3, which is based on the anchor station input series (see chapter 2), except that it includes only a single upwelling cycle. A maximum intra-patch chlorophyll *a* concentration of 15 $mg.m^{-3}$ was allowed. The daily estimates of sea surface temperature input into the model were assumed spatially homogeneous.

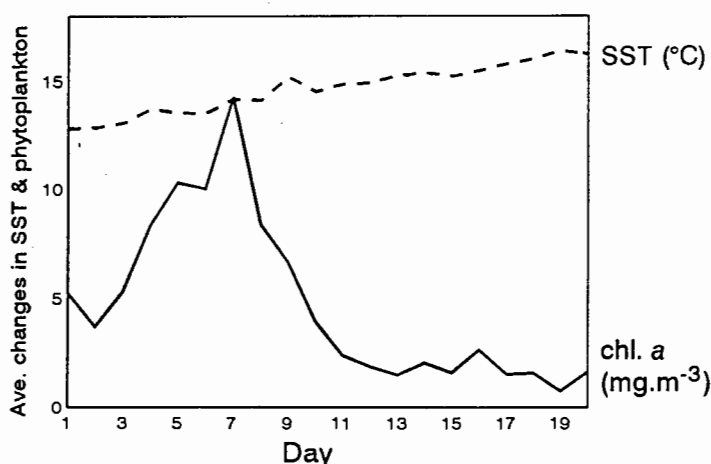


Fig. 4.3. Time series of the mean chlorophyll *a* concentration and sea surface temperature used as inputs into the model.

RESULTS AND DISCUSSION

Temporal Lag in Response to Patchiness

If a homogeneous environment is assumed, the temporally patchy chlorophyll *a* input series results in at most a 18% change in the predicted 20-day T_{biom} trend (Fig. 4.4). At a temperature of 15°C, which lies within the base-case temperature range, *C. carinatus* eggs take approximately 6 days to develop to copepodite stage CI individuals (equation 2.5). Consequently, in the model there is approximately a 6-day lag between the peak in primary production and the increase in the biomass of the copepodite stages.

As a preliminary means of investigating the effect of superimposing spatial patchiness on the temporal pattern of chlorophyll *a* abundance, it was assumed that in a heterogeneous environment the phytoplankton was aggregated in only one quarter of the total model area. The spatial dimensions and location of the individual patches in the model area were determined daily in a random fashion, and INT_p was set at 4. The average chlorophyll *a* concentration in the heterogeneous environment was slightly less than that in the homogeneous environment because of the upper chlorophyll *a* concentration limit allowed in the model.

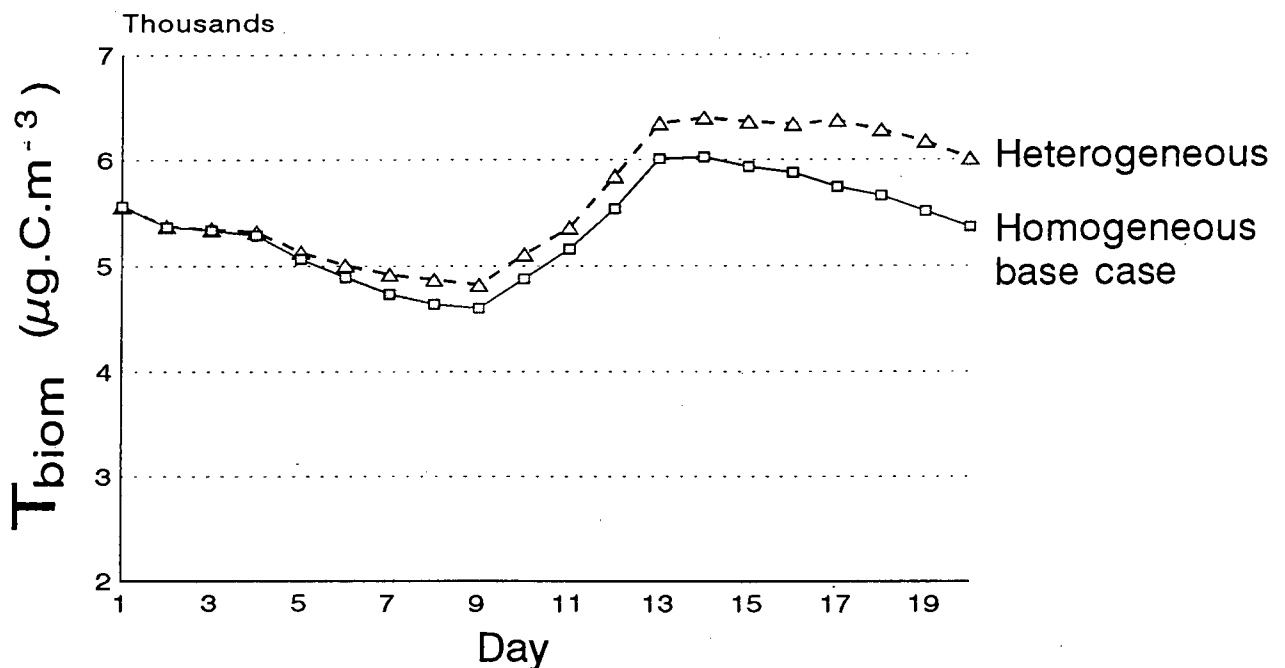


Fig. 4.4. The effect on T_{biom} of assuming that food for copepods is concentrated in patches covering one quarter of the environment. The base-case predicts T_{biom} as a function of homogeneously distributed food concentrations.

The predicted T_{biom} trend (Fig. 4.4) suggests that for high average chlorophyll a concentrations, there is only a small difference (maximum = 5%) in the average production rates and hence in the standing stocks of copepods in the two environments. This is because in the model copepods not in a food patch still have a good probability of finding a reasonable concentration of food so that average production rates are not drastically reduced by the spatial mismatch between the copepods and their food. An implicit consequence of the model equations is that the probability of a copepod finding food is proportional to the average chlorophyll a concentration. Furthermore, the above-average production rates in the food-rich patches do not drastically increase the overall average because, under favourable conditions, chlorophyll a concentrations are near-saturating anyway. The functional response of copepod egg production to chlorophyll a concentration (Fig. 2.2) therefore partly dampens the effect on T_{biom} of spatial patchiness during periods of high chlorophyll a concentrations.

Poor average feeding conditions:

Conversely, under less favourable conditions, the average production rate predicted for an area with a few above-average production areas and several below-average areas, is greater than that predicted for an area with an homogeneously distributed average production rate. In the homogeneous environment, there is a universal effect on local zooplankton aggregations of chlorophyll a concentrations falling below the grazing threshold level on day 10: egg production and development rates are retarded, and after even a short starvation period, the recovery of egg production is affected and the juvenile (particularly the naupliar stages) mortality rate M_{food} (see chapter 2) increases.

In the heterogeneous environment, while more subpopulations are adversely affected by the factors listed above, the persistence of high quality food patches permits the subpopulations in their vicinity to maintain high productivity rates. This overcompensates for the almost complete lack of food in other subregions.

As expected, there is a temporal lag in the response of T_{biom} to spatial patchiness, which manifests itself as a gradual amplification of the difference between the two T_{biom} trends (Fig. 4.4). This difference stabilizes with time so that under the present scenario spatial patchiness during unfavourable periods results in approximately a 12% increase in the predicted T_{biom} trend.

Temporal and Spatial Patchiness

To investigate further the relationship between temporal and spatial patterns of patchiness, 16-day simulations were run for each of a range of different levels of patchiness. Different levels of patchiness were simulated by changing the number of patches in a simulation. A value for PCHL was obtained for each day (from Fig. 4.3) and the degree of spatial heterogeneity in the model area increased further by randomly generating S_p and INT_p for each patch. Both S_p and INT_p were constrained in the range 1 to 4 (integers only).

The average phytoplankton biomass available to copepods on a daily basis was calculated as the mean of the chlorophyll *a* concentrations averaged over all model cells. The average chlorophyll *a* series obtained for each simulation was used to drive the homogeneous analog of each simulation. The ratio of T_{biom} in a patchy environment to that predicted in a homogeneous environment was plotted as a function of both time and the number of patches per 0.01 km^2 .

In the homogeneous environment, the initially high chlorophyll *a* concentrations are well above the grazing threshold level so that no food limitation of copepods is assumed to occur. In contrast, the inequitable distribution of food in a patchy environment means that even though average feeding conditions are good, part of the population will experience spatial mismatches with the available food. In a patchy environment, average copepod development rates will therefore be slightly less than that predicted in a homogeneous environment with a high average chlorophyll *a* concentration. This effect manifests itself rapidly on T_{biom} in the patchy environment ($BIOM_p$) because recruitment to the copepodite stage is retarded in the spatially mismatched copepod aggregations. The ratio $BIOM_p:BIOM_H$ is therefore initially less than one (Fig. 4.5), except where food patches were numerous or large enough to ensure that most individuals had access to a reasonable food patch. Because the position of patches is randomly determined in the model, the relative proportion of subpopulations which are food-limited is exacerbated in simulations with a more clumped spatial arrangement of food patches.

As before, the greatest differences between $BIOM_p$ and $BIOM_H$ arise in response to low average feeding conditions. At high levels of patchiness, average growth trends exceed those predicted for a homogeneous environment by almost 30%.

Fig. 4.5. The effect of different degrees of spatial patchiness on the ratio of total copepodite biomass predicted for a patchy environment ($BIOM_p$) to that predicted for an homogeneous environment with the same average food concentrations ($BIOM_H$). Spatial patchiness was increased by increasing the number of patches per 0.01 km^2 , while the size and density of individual patches was randomly determined in the range 1-4. Differences in population growth patterns in the two environments expand with time because of temporal variability in the daily standard intra-patch chlorophyll *a* concentration (PCHL) used to drive the model (Fig. 4.3), and because of the time for differences in copepod productivity to manifest themselves as a change in copepodite biomass.

The implication is that under some circumstances, the relative importance of spatial variability in food availability to determining average copepod growth rates in a region may exceed that of short-term temporal patterns of food availability. Mullin (1991) found that for two pelagic copepod populations in the Southern California Bight, mesoscale spatial variation in the biomass of phytoplankton was significant relative to larger-scale, seasonal variation. Furthermore, because the temporal variability in egg production rates exceeded the temporal variability in the mortality of the juvenile stages of the two copepod species (Mullin 1991), spatial variability in primary production levels may be an important determinant of copepod growth rates because of its potential impact on reproduction rates.

With a relatively low number of patches (and a random distribution of patch sizes and intensity), the distances between patches are too great to be adequately balanced by the average return from a patch, and $BIOM_p$ is slightly less than $BIOM_H$ (Fig. 4.5).

Changing Patch Intensity Gradients

To quantify the effect on T_{biom} of different geometric distributions of patches and intra-patch concentration gradients, 16-day simulations were run at levels of patchiness ranging from five to forty patches per 0.01 km^2 , in steps of five. For each patchiness level, 4 separate simulations were run. The total integrated chlorophyll *a* concentration was the same in all four simulations, but intra-patch chlorophyll *a* concentration was varied by changing INT_p by up to a factor of four times. Total integrated chlorophyll *a* concentration was kept constant by varying S_p . A schematic summary of the method employed is presented in Figure 4.6.

The predicted value of $BIOM_p$ on day 16 was recorded as a multiple of $BIOM_H(16)$ of the homogeneous analog of the four simulations. Because intra-patch chlorophyll *a* concentration was calculated as $INT_p \times PCHL$, average chlorophyll *a* concentrations increased with increasing levels of patchiness.

In a strongly spatially patchy environment, results suggested that, provided patches have sufficiently dense food concentrations, the average zooplankton biomass will be nearly 30% greater than that predicted for an homogeneous environment (Fig. 4.7, back left). With a large number of dense food patches, the majority of copepod aggregations have access to a high quality feeding area where their productivity is dramatically elevated relative to the background level. As the intra-patch chlorophyll *a* concentration is decreased in the model, patches increase in size so that the total

available food becomes distributed over a larger area. With a large number of patches, the limit of this process approaches the homogeneous situation. As INT_p is therefore decreased, the ratio $BIOM_p:BIOM_H$ tends to one at high levels of patchiness (Fig. 4.7, back right).

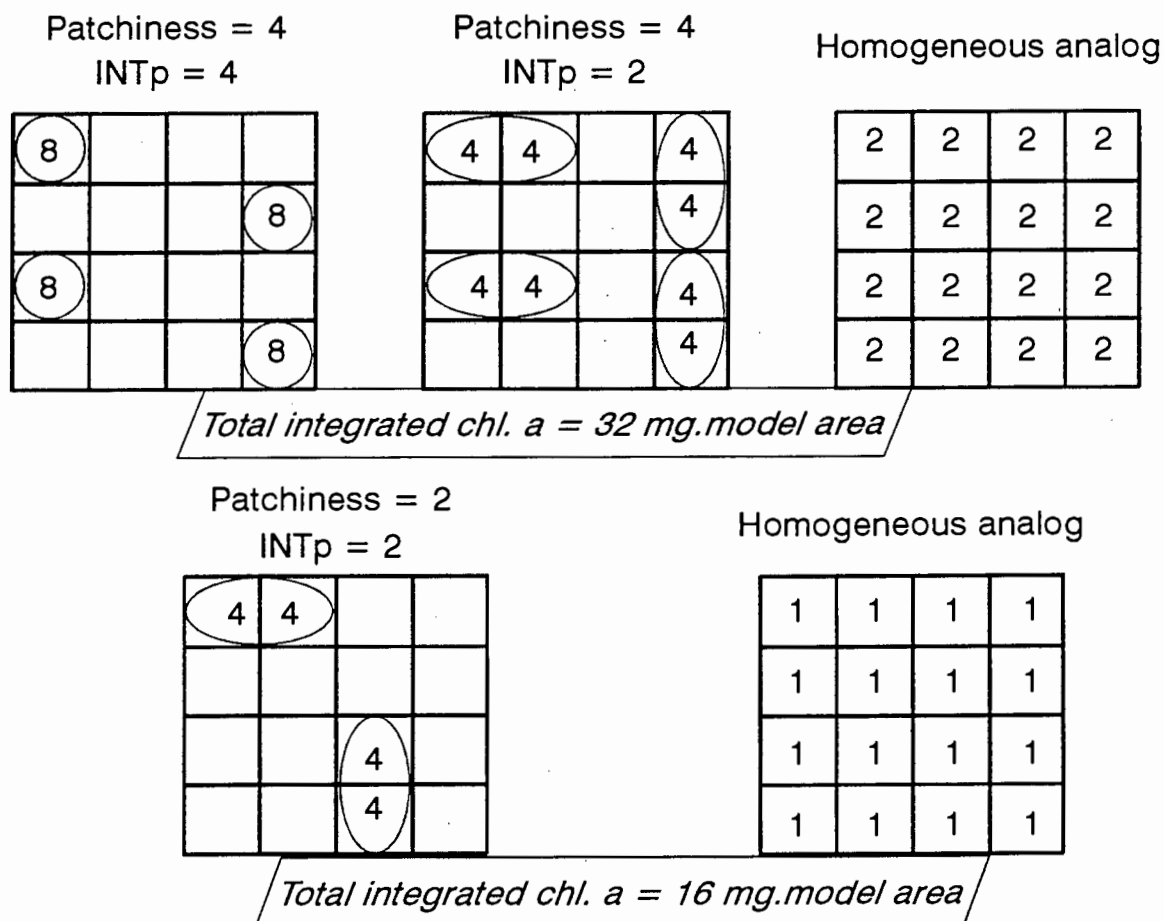


Fig. 4.6. Schematic illustration of the method used to investigate the effect, relative to a homogeneous analog, of variably aggregating total food concentration in an area into patches of different size and intensity. In the example $PCHL = 2$, and patch density is increased by increasing the patch intensity coefficient INT_p . For a constant number of patches, the total integrated chlorophyll a concentration is held constant but the size and density of individual patches is varied.

At low and intermediate levels of patchiness, dense food patches will be widely dispersed. Although copepods in the vicinity of these high quality patches have enhanced productivity rates, the patches are too widely spaced to be accessible to most subpopulations. Productivity is therefore slightly worse on average because there is little or no growth in too large a proportion of the total habitat (Fig. 4.7, front left).

Fig. 4.7. The effect of different numbers and densities of food patches on the ratio of total copepodite biomass (after 16 days) predicted for a patchy environment ($BIOM_P$) to that predicted for an homogeneous environment with the same average food concentrations ($BIOM_H$). Spatial patchiness was increased by increasing the number of patches per 0.01 km^2 . The same homogeneous analog was used for each patchiness level because the total integrated chlorophyll a concentration per food patch remained constant. Intra-patch chlorophyll a concentration was varied at each patchiness level by altering the spatial area occupied by the various food patches. Patches therefore become both larger and less dense as the inter:intra patch ratio is increased. At the same inter:intra patch ratio, the total integrated chlorophyll a concentration increases with an increasing number of patches.

As INT_p is decreased and intermediate numbers of patches become accessible to a greater proportion of the global population by virtue of their larger size, growth is better on average than that predicted for an homogeneous environment (Fig. 4.7, front right). This effect is most pronounced at intermediate than at low levels of patchiness because with only a few, albeit large, patches, average productivity rates are not great enough to compensate for the poorer average probability of a copepod locating a reasonable food patch.

There is thus a fine dynamic balance between the spatial arrangement and quality of patches in a heterogeneous environment, and the average productivity of copepod aggregations distributed randomly throughout the environment.

The disadvantages of the larger average distances between copepod and phytoplankton aggregations in a patchy environment are offset if patches are sufficiently dense. The model predicts that during unfavourable periods and at optimal levels of spatial patchiness, estimates of zooplankton production based on average feeding conditions will underestimate overall zooplankton productivity by approximately 30%.

The model prediction arises because of the effect of a patchy environment on the magnitude and functional response of egg production, as well as its effect on development and mortality rates. Energetic considerations are therefore not modelled explicitly but it should be noted that they may modify the above result depending on the trade-off between the energetic debts incurred through the greater distances travelled in a patchy environment and the energetic returns from feeding in a patch. It is energetically less expensive to feed on patches than on evenly distributed individuals (Horwood & Cushing 1978).

Trading off the Optimal Number and Quality of Food Patches

A simulation experiment was conducted to investigate further the hypothesis that average growth rates in a patchy environment are elevated relative to those in a homogeneous environment provided food patches are dense enough and not too widely spaced. In Figure 4.7, the total integrated chlorophyll *a* concentration increased with an increasing number of patches. In the present case, the total daily integrated chlorophyll *a* concentration remained constant for ten simulations, but was successively divided into more and more patches, so that INT_p was varied by up to a factor of ten times. S_p was held constant at one. Simulations were conducted using

100 cells, so that the number of patches varied from one to ten. The homogeneous analog assumed that average chlorophyll *a* concentrations over a ten day period were as shown in Fig. 4.8. The entire process was then repeated using average daily chlorophyll *a* concentrations equal to exactly twice that used for the first set of simulations. Total predicted copepodite biomass on day ten was plotted as a multiple of the relevant homogeneous analog.

For the low PCHL series, results suggested that with fewer than four patches, BIOM_P was as much as 32% less than BIOM_H (Fig. 4.9), despite the fact that chlorophyll *a* concentrations in these patches were at the maximum level. Because of the trade-off between inter-patch distances and the functional response of reproduction rates to patch intensity, the model predicts that growth rates are maximised at an intermediate patchiness level of 6 patches per 100 model cells.

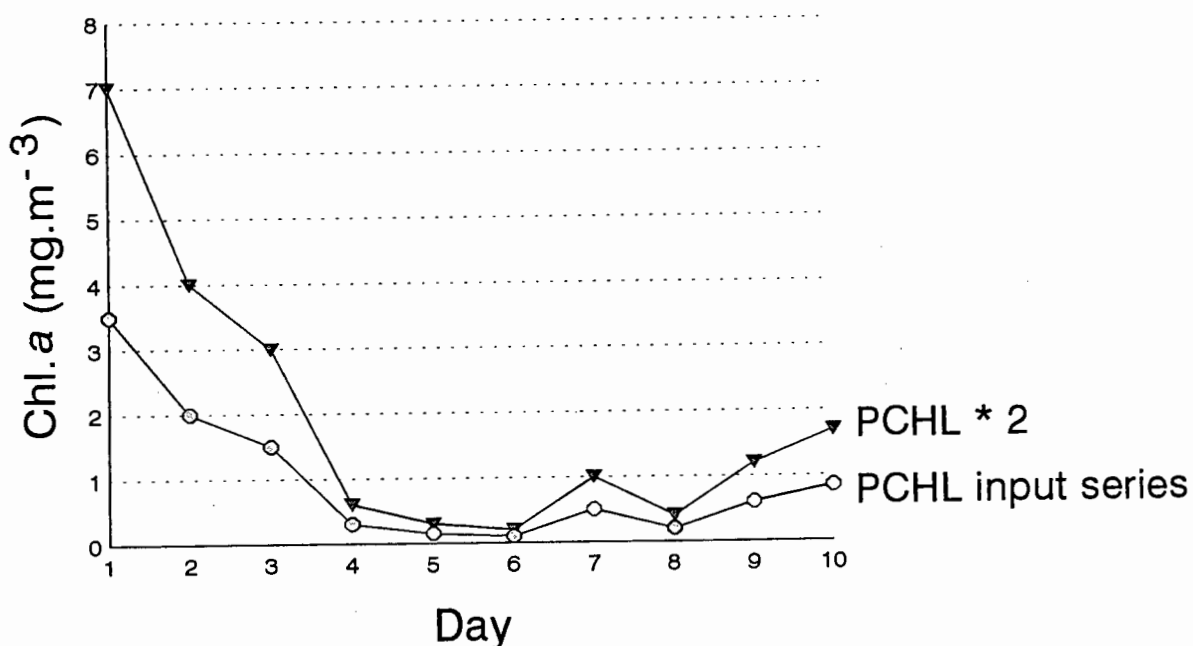


Fig. 4.8. Average chlorophyll *a* concentrations used as inputs in simulations which kept total integrated chlorophyll *a* concentrations constant, but varied the spatial pattern of primary productivity. The total integrated chlorophyll *a* concentration was successively divided between more and more food patches. Two separate sets of ten simulations each were conducted, with the second set using the PCHL*2 input series shown in the diagram.

For the higher PCHL series, growth rates are maximised relative to the second homogeneous analog at a patchiness level of 8 patches per 100 model cells. Because intra-patch concentrations are denser in the second set of simulations, average growth

rates are optimised at a greater number of patches. With only one patch (at the chlorophyll *a* saturation level), BIOM_P was 29% less than BIOM_H. With two patches, intra-patch chlorophyll *a* concentrations were still at the saturation level and hence the ratio BIOM_P:BIOM_H was relatively larger than in the first set of simulations because the probability of a local copepod aggregation finding a food patch is modelled as proportional to total food availability.

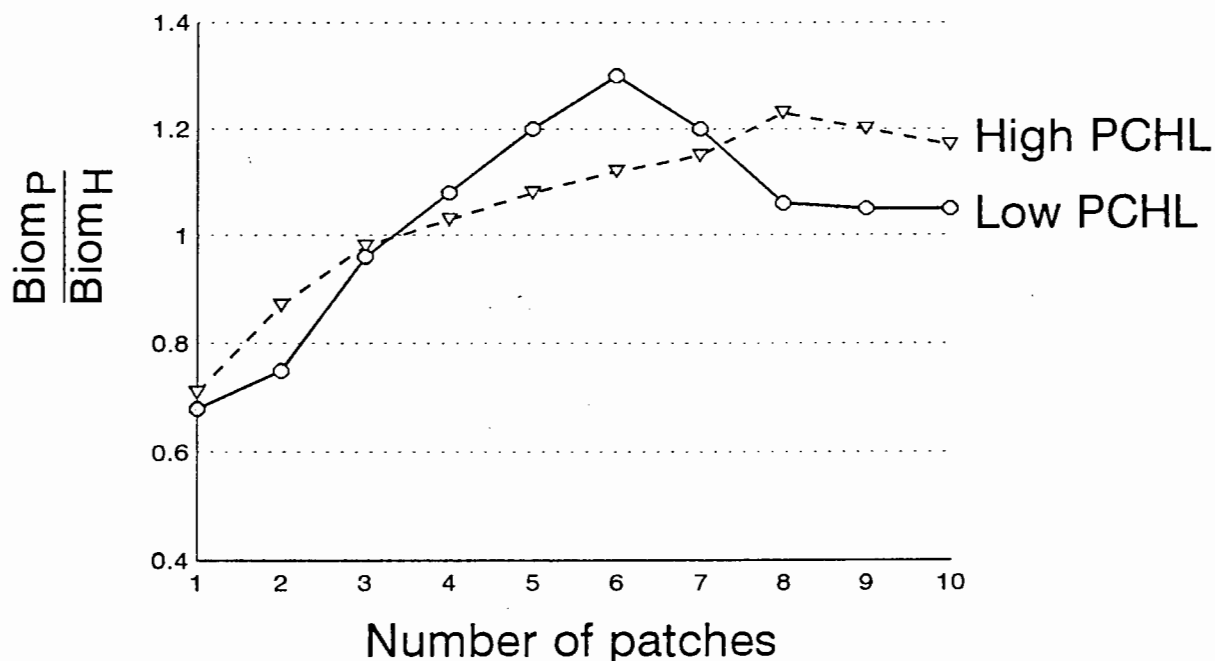


Fig. 4.9. The effect on the ratio BIOM_P:BIOM_H of redistributing the same total food concentration between differing numbers of food patches. The high PCHL curve represents simulations in which intra-patch chlorophyll *a* concentrations were twice those used to obtain the low PCHL curve.

CONCLUSIONS

Spatial variability in the distributions of zooplankton and phytoplankton populations was assumed to influence a local copepod aggregation's probability of finding a suitable food patch on which to feed. The model predicted that the effect of spatial heterogeneity on copepod productivity is more pronounced under poor than good feeding conditions.

If chlorophyll *a* concentrations are high and the average food concentration in a heterogeneous and homogeneous environment the same, food patches in the heterogeneous environment must either be very numerous or dense. Because average copepod productivity is correlated with the number and intensity of food patches, the

model predicts that patterns of productivity predicted for copepods in the heterogeneous environment are similar to those predicted for copepods feeding on high average food concentrations. Differences between the homogeneous and heterogeneous case are dampened to some extent during periods of high chlorophyll *a* concentration because of the functional response of copepod egg production to chlorophyll *a* concentration - reproductive rates in dense food patches are not dramatically enhanced relative to those based on high average food concentrations.

Conversely, with poor average food concentrations, significantly enhanced productivity rates in the food patches overcompensates for the almost complete absence of food elsewhere in the environment, so that average productivity rates exceed those predicted for a homogeneous environment with the same average food concentration. However, model results may be partially biased by failure to consider changes in predation risk associated with different patch utilisation strategies (Lima & Dill 1990, Saiz *et al.* 1993). Saiz *et al.* (1993) demonstrated experimentally the increase in egg production of the calanoid copepod *Acartia tonsa* when feeding in a patchy environment versus a homogeneous environment with the same average food concentration. In their experiments, although the presence a predator reduced the amount of time the copepods spent in food patches, the predator actually increased rates of egg production by the copepods. The exact mechanisms responsible for the complex results arising from the interaction of patchiness and predation in their experiments are presently unclear (Saiz *et al.* 1993).

Assuming the same average food concentrations in different habitats, model results indicated that there is a trade-off between the optimal number and intensity of food patches. For example, in a patchy environment, the disadvantages of the larger average distances that copepods have to travel in search of food may be offset if the energetic returns from feeding in a patch are sufficiently good. At optimal levels of patchiness, the model predicts that the average of growth estimates calculated for a number of different local copepod aggregations exceeds the average growth estimate predicted for a homogeneous environment by almost 30%. Under some circumstances, spatial matches and mismatches between zooplankton and phytoplankton may therefore influence patterns of copepod productivity as much as short-term temporal changes in food availability.

The implication of this study is that during periods of low food availability, such as between upwelling bouts, patterns of growth and survival in copepod populations in the field may be linked critically to the spatial arrangement of their food supply.

Once the relationship between hydrographic parameters, such as wind, and the spatial arrangement of phytoplankton populations has been quantified, the results of this study could be used to indicate tentatively how to modify model results to account for the effect of spatial heterogeneity. For example, during periods of poor food availability, model predictions which depend only on average measures of food availability may significantly underestimate average copepod production rates.

CHAPTER 5

**A DYNAMIC SIMULATION MODEL
TO INVESTIGATE THE RELATIONSHIP BETWEEN
SPATIAL AND TEMPORAL PATTERNS IN ANCHOVY AND
ZOOPLANKTON ABUNDANCE**

INTRODUCTION

The seasonality of fish spawning produces pulses of anchovy recruitment, resulting in seasonal impacts on zooplankton populations in the nearshore zone of the West Coast (Hampton 1987, Hutchings 1992). Moreover, intraseasonal variations in predation pressure occur because juvenile anchovy travel in a number of shoal groups (Hutchings 1991) and because they do not simultaneously impact all zooplankton populations in a broad horizontal area in the same way. It has been suggested that failure to consider the patchiness of predator or prey populations in aquatic systems may result in prey mortality rates due to predation being over- or underestimated by a factor of two or more (Williamson & Stoeckel 1990).

The model developed in chapter two does not simulate predators directly; rather, their effect is modelled indirectly by means of a density-dependent predator mortality function. This has several problems associated with it, one of the more obvious being that it assumes a mean fish density feeding on a mean plankton density. In reality, this is almost certainly not the case as not only are the fish clumped in their distribution, but their prey are also patchy.

Predator-induced mortality rates are notoriously difficult to determine empirically. To integrate the present model both spatially and temporally requires an estimate of the way in which the predator-induced mortality rate varies as a function of intra- and interseasonal variability in fish abundance, and the way in which changes in the spatial overlap of predator and prey populations affect this parameter.

Hutchings (1992) has suggested that the prey density available at a given fish density may be important along the West Coast because shoals of anchovy recruits moving through the restricted nearshore habitat require lots of food. Furthermore, he proposed that a critical dynamic balance exists during the winter recruitment period between the density of zooplankton prey populations, the rate of replenishment of depleted populations and the abundance of planktivorous fish.

Anchovy are opportunistic foragers, capable of switching between a filtering and particulate mode of feeding, with the latter being the dominant mode (James & Findlay 1989). They exhibit extremely flexible feeding behaviour, with both feeding behaviour and rate of food consumption being determined by the size and density of available prey (James & Findlay 1989). They are size-selective predators, and preferentially feed on relatively large items (1.0 - 20.0 mm diameter) (James 1987). Major components of their diet are calanoid copepods and euphausiids (James 1987). In terms of the impact on populations of the dominant copepod, *Calanoides carinatus*, the anchovy thus direct most of their feeding activity towards the CIV to CVI size classes. Anchovy stomachs sampled off the West Coast indicate that mesozooplankton contribute on average 40.7% of the total carbon content of the diet (Armstrong *et al.* 1991a).

The aims of this chapter are to investigate the effect on both zooplankton (*C. carinatus*) and fish (anchovy) populations of:

- a) the absolute and relative densities of both zooplankton and fish;
- b) the geometric distributions of the two species; and
- c) the degrees of synchrony in the population cycles and local abundance of the two species.

The above factors are presumably critical in determining the way in which pelagic fish and their food interact. A greater understanding of these effects should give some insight into the form of the predator mortality function to be used in the model and the critical parameters which modify this function. In addition, by quantifying the relative performance of anchovy under different feeding conditions, the model should identify some important criteria for successful recruitment of anchovy.

BACKGROUND TO THE MODEL

The time and space scales chosen in the present model are such that they are relevant to the observed properties of the organisms. A time-step of one day is used because the copepod biomass available to anchovy during their nightly forays in the model is calculated on the basis of daily updates in copepod population size. The spatial extent of the model is an area 10km X 10km, representing a sample window situated within 54 km of the coast and with one edge parallel to the coast. Most pelagic fish shoals are caught within 36 km of the coast (Thomas & Schulein 1988) and juvenile anchovies are known to occur close inshore along the West Coast, with the majority being present during the period May-July (Hampton 1987). The choice of the spatial area is further motivated by the fact that the model is directed at the active

component of the West Coast *C. carinatus* population - this component is restricted to the nearshore shelf zone where feeding and spawning occur (Verheye *et al.* 1991). Horizontal advection into and out of the model area is ignored, although this factor may be of some importance and is therefore incorporated into the model in the next chapter.

The spatial area is divided into a number of cells, each measuring 0.5km X 0.5km. The zooplankton population of each cell is assumed independent and modelled separately. The system thus has a number of local-scale models nested within a large-scale model, so that the effect of local-scale and large-scale processes on the overall trophic structure may be evaluated simultaneously. The model system (program listing: APPENDIX IV to thesis) uses the basic model developed in chapter two to simulate the population dynamics of local *C. carinatus* populations, and is therefore an extension of the basic model. The major program extensions revolve around attempts to realistically simulate predation patterns in a spatially and temporally heterogeneous framework, and the incorporation of calculations necessary to assess the relative performance of juvenile anchovies under various scenarios.

MODEL DESCRIPTION

Primary Production Input Series

As in chapter two, the model is driven by daily estimates of chlorophyll *a* concentrations and sea surface temperature. The base-case input series employed in all simulations (Fig. 5.1) is based on data in Brown & Henry (1985) and Verheye & Field (1992). Where applicable, upwelling cycles were simulated using the standard upwelling series presented in chapter two (Chapter two: Fig. 2.7, Brown & Hutchings 1987).

Initializing Prey Concentrations

A depth-weighted mean of the abundance of *C. carinatus* off Cape Columbine during a downwelling state in the month of June (Verheye *et al.* 1991) was used to obtain an initial abundance estimate N_1 for the prey population. Assuming a stable age structure and scaling this value upwards to account for the naupliar stage individuals, yielded an initial *C. carinatus* base-case abundance estimate of 135 copepods.m⁻³ and 58 prey (CIV-CVI) individuals.m⁻³.

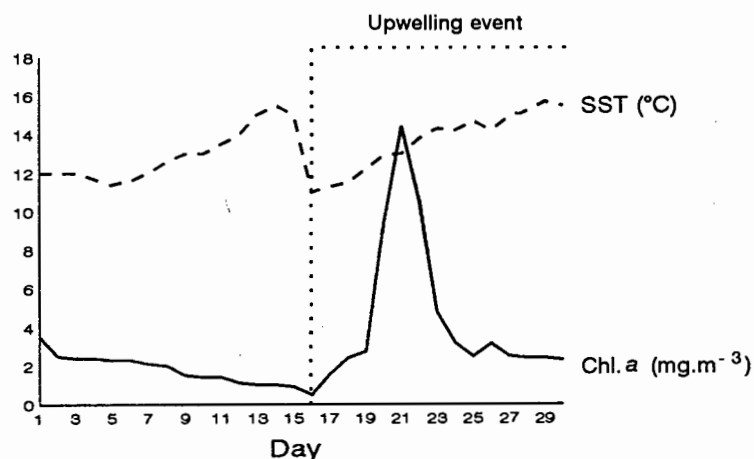


Fig. 5.1. The base-case chlorophyll *a* concentration and sea surface temperature series used as inputs in model simulations. The low chlorophyll *a* concentration values are characteristic of those measured along the West Coast during winter, when juvenile anchovies recruit in the region. Occasional upwelling events occur in the winter months (Andrews & Hutchings 1980), and these are simulated using the upwelling cycle shown.

Model equations were modified to model the CIV stage individuals separately from the CI-CIII stage individuals, and a stable initial population age structure of 30.5% NI-NVI, 27% CI-CIII, 17% CIV, 13% CV and 12.5% adults was assumed.

A summary of model constants and base-case parameter values is presented in Table 5.1, while model calculations and mathematical relationships are given in Appendix 5.1.

The Predator: Base-Case Anchovy Recruits

Along the West Coast of South Africa, anchovy recruits caught from April onwards are generally between 8 and 9 cm long (Hutchings and Boyd 1992). Anchovy birthdate distributions for 1984/85 and 1988/89 indicate that, because most fish are spawned during October (Waldron *et al.* 1992), the modal age-class along the West Coast in May is 7 months. Based on a Von Bertalanffy curve fitted to combined data from 1979 and 1983 to 1985, the caudal length of a 7 month old anchovy is 8.42cm. In the model, a base-case anchovy recruit therefore refers to an individual 8.4cm long, with a wet mass of 3.46g and a dry mass of 1.1g. The wet mass of a *L* cm long anchovy is calculated using the relation $0.0034L^{3.25}$ (Robinson 1966) and dry mass is calculated using a dry:wet mass ratio of 0.32 determined for anchovy (James *et al.* 1989b).

Growth rates of anchovy in the Benguela system are highly plastic (Shannon *et al.* 1992, Waldron *et al.* 1992). For example, anchovy recruits in 1989 and 1991

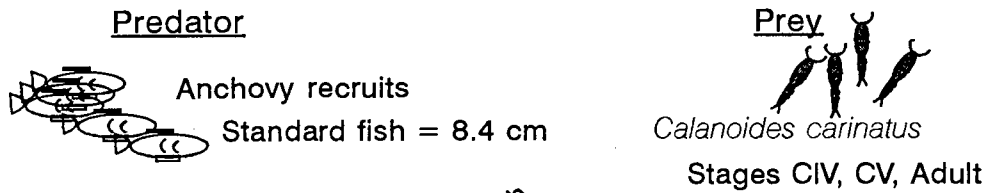
exhibited substantially slower growth rates than individuals in 1985. Thus while acoustic surveys conducted in June 1989 showed the anchovy recruits to have a modal length of 6.5cm, in June 1985 similarly aged fish had a modal length of 8.5cm (Waldron *et al.* 1992). The model developed here may be run with anchovy recruits of any size, but unless otherwise indicated, fish shoals are assumed to comprise 8.4 cm recruits. Length frequency distributions from commercial catch data in both 1985 and 1989 indicate that during the months of May and June, most anchovy recruits are *ca.* 8 cm long (Waldron *et al.* 1992).

Feeding Paths

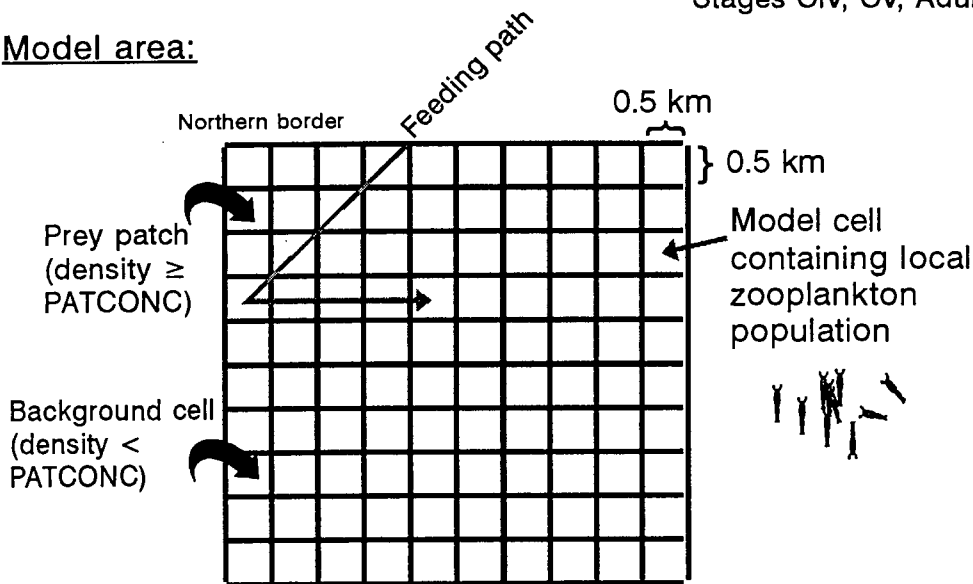
Pelagic fish shoals in the Southern Benguela system move mainly in a SE, S or SW direction, with 79% of fish shoals moving in a southerly direction (Thomas & Schulein 1988). The southward migration of anchovy recruits along the West Coast takes them towards their spawning grounds off the south-west and south coasts (Shelton 1986). Pulses of fish predation are modelled by variably partitioning total fish biomass into a number of shoals and by varying the daily migration rate of fish shoals into the model area. New shoals enter the model area at a random cell along the northern edge. A summary of the basic model structure is presented in Figure 5.2.

A stochastically determined feeding path is defined for each shoal and, where applicable, updated daily depending on the last cell reached on the previous day's feeding path. The maximum distance that may be travelled by an anchovy in one day is set at 15km. Fish shoals are never permitted to move in a northerly direction. If a shoal's feeding path intercepts the eastern or western border of the model area, the feeding path is randomly redirected from this point, so that it either continues in a direction parallel to the border or is deflected inwards away from the border. Fish shoals are thus only permitted to leave the model area along its southern border. This is to ensure that shoals remain in the area for long enough to estimate their total daily performance, and to standardize measures of the total biomass per day of fish present in the model area.

The distance travelled along a particular path by a shoal is determined by both the prey concentrations encountered en route and the size of the shoal, as explained below. The model cells through which a shoal actually passes are termed 'hit' cells. An individual shoal never backtracks through cells it has already encountered, but other shoals may move through its hit cells during the course of a night's feeding in the model.

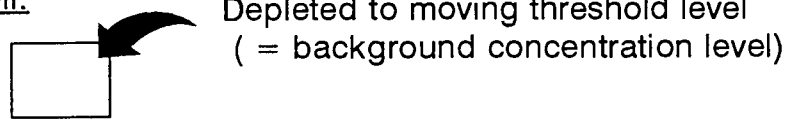


Model area:



PATCONC = threshold feeding concentration

One cell:



x copepods.m⁻³ consumed per shoal

No. fish = Shoal mass / Average fish mass

Consumption per 'hit' cell per fish:
 = $(x \cdot 500 \cdot 500 \cdot 15) / (\text{No. fish})$

Daily mortality rate in 'hit' cell:
 = $\frac{\text{Initial no.m}^{-3} - \text{Moving threshold}}{\text{Initial no.m}^{-3}}$

Fig. 5.2. A schematic diagram illustrating the basic structure of the present model. Shoals of anchovy recruits enter the model area along its northern border and proceed along randomly-determined feeding paths. Individual shoals stop and feed in cells on their feeding path which have prey concentrations in excess of the threshold feeding concentration (see text). These cells constitute prey patches as perceived by the fish. Prey patches are depleted by the fish. Prey consumption per cell integrated over a volume of 500x500x15m (see text). The predator-induced mortality rate in a cell is calculated as the proportion of prey individuals consumed. Total daily consumption per shoal depends on the number of prey patches encountered and the distance travelled.

Shoals still in the model area on the second day return to (or stay in) a cell adjacent to the last cell reached on the previous day's feeding path. If feeding conditions are unfavourable, the fish will quickly move away from this area, whereas if feeding conditions are favourable, it seems reasonable that fish might return to the same feeding area the following day.

Threshold Feeding Concentration

James and Findlay (1989) demonstrated in the laboratory that very low threshold prey concentrations were required to initiate particulate feeding in anchovy, with even single prey items being attacked in the experimental tank. Simple laboratory systems generally overestimate a predator's foraging efficiency however, because of the absence of refuges for the prey which are provided in the field by the habitat complexity (Diehl 1992). An estimate of the threshold prey density necessary to initiate particulate feeding in anchovy is central to understanding anchovy foraging behaviour in the field and also to defining an ecologically meaningful prey patch as perceived by a fish.

In the present model, the threshold feeding concentration is defined as the prey concentration required to maintain the standard metabolic rate (maintenance metabolism) of an anchovy. This approach seems logical because if an anchovy was to fulfil its energetic needs purely by preying on copepods, it would have to encounter individual prey at a rate equal to or greater than the threshold feeding concentration defined above. In the discussion which follows, copepod prey refers to *C. carinatus* individuals in stages CIV-CVI (the preferred prey of anchovy). An estimate of the threshold feeding concentration for a base-case anchovy recruit was obtained as follows:

The net energetic expenditure of a base-case anchovy engaged in particulate feeding is 20.48 J.h^{-1} (calculated from data in James 1989). Theilacker and Kimball (1984) estimate the energy content (E_c) of copepod prey as $20.58 \times 10^{-3} \text{ J}$ per μg prey material. The average dry weight for *C. carinatus* prey (stages CIV-CVI) is $57.4 \mu\text{g}$ (calculated from Verheye 1991, using mean population abundance data for the month of June). The mean absorption efficiency of anchovies feeding on zooplankton is 71.4% (James *et al.* 1989a) and the estimated net energetic value of an average copepod prey item is thus *ca* 0.84 J. To meet its energetic requirements whilst feeding, a standard anchovy therefore requires approximately 24.3 copepods per

hour. Assuming a 50% capture efficiency, it follows that a feeding individual needs to encounter at least 0.013 copepods per second (or one copepod per 74 secs).

The reactive distance of an anchovy to a particular food particle is a function of prey length (James & Findlay 1989). For a large *C. carinatus* individual, the reactive distance of a 10 cm anchovy is approximately 10 cm (James & Findlay 1989). The reactive distance of a 8.4cm anchovy is therefore similarly assumed to be one body length (BL). In terms of searching for copepod prey, the visual field of a base-case anchovy is therefore *ca* $1.24 \times 10^{-3} \text{ m}^3$ (calculated as $2/3\pi r^3$ with $r=8.4\text{cm}$). A single anchovy swimming at the mean recorded speed of $1.7 \text{ BL}\cdot\text{s}^{-1}$ (James & Findlay 1989) moves through approximately $1.7 \text{ visual fields}\cdot\text{s}^{-1}$. It follows that an individual would have to encounter 0.013 copepods per 1.7 visual fields, or 6.2 copepods per cubic metre of water.

The threshold feeding concentration used in the model is therefore 6 copepod prey individuals. m^{-3} and a patch of zooplankton is defined as any cell with a concentration of prey that exceeds this threshold level. Expressing the threshold concentration in terms of numbers rather than biomass assumes implicitly that the fish are able to use prey encounter rate (or intercatch interval) as a measure of their feeding success.

Moving Threshold of Anchovy

Several studies have attempted to determine the strategy a predator should employ in using a patchy environment in order to maximise its net rate of food intake while foraging (MacArthur & Pianka 1966, Krebs *et al.* 1974). An efficient predator is able to discern patches of high profitability, and the threshold below which it is no longer worthwhile remaining in the present patch (Krebs *et al.* 1974). The moving threshold used in this model refers to the prey concentration at which a predator decides to leave a depleted patch and move on in search of another. Optimal foraging models of patch feeding predict that the moving threshold is equal to the average rate of food intake for the habitat as a whole. The moving threshold is therefore higher in a rich habitat than in a poor one (Krebs *et al.* 1974). He and Wright (1992) demonstrated that when prey density in a lake was low but not limiting, consumption by a piscivorous predator accounted for a larger relative change in prey biomass than when prey biomass was high, supporting the above arguments. Even when food is not strictly distributed in patches with no food between the patches, recent models suggest that an optimal predator will employ a discrete exploitation policy in a continuous environment (Kacelnik & Bernstein 1988). The present model uses these

concepts to describe anchovy foraging behaviour. The moving threshold is thus taken as the level at which the prey concentration within a depleted patch is the same as the average background concentration.

This approach assumes that the stimulus for a shoal to leave a depleted patch is the patch:background prey concentration ratio rather than the prey:predator ratio. The former suggests that anchovy respond to the average feeding conditions they encounter in the environment while the latter suggests that they respond to the individual prey capture rate or *per capita* prey availability. The former seems more logical because if the anchovy movements are tied evolutionarily to optimise the use of a patchy environment, then it would pay them to stay in a patch until it is depleted to the background level, irrespective of the size of the shoal. On the other hand, the second approach would result in larger shoals leaving a patch with a higher remaining prey concentration than would smaller shoals. This strategy is clearly disadvantageous if the prey concentration in the abandoned patch is higher than the background concentration, as the larger shoal would still have done better by remaining in the patch. The moving threshold is therefore considered independent of the number of predators ie. different sized shoals deplete prey patches to the same level and it is only the time taken to deplete a patch which varies. Increasing the number of predators in the model will thus still have the effect of increasing the absolute or integrated prey depletion rate.

Analytically, the moving threshold is calculated as the average background prey concentration or, specifically, the number of *C. carinatus* individuals (stages CIV-CVI) averaged over all cells with a prey concentration less than or equal to the threshold feeding concentration. The moving threshold thus has the threshold feeding concentration as its maximum value.

Anchovy do not have perfect knowledge and thus cannot predict the potential intake rate in every patch in advance - patches are exploited by sampling them as they are encountered. The moving threshold is updated daily in the model according to the average background prey concentration characterizing the environment. This assumes that anchovy update their foraging techniques daily, in response to gradients in prey availability. This is not an unrealistic assumption as James and Findlay (1989) demonstrated that anchovy feeding behaviour is very flexible and highly opportunistic, presumably in response to the variable environment in which they occur.

Rate of Prey Depletion

Anchovy in the model are assumed to exhibit a prey-dependent functional response (see Appendix 5.2). Feeding activity by anchovy has been shown to result in an exponential decline in the food concentration with time, regardless of the feeding mode employed or the size of the prey items (James & Findlay 1989). The rate at which anchovy are able to deplete a concentration y of *C. carinatus* individuals in the laboratory is described by the relation $y = 361.4e^{-0.18t}$, where y is concentration in $\mu\text{g dry wt l}^{-1}$ and t is time in minutes (James & Findlay 1989). The rate of prey depletion is modelled using this equation and by converting prey concentration from dry weight per unit volume to no.m^{-3} . Prey concentration is calculated simply as the difference between initial concentration and the moving threshold level. Prey depletion rates are standardized for different numbers of predators by assuming that the rate of prey depletion is directly proportional to the number of predators. Since *C. carinatus* prey are generally small (prosome lengths in the range $1336\mu\text{m}$ (CIV) - $2041\mu\text{m}$ (female CVI) - Verheye 1991), it seems reasonable to assume that handling times are short and are similar for different *C. carinatus* prey individuals. Handling time is therefore ignored.

Foraging constraints

Three factors are thought to be important in limiting the cumulative daily rate of prey depletion: the maximum distance travelled by an anchovy (dealt with in a previous section), their physiological satiation level and the time available for foraging on zooplankton. Following Cochrane *et al.* (1991), a maximum satiation level of 10% of shoal wet biomass per day was used to constrain the maximum amount that could be ingested daily by each shoal.

James (1987) showed that anchovy on the West Coast exhibit marked diel synchrony in foraging, with peak activity between dusk and midnight (19h00-24h00) on the West Coast. A second but less intense foraging peak occurs between midnight and dawn (24h00-06h00) (James 1987). Foraging effort is reduced at other times (although *E. capensis* forage at low intensity throughout the day) (James 1987). The maximum total daily foraging time (T_{total}) available to an anchovy in the model is set at 12 hours, and includes the time spent searching for prey.

The total time to deplete each prey patch was calculated as the sum of the time required to deplete that particular patch and the travelling time required to reach the

patch. Travelling time was estimated using the mean swimming speed for anchovy (1.7 BLs^{-1} , James & Findlay 1989) and the distance covered between patch centres. The average distance traversed by a fish entering and exiting a model cell is taken as the diagonal distance (0.707km) of the cell.

To summarize: although the cumulative energy intake within a patch is the same for a small or large number of predators, the *per capita* gain decreases with an increasing number of predators. This is partly compensated for by the larger number of predators exploiting proportionately more patches per unit time. The relationship between total prey depletion in the model area and predator density is nonetheless not perfectly linear because although individual energetic gain per unit time spent in a patch is the same for a small and large number of predators, a larger number of predators will incur a greater total travelling time.

Impact of Predation on *C. carinatus* Population Structure

In the present model, prey risk in each of the cells depends only on the probability of the patch being detected by a predator. The question of whether the predator mortality function in the present system should be density-dependent or density-independent is then simply a matter of scale, with density-dependence manifesting itself increasingly with increasing spatial scale.

Patches of zooplankton which lie in the feeding path of a shoal of anchovies are all depleted to the moving threshold level. The model assumes that prey above the preferred size are encountered sequentially (random ingestion of CIV to CVI stage individuals) and hence that they are depleted in the same proportions as they occur in the patch. The model does not account for the incidental ingestion of smaller copepods while filter-feeding or during particulate feeding. The mortality (due to predation) of these smaller individuals is modelled as described in chapter two. Also, the model describes only the interactions between a single zooplankton and fish species and all other predation is therefore modelled as a constant. This is a simplification of the real situation because feedback relationships may well exist between the model animals and other predators or prey. Complex interactions could occur because, in selecting large prey, size-selective predators also remove invertebrate predators, which are generally large, and in this way they indirectly reduce predation on small zooplankton (DeVries & Steyn 1992).

Mortality due to abiotic factors, such as adverse feeding conditions, is modelled as before (see chapter 2), but because model cells not on a shoal's feeding path are still subjected to some mortality due to biotic factors, a constant low background mortality rate (M_{back}) of 0.05d^{-1} is assumed. This parameter is included for reasons of biological realism, and because of the uncertainty surrounding the choice of an appropriate value, the effect of changes in its value is assessed in the sensitivity analysis.

Estimating Absolute Prey Abundance in Model Cells

With the exception of males and spermatophore-bearing females, *C. carinatus* adults and late copepodites ascend into the upper 15m of the water column at night (Verheye & Field 1992). Mean migration amplitudes for CIV, CV and adults range from 5.5m (CIV, relaxation period) to 18.5m (adults, advection period) (Verheye & Field 1992). The maximum vertical height between the nighttime weighted mean depths (WMD) of the older developmental stages of *C. carinatus* is *ca.* 17m (Verheye & Field 1992). Copepod prey abundance measures quoted for each cell are therefore assumed to represent the number. m^{-3} averaged over a 15m depth range. Model cells therefore consist of 500 x 500 x 15 one cubic metre subcells.

The spatial arrangement of copepods in each cell is not modelled explicitly or assumed to influence anchovy foraging behaviour as the fish are assumed able to integrate their food supply over the entire volume occupied by a model cell. Thus while the fish experience a patchy distribution of prey on scales larger than the size of individual cells (0.5km x 0.5km), feeding behaviour within each cell is modelled independently of smaller scale prey distribution.

Shoals of anchovy recruits disperse after dark and generally migrate to the upper 20 metres of the water column (James 1987). Echochart recordings suggest that anchovy concentrate over a depth range of approximately 10 metres at night, although exact estimates are difficult to obtain as the upper 10 metres of the water column cannot be examined acoustically (Hampton 1987, James 1987, Wrzesinski 1987b, Pillar & Barange 1993). Anchovy schooling behaviour breaks down during particulate feeding (James & Findlay 1989). Anchovy shoals are therefore assumed to disperse and fill the entire volume upon encountering a prey patch in the model. The diffuse nature of feeding shoals presumably decreases the overlap of the visual fields of the fish (Eggers 1976), lending support to the model assumption that competition between feeding fish is minimised.

Estimating Consumption by the Anchovy

Individual fish in anchovy schools all behave similarly when feeding and hence it is assumed that individual fish obtain equal portions of the available food (James & Probyn 1989).

A *per capita* consumption value (μg) for each shoal in each model cell was calculated as:

$$\text{Consump} = \frac{\sum_{i=1}^3 C_i B_i}{F} \quad (5.1)$$

where C_i and B_i are respectively the number consumed per cell (no. $375 \times 10^4 \text{m}^{-3}$) and the mean individual body weight (g.dry wt) (from Verheye 1991) of copepodite stages CIV ($i=1$), CV ($i=2$) and CVI ($i=3$). F is the number of fish in the shoal, ie.

$$F = \frac{\text{Shoal Mass}}{\text{Average Fish Mass}} \quad (5.2)$$

Daily *per capita* consumption estimates for each shoal are calculated as the sum of prey consumed in each patch encountered. These values are then used to calculate the percentage dry body mass consumed per shoal per day to enable comparisons to be made between the rate of intake of food by various shoals in the model.

Calculating Simplified Net Energy Budgets for the Anchovy

Anchovy obtain the bulk of their nutritional requirements by particulate feeding upon mesozooplankton and macrozooplankton (James *et al.* 1989b). While their diet is supplemented to some extent by filter-feeding upon dense phytoplankton and microzooplankton aggregations, the overall contribution by filter-feeding to net energetic intake is small (James *et al.* 1989b). In the model it is therefore assumed that the energetic gains derived from filter-feeding are just sufficient to maintain the standard metabolic rate of the fish during the day. Only particulate feeding therefore provides for scope in growth. Gross daily energetic gain during particulate feeding is calculated as daily *per capita* consumption times the energy content of copepod prey (see Appendix 5.1 for mathematical formulations). A mean dry weight absorption efficiency of 71.35% is used (James *et al.* 1989a).

Gross daily energetic losses due to particulate feeding are estimated for each shoal using model estimates of the total time spent feeding (hours) in prey patches and the total time spent travelling (hours) between patches. Particulate feeding causes a two to six fold rise in the routine respiration rate (James & Probyn 1989). The mean measured respiration rates for anchovy in an active (swimming) state and engaged in particulate feeding are respectively $0.282 \text{ mg.O}_2\text{.g}^{-1}\text{wet wt.hr}^{-1}$ and $0.414 \text{ mg.O}_2\text{.g}^{-1}\text{wet wt.hr}^{-1}$ (James & Probyn 1989). These values are converted to $\text{J.fish}^{-1}\text{.hr}^{-1}$ using the relations: $1 \text{ mg.O}_2 = 3.42 \text{ cal}$ and $1 \text{ cal} = 4.184\text{J}$.

Net energetic gain ($\text{J.fish}^{-1}\text{.d}^{-1}$) per fish per shoal per day is calculated simply as the difference between energetic gains from particulate feeding and energetic losses attributable to the metabolic costs of feeding and swimming in search of food.

Simulating Growth in Caudal Length in Anchovies

Juvenile fish with positive energy balances were assumed to channel the excess joules into growth processes. Following Nonacs *et al.* (1994), excess calories are transposed into biomass increase using Hunter and Leongs' (1981) calculated relationship of the energetic content $6.151L^{3.195}$ of a L cm long Northern Anchovy *Engraulis mordax*. Excess energetic gains were added to a fish's existing caloric biomass and then back-calculated into a new length (Nonacs *et al.* 1994).

The daily growth in caudal length (cm.d^{-1}) of a base-case anchovy recruit is therefore calculated as:

$$G = \left(\frac{23276 + E_{\text{net}}}{25.736} \right)^{\frac{1}{3.195}} - 8.42 \quad (5.3)$$

where E_{net} is the net energetic gain ($\text{J.fish}^{-1}\text{.day}^{-1}$).

Growth rates calculated in the model are compared with field estimates (Waldron 1994) of anchovy growth rates. To achieve the mean growth rates of 0.04 and 0.03 cm.day^{-1} observed in 1985 and 1989, base-case anchovy recruits require E_{net} values of 355 and $266 \text{ J.fish}^{-1}\text{.day}^{-1}$ respectively.

Calculating Shoal Dimension Parameters

Laboratory observations of anchovy schooling behaviour suggest that schools are generally twice as long as they are broad (James & Findlay 1989). To estimate shoal

dimension parameters, the surface area A occupied by an anchovy shoal was assumed to be elliptical and hence calculated as πab , where a and b are respectively half the minor and major axes of an ellipse, and $b=2a$. Thus:

$$A = 2\pi a^2 \quad (5.4)$$

To obtain average estimates of a , the following method was employed: If shoal surface area is approximately elliptical in the field, acoustically-determined estimates of shoal width (sw) should fall in the range $2a$ to $2b$ (Fig. 5.3). If the actual value of sw depends on the orientation Θ of the shoal relative to the ship at the time of measuring, an expression is required to calculate sw as a function of Θ . Accordingly, a function relating Θ and x , where $x = \frac{1}{2}sw$, was derived (Fig. 5.3).

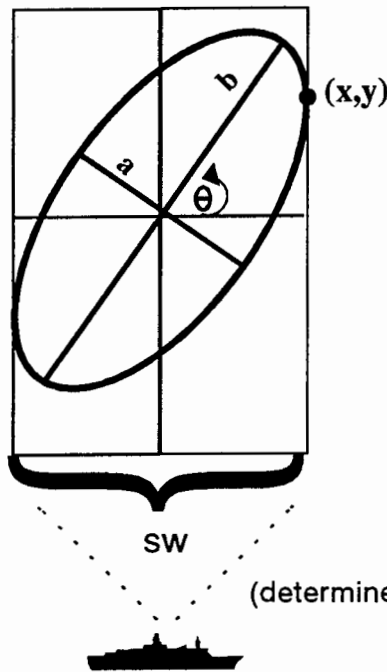
The relationship between the actual dimensions of a shoal in the field and acoustically-determined estimates of sw was explored using the equation derived above and a simulation model (Appendix 5.3). Assuming a random distribution for Θ , and substituting $a=1$ and $b=2$, simulations were run to calculate the average sw value measured when shoals were orientated randomly relative to a ship's acoustic equipment in each instance. As the number of runs was increased, simulations predicted that the mean of the sw values measured tends to a limit of 3.04. On average, the measured value of sw is therefore approximately 3.04 a or 1.52 times the minor axis of an elliptical-shaped shoal. An average estimate of a , necessary to calculate average shoal size and volume, was therefore obtained using the relation:

$$a = 1/3 sw \quad (5.5)$$

Shoal surface area: Using acoustically-determined shoal width measurements (Table 5.2) obtained for anchovy recruits during winter (Wrzesinski 1987a), the above approach suggests that the average surface area of an anchovy school (not engaged in feeding) is $3.69 \times 10^{-4} \text{ km}^2$. A maximum surface area value of $A = 1.92 \times 10^{-2} \text{ km}^2$ was calculated by assuming that the maximum observed shoal width (Table 5.2) is $2b$ (ie. $\max b = 0.1105 \text{ km}$).

Shoal volume: Using average and maximum shoal depth estimates of 6 and 32 metres respectively (Table 5.2), yields corresponding shoal volume estimates of $2.24 \times 10^{-6} \text{ km}^3$ and $6.14 \times 10^{-6} \text{ km}^3$, if shoal depth is assumed constant.

Calculating Shoal Dimension Parameters



Elliptical shoal surface area assumed

From empirical observations:

$$b = 2 \cdot a$$

θ = angle of orientation of shoal relative to ship

$$sw = 2 \cdot x$$

Require $a = f(sw)$

Shoal width (sw)
(determined acoustically from the ship)

Equation of rotated ellipse:

$$\frac{(x \sin \theta + y \cos \theta)^2}{a^2} + \frac{(x \cos \theta - y \sin \theta)^2}{b^2} = 1 \quad (1)$$

Require (x,y) s.t. $\frac{dy}{dx} = \infty \equiv \frac{dx}{dy} = 0$

Thus differentiate (1) w.r.t. y \rightarrow eqn. (2)

To solve for x,y, rotate the ellipse by $-\theta$
to get it into normal form ie. $x = x' \cos \theta + y' \sin \theta$
 $y = -x' \sin \theta + y' \cos \theta$

Now use (1) & (2) to solve for x' & y'

The required distance x is then the projection onto the horizontal axis

Solution:

$$x = \sqrt{\frac{b^4}{a^2 \tan^2 \theta + b^2}} \cos \theta + \sqrt{\frac{a^4 \tan^2 \theta}{a^2 \tan^2 \theta + b^2}} \sin \theta$$

Fig. 5.3. Summary of the assumptions and calculations used to derive a function describing the relationship between acoustically-determined measures of shoal width, and the actual dimensions of a shoal in the field.

Shoal biomass: In most acoustic surveys, errors in absolute biomass estimates arise primarily because of uncertainty in the target-strength expression used (Hampton 1987). The target-strength expression used by Wrzesinski (1987a) underestimates absolute biomass by a factor of approximately two (I. Hampton, pers. comm.) and hence the shoal density estimates in Table 5.2 are doubled in the following calculations. Based on the empirical observations of Wrzesinski (1987a), estimated average and maximum shoal sizes are therefore 0.755 tons and 832 tons respectively. Model simulations were therefore conducted using anchovy shoal size in this range.

Table 5.2. Acoustically-determined shoal parameters for anchovy recruits along the West Coast of South Africa (from Wrzesinski 1987a).

	Shoal thickness(m)	Shoal width(m)	Density (g.m ⁻³)
MINIMUM	1	0.02	5.79
MAXIMUM	32.1	220.5	677.4
MEAN	5.8	22.9	168.7
S.D.	3.82	30.6	156.1

Calculating Shoal Packing Densities

For comparative purposes, and to ensure that model representations were biologically realistic, shoal packing densities were calculated simply as the average number of shoals per km². Discrete shoals are obviously separated from one another in space by some minimum distance. Shoal width parameters were used to estimate the average horizontal distance between shoals because the earlier calculations (equation 5.5) revealed that, on average, sw may be approximated by the mean of the major and minor axes of an ellipse. In general, the distance between shoals was calculated as sw1-sw2, where

$$sw1 = (4.5 \times A_1/\pi)^{1/2} \quad (5.6)$$

(from equations 5.4 and 5.5) and A_1 is the average area available per shoal (see Fig. 5.4). The parameter sw2 was calculated similarly, but A_2 , which represents the area actually occupied by a shoal, was substituted for A_1 .

Assessing Shoal Packing Densities

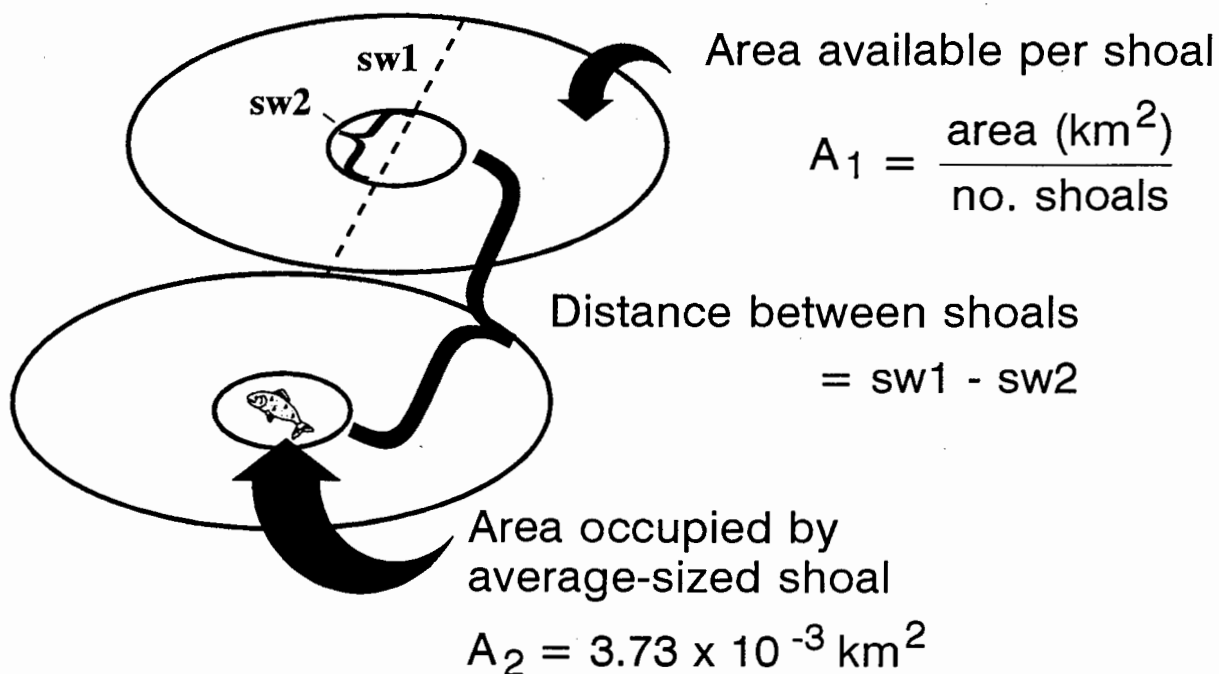


Fig. 5.4. A schematic diagram illustrating the method used to calculate the average horizontal distance between two shoals in a region with a mean shoal packing density of $1 / A_1$ shoals.km⁻². Assuming an elliptical shoal surface area, the shoal width parameter sw is approximately the mean of the major and minor axes of the ellipse (see text, equation 5.5). It is therefore used to estimate average distances between shoal boundaries.

Division of Total Fish Biomass into Discrete Shoals

The densest anchovy recruits along the West Coast occur in the St Helena Bight, between Cape Columbine and Lambert's Bay, where persistent aggregations of fish are found (Hampton 1987, Armstrong *et al.* 1991a). Average recruit biomass estimates for this region range from 23 tons.km⁻² (May 1986 survey) and 49 tons.km⁻² (May/June 1985 survey) to 65 tons.km⁻² (June 1986 survey) (Hampton 1987). The maximum average fish density per model cell is therefore *ca.* 16 tons.¼km⁻².

Simulating such a high fish density in the model using average-sized shoals would necessitate partitioning fish biomass into approximately 22 shoals per model cell. Because of computer limitations, the maximum number of shoals per simulation is approximately one third the number of model cells. When simulating high fish densities, much larger than average shoal sizes are therefore used. For example, at high fish densities, a shoal size of 50 tons corresponds to a shoal packing density of approximately 1 shoal.km⁻², or 1 shoal per four model cells. These larger shoals may alternatively be envisaged as comprised of a number of smaller shoal groups (Hutchings 1992), which all move in approximately the same direction in search of food and which collectively occupy an area smaller than 0.25 km² at any one time.

RESULTS AND DISCUSSION

Unless stated otherwise, in all instances results represent the mean (\pm standard deviation) of 100 simulations.

Simulations Along the West Coast

Acoustic studies on the abundance and distribution of anchovy recruits off the West Coast reveal large local differences in recruit biomass, with densities ranging from less than 5 tons.km⁻² to over 100 tons.km⁻² (Hampton 1987). As a preliminary means of comparing model predictions under a range of different fish density scenarios, the same base-case prey concentration was assumed for the entire West Coast region, but separate simulations were run for each of four strata used by Hampton (1987). Fish density in each stratum was simulated using estimates of anchovy recruit biomass from an acoustic survey conducted in June 1986, when large recruitment strength was detected (Hampton 1987) (Fig. 5.5a).

To standardize model output, it was assumed that total fish biomass in each stratum was equally partitioned into n shoals of size nine tons each, yielding shoal packing densities ranging from 1 shoal.km⁻² in stratum D to 7 shoals.km⁻² in stratum C. The latter estimate suggests an area of 0.143 km² per shoal, and hence corresponds to average-sized shoals being distributed approximately 430 m apart, which is not biologically unrealistic.

Quantifying M_{pred} : As expected, preliminary results suggest that the proportion of copepod prey biomass removed on a daily basis (M_{pred}) by the fish is directly proportional to fish biomass (Fig. 5.5b). Model-predicted estimates of M_{pred} ranged from 0.27 d⁻¹ at moderate fish densities to 0.86 d⁻¹ at high fish densities.

On a local scale, the daily predator-induced mortality rate within individual cells ranged from zero (in cells not on any shoal's feeding path) to 0.93 d⁻¹ (in 'hit' cells with initially high prey concentrations). The model therefore simulates a patchy distribution of predation intensity so that there is no correlation between fish density and prey mortality rates at small scales, versus a clear correlation at scales larger than 25 km². Correlations between predator and prey densities are only to be expected at scales larger than the dimensions of the aggregations of the predator and prey (Rose & Leggett 1990). Field observations of extremely low copepod abundance in areas

of high fish abundance (Painting & Huggett 1989) lends credence to the high local model-predicted mortality rates.

The average and maximum specific production rates (ie. P/B = total daily production to total biomass ratio) measured in the field for copepod stage CI to CV *C. carinatus* individuals are respectively 0.139 d^{-1} and 0.233 d^{-1} . The model therefore predicts that if fish are present on a permanent basis at densities in excess of 9 tons.km^{-2} , fish predation is of a higher order of magnitude than the production of food ie. copepod turnover rates are too slow to sustain fish growth. Model simulations therefore suggest that for fish resident in an area, fish predation rates match the average and maximum specific production rates at fish densities of approximately 1 ton.km^{-1} and 3.5 tons.km^{-2} respectively. The persistent presence of patchily-distributed anchovy aggregations has been observed to impact notably on local zooplankton densities (Armstrong *et al.* 1991a). If fish predation pressures in the field exceed prey turnover rates, other mechanisms, such as the temporal and spatial segregation between cohorts of recruits (Lambert 1984, Hutchings 1992) must exist to synchronize the overlap between peak fish density and prey abundance.

Quantifying fish performance: Several authors (eg. Cook & Armstrong 1986, Daan *et al.* 1990, Emlen *et al.* 1990, Persson & Greenberg 1990) have demonstrated that fish growth and survival rates are density-dependent, particularly in the early life stages. The model predicted that the rate of intake of food by anchovy at high densities is a negative function of recruit biomass (Fig. 5.5d) and therefore that food availability is density-dependent. Armstrong *et al.* (1991a) estimate that anchovy populations along the West Coast consume about 1.88% of dry body mass per day. Corresponding model-predicted averages vary from 0.62 to 4.4% ($x=2.41$, $SE=0.84$) of dry body mass per day, suggesting that model results are biologically realistic. With the exception of simulations run using much higher prey:predator abundance ratios, fish feeding behaviour in the model was never constrained by the maximum satiation level but by the time available for foraging, or, under poor feeding regimes, by the maximum distance travelled.

The relationship between the percentage body weight consumed by an individual in a shoal and its estimated daily net energetic gain predicted by the model was not simple but depends on a number of parameters: specifically, the predator:prey abundance ratio and shoal size. This is because net energetic gain E_{net} is in some sense a measure of the trade-off between the rate of food consumption and the energy expended in search of food.

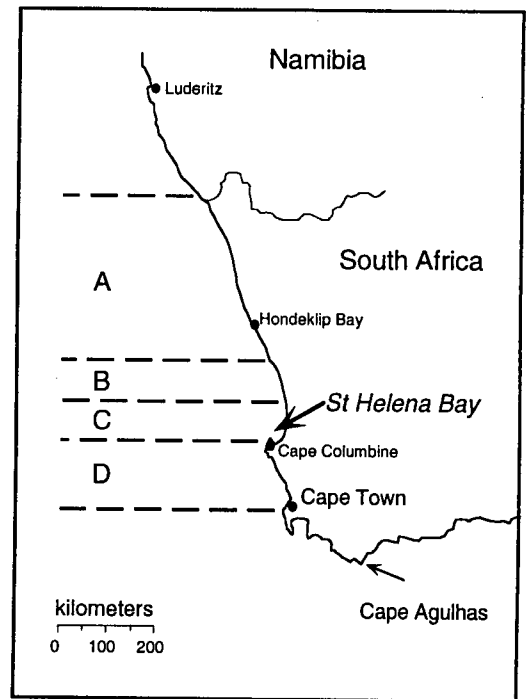
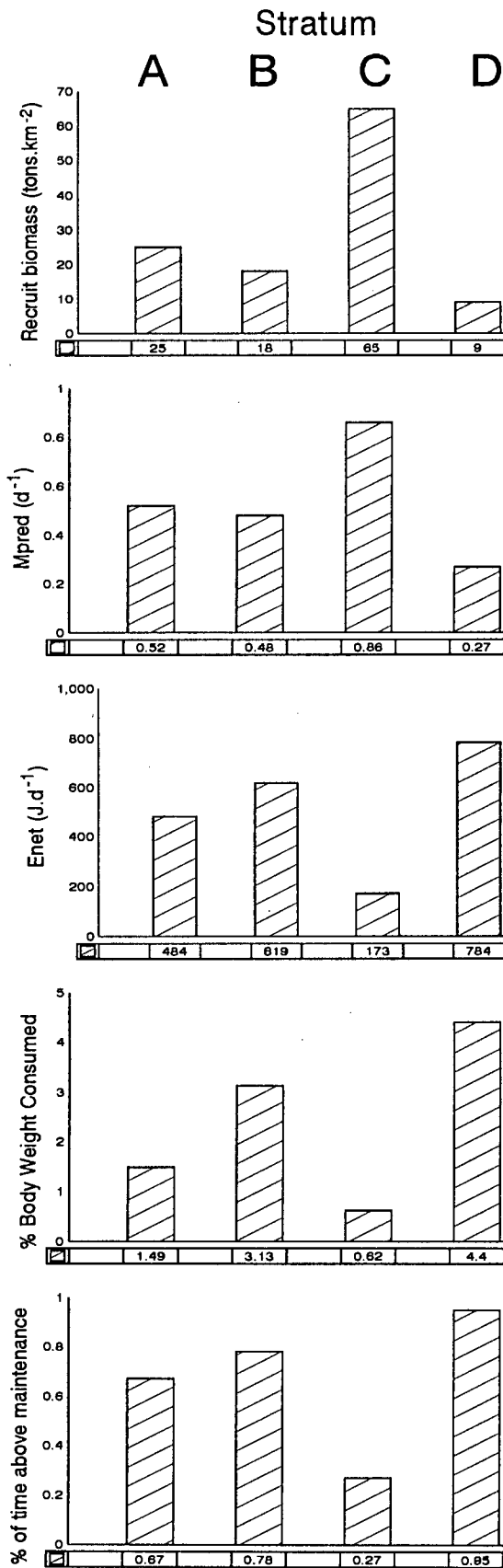


Fig. 5.5. Model-predicted estimates of the values of b) the predator-induced mortality rate M_{pred} , c) net energetic gain E_{net} , d) the percentage body weight consumed and e) the percentage of time that shoals are above their maintenance level, for each of four regions containing different anchovy recruit densities along the West Coast. Strata are those depicted in Hampton (1987) and are shown alongside.

The model predicted that the seven-fold increase in fish biomass between areas C and D leads to approximately a 4.5-fold decrease in the average net energetic gain per fish in the two regions (Fig. 5.5c). This suggests that growth in different regions may vary dramatically depending on *per capita* prey availability. Regional differences in growth are probably less dramatic in the field because it is unlikely that fish will distribute themselves evenly throughout the environment - rather, predators usually vary proportionately with their prey (Steele & Henderson 1992). More realistic simulations should therefore depict the higher fish densities in stratum C as coincident with higher prey densities in the region.

The coefficient of variation attached to model-derived estimates of E_{net} increased with increasing fish biomass as more shoals competed with each other in the model - shoals following in the wake of earlier shoals were unable to obtain sufficient food to maintain themselves, while shoals arriving first in an area of dense prey were able to quickly attain their maintenance rations. The average percentage of time that fish were above their maintenance ration therefore decreased with increasing fish biomass (Fig. 5.5e).

The Importance of Spatial Segregation

An important result which emerged from all model simulations was that model predictions are highly sensitive to the spatial rearrangement of fish biomass. Simulations were run using the same total fish biomass but with total biomass variably partitioned into different numbers of shoal groups. Although *per capita* prey availability remained constant in all simulations, changes in the geometric distribution of shoals resulted in more than five fold differences in the predicted net energetic gain per day (Fig. 5.6a). This is because shoals interfere more with each other at higher packing densities. For example, a shoal might deplete a prey patch situated on another shoal's feeding path, resulting in the second shoal incurring a greater travelling cost in searching for food. Thus although some shoals still do well at high packing densities, on average, the performance of shoals will be worse because of a density-dependent effect which manifests itself at the scale of a shoal, rather than at the scale of an individual. One implication of this model result is that if density-related changes in recruit dispersal behaviour occur in the field, the net effect on the system's dynamics is a non-linear density-dependent function of higher order than if concomitant changes in spatial structure did not occur with increasing fish density.

With fewer shoals, a larger number of prey 'refuges' or cells with high prey concentrations survive, so that when predation impact is averaged over all cells, the average will not be the same for a small number of shoals as for a large number of shoals. A more evenly distributed predation pressure therefore results in higher average M_{pred} estimates (Fig. 5.6b).

Because individual shoals are able to integrate their food supply over a fairly large area, it seems reasonable to expect model predictions to tend to a limit as shoal packing density is increased beyond some critical value. Model results (Figs. 5.6a&b) suggest that a reasonable estimate of this critical value is 10 shoals per 25 km² or 1 shoal per 2.5 km². To avoid inconsistencies in model predictions as a result of differences in shoal spatial segregation patterns, a minimum shoal packing density of one shoal per 2.5 km² was therefore employed in the model. Assuming average-sized shoals have a biomass of 0.755 tons (Wrzesinski 1987a), shoal packing densities in the field are approximately 3 shoals per 2.5 km² at low recruit biomass estimates of 1 ton.km⁻².

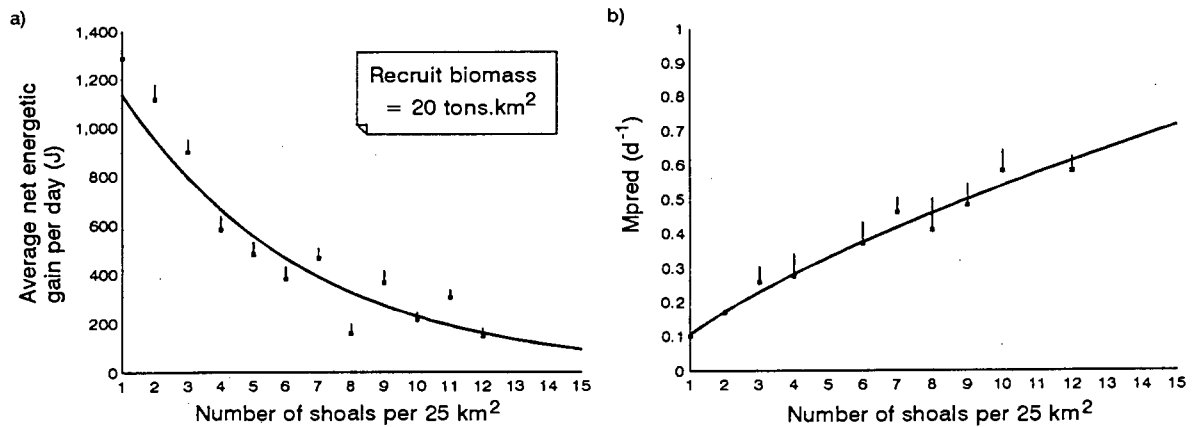


Fig. 5.6. The effect on a) E_{net} and b) M_{pred} of dividing the same total fish biomass into successively more shoal groups. Points on the graph in (a) represent the means (+S.E.) of 100 simulations, calculated using daily means for n evenly-sized shoals. Points in (b) are the means (+S.D.) of the M_{pred} estimates obtained for each of 100 simulations.

The Effect of Predator:Prey Abundance Ratios on Model Predictions

To investigate the effect on model predictions of varying prey abundance levels, one hundred simulations were run using an average fish density of 10 tons.km⁻², with shoal packing density in each simulation generated randomly in the range 0.4 to 1 shoal.km⁻². Mean base-case M_{pred} and E_{net} values were thus obtained and the

procedure then repeated for a number of scenarios in which prey abundance was varied by a factor of up to four times (Fig. 5.7). The entire procedure was then repeated using average fish densities of 50 and 100 tons.km⁻².

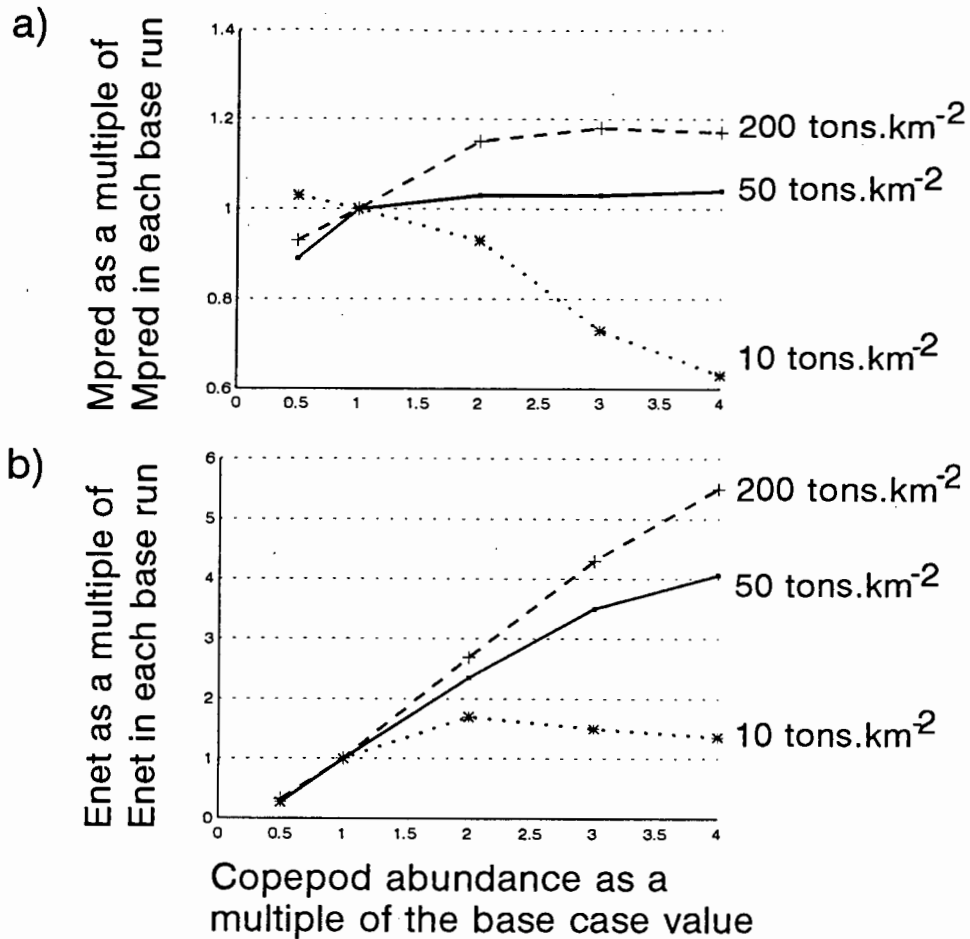


Fig. 5.7. The effect on a) M_{pred} and b) $Enet$ of varying prey abundance levels, and the sensitivity of this relationship to varying fish densities.

M_{pred} measures the averaged proportion of prey biomass removed by the fish. At extremely high fish densities (200 tons.km⁻²), the base-case M_{pred} mean is obviously high. If prey abundance is doubled, there are still enough fish to deplete all available prey to approximately the same background level as before, but because initial prey concentrations in each cell are now higher, average M_{pred} estimates will increase accordingly (Fig. 5.7a). Doubling prey abundance again causes only slight further increases in M_{pred} as fish are already removing almost the maximum proportion of prey.

At low fish densities (10 tons.km^{-2}), fish are not constrained by prey availability but remove as much copepod biomass as possible subject to their own foraging constraints. Increasing prey abundance does not therefore further increase the absolute amount of prey consumed. The ratio of prey consumed to prey abundance (M_{pred}) will therefore decrease as copepod abundance is increased.

Because at low fish densities the fish are already consuming the maximum amount possible, the average daily net energetic gain per fish is essentially independent of prey abundance, for prey concentrations in excess of the base-case value (Fig. 5.7b). In contrast, at high fish densities, the base-case prey concentration is limiting (low *per capita* prey availability) so that there is a dramatic increase in E_{net} with increasing prey concentration. A similar pattern is observed at intermediate fish densities (50 tons.km^{-2}), except that increases in E_{net} start levelling off after about a three-fold increase in prey abundance. At higher prey concentrations, the fish are again removing the maximum amount possible.

Quantifying M_{pred} and E_{net}

The sensitivity of model predictions to prey abundance levels is a nonlinear function of predator abundance. This highlights the necessity of quoting model predictions as a function of a predator:prey abundance ratio. The index adopted here represents the ratio of the average fish biomass (tons.km^{-2}) to the average copepod prey abundance (no.CIV-CV.m^{-3}).

As a preliminary means of quantifying the best form of a predator-induced mortality rate to be used to temporally integrate the model developed in chapter two over the winter season, model-derived estimates of M_{pred} are furnished as a function of the predator:prey abundance ratio (Fig. 5.8). Values of M_{pred} represent the predicted average proportion of *C. carinatus* prey removed by a certain relative density of fish moving through an area along the West Coast, assuming that density-related changes in recruit dispersal occur. Under food limiting conditions, M_{pred} plateaus at a constant high value of *ca.* 0.88 d^{-1} . High fish densities thus deplete zooplankton populations within a limited area to such an extent that it is no longer energetically viable for the fish to continue particulate feeding (hence the small number of (widely-dispersed) prey individuals which survive). Under this scenario, fish will either move on in search of new prey patches, or they must switch to a filtering mode of feeding, which generally offers substantially poorer energetic rewards.

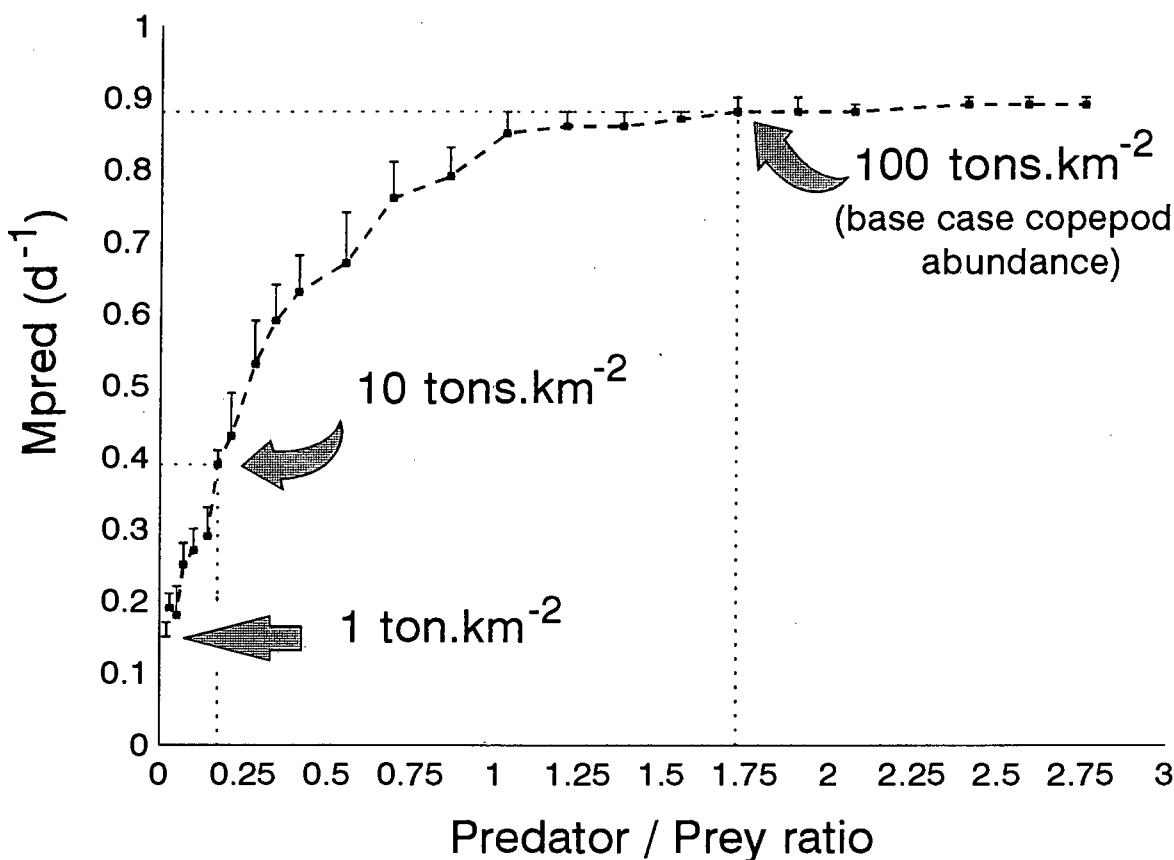


Fig. 5.8. Model-predicted estimates of the predator-induced mortality rate M_{pred} as a function of a predator:prey abundance ratio. The predator:prey ratio measures the average anchovy recruit biomass (tons.km^{-2}) feeding on *C. carinatus* prey (CIV-CVI stage) individuals (no.m^{-3}). A base-case prey abundance of 58 m^{-3} was used in the simulations. The figure shows the predicted average proportion of prey biomass removed by anchovy recruits occurring at different densities in a $10 \times 10 \text{ km}^2$ area along the West Coast shelf region. Points on the graph represent the mean M_{pred} value (+SD) when averaged over 100 simulations and 400 model cells.

Along the West Coast, marked inter-annual variations in average anchovy growth rates are manifest (Waldron *et al.* 1992). The present model predicts that density-dependent food-limitation elicits dramatic variability in juvenile anchovy growth rates. Figure 5.9 represents a crude attempt to quantify fish performance (in terms of net energetic gain only) as a function of *per capita* prey availability. Since *per capita* prey availability is both spatially and temporally dynamic, instantaneous growth rates may be expected to fluctuate about some average value, with the overall average observed in any one year (eg. 0.03cm.d^{-1} in 1989 vs 0.04cm.d^{-1} in 1985) increasing with increasing prey availability. If selective predation mortality of slow-growing

individuals occurs in the field, the average observed growth rate will be higher than that predicted by the model, and this mechanism will act to dampen variability in growth rates.

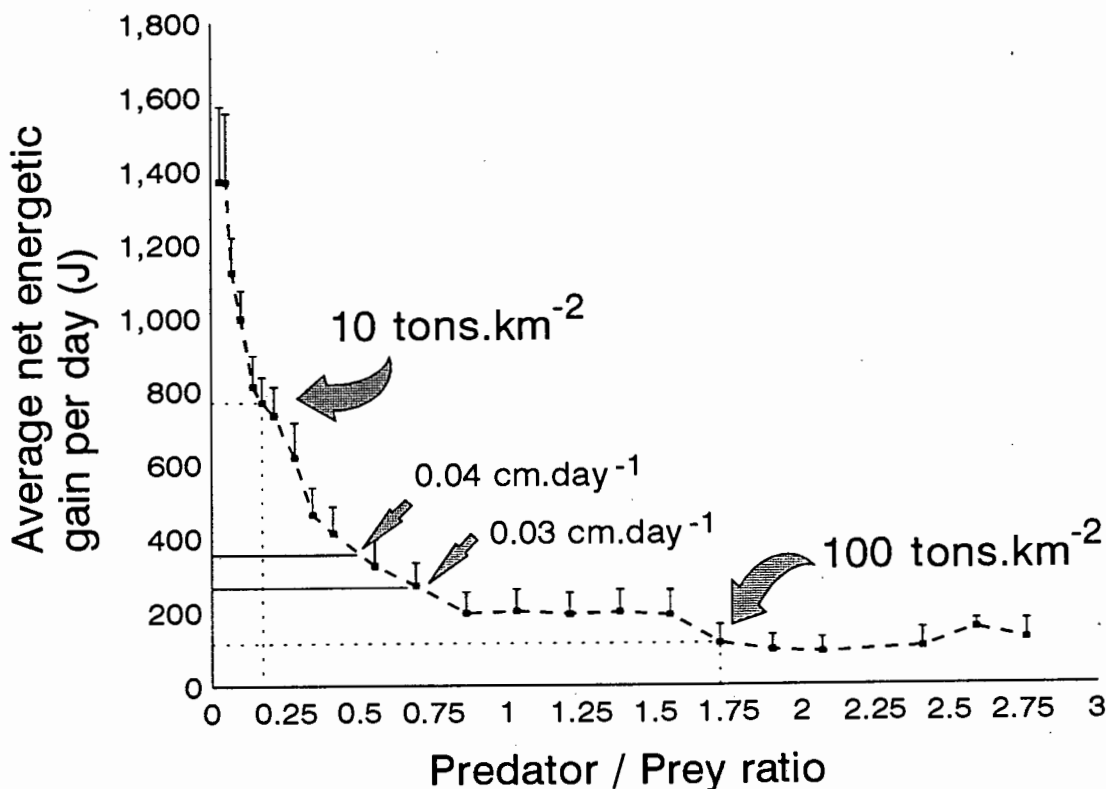


Fig. 5.9. Model-predicted estimates of the average daily net energetic gain E_{net} of anchovy recruits as a function of a predator:prey abundance ratio. The predator:prey ratio measures the average anchovy recruit biomass (tons.km^{-2}) feeding on *C. carinatus* prey (CIV-CVI stage) individuals (no.m^{-3}). A base-case prey abundance of 58 m^{-3} was used in the simulations. In each simulation, E_{net} is calculated as the mean of the E_{net} values predicted for all shoals in the model area. The points on the graph represent the mean of 100 such means, along with the associated standard error. As explained in the text, positive energy balances are used to estimate the daily growth in caudal length of a base-case anchovy recruit. The E_{net} values required to achieve the mean growth rates of 0.04 and 0.03 cm.d^{-1} observed in 1985 and 1989 respectively are highlighted.

TESTING THE MODEL'S SENSITIVITY TO RELEVANT PARAMETERS

The primary aims of the present model were to quantify the predator-induced mortality rate M_{pred} and to assess the performance of the predator under various scenarios. The sensitivity of the model was therefore tested by determining to what degree model-predicted M_{pred} and E_{net} estimates depend on the parameter values

chosen and the underlying model assumptions. Model parameters were varied one at a time and one hundred five-day simulations run under each scenario. Each simulation took *ca.* 80 seconds using a 386 IBM microcomputer. A separate program (APPENDIX II to thesis) computed the mean and standard deviation of the M_{pred} estimates for each of the five days, and the mean of these daily estimates was then compared with the mean of 0.302 d^{-1} (SE = 0.034, $n=100$) obtained for the base-run. Mean Enet values under each scenario were obtained by pooling Enet values for each individual shoal for each of the five days and for all one hundred simulations, and comparing the mean obtained with the base-case value of $603 \text{ J.fish.d}^{-1}$ (SD = 193). Base-case simulations used a mean fish biomass of 5 tons.km^{-2} and a mean shoal packing density of $0.5 \text{ shoals.km}^{-2}$. The results of a sensitivity test are only presented if a fifty per cent change in the test parameter resulted in at least a 5% change in the model predictions.

Sensitivity to foraging constraints

The model exhibited a greater degree of sensitivity to total available foraging time (T_{total}) than to the limit on the maximum distance travelled per day (Maxdist) (Figs. 5.10 a&b), and was relatively insensitive to the maximum satiation parameter (Satiat). Increases in both T_{total} and Maxdist resulted in proportionately smaller changes in M_{pred} and Enet than equivalent decreases in their value. This suggests that even without any foraging constraints, model-predicted Enet and M_{pred} values would tend to a limit determined by *per capita* prey availability. If fish could forage equally efficiently throughout the day and night, the model predicts that at a constant high predator:prey ratio, they would be able to increase their average net daily energetic gain by a maximum of *ca.* 75%. The percentage of time that shoals were above their maintenance level (MAINT) was relatively independent of changes in T_{total} and Maxdist. At constant predator:prey ratios, MAINT is primarily a function of the spatial segregation of shoals because of inter-shoal competition effects.

Does foraging time increase with increasing fish density? The above simulations could be interpreted as quantifying the adaptive control of foraging effort. Food availability may determine foraging effort in fish (Abrams 1991) and natural selection should favour increasing foraging time and hence predation risk as juvenile fish density is increased (Walters & Juanes 1993). If predator density is doubled in the model, the above results predict that individual fish would need to increase foraging effort by approximately one third to achieve the same relative increase in growth.

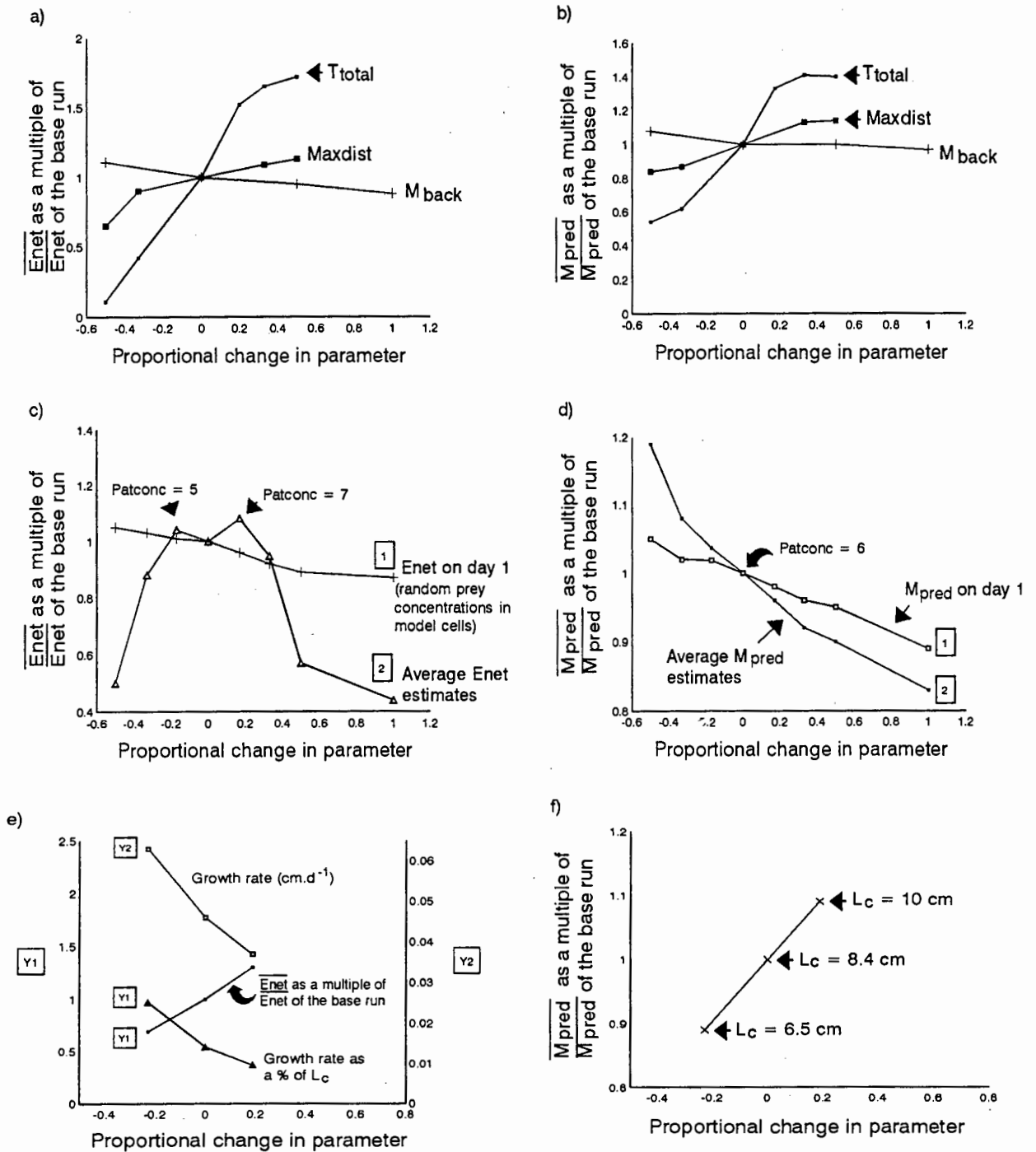


Fig. 5.10. Comparison of the model's sensitivity to different parameters. The curves show the effect on the mean base-case value of a) $\overline{E_{net}}$ and b) $\overline{M_{pred}}$ when the foraging constraints ($Maxdist$ and T_{total}) and the background prey mortality rate (M_{back}) were varied one at a time. The curves in c) and d) show the effect of changes in the threshold feeding concentration ($PATCONC$) on $\overline{E_{net}}$ and $\overline{M_{pred}}$ respectively, for cases 1 and 2 described in the text, while curves e) and f) show the model's sensitivity to differences in the caudal length L_c of the fish used in the simulation.

Density-dependent effects on fish growth rate may manifest themselves not so much because of food availability but because predation mortality on the fish increases with increasing density (Walters & Juanes 1993). The nonlinear relationship between fish density and fish growth rates emphasizes the importance of trying to quantify the way in which density-dependent effects affect habitat use and population survival.

Sensitivity to the Background Mortality Rate

Changes in the value of M_{back} resulted in proportionately smaller changes in model predictions (Figs. 5.10 a&b), suggesting that model predictions are not overly sensitive to the assumption that $M_{\text{back}} = 0.05$. This is because M_{back} is small relative to M_{pred} .

Sensitivity to the Threshold Feeding Concentration

The model was both quantitatively and qualitatively sensitive to the choice of PATCONC because changes in its value produced both substantial and nonlinear changes in model predictions (Fig. 5.10c). Decreasing PATCONC is equivalent to relaxing the stringency of the rule defining what constitutes a patch as perceived by a fish and which areas are therefore profitable for the fish to stay and feed in. In the short term the model predicts that E_{net} will be higher (Fig. 5.10c, curve 1) because the fish stop and feed in virtually every model cell ie. they effectively encounter more 'patches'. The increase in E_{net} is small because the additional energetic gain derived from feeding in low concentration areas is correspondingly small. When integrated over larger time or space scales however, the model predicts that it is disadvantageous to stop and feed in these low concentration areas (Fig. 5.10c, curve 2). This is presumably because, with time, the average prey concentration drops and prey populations are depleted to such an extent that they hardly recover between predation bouts. Under this scenario, shoals will be forced to stay and feed in areas with prey concentrations below that required to maintain their maintenance ration.

Conversely, if PATCONC is increased, E_{net} will initially be worse than the base-case value because fewer 'patches' are encountered. Because the fish are repeatedly 'underexploiting' the available prey, they deplete prey patches faster and move on in search of others, so that with time shoals encounter fewer and fewer patches. The model predicts that despite the higher average background prey concentrations under this scenario, the trade-off between the reduced frequency at which patches are encountered (ie. increased travelling cost) is not adequately balanced by gains

accrued from the faster turnover rates in background model cells. The implication is that it is not advantageous for shoals to forfeit 'average-quality' prey patches in preference to fewer 'high-quality' prey patches. This prediction might fail in the field if fish entering a relatively pristine area with high prey concentrations can accurately assess the average prey environment and are able to locate dense prey aggregations.

Predicted optimum patch choice strategy: The model predicted that average net energetic intake is maximised for values of PATCONC in the range 5-7 prey individuals.m⁻³. This result is of interest because the model prediction, which arises from the trade-offs between the various costs and benefits associated with each patch choice strategy, corresponds well with the theoretically-derived estimate employed in the model. While it seems intuitively obvious that it is sub-optimal for fish to stop and feed in areas with prey concentrations below that required to maintain their standard metabolic rate, it is less obvious that the optimal strategy should be to stop and feed in all prey patches with concentrations greater than PATCONC, as predicted by the model result. Thus although the model is sensitive to the choice of PATCONC, the above arguments corroborate the use of the base-case value.

The exact value of PATCONC has a much smaller effect on M_{pred} estimates. As expected, M_{pred} decreases with increasing PATCONC as, when averaged over all model cells, a proportionately smaller percentage of the prey population is removed in each instance.

The Effect of Fish Size on Model Predictions

The different locomotory capabilities of adult and juvenile (and synonymously large and small-sized) fish means that the older life history stages of pelagic fish are more efficient integrators of spatial and temporal variability in food availability than the younger stages (Kjørboe 1991). The effect of differing fish size on model predictions was tested by partitioning the same shoal biomass into F fishes of (a) size $L_c = 6.5\text{cm}$ ($F_{weight} = 1.49\text{g}$) and (b) size $L_c = 10\text{cm}$ ($F_{weight} = 6.05\text{g}$). Because the reactive distance (RD), swimming speed and the quantity of prey required to attain its maintenance ration are all functions of an anchovy's size, a value for PATCONC was recalculated for each case, using the same method as before. In accordance with theoretical predictions (Lasker 1975, 1978, Schmitt 1986), calculations suggested that smaller fish require a higher threshold feeding concentration: values of PATCONC obtained for cases (a) and (b) were respectively ten and four prey individuals.m⁻³. If shoal biomass is held constant, the foraging

efficiency of a shoal comprised of large fish may be further enhanced relative to that of a shoal comprised of smaller fish because the collective search volume is larger in the former case. This is because the distance between neighbouring fish in an aggregate increases with increasing fish size (Serobrov 1976, Pitcher & Partridge 1979, Pitcher *et al.* 1985).

To account for the fact that larger fish integrate food availability over larger areas (Kjørboe 1991), Maxdist was adjusted as a linear function of swimming speed (measured in $\text{BL}\cdot\text{s}^{-1}$), yielding estimates for case (a) and (b) of 11.6 and 17.8 km respectively. Respiratory costs were modified as a linear function of F_{weight} since they are standardized in units of $\text{J}\cdot\text{g}^{-1}\cdot\text{hr}^{-1}$ in the model.

The model predicted that although the initial predator:prey abundance ratio was the same, Enet increased in an almost exponential fashion with increasing fish size (Fig. 5.10e). However, the superior foraging and locomotory abilities of larger fish also results in a less equitable partitioning of the available food resources due to greater inter-shoal competition effects: the model predicts that the percentage of shoals that are above their maintenance ration level in case (a) (MAINT = 65%) is on average 0.14 times higher than the corresponding percentage (MAINT = 57%) predicted for case (b).

Transposing excess joules into growth results in a reversal of the above pattern (Fig. 5.10e), with growth rate decreasing with increasing fish length and in a manner consistent with the theoretical predictions of a von Bertalanffy-type growth curve. Relative growth rates (calculated as a percentage of fish length in each instance) also decrease with increasing fish length (Fig. 5.10e).

Growth in absolute fish biomass: Given that a fish's volume is approximately proportional to the cube of its length, the volume V_1 of a 6.5 cm long anchovy is approximately 0.275 times that of the volume V_2 of a 10 cm long anchovy. Using the growth estimates obtained from the above simulations ($\delta L_1 = 0.063 \text{ cm}\cdot\text{d}^{-1}$; $\delta L_2 = 0.037 \text{ cm}\cdot\text{d}^{-1}$), suggests that, on average, the same initial predator:prey abundance ratio produces a proportionately greater volume (and hence mass) increase in small fish than in large fish ($V_1/V_2 = 0.2796$). Because both total fish biomass and shoal packing densities are the same in case (a) and (b), this implies that the same food environment produces approximately an extra 17 kg growth in fish mass per km^2 per day when shoals are comprised of small versus large fish.

Because larger fish are more efficient foragers than smaller fish, they remove a greater absolute quantity of prey and hence the proportion of prey removed (M_{pred}) increases with increasing fish length (Fig. 5.10f). Changing fish length in the model results in proportionately smaller changes in M_{pred} , suggesting that the present attempts to quantify the predator-induced mortality rate are not overly dependent on fish size.

The Effect of Shoal Size

To test whether or not different sized shoals performed differently in the model, the same total fish biomass was variably partitioned into shoals of different size, in such a way that shoal packing density remained constant. The average anchovy density in each simulation was 7.2 tons.km^{-2} and a shoal packing density of $0.4 \text{ shoals.km}^{-2}$ was used. Simulations were run until 100 Enet values were obtained for each of a range of shoal sizes.

The model predicted that Enet is optimised for shoal size approximately in the range 10 to 50 tons (Fig. 5.11a). The optimum range predicted by the model results because of the trade-off between *per capita* consumption per prey patch encountered and the speed of movement (or foraging volume searched) of various sized shoals.

The consumption per unit time spent feeding of at least some small shoals is higher than that of any of the larger shoals in the model area - maximum percentage of dry body mass consumed per day: 7.87% (shoal size = 5 tons) vs 2.69% (shoal size = 50 tons). However, because of competition with other shoals, the probability of an individual shoal encountering a prey patch decreases with decreasing shoal size in the model, so that on average smaller-sized shoals do worse than medium-sized shoals. Above a critical shoal size Enet declines again because decreases in *per capita* consumption per patch cell are not adequately balanced by the increased speed of movement through the environment.

Net energetic budgets in the model vary not only because of changes in energetic gain, but also because of changes in the relative amounts of time spent travelling and feeding. The distance a shoal travels along its feeding path on any one day depends on the prey concentrations encountered en route. If prey availability is doubled, the rate of movement of all shoals through the model area therefore decreases. At higher prey concentrations there is therefore less of a clear distinction between the performance of different-sized shoals (Fig. 5.11b). Also, because at high prey

concentrations the *per capita* consumption per patch cell encountered is less restrictive for a large shoal than is the case at lower prey concentrations, the optimum predicted shoal size increases slightly with increasing prey concentration.

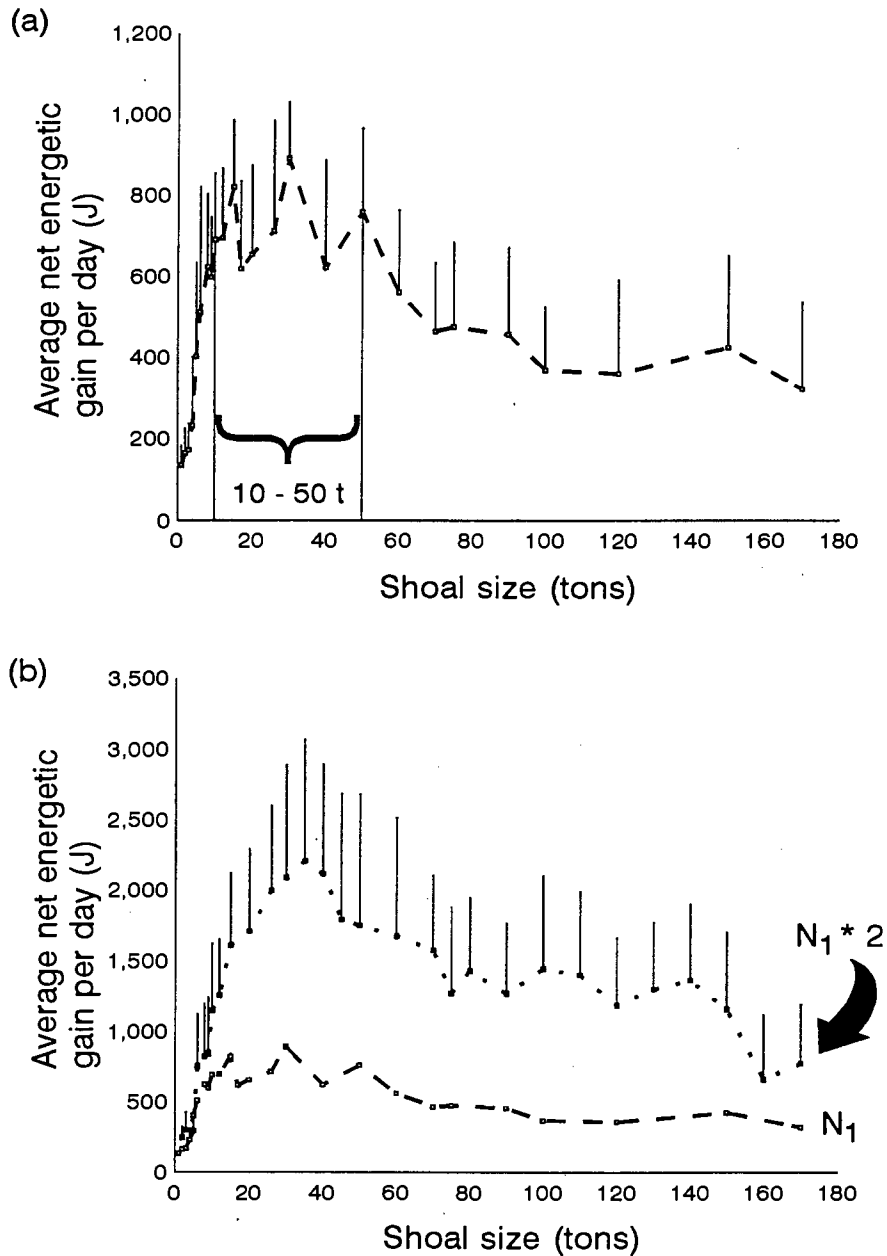


Fig. 5.11. The effect of shoal size on model-predicted net energetic gain E_{net} estimates (a), and the way in which prey availability modifies this relationship (b). Points on the graph represent the mean (+SD) of 100 E_{net} values predicted for a shoal of size as shown. Total anchovy biomass is variably partitioned in each simulation so that shoals of a certain size co-occur with a range of different-sized shoals in the different simulations, thereby compounding the variance of mean E_{net} estimates. In (b), simulations are repeated but the initial prey abundance estimate N_1 is doubled.

The above results suggest that in exploiting a patchy prey source, net energetic gain is maximised at intermediate shoal sizes. This prediction is incongruous with the empirical observation that average shoal size in the field is much smaller (Wrzesinski 1987a). This highlights the fact that other factors such as the energetic costs of maintaining a coherent school structure or the relationship between shoal size and susceptibility to predators may be more important in determining optimal shoal size. Anchovy form a significant component of the diet of many vertebrate predators off the West Coast, including juvenile Cape hake *Merluccius capensis* (Punt *et al.* 1992, Pillar & Barange 1993), South African fur seals *Arctocephalus pusillus* (Wickens *et al.* 1992), African penguins *Spheniscus demersus* (Laugksch & Adams 1993), squid, fish species such as snoek *Thryxites atun* and yellowtail *Seriola lalandi*, and several odontocete cetacean species (Sekiguchi *et al.* 1992). The major predators of anchovy are juvenile Cape hake which, excluding the fishery, account for approximately half of all anchovy predation (Wickens *et al.* 1992). Juvenile hake switch from being planktivorous to being almost exclusively piscivorous in areas of high anchovy recruit abundance (Pillar & Barange 1993), suggesting that smaller anchovy shoal size may be selected for in the field as it minimizes predation. The implication is that because of the simplistic model construction and consequent failure to account for the way in which predators on anchovy may in turn modify their foraging behaviour, the present model possibly overestimates Enet.

Effect of Increasing Prey Patchiness

To test the effect of different spatial arrangements of prey biomass on model-predicted fish performance, the starting prey concentration in each model cell was initialized by generating a series of gaussian random numbers with a mean equal to the base-case N_1 value and with random numbers constrained in the range \pm a variable percentage. Mean Enet and M_{pred} values (from 100 simulations) were then compared with predictions obtained using the base-case, which assumed an even initial prey distribution. The entire process was then repeated using a mean N_1 value three times larger than the base-case N_1 value.

The model predicted that at high prey concentrations, Enet is less sensitive to spatial prey patchiness than at low prey concentrations (Fig. 5.12a). This is so because in the former case prey concentrations in most cells are above the PATCONC level, and patches are generally of high quality (in terms of their energetic content), and hence spatial variability in prey concentration is not overly important because fish seldom have to travel long distances to attain their maintenance ration.

At lower overall prey concentrations, E_{net} decreased as the variance in prey concentration between the various model cells was increased (Fig. 5.12a, curve 2). Increasing prey spatial heterogeneity both decreases the probability of an individual shoal finding food and changes the ratio of energetic gain to energetic expenditure. Although the greater travelling costs incurred in a more patchy environment may be balanced by the greater energetic benefits of feeding in a high quality prey patch, the model predicts that MAINT decreases with increasing spatial heterogeneity. This suggests that, because of the greater variability attached to a shoal's probability of finding a prey patch, utilisation of the available resources by the various shoals is less equitable. The net effect is that, on average, shoal performance is worse.

For similar reasons to those discussed above, at high prey concentrations the value of M_{pred} is relatively independent of spatial prey patchiness, whereas at lower prey concentrations M_{pred} decreases with increasing spatial heterogeneity (Fig. 5.12b).

The prediction that, on average, fish do better by feeding on more average-quality patches than on fewer higher-quality patches is consistent with the earlier prediction (Fig. 5.10c) that, on average, it does not pay shoals to forfeit poorer quality prey patches in their search for those of high quality.

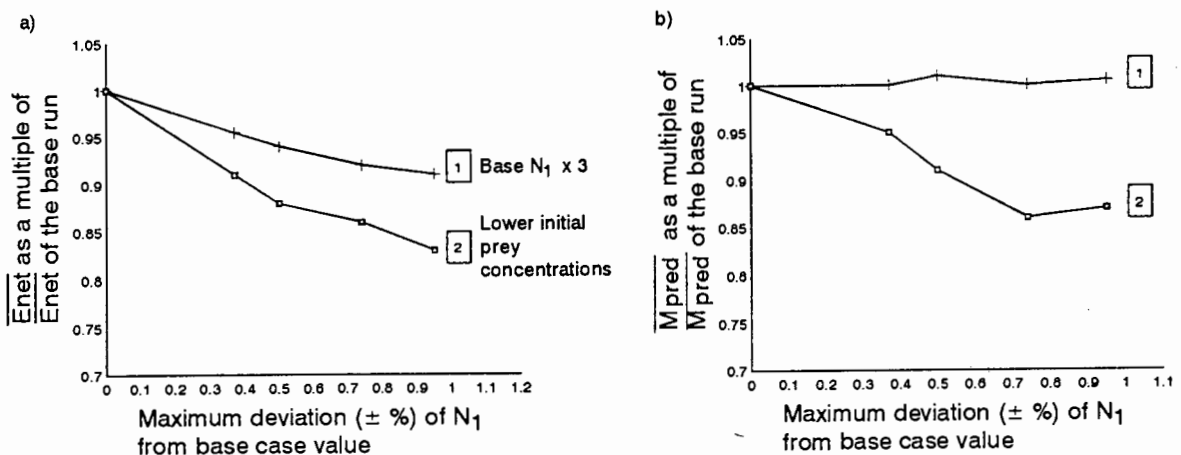


Fig. 5.12. The effect on the mean base-case a) E_{net} and b) M_{pred} value of increasing the variance in the initial spatial distribution of prey concentration. Case 1 uses a mean initial prey abundance value N_1 of 58 prey individuals. m^{-3} , while case 2 has $N_1 = 172$ prey individuals. m^{-3} . Inter-cell prey concentration variability is increased by increasing the maximum permissible deviation from the mean when randomly generating prey concentration in each cell.

The Effect of Faster Feeding Rates

Doubling feeding rates (FR) in the model resulted in approximately a 58% increase in E_{net} (Fig. 5.13b vs d). While faster feeding rates imply a higher energetic

gain:expenditure ratio, as well as an energetic bonus due to the increased time available for foraging, the positive effects are dampened to some extent when averaged over longer time scales because of increased density-dependent effects in the model. This is illustrated by the fact that if prey availability is doubled, a relatively larger increase in Enet occurs when FR is doubled (Fig. 5.13e).

Since the classic paper of Rothschild and Osborn (1988) which asserted that turbulence may enhance predator-prey encounter rates and hence zooplankton feeding rates, much attention has focused on the role of turbulence in mediating growth rates in the field. Small-scale turbulence has been shown to increase ingestion rates and gross-growth efficiency in copepods (Marrase *et al.* 1990, Saiz & Alcaraz 1992b, Saiz *et al.* 1992, Kiørboe 1993), and there is mounting theoretical, experimental and field evidence that turbulence enhances the encounter rates (and hence feeding rates) between zooplankton predators and their prey (Sundby & Fossum 1990, MacKenzie & Leggett 1991, Yamazaki *et al.* 1991).

MacKenzie and Kiørboe (1993) recently determined experimentally that attack rates of small cod larvae are 2.3-fold higher in turbulent than in calm water. Furthermore, they established that the effect of turbulent water motion on feeding rates is greater at low prey densities than at high prey densities. At high (saturating) prey densities the increase in prey density perceived by planktonic predators (due to turbulence-induced transport of prey individuals into a predator's visual range) is negligible relative to the already high prey densities.

To compare tentatively model predictions under a calm and turbulent regime, simulations were run in which it was assumed that the entire model area was subject to increased turbulence, but that fish feeding rates were only enhanced (by a factor of 2 relative to the base-case) in model cells with prey concentrations less than some low threshold prey concentration. The model predicted that if, under a turbulent regime, only one fifth of hit cells encountered by the fish result in an increase in the feeding rate FR, the increase in Enet relative to the base-case is disproportionately higher than when FR is constantly doubled (Fig. 5.13c vs b). Furthermore, if this mechanism really applies, the model predicts that turbulence-mediated enhanced feeding rates at low prey densities results in an increase in Enet equal to half that predicted assuming FR is constant but absolute prey abundance is doubled. The implication is that if anchovy feeding rates are mediated by physical processes, correlations between prey abundance and fish growth rates may be obscured.

Food concentrations and turbulence: The results obtained above remained similar when FR was increased in anywhere between 12 and 30 per cent of the hit cells encountered by shoals. However, when simulations were rerun using a higher total prey abundance level, and assuming turbulence similarly enhanced FRs, only slight increases in Enet occurred relative to Enet of the base-run (which used the higher prey abundance level but held FR constant) (Fig. 5.13f vs d). The model therefore predicts that, in accordance with theory, the effect of turbulence-mediated elevated feeding rates is greatest at low prey densities.

Two additional points are worth mentioning. Firstly, if fish need to be less active in turbulent than in calm water, then the resultant decrease in their active metabolic costs (MacKenzie & Kiørboe 1993) means that the effect of turbulence on fish growth rates may be even more pronounced than estimated here. This highlights the need to explore further the effects of turbulence (Kiørboe 1993). Secondly, it is likely that there is an optimum range of turbulence levels which maximise feeding rates (MacKenzie *et al.* 1993). Overall feeding success may be reduced with greater turbulence if, for example, dense prey patches are dissipated (Kiørboe 1993). Because wind speed explains more than half the variance in the dissipation of surface layer turbulence, future plankton studies should record this variable (MacKenzie & Leggett 1993).

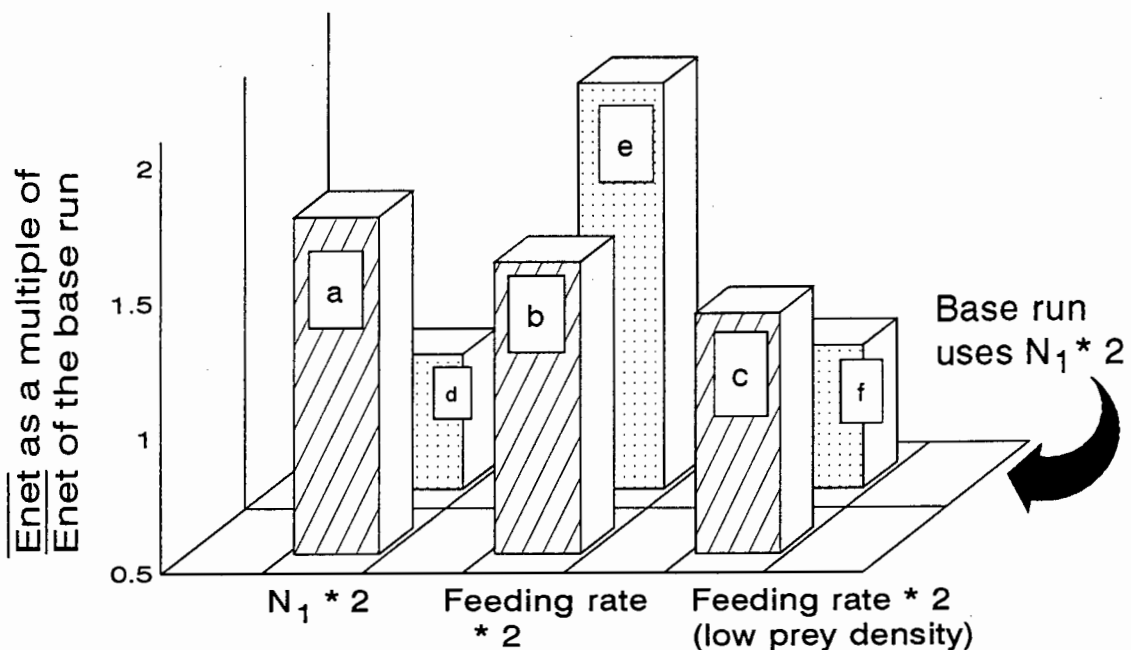


Fig. 5.13. Simulation experiments to investigate the effect of a turbulence-mediated increase in fish feeding rate on model-predicted Enet values, and the way in which prey concentration modifies this relationship. See text for further explanation.

The Problem of Spatial Autocorrelation

A detailed analysis of the model's sensitivity to all underlying functional forms and all aspects of its structure would necessitate fundamentally reworking the computer program into a more complicated form, and hence only brief discussions of the hypothesized effects of some underlying model assumptions are presented. The initial formulation of the model assumes that anchovy encounter prey patches sequentially in what is essentially a Poisson process. Real distributions are not necessarily random, however, as prey patches are spatially correlated due to local hydrodynamic or biological processes (Haury *et al.* 1978). If the movements of anchovy are not random and the fish are able to increase their probability of detecting a prey patch by using chemical or other cues, the present model may under-estimate their potential predatory impact on zooplankton populations.

A related problem concerns the speed at which predators assess the average density of resources in their environment. If prey patches are spatially correlated, the environment may be thought of as having a coarser grain than if prey patches are distributed randomly. Bernstein *et al.* (1991) suggest that in a coarse-grained environment predators form an inaccurate estimate of average feeding conditions and this may then affect their judgement as to when to move away from areas of low prey density. Conversely, in a fine-grained environment, or with random movements of the predators, the predators rapidly form a 'correct' estimate of average prey density (Bernstein *et al.* 1991) and they may therefore integrate their food supply more effectively over the available area. The degree of spatial autocorrelation may therefore have some effect on the overall rate of prey depletion, but the magnitude of this effect is presently unknown.

The Moving Threshold Assumption

The rule governing the extent to which fish deplete prey patches in the model assumes implicitly that the primary stimulus mediating patch use is that of optimizing food intake. However, several authors (eg. Brown 1988, Abrahams & Dill 1989, Sih 1992, Nonacs *et al.* 1994) have highlighted the potential role of predation in determining the strategy a predator should use in exploiting food patches. Using a behavioral model of the foraging behaviour of northern anchovy, Nonacs *et al.* (1994) predicted that fish maximize survival by selectively avoiding zooplankton patches with a high associated predation risk.

As a crude means of approximating the relative importance of the way in which the above aspect of anchovy foraging behaviour is defined in the model, simulations were run in which it was assumed that the fish remove only a certain proportion of prey from a patch before moving on in search of another. As before, the base-case assumed that fish deplete prey patch populations to the average background level.

The model predicted that if the trade-off between growth rate and lessening predation risk dictates that fish should minimize the time spent in a prey patch and so exploit only half of the available prey for example, then E_{net} will be reduced to 68% of the base-case value (Fig. 5.14). If it is assumed that fish remove as little as one third of the available prey per patch cell encountered, then the ratio $E_{net}:E_{net}(\text{base})$ decreases disproportionately (Fig. 5.14) as fish incur a greater travelling cost for the same energetic gain. To accurately assess net fish survivorship under these conditions requires an estimate of the decrease in predation risk associated with each particular strategy. Model results therefore suggest that fish growth rates may be significantly reduced by predator-induced sub-optimal utilisation of prey patches. Furthermore, the quantitative sensitivity of both E_{net} and M_{pred} estimates to the level to which the fish deplete prey patches highlights the importance of the moving threshold assumption.

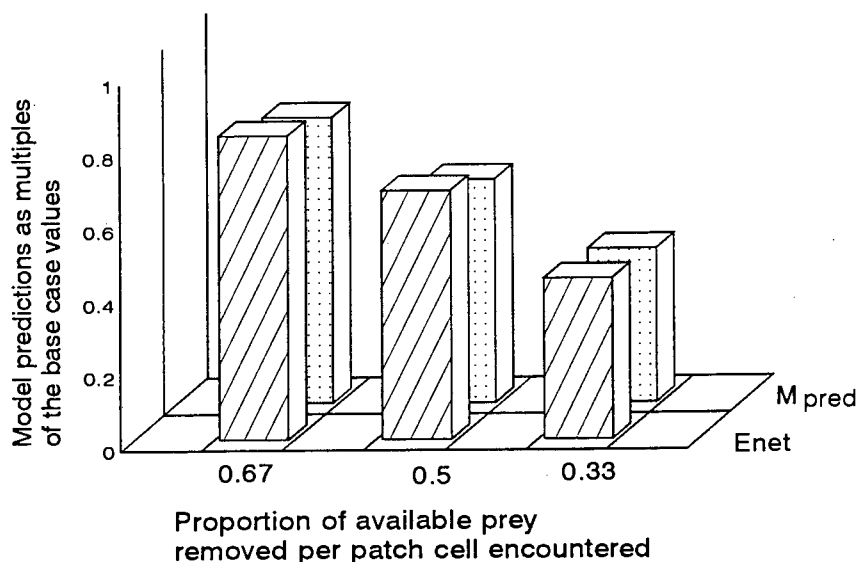


Fig. 5.14. Simulation experiments to investigate the effect on model predictions of predator-induced sub-optimal utilisation of prey patches. See text for explanation.

The Importance of Temporal Segregation

To gain insight into the way in which fish growth rate is affected by temporal matches and mismatches between the anchovy and their prey, the following 35-day simulation experiment was conducted:

The model area was initialised with the same base-case prey concentration in each cell and the rate at which fish shoals succeeded one another through the area was varied from once every day to once every five days or less. Shoals remained in the model area for between one and three days, with improved feeding conditions retarding the speed of movement through the area. Fish density was held constant at 10 tons.km⁻² when fish were present in the area. For each scenario, average growth rates were used to predict the growth in caudal length of a base-case anchovy over a period of one week. Predicted growth patterns were compared to observed growth patterns, assuming a constant value of 0.03 cm.d⁻¹ (1989 data) and 0.04 cm.d⁻¹ (1985 data) (Waldron 1994).

Model results suggested that at densities of 10 tons.km⁻², anchovy permanently resident in the same area quickly deplete the available prey and so are unable to sustain a growth rate of 0.03 cm.d⁻¹ (Fig. 5.15). A five day gap in predation pressure was necessary to allow prey populations to recover sufficiently to sustain growth at the level observed in 1989. To achieve the growth rates observed in 1985 necessitated doubling the initial prey abundance in the model (Fig. 5.15). At a higher fish density of 20 tons.km⁻², an eight day gap in predation pressure was necessary to simulate the 1989 growth patterns.

Model predictions are approximately consistent with the observation that, provided feeding conditions are favourable, copepods can double their biomass within about five days (Peterson *et al.* 1990, 1992, Verheye 1991, Walker & Peterson 1991). Hutchings (1992) suggested that if anchovy shoal groups follow too closely behind one another, reductions in the fish's scope for growth will occur because of temporal mismatches between zooplankton production and fish abundance. Anchovy are known to exhibit life history traits such as iteroparity which render them well-adapted to inhabiting a highly variable environment (Shelton 1987). Hutchings (1992) proposed that iteroparity functions in increasing the carrying capacity of a narrow shelf region such as the West Coast, where density-dependent food limitation may occur. Model predictions corroborate theoretical predictions emphasizing the importance of temporal segregation between anchovy shoal groups to anchovy feeding success, and ultimately to growth and survival rates. Moreover, because

adult anchovies on the Agulhas Bank require sufficient food resources for sustained serial spawning, food limitation on the Agulhas Bank may indirectly contribute to recruitment failure if the protracted spawning season in turn induces severe density-dependent food limitation along the West Coast during the recruitment period.

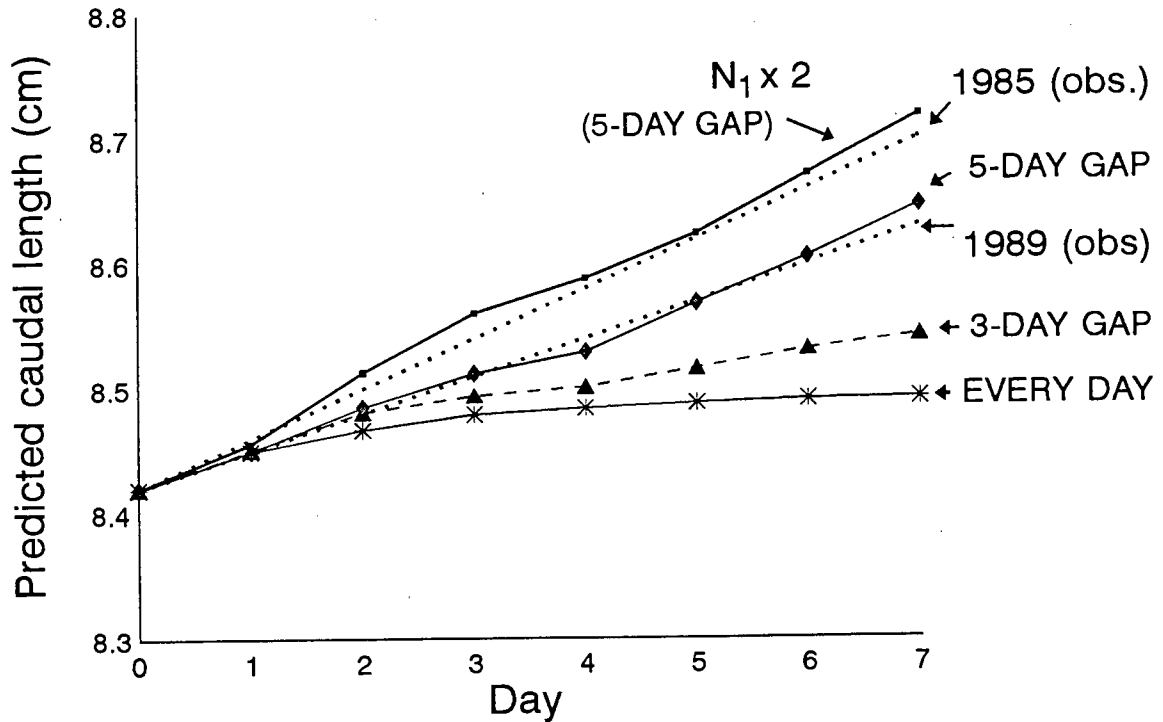


Fig. 5.15. The predicted growth in caudal length of an anchovy recruit when shoals succeed one another through an area at the rates shown.

Temporal Segregation and Fish Size

To summarize some of the relationships between temporal segregation, fish size and prey abundance, simulations were run in which it was assumed that shoals of recruits passed through an area on average once every five days. A mean fish density of 10 tons.km⁻² was used, but with shoals being comprised of fish having a caudal length of a) 8.4 cm (base-case), (b) 6.5 cm and (c) 10 cm. Shoal packing density was varied randomly in the range 0.4-0.8 shoals.km⁻². Simulations were then repeated but the initial prey abundance was doubled. For each scenario, net energetic gain was averaged over a two-week period.

As before, net energetic gain increased with increasing fish size, but because small fish require less food to achieve the same growth rate as a large fish, growth rate

decreased with increasing fish size (Fig. 5.16). When prey abundance was doubled, a proportionately larger difference was manifest between the predicted growth rates of 6.5 cm fish under the sparse and dense prey scenarios, than for 10 cm fish (Fig. 5.16). This is because at dense prey concentrations, the superior ability of larger fish (relative to smaller fish) to integrate spatial and temporal variability in food availability becomes less important. It suggests also that growth rates of the younger life history stages may be more variable than those of the older stages. To simulate differences in average growth rate on the same scale as that observed in the field necessitates doubling the initial prey abundance available to base-case recruits. To induce the same variability in growth rates of the younger stages, a smaller increase in prey abundance is necessary. To achieve the same growth in fish biomass in an area, larger fish require nearly twice as dense initial prey concentrations as smaller fish.

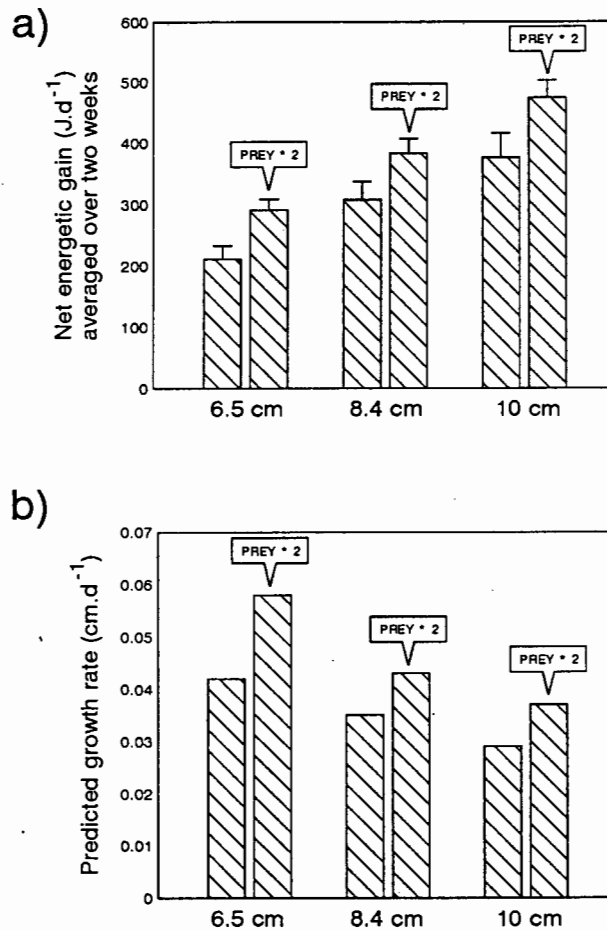


Fig. 5.16. Model-predicted average net energetic gain (a) and the average predicted growth in caudal length (b), of anchovy recruits of different size and under two different prey abundances. Total fish biomass is the same in all simulations and it is assumed that there is a 5-day gap in the rate at which shoals succeed one another through an area.

To what extent is food limitation of juvenile (versus larval) fish an important predictor of recruitment variability? The "match-mismatch" hypothesis of Cushing (1972, 1990) assumed implicitly that very young fish larvae rely critically on adequate food concentrations, and hence that the timing of spawning is constrained to ensure that first-feeding larvae appear in synchrony with seasonal plankton blooms. Subsequent work has focused on, *inter alia*, temporal matches between larval fish and zooplankton prey abundance (eg. Sherman *et al.* 1984, Sinclair & Tremblay 1984), while studies on northern anchovy larvae have stressed the importance of food microdistribution in determining fish growth and survival rates (Lasker 1975, 1978, Vlymen 1977). In contrast, Bollens *et al.* (1992) recently demonstrated that significant lags occur between the seasonal abundance patterns of fish larvae and zooplankton populations in a temperate fjord. They suggest that predation and food limitation in the later life history stages of fish may be more important in constraining the timing of spawning. Smith (1985) also hypothesized that variability in the growth rate of the late larvae and early juveniles of the northern anchovy may affect the magnitude of recruitment.

Peterman *et al.* (1988) highlighted the lack of correlation between year-class strength in northern anchovy and the abundance of the early life history stages. Butler (1989) found that food was not growth limiting in northern anchovies until the fish reached a certain size (4cm in El Niño years and 6.5cm in "normal" years). He proposed that this occurs because the ration necessary to sustain fish growth increases with increasing fish size, but there is a concomitant decrease in the density of suitably large food particles with increasing size (Sheldon & Parsons 1967, Sheldon *et al.* 1972).

In the Southern Benguela region, the appearance of anchovy larvae is generally coincident with peak prey availability during the upwelling season. Peaks in fish biomass, which occur later in the season, therefore lag both peak prey abundance and production by several months. The timing of spawning in this system may be constrained by several mechanisms acting in concert: for example, food availability on the spawning grounds, larval transport mechanisms and predation. Since the West Coast is dominated by large phytoplankton cells during the summer upwelling season, anchovy larvae might for example gain some protection from predation by co-occurring synchronously with large numbers of similar-sized prey organisms. Whatever the causative mechanism, a dominant negative trade-off arising from this spawning strategy seems to be the overlap between peak anchovy recruit biomass and

that if the late larval/early juvenile stages of fish do indeed pass through a critical period with large food requirements (Bollens *et al.* 1992), then the availability of sustained abundances of food along the West Coast may be a critical "bottleneck" contributing to recruitment success in anchovy (Hutchings 1992, Hutchings & Boyd 1992). This "bottleneck" might of course only constrict sufficiently to affect year-class strength in those years in which *per capita* prey availability is below some critical level. Under food limiting conditions, the importance of reduced growth rates in determining recruitment failure may be further exaggerated if growth rates are correlated with vulnerability to gape-limited predators, or if they impair escape responses (Fogarty *et al.* 1991).

The Impact of Predation Pulses on Spatial Patterns of Prey Abundance

To illustrate the effect of different temporal patterns of predation pressure on the spatial patterns of prey abundance, ten horizontally-adjacent model cells were chosen at random and the number of naupliar stage individuals, early copepodite stage individuals and prey (CIV-CVI) individuals per cubic metre was recorded on both day four and day ten. Initial prey concentrations were the same in all model cells, and an average fish density of 10 tons.km⁻² was used. Transitory shoals were assumed to pass through the model area on days two, three, eight and nine only. Resident shoals remained in the model area for the duration of the simulation.

Model results suggested that constant high fish densities dampen the spatial variability in copepod abundance (Fig. 5.17). Pulsed predation pressure presumably permits some copepod patches to avoid detection and allows locally depleted populations a short respite in which to recover some growth, thereby inducing a greater level of spatial patchiness. The greater variability in prey abundance in the latter scenario in turn amplifies the spatial variability in the abundance of the naupliar stage individuals, because of the different numbers of reproductive females in the various model cells.

The model predicts a relatively low degree of spatial variability in the patterns of abundance of the early copepodite stages because of damping mechanisms such as mortality of the naupliar stages, and because a longer time period is required for the effects of a predation pulse to manifest themselves at this level. Hence, the greater spatial variability in early copepodite population abundance patterns on day ten than on day four (Fig. 5.17) is presumably due to the passage of fish through the area

several days previously (on days two and three). Again, no such effect is evident under the assumption that shoals are resident in an area.

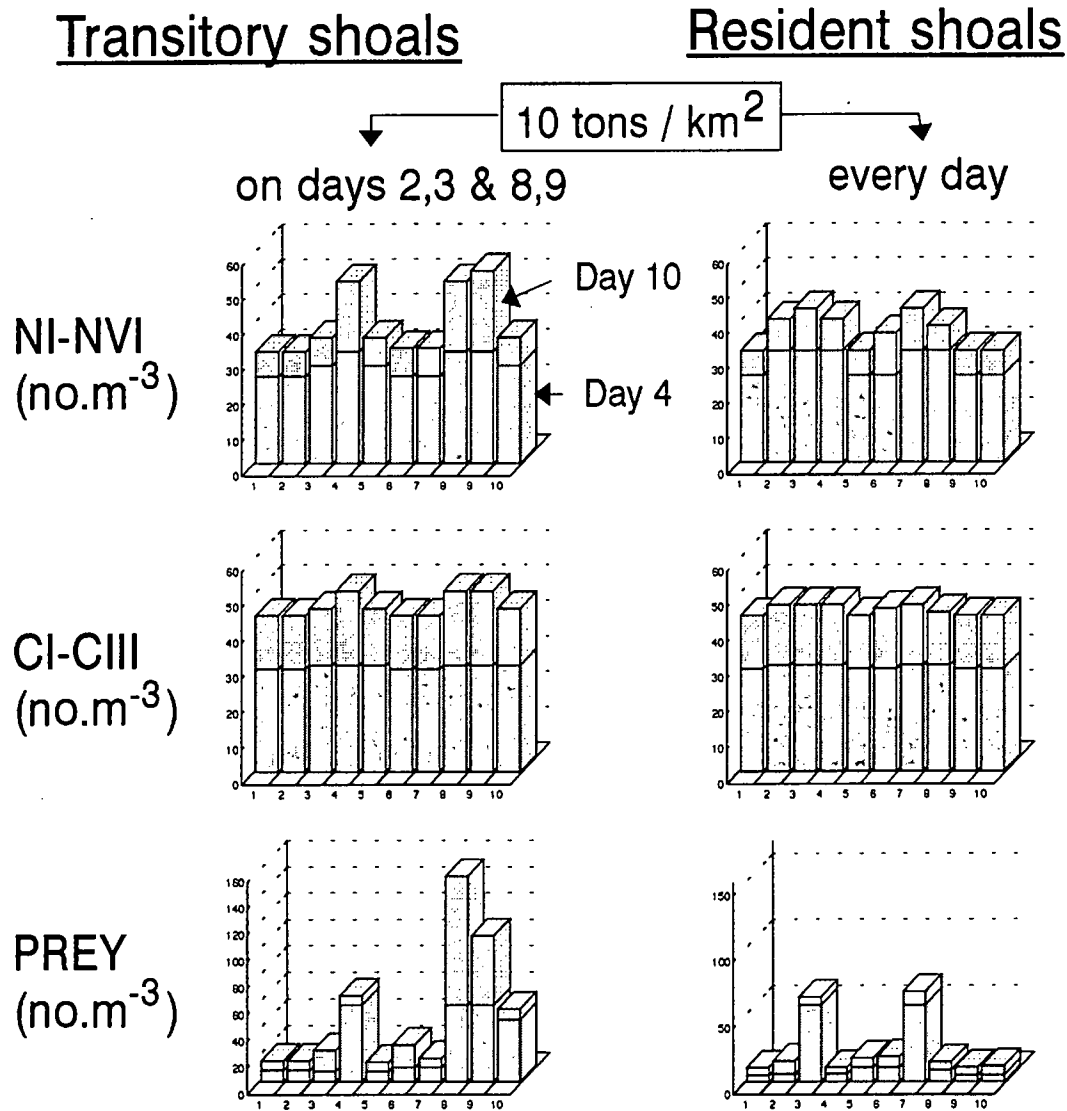


Fig. 5.17. The effect of different temporal patterns of predation pressure on the level of variability in spatial patterns of prey availability predicted by the model.

Direct and Indirect Effects of Predation on Copepod Population Dynamics

The effects of size-selective predation on size-structured populations are complex and are discussed elsewhere in this thesis (chapter three). Copepod populations may exhibit other mechanisms, such as the shoreward advection of overwintering CV stage individuals during downwelling events (Verheye & Field 1992), to compensate for local predatory losses. This mechanism is incorporated into the model in the next chapter.

CONCLUSIONS

The model predicted that high densities of juvenile anchovies concentrated in the restricted nearshore zone along the West Coast may dramatically deplete local prey populations, resulting in strongly density-dependent patterns of food availability. At base-case prey concentrations, the model predicted that predation rates by resident fish are on the same scale as average and maximum copepod production rates when fish densities are approximately 1 ton.km^{-2} and 3.5 tons.km^{-2} respectively. Mechanisms such as temporal and spatial segregation play an important role in synchronizing the relationship between fish predation pressure and prey turnover rates.

Model simulations suggest that spatial and temporal variability in *per capita* prey availability may elicit dramatic variability in juvenile anchovy growth rates, but there is a correlation between the overall average growth rate and absolute prey availability. To simulate the observed level (Waldron 1994) of inter-annual variability in anchovy growth rates, necessitated doubling the initial prey abundance in the model. The average percentage of time that fish were above their maintenance level decreased with increasing fish biomass.

The model provides a preliminary means of quantifying the predator-induced mortality rate in copepod populations subject to varying levels of fish predation pressure. Model predictions are highly sensitive to the spatial arrangement of fish biomass and to the temporal overlap between fish and prey abundances. Mechanisms which permit spatial and temporal gaps in predation pressure are highlighted as more important in determining anchovy feeding success than absolute prey availability. The implication is that, when averaged over large time and space scales, the synchrony between predator abundance and prey production or turnover rates is more critical than absolute *per capita* prey availability.

Fish foraging behaviour in the model was constrained most often by the time available for foraging. Nonlinearities between fish density and fish growth rates may be exaggerated if fish increase foraging effort in response to increasing fish density (Walters & Juanes 1993), although the associated increase in predation risk remains to be quantified.

The model predicted that juvenile anchovies require high sustained abundances of food, and it is disadvantageous in the long run for shoals to seek out 'high-quality'

prey patches in preference to exploiting all prey patches encountered. Model predictions suggested tentatively that mean fish aggregation size may be less than optimal in the field if fish trade-off increased energetic gain in favour of a reduced predation risk. Furthermore, if patch utilisation strategy is linked more closely to predation risk than to energetic considerations, the model predicts that anchovy growth rates may be substantially less than the maximum possible.

Under conditions of density-dependent food limitation, the proportion of shoals below their maintenance ration increases with increasing spatial heterogeneity of prey, so that, on average, model fish do worse in a highly patchy environment. Predictions of both fish feeding success and prey mortality rates which are based on biotic considerations (such as *per capita* food availability) only, may significantly underestimate actual trophic transfer processes in the field by ignoring the role of physical processes such as turbulence in mediating feeding rates under certain conditions. Model results corroborated the prediction that the effect of turbulence-mediated elevated feeding rates is greatest at low prey densities.

Based on energetic considerations only, the model predicts that to achieve the same absolute growth in fish biomass, large fish require a higher absolute prey abundance than small fish. In the field the same food environment will not necessarily produce a greater net increase in absolute fish biomass if predation risk is size-dependent, as seems likely. Nonetheless, the model lends support to the suggestion of Bollens *et al.* (1992) that the juvenile stages of fish pass through a critical period with large food requirements. Variability in the growth rate of late juvenile anchovies may therefore affect the magnitude of recruitment biomass in years where strong density-dependent effects are manifest with respect to food availability.

Table 5.1. Summary of model parameters and constants.

Parameter	Notation	Units	Base case value
Threshold feeding concentration	PATCONC	no.m ⁻³	6
Anchovy caudal length	L _c (=BL)	cm	8.42
Average travelling speed	V _{swim}	BL.s ⁻¹	1.695 [#]
Average swimming speed	V _{feed}	BL.s ⁻¹	2.412 [#]
Reactive distance(anchovy to prey)	RD	cm	1 BL [#]
Maximum daily distance travelled	Maxdist	km.d ⁻¹	15
Available foraging time	T _{total}	hours.d ⁻¹	12
Maximum satiation value	SATIATE	-	10% of F _{weight}
Feeding rate (secs per copepod)	FR	s	5.24 [*]
Assimilation efficiency	* ASS	-	0.71 ^{\$}
Area of a model cell	A _{cell}	km ²	0.25
Surface area of a shoal	A	km ²	■
Average shoal mass	S _{base}	tons	0.755
Initial prey abundance estimate	N ₁	no.m ⁻³	58
Background mortality rate	M _{back}	d ⁻¹	0.05

from James & Findlay (1989).

* based on an observed clearance rate of ca. 400 μg.dry wt.l⁻¹. *C. carinatus* per 33 minutes per 46 fish (James & Findlay 1989).

\$ James *et al.* (1989a).

■ calculated as area of an ellipse πab, with b = 2a (see text).

APPENDIX 5.1. Summary of Model Calculations and Mathematical Relationships

Define two types of model cells:

Patch cell - a model cell with a prey concentration which exceeds the threshold feeding concentration PATCONC.

Background cell - a model cell with a prey concentration \leq PATCONC.

Model cells which lie on a shoal's feeding path are termed 'hit' cells.

Let $i = 1$ to 3 represent *Calanoides carinatus* copepodite stages CIV, CV and CVI respectively. The following quantities are calculated each day in the model.

Moving Threshold level of copepodite stage i :

$$MT_i = \frac{\sum_{j=1}^b COP_{i,j}}{b}$$

where $COP_{i,j}$ is the number.m⁻³ of copepodite stage i individuals in background cell j , and b is the total number of background cells.

Total number of copepod stage i individuals consumed per patch cell:

$$C_i = (INIT_i - MT_i) \times V_{\text{patch}}$$

where $INIT_i$ is the initial number of prey individuals present in a cell before the predators arrive, and $V_{\text{patch}} = 3.75 \times 10^6 \text{ m}^3$ is the volume over which prey concentrations are integrated.

Number of fish in a school:

$$F = \frac{S}{F_{\text{weight}}} \times 10^6$$

where S is shoal mass (tons) and F_{weight} is the mass (g) of an individual anchovy.

Daily per capita consumption per fish in shoal sh (g.dry wt.fish⁻¹):

$$D_{\text{consump}_{sh}} = \frac{\sum_{k=1}^h \sum_{i=1}^3 C_{i,k} B_i}{F}$$

where B_i is the mean individual body mass (g.dry wt) of copepodite stage i and h is the number of patch cells 'hit' by shoal sh .

Standard length L_C (cm) for an anchovy of age t years (from Waldron 1992):

$$L_C = 14.8 \times (1 - e^{-1.367(t + 0.032)})$$

Diagonal length (km) of a model cell:

$$d = \sqrt{0.5^2 + 0.5^2}$$

Total daily distance travelled in search of food by a foraging shoal sh (km.fish⁻¹):

$$\text{Mindist}_{sh} = h \times d$$

where h is the number of 'hit' cells through which the shoal swims.

Total time per day (hours) spent particulate feeding by shoal sh :

$$\text{Timefeed}_{sh} = \frac{\left[\sum_{k=1}^h \sum_{i=1}^3 C_{i,k} \right] \times FR}{F \times 3600}$$

where FR is the feeding rate (secs.fish⁻¹.copepod) (see Table 2).

Total time per day (hours) spent swimming in search of food by shoal sh :

$$\text{Timetravel}_{sh} = \frac{\text{Mindist} \times 10^5}{V_{\text{swim}} \times L_c \times 3600}$$

where V_{swim} (BL.s⁻¹) is the average travelling speed (see Table 2).

Daily per capita energetic expenditure (J) by a fish in shoal sh whilst searching for food or engaged in particulate feeding:

$$\text{Eloss}_{sh} = \text{Timefeed}_{sh} \times R_f + \text{Timetravel}_{sh} \times R_s$$

where the respiratory costs due to the fish's feeding and swimming behaviours are respectively $R_f = 5.92 \text{ J.hr}^{-1}$ and $R_s = 4.03 \text{ J.hr}^{-1}$ (adapted from James & Probyn 1989).

Daily per capita energetic gain (J) from particulate feeding by a fish in shoal sh :

$$\text{Egain}_{sh} = \text{DCONSUMP}_{sh} \times E_{\text{cop}} \times \text{ASS}$$

where $E_{\text{cop}} = 2.87 \times 10^3 \text{ J.g}^{-1}$ dry copepod mass (Theilacker & Kimble 1984) and ASS is the assimilation efficiency for anchovies (James *et al.* 1989a).

Daily net energetic value for a fish in shoal sh :

$$E_{net_{sh}} = E_{gain_{sh}} - E_{loss_{sh}}$$

Energetic value (J) of a fish L_c cm in length (from Hunter & Leong 1981):

$$E_{fish} = 25.736 \times L_c^{3.195}$$

Backcalculating (after Nonacs *et al.* 1993):

Growth rate ($\text{cm} \cdot \text{d}^{-1}$) of a fish L_c cm in length and in shoal sh :

$$G_{sh} = \left(\frac{E_{fish} + E_{net_{sh}}}{25.736} \right)^{\frac{1}{3.195}} - L_c$$

Calculation of average predator-induced mortality rates for copepod populations:

Daily mortality rate (d^{-1}) in patch cell x 'hit' by predators:

$$M_c = \frac{\sum_{i=1}^3 INIT_i - \sum_{i=1}^3 MT_i}{\sum_{i=1}^3 INIT_i}$$

Average daily mortality rate (d^{-1}) over entire model area:

$$\overline{M_{pred}} = \frac{\sum_{x=1}^P M_x}{(p + b)}$$

where p , b are respectively the number of patch and background cells.
Obviously $p + b =$ total number of model cells.

APPENDIX 5.2. Justification for the use of a prey-dependent rather than ratio-dependent functional response in the model.

In conventional predator-prey models it is usually assumed that the functional response of predators (the amount of prey consumed per predator per unit time) depends only on absolute prey density (prey-dependent trophic function). This approach assumes that there is no interference among consumers and hence that consumer density does not have any direct effects on the *per capita* consumption rate (Ginzburg & Akçakaya 1992). Several authors have highlighted the inadequacy of using such an approach in some instances, arguing that the functional response of predators depends on the *per capita* prey availability i.e. on the prey:predator ratio (ratio-dependent trophic function) (eg. Arditi & Ginzburg 1989, Arditi & Akçakaya 1990, Arditi *et al.* 1991a,b, Akçakaya 1992, Berryman 1992b). Furthermore, it has been hypothesized that the degree of spatial and temporal heterogeneity determines the form of dependence: heterogeneous distributions are thought to be associated with ratio-dependence and homogeneous distributions with prey-dependence (Arditi & Ginzburg 1989, Arditi *et al.* 1991, Arditi & Saïah 1992).

These arguments raise the question of whether to model the anchovy-zooplankton system as having a prey-dependent or ratio-dependent functional response. The view adopted here is that when integrated over a time-scale of one day, the functional response will be approximately the same for a small or large number of predators as any potential disadvantages of increased mutual interference are offset by other mechanisms. These include:

- a) Minimisation of interference due to the characteristic feeding behaviour of anchovy: laboratory experiments conducted by James and Findlay (1989) on anchovy have shown that schooling breaks down immediately after the initiation of particulate feeding, with the fish acting independently within a loose aggregation. This behaviour serves to both increase the predator-prey encounter rate and it decreases the overlap of the visual fields of the fish (O'Connell 1972, Eggers 1976).
- b) Increasing the number of searching predators in a patchy environment increases the potential *per capita* rate of consumption: Because a larger aggregation of fish will have a larger leading edge to the shoal and therefore a larger collective visual field, the probability of detecting a prey patch will increase with increasing predator density;
- c) Increasing predator density may increase the prey availability/unavailability ratio: Individual copepods are able to respond to the presence or absence of fish and Bollens and Frost (1991a) have suggested that rapid evasive responses by individual

zooplankton to predators may be much more common and effective in pelagic environments than previously supposed. These changes in predator avoidance behaviour are mediated by visual cues or mechanical stimuli (Bollens & Frost 1989). Any shoal above a critical minimum size should elicit a similar escape response in a patch of copepods. If that is the case, then individual escape time is independent of predator density and a greater number of predators may be able to catch proportionately more copepods in a patch. In this way they may increase the ratio of available to unavailable prey within a patch, and hence prey capture efficiency.

In support of the above arguments, empirical studies of group foraging have shown that food patches may be located faster by foraging groups as information about the location of the food is conveyed within the group. If the schooling behaviour of anchovy increases prey capture efficiency in addition to search efficiency, it seems likely that the integrated functional response will be the same for a small or large number of predators.

APPENDIX 5.3. A simulation model to explore the relationship between acoustically-determined estimates of the shoal dimension sw , and the actual dimensions of an elliptically-shaped anchovy shoal orientated at a random degree Θ to a ship's acoustic equipment.

```

! PROGRAM TO DETERMINE SW AS A FUNCTION OF A1 AND A2 (INTERCEPTS OF
ELLIPSE)
CLEAR
INPUT PROMPT "Number of simulations required...":h
DIM n(10000)
RANDOMIZE
SET WINDOW 0,pi/2,0.5,2.5
PLOT 0,0.5;pi/2,0.5
PLOT 0,0;0,2.5
FOR theta = 0.0157 to pi/2 step 0.0157
  LET dist1 = cos(theta)*sqr(1/(1+4*tan(theta)^2))
  LET dist2 = sin(theta)*sqr(16/(1/tan(theta)^2 + 4))
  LET dist = dist1 + dist2
  PLOT theta,dist;
NEXT theta
GET KEY uu
CLEAR
FOR i = 1 to h
  LET theta = rnd * pi/2
  LET dist1 = cos(theta)*sqr(1/(1+4*tan(theta)^2))
  LET dist2 = sin(theta)*sqr(16/(1/tan(theta)^2 + 4))
  LET dist = dist1 + dist2
  IF dist > 1 and dist < 1.1 then LET n(1) = n(1) + 1
  IF dist > 1.1 and dist < 1.2 then LET n(2) = n(2) + 1
  IF dist > 1.2 and dist < 1.3 then LET n(3) = n(3) + 1
  IF dist > 1.3 and dist < 1.4 then LET n(4) = n(4) + 1
  IF dist > 1.4 and dist < 1.5 then LET n(5) = n(5) + 1
  IF dist > 1.5 and dist < 1.6 then LET n(6) = n(6) + 1
  IF dist > 1.6 and dist < 1.7 then LET n(7) = n(7) + 1
  IF dist > 1.7 and dist < 1.8 then LET n(8) = n(8) + 1
  IF dist > 1.8 and dist < 1.9 then LET n(9) = n(9) + 1
  IF dist > 1.9 and dist < 2 then LET n(10) = n(10) + 1
  LET sum = sum + dist
NEXT i
SET WINDOW 1,10,0,h
LET avg = sum /h
PRINT "The average shoal width parameter is",avg
FOR s = 1 to 10
  PLOT s,0;
  PLOT s,n(s)
NEXT s
END

```

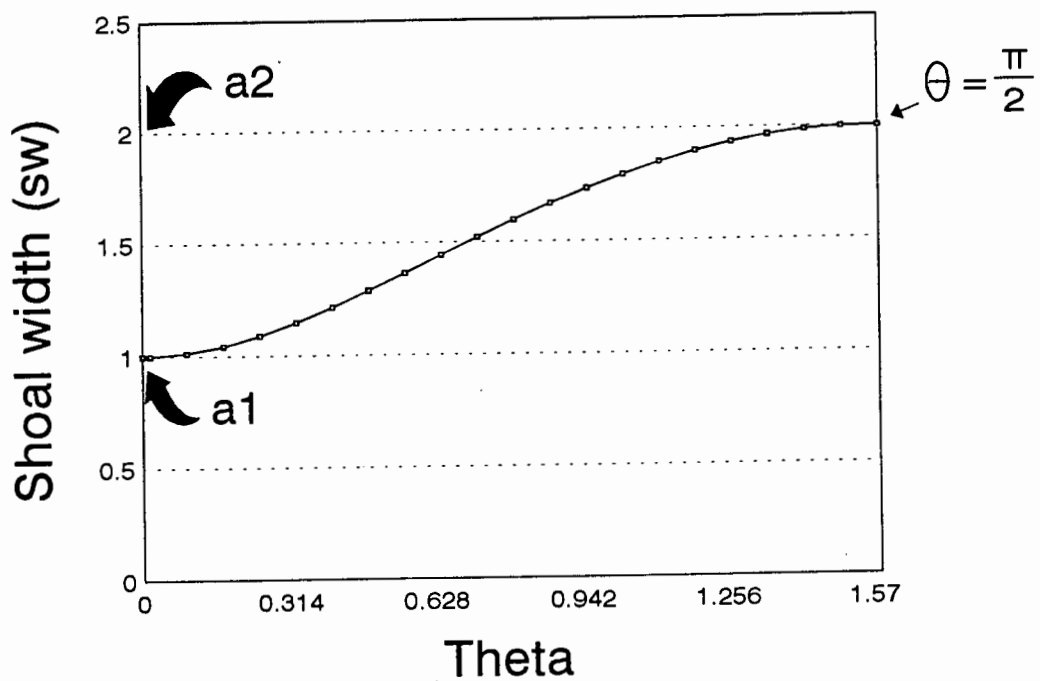


Fig. A5.3.1 A plot of the derived function x , where $x = \frac{1}{2}sw$, against Θ , where Θ is the angle of orientation of a shoal relative to a ship. For any angle Θ , the function describes the relationship between the empirically determined shoal width parameter and the actual dimensions of a shoal, where $a (=a1)$ is assumed equal to $\frac{1}{2}b (=a2)$. The program listed above generates large numbers of random Θ values, and then calculates the average corresponding x value. Because $x = \frac{1}{2}sw$ and the derived equation relates x to the true shoal parameters a and b , backcalculating provides an estimate of average shoal size in the field.

CHAPTER 6

MODELLING ANNUAL PATTERNS OF ZOOPLANKTON PRODUCTIVITY

INTRODUCTION

In the Southern Benguela system, the oceanography is dominated by pronounced seasonal wind cycles (Andrews & Hutchings 1980). Upwelling-favourable southeasterly winds predominate during the months September to April, while northwesterly winds are common during the winter months (May to August) (Andrews & Hutchings 1980). Cold nutrient-rich upwelling waters give rise to dense blooms of phytoplankton during the upwelling seasons (Brown & Henry 1985), favouring the growth and survival of herbivorous copepods such as *Calanoides carinatus* (Armstrong *et al.* 1991, Verheye *et al.* 1991). In contrast, although occasional upwelling occurs during winter (Andrews & Hutchings 1980), reduced upwelling, poorer light levels, lower nutrients in the source waters, and increased turbulence levels over this period combine to significantly dampen winter production rates (Brown & Henry 1985). Large shoals of anchovy recruit along the West Coast during autumn and winter (Crawford *et al.* 1980, Hampton 1987), and may severely deplete co-occurring zooplankton populations (Painting & Huggett 1988).

In temperate pelagic ecosystems, copepod annual cycles are controlled by a complex combination of seasonal variation in food limitation and predation (Roff *et al.* 1988). Furthermore, hydrodynamics may play a substantial role in determining spatial and temporal patterns of abundance (Legendre & Demers 1984, Roughgarden *et al.* 1988). The exact mechanisms controlling seasonal abundance cycles are presently poorly understood. However, positive correlations exist between the size of overwintering copepod populations and the population size manifest in the subsequent summer (Colebrook 1982, Roff *et al.* 1988).

Zooplankton biomass in the Southern Benguela system peaks during spring and summer and declines to a minimum during winter (Shannon & Pillar 1986). By applying a three-month running mean to their monthly data, Andrews & Hutchings (1980) found evidence of distinct seasonal patterns of zooplankton abundance and documented two- to three-fold seasonal differences in zooplankton standing stocks off the Cape Peninsula. Shannon and Field (1985) estimated that zooplankton production in the active upwelling area of the Southern Benguela, an area covering some 40 000 km², fluctuates annually between 2 and 6.7 million tonnes of carbon.

Seasonal fluctuations in the abundance of *C. carinatus* in the Southern Benguela system are reduced relative to those characteristic of populations which occur further north (Verheye *et al.* 1991). This is largely attributable to the division of the population into an "active" nearshore component and a short-term resting phase during winter. The latter phase comprises copepodite stage CV and adult females in temporary developmental arrest in the deeper layers of the outer shelf region (Verheye *et al.* 1991). During winter and spring upwelling events, the deep offshore resting phase component is advected shorewards, and plays an important role in restocking inshore populations (Verheye *et al.* 1991).

The aim of this chapter is to integrate temporally the basic model developed in chapter two by accounting for seasonal variations in the system's dynamics. As a rough means of assessing model predictions, chlorophyll *a* concentration and sea surface temperature data from 1971 and 1972 (Andrews & Hutchings 1980) are used as inputs into the model and the output is compared with the mean observed zooplankton standing stocks in each year.

METHODS

Temporal Integration of the Basic Model

The model developed in chapter two was directed at the dynamics of *Calanoides carinatus* during the summer upwelling season. To extend the basic model to simulate annual patterns of zooplankton productivity necessitated consideration of the following:

- a) inter-seasonal changes in temperature and primary productivity trends;
- b) changes in the mortality rate of *C. carinatus* stages CIV-CVI, concomitant with seasonal variation in the biomass of anchovy, which selectively prey on these size classes; and
- c) the shoreward advection of overwintering CV stage individuals during downwelling events (Verheye & Field 1992).

a) Chlorophyll *a* and Temperature Input Series

Mean monthly chlorophyll *a* and sea surface temperature (SST) data from January 1971 to December 1972 were used to derive annual input series for the years 1971 and 1972. The data were obtained during monthly Upwelling-Monitoring Cruises run due north-west from the Cape Peninsula by Andrews and Hutchings (1980). The

two-day monitoring cruise measurements presently represent the only continuous annual series for the region, but it should be borne in mind that the data are biased to varying degrees by upwelling and downwelling cycles of 5 to 13 days, so that the monthly means are not necessarily always truly "typical" (Hutchings, pers. comm.). The results of the present simulation exercise therefore provide only a very general test of the model.

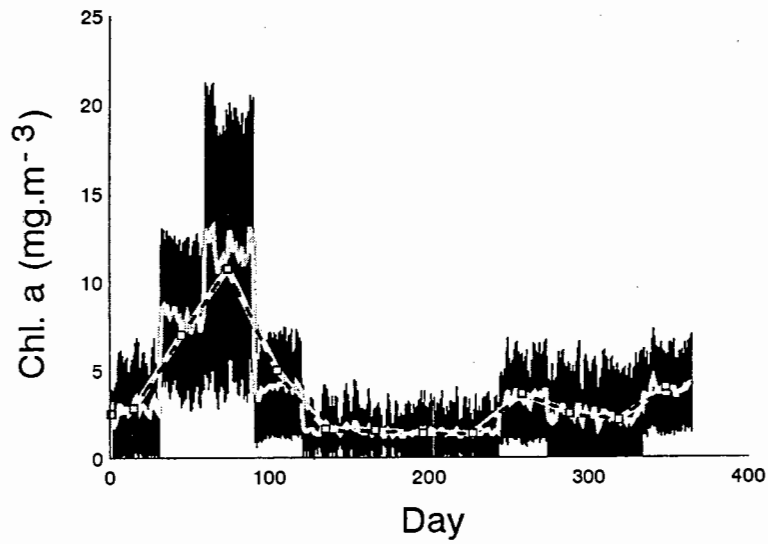
Simulating Intra-Seasonal Variability

To construct realistic and continuous input series which simulated day-to-day variability in the driving variables - chlorophyll *a* and SST, whilst simultaneously ensuring that monthly averages reflected the underlying seasonal trends, the following method was used:

During the peak upwelling season (September - April), a random number of upwelling cycles (range: 1-3 per month) was allowed in the model. To account for occasional upwelling events during the quiescent period May to August, the number of upwelling cycles in each of these months was randomly set at zero or one. Upwelling cycles were simulated using a characteristic 7-day cycle derived from data in Brown and Hutchings (1987) (Fig. 3.1). The start of each upwelling cycle was randomly determined, while successive upwelling cycles started at least four days apart.

To generate input values for the remaining days of each month, gaussian random numbers were generated in such a way that monthly means in the model were approximately the same as the monthly means calculated in Andrews and Hutchings (1980). Because chlorophyll *a* concentrations are denser and more variable during the upwelling season (Brown & Henry 1985), the standard deviation used to generate the chlorophyll *a* input series was set as a fraction (0.25) of each monthly mean. A standard deviation of 2°C was used to generate the SST input and a minimum of 8°C allowed (Andrews & Hutchings 1980). As in chapter three, successive runs produce two probability distributions of input values that represent the most probable mean pattern of chlorophyll *a* and SST respectively, based on the constraints outlined above. Based on several (10-100) runs, one may then predict the mean expected pattern of zooplankton abundance in 1971 and 1972, assuming that intra-seasonal variability is approximately the same in the two years, but monthly means differ. The means and standard deviations of the 1971 and 1972 chlorophyll *a* and SST input series are presented in Figures 6.1 and 6.2 respectively.

a) 1971



b) 1972

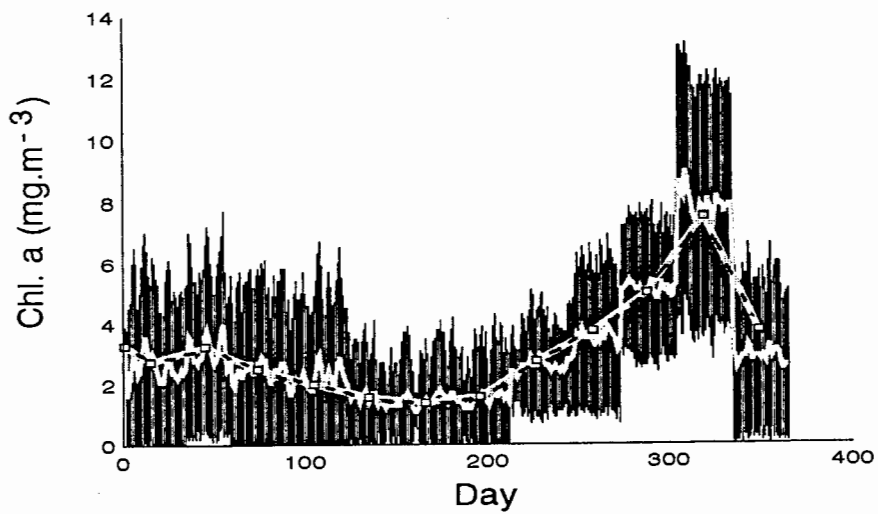
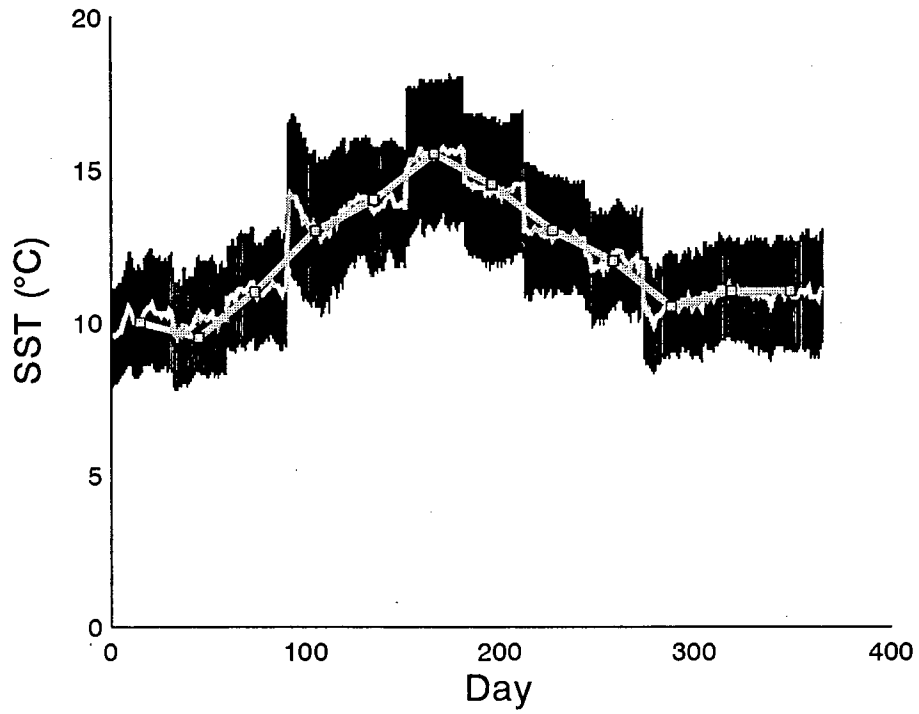


Fig. 6.1. The observed mean monthly chlorophyll *a* concentrations (mg.m⁻³) (dashed lines) measured off the Cape Peninsula in a)1971 and b)1972 (Andrews & Hutchings 1980), and used to generate input series for the model. The solid line represents mean (\pm S.D., $n=10$) daily chlorophyll *a* concentrations used to drive the model over a period of one year.

a) 1971



b) 1972

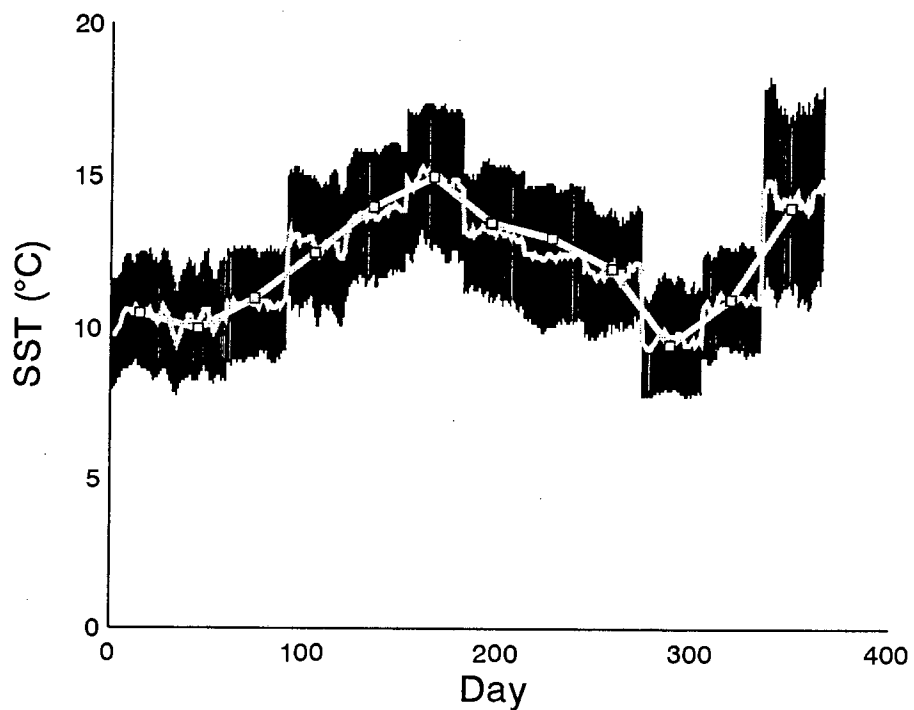


Fig. 6.2. The observed mean sea surface temperatures ($^{\circ}\text{C}$) (dashed lines) measured off the Cape Peninsula in a)1971 and b)1972 (Andrews & Hutchings 1980), and used to generate temperature input series for the model. The solid line represents mean (\pm S.D., $n=10$) daily sea surface temperature (SST) used to drive the model in each year.

Initializing *C. carinatus* Concentrations

A characteristic abundance estimate for *C. carinatus* during the upwelling season was obtained using the overall mean value observed during the 27-day time series held in March-April 1987 in St Helena Bay (Verheye 1991). A stable initial population age structure of 30.5% NI-NVI, 27% CI-CIII, 17% CIV, 13% CV and 12.5% adults was assumed. The abundance value was scaled upwards to account for the naupliar stage individuals, yielding an initial *C. carinatus* abundance estimate $N_1(1971)$ of 468 copepods.m⁻³, of which 198 individuals.m⁻³ constitute potential prey (CIV-CVI).

Mean zooplankton standing stocks measured during the Upwelling-Monitoring Cruises in January 1971 and January 1972 differed by a factor of 1.9 (Andrews & Hutchings 1980). The same order of magnitude difference was therefore used to initiate the *C. carinatus* abundance estimates in the 1971 and 1972 model series, yielding a $N_1(1972)$ estimate of 889 copepods.m⁻³ and 378 prey individuals.m⁻³

b) A Seasonal Increase in the Predator-Induced Mortality Rate

Along the West Coast, the relative abundance of the older life stages of *C. carinatus* decreases during winter (Verheye *et al.* 1991). A major causative factor is thought to be the increase in the biomass of recruits present in the area at this time (Verheye *et al.* 1991).

The basic model developed in chapter two assumed a steady-state predator-induced mortality rate M_{pred} of 0.10 d⁻¹ throughout the upwelling season. A rough estimate of an appropriate value for this parameter during the winter recruitment period (May to September) was obtained as follows:

Assuming that effort levels in the South African purse seine fishery remained approximately constant from 1971 to 1986, annual changes in catch statistics provide a proportional index of stock biomass (Clark 1976). Anchovy catch statistics for 1971 and 1972 are respectively 58% and 87% that reported in 1985 and 41% and 62% that reported in 1986 (Bergh & Butterworth 1987, Hampton 1992). Acoustically-derived estimates of average anchovy recruit biomass for the inshore region between Cape Town and Cape Columbine during May/June 1985 and 1986 (Hampton 1987), suggest average recruit biomass estimates of 11 and 17 tons.km⁻² in this region for 1971 and 1972 respectively.

The abundance of the older stages (CIV to adults) of *C. carinatus* is reduced by about half during winter (Verheye *et al.* 1991). Predator:prey ratios (tons.km⁻²:no.m⁻³, see chapter 5) for 1971 and 1972 were therefore calculated as $11/(0.5*198) = 0.11$ and $17/(0.5*378) = 0.09$ respectively. For a predator:prey abundance ratio in this range, the model developed in chapter five (Fig. 5.8) predicts an average value for M_{pred} of approximately 0.15 d^{-1} . Because of the uncertainty attached to estimates of this parameter, and for comparative purposes, the same value of M_{pred} is used for the 1971 and 1972 series. It should be borne in mind that for present purposes the exact value of M_{pred} is less important than the fact that M_{pred} increases over the winter recruitment period. Furthermore, the value chosen is realistic because it lies between the average (0.139 d^{-1}) and maximum (0.233 d^{-1}) specific production rates (ie. P/B = total daily production to total biomass ratio) measured in the field for copepod stage CI to CV *C. carinatus* individuals (Verheye 1991).

c) The Role of Advection in Restocking Nearshore Populations

Precise quantification of the rate at which "overwintering" *C. carinatus* individuals are advected towards the nearshore region is beyond the scope of this work. However, because this mechanism plays an important role in permitting the perennial presence of nearshore *C. carinatus* populations, this feature was incorporated into the model using randomly-determined estimates constrained within a reasonable range.

Changes in the physical environment (Andrews & Hutchings 1980) and upwelling-induced advective processes (Verheye 1991) can produce as much as four-fold differences in zooplankton standing stocks (Andrews & Hutchings 1980) and in the abundance of the copepodite stages of *C. carinatus* (Verheye 1991). Mean abundance estimates for copepodite stage CV and adult females during the month of June are respectively 13 and 5 m^{-3} (Verheye *et al.* 1991). With the onset of each upwelling cycle during the months June to September, it is therefore assumed in the model that the nearshore *C. carinatus* population is restocked with between two and four times the mean winter abundances of CV and adult female individuals.

Quarterly Variations in Population Age Structure

To examine further to what extent the model is capable of simulating the dynamics of *C. carinatus*, predicted seasonal variations in age structure were compared with observed quarterly variations in *C. carinatus* copepodite abundance off Cape Columbine in March, June, October and December 1974 (Verheye *et al.* 1991).

Mean chlorophyll *a* concentration and sea surface temperature recorded for each of these months (Verheye *et al.* 1991) were used as inputs into the model and averages for the remaining months were obtained using the 1972 input series from Andrews and Hutchings (1980). The mean abundances of copepodite stages CI-CIV, copepodite stage CV and adults were calculated for each of the four months, and used to calculate mean population age compositions.

RESULTS AND DISCUSSION

Seasonal Trends Predicted for 1971

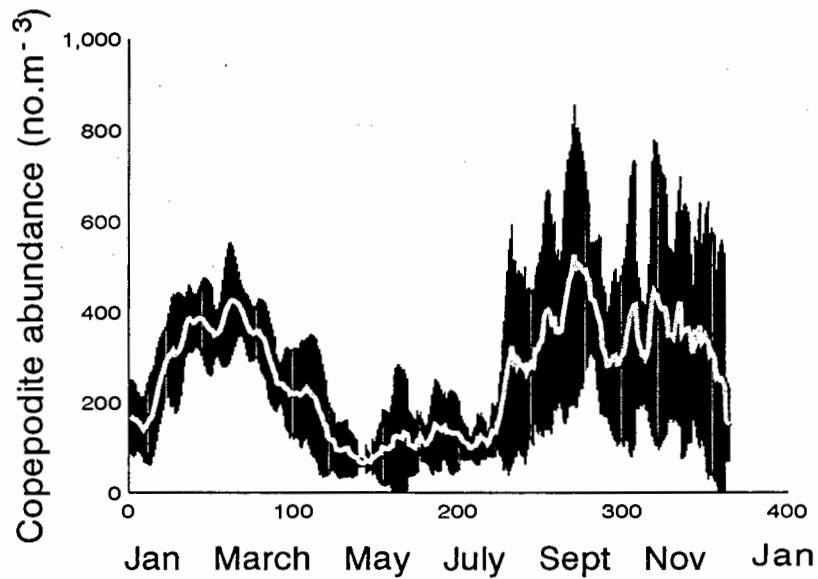
In response to the relatively high mean chlorophyll *a* concentrations in the first quarter of 1971 (Fig. 6.1a), there is a dramatic increase in the abundance of the copepodite stages predicted by the model (Fig. 6.3a). However, the model predicts an initial decline in the biomass (T_{biom}) (mg.C.m^{-3}) of the copepodite stages (Fig. 6.4a). This is because there is a time lag of approximately three weeks before the elevated reproduction rate (in response to the favourable feeding conditions) manifests itself as an increase in biomass. The model is initialized assuming a stable age structure and the model therefore probably underestimates the initial relative abundance of the older stages. However, independent of the initial age structure (see Fig. 3.6) and predicted initial decline, the population biomass soon settles and fluctuates about the initial value (Fig. 6.4a). The period of the fluctuations is approximately 20 days.

At the end of the upwelling season, population biomass declines steeply and falls to a minimum in early June, equal to approximately half the initial value (Table 6.1). Following the resumption of frequent upwelling, there is a sharp increase in copepodite biomass towards the end of September. The model predicts that average copepodite biomass at the end of 1971 was approximately 1.92 times that at the start of the same year. This corresponds extremely well with the observed 1.9-fold difference between mean zooplankton standing stocks in December and January 1971.

Moreover, the 4.13-fold difference between the average minimum and maximum T_{biom} values predicted by the model is commensurate with the 4-fold difference observed between the minimum and maximum zooplankton standing stocks in 1971 (Table 6.1). The model predicts almost an eight-fold difference between peak

copepodite abundance (March and October) and the minimum copepodite abundance level (May/June).

a) 1971



b) 1972

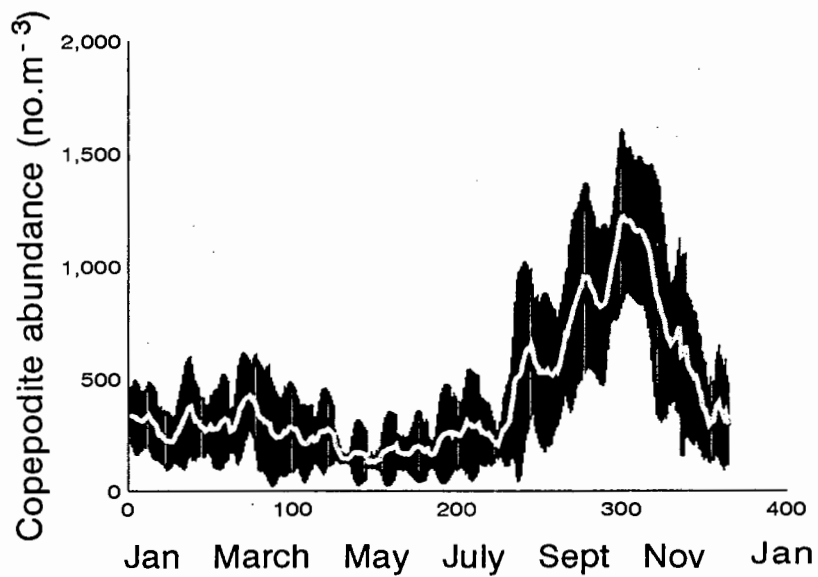


Fig. 6.3. The seasonal variation in copepodite abundance (no.m⁻³) predicted for a)1971 and b)1972. The graphs show the mean (\pm S.D.) of 10 runs based on mean observed monthly differences in chlorophyll *a* concentration and sea surface temperature, but with different intra-seasonal variation in these parameters in each run.

Seasonal Trends Predicted for 1972

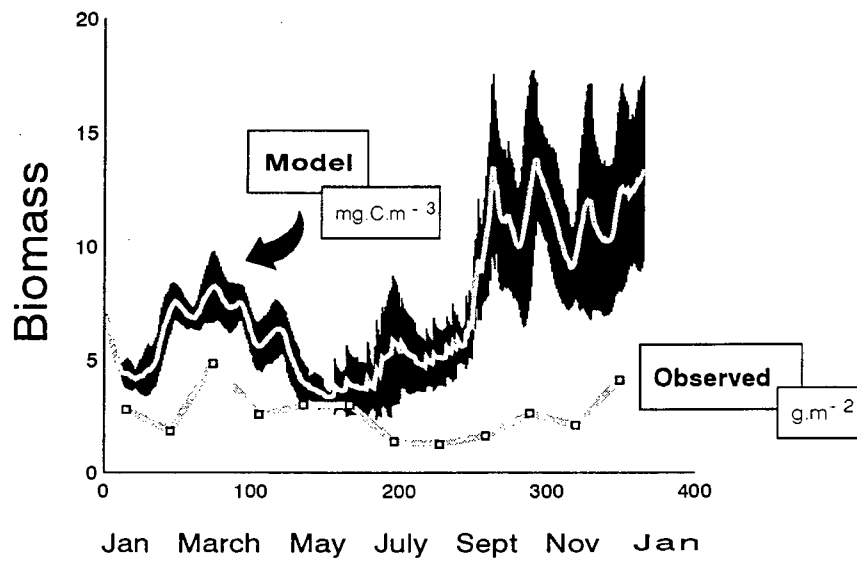
The dampened copepodite biomass trend predicted for the first quarter of 1972 mirrors the relatively flat mean chlorophyll *a* input series (Fig. 6.1), as well as the observed pattern of mean zooplankton standing stock over this period (Fig. 6.4b). The model predicts a less distinct seasonal peak in copepodite abundance in 1972 than in 1971 (Fig. 6.3). Concomitant with the increase in both mean chlorophyll *a* concentration and sea surface temperature (which accelerates copepod development rates), there is a dramatic increase in the mean copepodite biomass trend predicted for the last quarter of 1972 (Fig. 6.4b).

The model predicts a 4-fold difference between the average minimum and maximum copepodite biomass estimates furnished by the model, and a 9.6-fold difference between the peak (October) and minimum (May/June) copepodite abundance levels (Table 6.1).

Table 6.1. Model-predicted copepodite abundance (no.m⁻³) and biomass *Tbiom* (mg.C.m⁻³) estimates for 1971 and 1972. The table lists the values used to initialise the model in the two years, the values (mean of 10 runs) predicted at the end of each year, the range in model averages predicted for the year, and the average coefficient of variation (C.V.) attached to the average *Tbiom* trend predicted from 10 runs.

		Copepodite abundance	Copepodite biomass
1971	Initial value	169	6 968
	Final value	151	13 377
	Minimum	66	3 350
	Maximum	526	13 841
	Mean C.V.		0.23
1972	Initial value	337	13 237
	Final value	296	14 073
	Minimum	127	6 450
	Maximum	1 220	25 633
	Mean C.V.		0.25

a) 1971



b) 1972

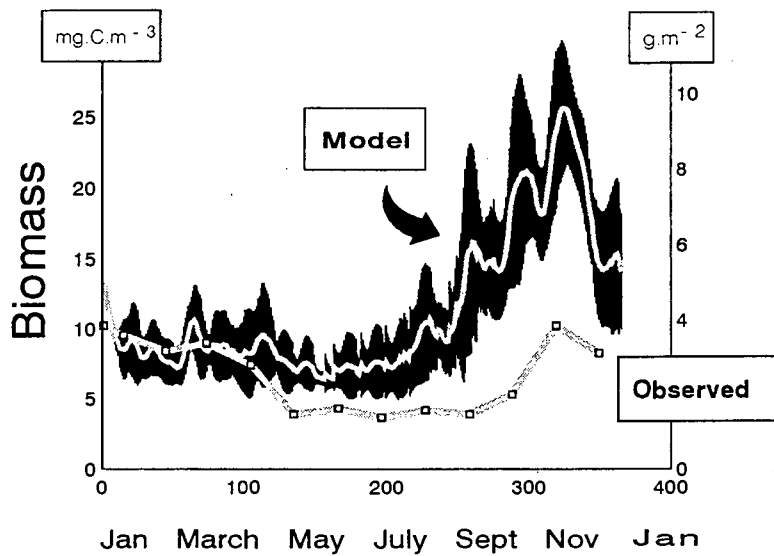


Fig. 6.4. A comparison between model-predicted copepodite biomass (mg.C.m^{-3}) estimates for a)1971 and b)1972, and corresponding zooplankton standing stocks (g.m^{-2}) observed during monthly surveys conducted off the Cape Peninsula from October 1970 to March 1973 (Andrews & Hutchings 1980). The graphs show the mean (\pm S.D.) of 10 runs. For ease of viewing, the two figures are not plotted on the same scale. The difference in starting values in 1971 and 1972 is commensurate with that observed in the two years.

At the end of 1972, the predicted copepodite biomass trend declines in the same manner and to approximately the same value as that observed during December 1972 and January 1973 (Fig. 6.4b, Andrews & Hutchings 1980).

Dampening the Seasonal Signal

The copepodite biomass trends presented in Fig. 6.4 represent the mean of ten runs. A small number of runs was used for comparative purposes because of the variability in the observed data series. The use of ten runs was further justified on the grounds that the average coefficient of variation attached to model estimates (Table 6.1) decreased by less than 0.05 when the number of runs was increased from ten to one hundred. This is because although there are random factors in the model (the input series and advection rates), these are constrained within fairly narrow ranges.

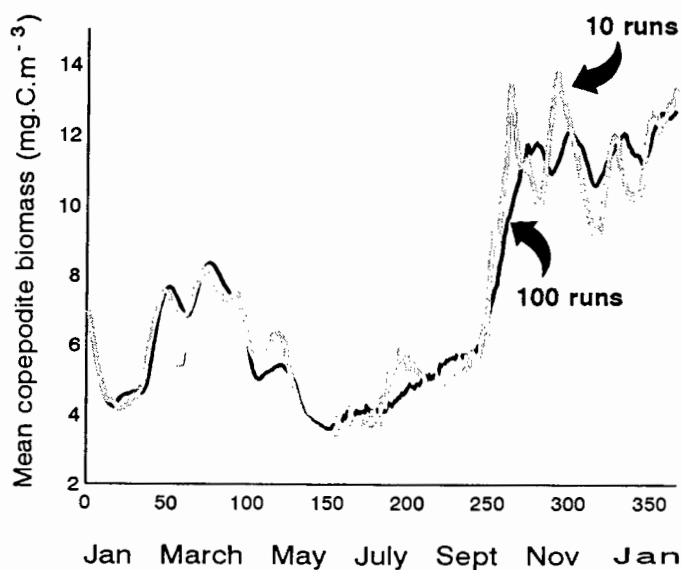
Mean predicted seasonal signals are dampened slightly when the number of runs is increased (Fig. 6.5). Model results nonetheless predict 3.5- and 3.7-fold differences between the average maximum and minimum biomass estimates for 1971 and 1972 respectively.

Model averages may be envisaged as representing spatially integrated averages determined for a number of discrete 'subpopulations', each subject to local differences in physical and primary productivity characteristics. Model averages therefore test the effect of superimposing temporal variability on spatial variability, and the results suggest that there is an overriding seasonal signal - temporal variability (on a time scale of one year) is significant relative to spatial variation in population parameters. It should be noted however that on a shorter temporal scale, results obtained in chapter four suggested that spatial variability in food availability may exceed temporally-induced variability under some circumstances.

Assessing Seasonal Variations in Age Structure

Comparisons between model-predicted and observed quarterly variations in population age structure indicated that the model provides a reasonable approximation to the observed age structure in all months except October (Fig. 6.6). The decrease in the proportional abundance of the older stages in June may be partly ascribed to the increase in size-selective predation upon the largest individuals from April onwards.

a) 1971



b) 1972

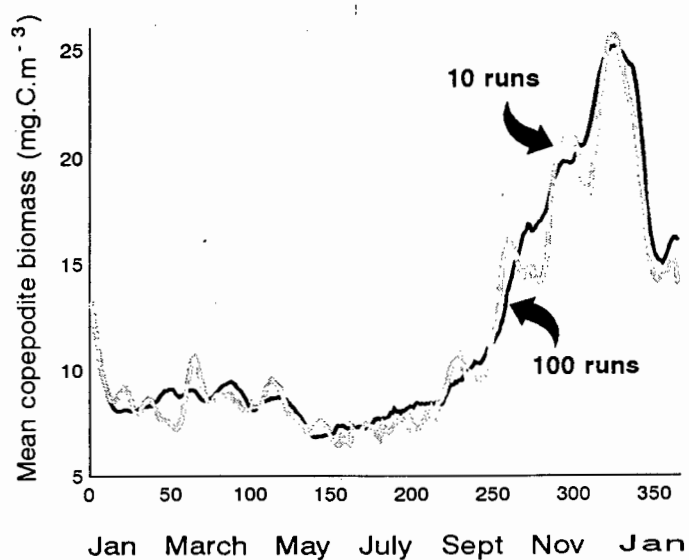


Fig. 6.5. The effect on the mean pattern of copepodite biomass (mg.C.m⁻³) predicted for a)1971 and b)1972, of increasing the number of model runs from 10 to 100. For ease of viewing, the standard deviations attached to model estimates are not shown. However, they are very similar to those presented in Fig. 6.4 as the coefficient of variation attached to model estimates decreased by less than 0.05 when the number of runs was increased as shown.

Size-selective predation is often invoked to explain the inverse relationship between predator density and the average size of zooplankton populations (Zagarese 1991). However, although the intensity of this relationship is closely correlated with the size of the prey individuals targeted, in a closed system, a decrease in average population size occurs whenever there is an increase in mortality losses - this is because a population's average age, and synonymously size, decreases as dead individuals are replaced by younger ones (Zagarese 1991). Increases in mortality due to starvation during winter may therefore also play a role in exacerbating the low proportional abundance of the older copepodite stages over this period, even though it is the younger stages which are most susceptible to starvation (Borchers & Hutchings 1986).

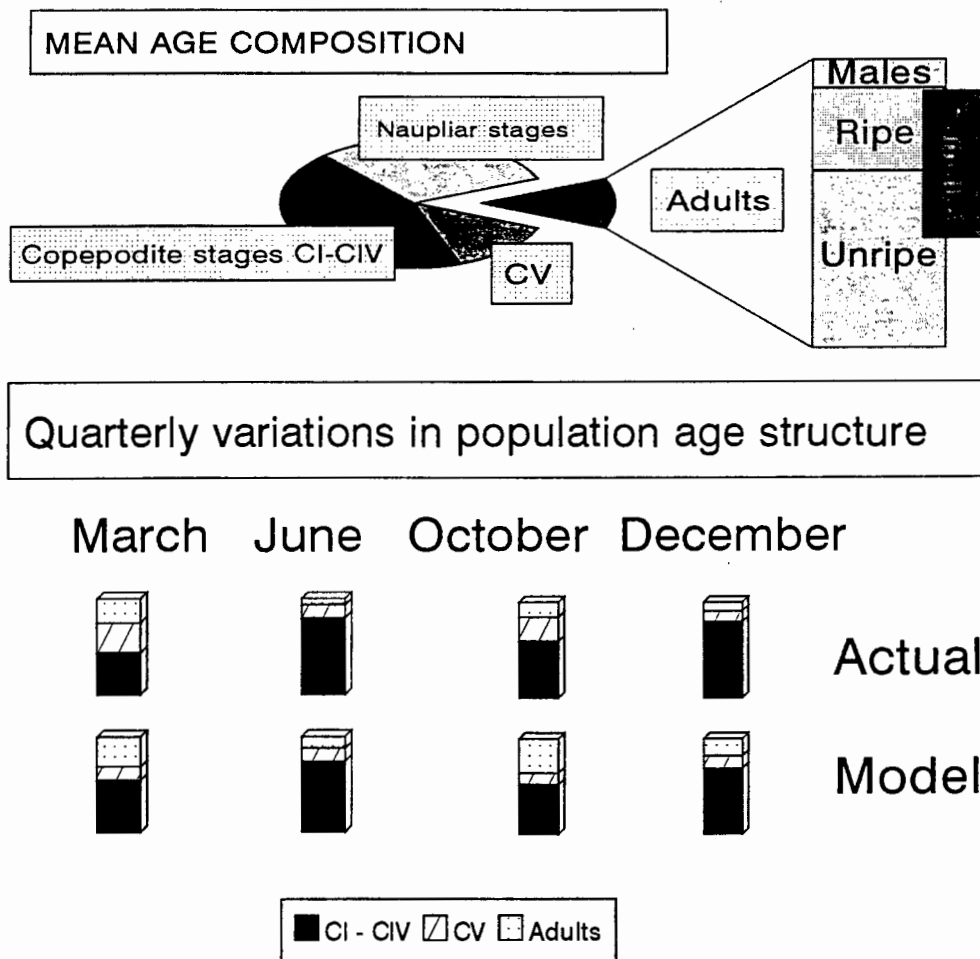


Fig. 6.6. A comparison between model-predicted quarterly variations in population age structure and that observed off Cape Columbine in March, June, October and December in 1974 (Verheye *et al.* 1991).

The model results underestimated the proportional abundance of the younger copepodite stages in October. The most plausible explanation is that the number of CV and adult females which are advected shorewards during the preceding month is set unrealistically high in the model. However, size structure relationships within zooplankton populations are complex and may be influenced, either directly or indirectly, by a suite of factors acting alone or in combination (Kerfoot & Sih 1987). For example, by selectively feeding on large prey, planktivorous fish such as anchovy may indirectly reduce the mortality of the younger stages because they simultaneously remove large invertebrate predators, such as chaetognaths, which prey on these individuals (De Vries & Stein 1992). Another factor which may be important concerns the quarterly variations in the cross-shelf distribution of the various life history stages of *C. carinatus* (Verheye & Field 1992). This seasonal reshuffling of population age structure is related to ontogenetic differences in their vertical migratory behaviour (Verheye & Field 1992) and should possibly be incorporated in improved versions of the present model.

The proportional increase in the numbers of the younger stages in December (Fig. 6.6) is as a result of pulses of upwelling over this period which give rise to renewed reproduction. The slight disparity between the observed values and the model predictions may be partly due to the relatively warm sea surface temperatures assumed over this period in the model (Fig. 6.2b).

CONCLUSIONS

The ability of the basic model developed in this thesis to provide an index of zooplankton productivity is supported here by the corroboration of model results with an independent data set, as well as the ability of the model to reconstruct reasonably accurately observed seasonal variations in population age structure. Both environmental factors and biological interactions such as predation can play a role in regulating the size structure of copepod populations.

The predictions from the temporally integrated model developed in this chapter support the empirical observations (Andrews & Hutchings 1980, Verheye *et al.* 1991) that a distinct annual cycle in *C. carinatus* biomass occurs. Because the empirical data used in this chapter were obtained from specific regions and hence do not represent the average over the entire West Coast, model predictions are not expected to depict the overall average observed period and amplitude of annual copepod cycles. Spatially integrated averages for the Cape Columbine - Cape Peninsula area

suggest that copepod biomass increases seasonally from about November to a maximum in March, and then declines again to a minimum during the winter months (Pillar 1986, Verheye *et al.* 1992). The respective presence and absence of a peak in copepodite biomass predicted for the month of March in 1971 and 1972 effectively mirrors the chlorophyll *a* concentration input series, and is at most a depiction of changes in annual copepod cycles in a local region. Measurements made off Cape Columbine in March 1974 (Verheye 1989) and March 1983 (Painting 1989) indicates that a 4.7-fold inter-annual difference was manifest in *C. carinatus* biomass, supporting the contention that identification of representative seasonal variability in the biomass of copepods necessitates consideration of larger spatial and temporal scales.

Comparison with empirical data (Pillar 1986, Verheye *et al.* 1991) suggests that the model-predicted increase in *C. carinatus* copepodite biomass from October onwards is at least one month premature. This highlights the fact that there are still considerable gaps in our understanding of the mechanisms controlling copepod annual cycles. Although advances have been made in elucidating the contribution of physical transport processes and population maintenance mechanisms to copepod population dynamics in the Southern Benguela region (eg. Verheye & Field 1992), the construction of annual models is impeded by the need to quantify the scale of input terms accounting for these processes. Gaps in our understanding of copepod population dynamics are similarly highlighted by the model's substantial overestimation of the proportional abundance of the older *C. carinatus* stages during October. Errors in population age composition predicted by a model are amplified because of the disproportionate contribution of the larger stages to biomass calculations (cf. Figs. 6.3 & 6.4). Research is necessary to identify which of a suite of factors (eg. advective processes, indirect feedback processes, mixed layer depth, seasonal dietary shifts) are most important or could contribute significantly to reducing errors in model predictions.

Model results indicated a strong link between predicted copepodite biomass trends, and the pattern and magnitude of inter-seasonal variations in chlorophyll *a* concentration and sea surface temperature. Inter-annual variations in these two parameters significantly alter predicted seasonal patterns of copepodite biomass in any particular year.

Using observed mean chlorophyll *a* concentration and sea surface temperature data from 1971 and 1972, the model provided a good qualitative approximation to the

mean pattern of zooplankton biomass observed in the two years. Significantly different trends were predicted for the two years, and the predicted scale of seasonal fluctuations was commensurate with observed differences between summer biomass maxima and winter biomass minima. However, results need to be viewed in the light of several reservations which are discussed below.

Dramatic short-term temporal variability and spatial patchiness, characteristic of the West Coast upwelling region, together conspire to render as dubious the use of data collected over short time scales or in a "snapshot" fashion, as proximates of "typical" monthly means for the region. Model predictions are therefore based on data input series which do not necessarily accurately reflect the true scale of inter-seasonal and inter-annual fluctuations. Greater confidence may be attached to the monthly means (Verheye *et al.* 1991) used for the months March, June, October and December, in the section on comparisons of quarterly variations in *C. carinatus* population age structure.

Comparisons between predicted *C. carinatus* copepodite biomass trends with seasonal changes in zooplankton standing stock measured during the Upwelling-Monitoring cruises are only meaningful if it is assumed that mesozooplankton species such as *C. carinatus* constituted a significant and fairly constant proportion of total zooplankton biomass. Based on monthly Bongo net (mesh size 300 μm) surveys undertaken between August 1977 and August 1978, Pillar (1986) estimated that copepods and euphausiids together constituted, in approximately equal proportions, as much as 90 to 95 per cent of the total zooplankton biomass sampled along the West Coast. The zooplankton biomass estimates presented in Andrews and Hutchings (1980) mainly reflect copepod biomass, because Pillar (1984) showed that the WP-2 (200 μm) sampling nets they used greatly underestimated the macrozooplankton contribution. The annual zooplankton trend used for comparative purposes in this chapter is therefore not significantly obscured by the presence of euphausiids, which exhibit large biomass fluctuations with no evidence of seasonality (Pillar 1986). Consideration of the percentage contribution of *C. carinatus* to total mesozooplankton biomass measured off Cape Columbine in the months March (23%), June (15%), October (16%) and December (18%) (Verheye 1989), suggests that *C. carinatus* may provide a reasonable index of mesozooplankton biomass fluctuations. The contribution of smaller zooplankton groups to the zooplankton biomass trend under discussion remains unquantified, and may explain some of the variability between the model-predicted *C. carinatus* and the observed zooplankton biomass trends.

Low-chlorophyll waters and high starvation- and predator-induced mortality rates during winter result in the model prediction that *C. carinatus* populations are unable to successfully sustain themselves over this period without the population "boosts" provided by occasional winter upwelling events and population restocking due to transport processes. However, the postulated importance of phytoplankton as a predictor of copepod egg production rates during winter is in need of further investigation. Ohman and Runge (1994) recently demonstrated that *Calanus finmarchicus* maintains high egg production rates in chlorophyll-poor waters through predation on microzooplankton. Furthermore, the dietary significance of microzooplankton is disproportionately exaggerated because of the organic and inorganic composition of prey such as ciliates, and the rapid clearance rates attained whilst feeding on certain microzooplankton groups (Ohman & Runge 1994). The ability of omnivorous copepods to adjust their feeding habits to accommodate food web shifts may therefore be a critical mechanism sustaining populations over the winter period (Urban *et al.* 1992). The role of this hitherto neglected facet in the Southern Benguela system warrants further attention. The principal aim of this thesis was to construct a model to simulate patterns of zooplankton productivity during the summer upwelling season. The implication from the above is that while the basic model developed in this thesis has made major contributions towards this aim, its use should only be extended with caution to model seasonal variations in zooplankton biomass, because of uncertainties regarding the use of phytoplankton abundance and composition measures as predictors of copepod fecundity during winter (Kleppel *et al.* 1991, Urban *et al.* 1992, White & Roman 1992, Ohman & Runge 1994).

CHAPTER 7

SYNTHESIS
TOWARDS PREDICTING ZOOPLANKTON
PRODUCTIVITY IN THE SOUTHERN BENGUELA
UPWELLING REGION

"Sandwiched between fish and phytoplankton ... are the zooplankton, a heterogeneous assemblage of herbivores, omnivores and invertebrate predators that ultimately draw energy from primary producers and bacteria, yet serve as essential forage items for fish during crucial recruitment stages."

Kerfoot & DeAngelis 1989

Evaluation of Modelling Efforts

This study revolves around the construction of a basic model to simulate the dynamics of the calanoid copepod *Calanoides carinatus*, which is the dominant copepod in terms of biomass along the West Coast region of the Southern Benguela system (see Fig. 2.5 for a summary of model structure). The model is driven by satellite-derived images of chlorophyll *a* concentration and sea surface temperature. This confers a distinct advantage over previous models developed for the region because it greatly reduces the number of model linkages, and circumvents the need to measure and incorporate an array of parameters needed, for example, to drive models which explicitly simulate primary production. The basic model incorporates only those mechanisms considered essential in driving copepod population dynamics. This helps to highlight the basic functioning of the system and permits a stepwise assessment of the relative importance of a suite of additional parameters and mechanisms.

The model is designed to estimate patterns of zooplankton productivity as a function of a set of easily measured hydrographic parameters. It is a first attempt at constructing a model which can be used to predict patterns of food availability for planktivorous fish, such as the commercially important anchovy. In terms of the aims discussed in chapter one, the modelling exercise was successful.

The model simulates the timing and scale of a copepod population's response to pulses of primary production, as well as the population's performance between upwelling bouts. Model output was compared with field data collected during a 27-

day anchor station study conducted in St Helena Bay. Substantial fluctuations were evident in the observed data and the point of the exercise was only to test whether or not the model was capable of capturing the basic trend. Model output provided a reasonable approximation of the average observed patterns of abundance of *C. carinatus*, supporting the use of the model as a tool for predicting within-season changes in patterns of secondary production.

The Achilles' Heel of the Population Dynamics Approach

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 nonlinear relationships may operate in the field if, for example, large temporal variability is evident in either the viability or mortality of copepod eggs (eg. Ianora *et al.* 1992). The imperfect relationship between fecundity and recruitment to the first naupliar stage is nonetheless here deemed less serious than the trophodynamic link between copepod feeding history and reproductive output.

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 (Hutchings, pers. comm.). A potential Achilles' heel of the present model therefore exists in the relationship between food abundance and copepod fecundity. 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 régime, which cannot be detected using standard sampling gear or techniques. If feeding history is an important factor controlling the production of calanoid eggs (Attwood & Peterson 1989), then traditional shipboard egg-production incubation methods may similarly yield inconsistent results.

One way to resolve this issue is to focus on a sampling program which attempts to track a local copepod population, rather than attempting broad-scale correlations based on data collected in a 'snapshot' fashion. The scale of sampling efforts is obviously restricted to some degree by the state-of-the-art in sampling gear, but there is a need to collect data on a range of different spatial scales. For example, improved

correlations between food abundance and fecundity might be obtained if the sampling scale is reduced sufficiently to allow accurate quantification of both the scale and magnitude of food patches available to copepods.

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. *C. carinatus* stages have been observed aggregating in areas with rapid phytoplankton growth rates (Verheye & 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 chlorophyll *a* concentration data (as an index of food abundance) or consideration of vertical changes in chlorophyll *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 (see Fig. 2.1). 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.

Food Quality and Egg Viability: 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 (Harris *et al.* 1993, Ianora & Poulet 1993, Ohman & Runge 1994). 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 & Capuzzo 1990, Ianora & Poulet 1993, Head & Harris 1994). Ianora and Poulet (1993) demonstrated a 4-6 fold difference in the hatching success of eggs of the copepod *Temora stylifera*, in response to changes in the copepod's diet. This stresses the need to quantify the relative contribution of copepod egg viability to enhancing or impeding the flow of energy through food webs in the southern Benguela system. Field studies correlating copepod egg production and phytoplankton species composition could assist in clarifying whether or not a significant proportion of the variability in copepod egg production and hatching success is attributable to this factor.

Reviewing the Model's Sensitivity

Model predictions were evaluated over a range of parameter values because of the difficulties of obtaining precise estimates of field parameters and the gaps in our understanding of some of the underlying ecological processes (Gladstein 1991). The model was robust with respect to most of its parameters and showed greatest sensitivity to parameters which are difficult to determine empirically, such as the copepod egg and adult mortality rates (Fig. 3.25). Because changes in adult abundance are quickly mirrored as changes in the rate of reproduction, copepod population dynamics are more sensitive to the abundance and survival rates of the adult and older stage individuals than to the corresponding values for the younger stages. This suggests that field sampling efforts should continue to focus on the larger, and synonymously older, stage classes rather than the hitherto neglected naupliar stage classes, although the latter group may be more important in a different context.

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 (eg. 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, Pillar *et al.* 1992). 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).

Model structure could be improved through the correct choice of population growth rates. Traditionally, such rates are simply extrapolated from average rates determined in the laboratory. There is a growing body of evidence suggesting that because of the order of magnitude higher mortality rates in the field, *in situ* marine copepod populations are subject to strong selective forces which ensure the survival of only the fittest individuals. Individuals with reduced fitness are more susceptible to both physiological and predatory sources of mortality (Lopez 1991, Carlotti & P. Nival 1992, Saiz *et al.* 1993). From a modeller's point of view, this is important because it suggests that modelling *in situ* zooplankton productivity rates requires

consideration of maximal rather than average rates of growth, development and survival under various sets of environmental conditions.

Crowder *et al.* (1992) demonstrated that large variance in growth rate among individual fish, and size-dependent predation effects, indicate that survivors are not average individuals. They therefore suggest that the performance of populations subject to high variance in individual behaviour, physiology or vital rate functions cannot simply be estimated as the sum of "average" individuals. Improvements on the basic model presented here could therefore be made by examining more fully the implications of individual variability on population dynamics (MacKenzie *et al.* 1990, Crowder *et al.* 1992), possibly through the use of individual-based models (DeAngelis & Gross 1992). Klein Breteler *et al.* (1994) propose that improved estimates of the duration of copepod life stages may be obtained by using an appropriate probability distribution function to account for individual variability among instars. Individual variability of other population dynamics variables, such as feeding behaviour (Turner *et al.* 1993), has been demonstrated in the laboratory. However, Paffenhöfer (1994) recently stressed that in some cases measured variability is attributable largely to the methods employed, and hence that variability in feeding rates for example, due to individual variability, is low relative to the effects of food concentration.

The Importance of Spatial Patchiness

Spatial variability in patterns of zooplankton and phytoplankton abundance manifest on a range of different scales and result from the interaction of various physical and biological processes. The effect of fine-scale spatial patchiness on mesoscale patterns of copepod productivity was investigated by quantifying the way in which different patch attributes modify the trophic transfer process from phytoplankton to zooplankton. This process was modelled by assuming that spatial patchiness affected the relative distributions and hence the degree of 'overlap' between zooplankton and phytoplankton populations. Model results suggested that under some circumstances, spatial variability in phytoplankton availability is more critical to determining average copepod growth rates than short-term temporal variability in phytoplankton abundance.

The effect of spatial patchiness on model predictions is more pronounced under poor than good average feeding conditions. During unfavourable periods and at optimal levels of spatial patchiness, simulations indicate that estimates of zooplankton

production based on average feeding conditions will underestimate overall zooplankton production by approximately 30%. There is a fine dynamic balance between the spatial arrangement and quality of patches in a heterogeneous environment, and the average productivity of copepod aggregations distributed randomly throughout the environment. For example if, albeit high quality, food patches are too widely spaced to be accessible to most local copepod aggregations, productivity on average is worse, because there is little or no growth in too large a proportion of the total habitat. The implication of these results is that more research should focus on attempting to quantify the scale of spatial patchiness in the Southern Benguela region, as well as the factors which potentially modify the spatial arrangements of zooplankton and phytoplankton biomass. This study provides a first and rough means of quantifying the scale of errors in spatial averaging which occur due to spatial matches and mismatches between zooplankton and phytoplankton populations.

Quantifying Mortality Rates Using a Simulation Approach

Temporal and spatial variability in the rate of predation on copepods by one of its major predators, the anchovy, occurs because the seasonality of fish spawning produces pulses of anchovy recruits which generally travel southwards down the West Coast from April onwards (Hampton 1987, Hutchings & Boyd 1992). Predator-induced mortality rates are notoriously difficult to determine empirically and hence a simulation approach was used to estimate the way in which this parameter varies as a function of intra- and interseasonal variability in predator abundance. The model predicts that predation rates by resident fish are commensurate with the average and maximum specific copepod production rates at fish densities of approximately 1 ton.km^{-1} and 3.5 tons.km^{-2} respectively.

Marked changes in the growth rates of juvenile anchovies (Waldron *et al.* 1992) may be an important factor determining recruitment strength to the pelagic purse-seine fishery in South African waters (Hutchings & Boyd 1992). The model developed in this study explored the effect on growth parameters of different geometric distributions and degrees of synchrony in the abundance of anchovy and its prey. Predicted growth trends were strongly density dependent. The spatial arrangement of fish biomass and the temporal overlap between fish and copepod abundances significantly modify both anchovy and copepod growth estimates. Absolute prey availability is less important in determining anchovy feeding success than mechanisms which permit spatial and temporal gaps in predation pressure. This

highlights the inadequacy of using measures of absolute prey abundance as correlates of fish growth rate without a fuller understanding of the way in which underlying mechanisms modify this relationship. The present study complements field studies in that it can explicitly simulate the synchrony between predator abundance and prey production rates, which are more critical to anchovy feeding success than absolute *per capita* prey availability.

For juvenile anchovies, model results suggested that the ration necessary to sustain fish growth increases with increasing fish size. Furthermore, because model results indicate that the juvenile stages pass through a critical period with high food requirements (Bollens *et al.* 1993), the availability of sustained high abundances of food along the West Coast may be a critical "bottleneck" contributing to recruitment success in anchovy. The importance of this factor in determining anchovy recruitment success and the value of the present model as a predictive tool for management will be assessed in the future by comparing model-predicted patterns of intra- and interseasonal variability in secondary productivity along the West Coast with anchovy recruitment success over the same period.

***C. carinatus* Productivity as an Index of Zooplankton Productivity**

Predictions generated using a temporally integrated form of the basic model suggested that the model is capable of providing a reasonable index of zooplankton productivity: model-predicted patterns of copepod standing stock generated using observed chlorophyll *a* concentration and sea surface temperature data for 1971 and 1972 (Andrews & Hutchings 1980) were similar to observed patterns of zooplankton biomass in these years. Model results are consistent with the empirical observation that distinct seasonal changes in copepod biomass occur, and the predicted scale of seasonal fluctuations in abundance is commensurate with observed differences (Verheye *et al.* 1991). However, predicted biomass fluctuations are somewhat exaggerated relative to observed values, and the predicted post-winter increase in copepod biomass occurs one month too early in the model. This highlights the fact that there are still considerable gaps in our knowledge of the mechanisms controlling copepod annual cycles, and the role of several additional factors needs to be quantified before annual patterns of copepod productivity can be successfully modelled in the Southern Benguela system. Specifically, there is a need to assess the role of, and quantify the dietary significance of, microzooplankton in sustaining copepod populations during the low-chlorophyll winter months (see eg. Ohman & Runge 1994). The effect on copepod population dynamics of changes in the cross-

shelf distribution of the various life cycle stages, as well as the role of advection in restocking nearshore populations during winter and spring (Verheye & Field 1992) could be investigated more fully in the future by coupling the present model with a more detailed physical model of transport processes in the region.

Size Relationships, Indirect Interactions and Processes Modulating the Trophic Transfer Process

Modelling exercises in this study are used to explore the effect of a single size-selective predator on a single zooplankton species, the dynamics of both groups being superimposed on a temporally and spatially heterogeneous environment. Simplification of the multitude of interactions characterising natural pelagic systems is essential because predicted zooplankton population size structure relationships are complex and dynamic. Effects need to be isolated or identified to provide some insight into the processes operating in these systems. For example, simulation results suggest that, for *C. carinatus*, a steady state population age composition is attained when the predator-induced mortality rate M_{pred} remains constant at 0.1 d^{-1} (Fig. 7.1a). During periods of frequent upwelling (and associated enhanced rates of reproduction), the proportional abundance of the younger stages increases, but the relatively poor starvation tolerance limits of this group causes a decrease in their proportional abundance during unfavourable conditions (see Fig. 2.12). Simulations suggest that the magnitude of population age structure shifts induced by "bottom-up" processes such as primary production levels (versus "top-down" controlling processes such as predation) is largely mediated by temperature. The gradual increase in water temperature subsequent to an upwelling event presumably permits individuals to develop rapidly and hence to "escape" into older size classes before feeding conditions deteriorate.

If predators are modelled explicitly as described in chapter five, and shoals of juvenile anchovies (average biomass = 13 tons.km^{-2}) selectively prey on large (CIV, CV and ADULT) *C. carinatus* individuals, the proportional abundance of the older stage individuals decreases as expected (Fig. 7.1b). However, it is interesting to note that the model predicts only a minor increase in the relative abundance of the naupliar stage individuals. This is because the selective removal of large fecund females from the population simultaneously reduces the rate at which new offspring are produced. Following the passage of a size-selective predator, the model therefore predicts that the increase in the relative abundance of the younger stages is almost wholly attributable to copepodite stages CI to CIII. No field data exist to compare

naupliar stage abundance estimates with model predictions, but results are approximately in accordance with the observation that copepodite stage CI constitutes almost 30 per cent of *C. carinatus* copepodite abundance measured off Cape Columbine in June (when high densities of anchovy recruits occur in the region) (Verheye *et al.* 1991). Conversely, late copepodites are more dominant than early copepodites in the months March and October, when large shoals of anchovy recruits are scarce (Verheye *et al.* 1991).

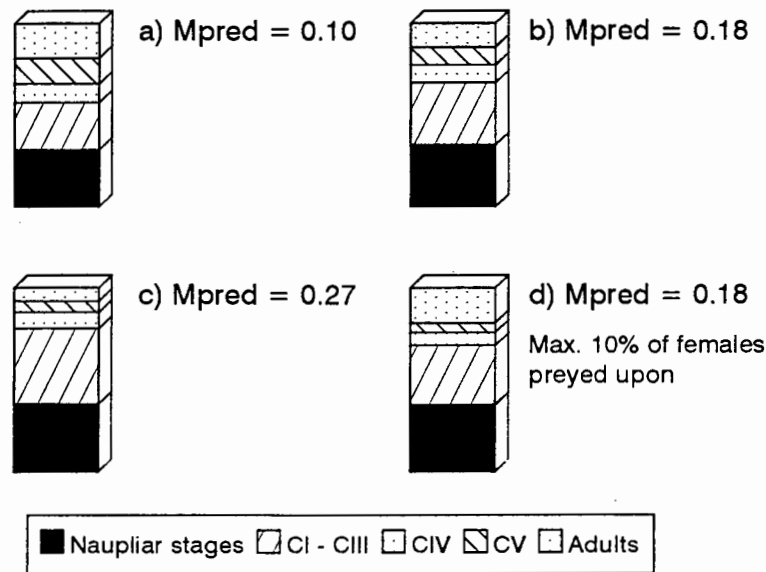


Fig. 7.1. The effect on *C. carinatus* population stage class structure of changing the magnitude and focus of predation pressure. The base-case (a) assumes an even predator-induced mortality rate M_{pred} of 0.10 d^{-1} operates on all stage classes. In (b), size-selective planktivorous fish (average biomass = 13 tons.km^2) are explicitly simulated preying on stage classes CIV to adult. Scenario (c) shows the predicted stage class structure following the passage of twice as many fish as in (b). In (d) it is assumed that the same biomass of fish is present as in (c), but their feeding is constrained by the assumption that the fish are able to locate a maximum of 10% of adult females, which are assumed to possess superior predator avoidance strategies. Note that in (d) the proportion (M_{pred}) of copepod individuals removed through predation is the same as that predicted for case (b), which assumes half the fish biomass used in (d), and no adult female refuge from predation.

If the biomass of anchovy recruits moving through an area with an initial *C. carinatus* abundance estimate of $400 \text{ copepods.m}^{-3}$, is assumed to double, the model-predicted predator-induced mortality rate M_{pred} increases from 0.18 d^{-1} to 0.27 d^{-1} . Predicted shifts in population stage structure are similar to those described above, but the magnitude of the effects is amplified (Fig. 7.1c). The implication of this model result is that while copepodite abundance in an area may be only 26% greater than copepodite abundance in an area with twice as many fish, predicted copepodite

biomass estimates suggest that copepodite biomass will be as much as 60% greater in the area impacted by fewer fish. The effect of predators on prey population size structure may therefore exacerbate density-dependent food limitation feedback processes, rendering approaches considering only simple numerical effects of predators inadequate.

Knowledge of size relations is therefore central to understanding both the effect of predation on plankton communities and the energetics of predators feeding on the plankton. This point is further illustrated if it is assumed for example that adult copepod females, which occur at greater depths in the water column than the other stage classes (Verheye & Field 1992), are less susceptible to predation. Ovigerous females of several copepod species are thought to frequent deep water as a means of reducing predation risk (*see* Bollens & Frost 1991b, for a review of the trade-offs). Assuming a maximum of, say, 10% of adult females constitute potential prey, and using the greater of the two fish biomass estimates (anchovy recruit biomass = 26 tons.km⁻²), the model predicts an M_{pred} value of 0.18, which is the same as that predicted for an area with half the number of fish but no adult female refuge from predation. Although M_{pred} is the same in these two scenarios, the predicted copepodite biomass in the former case is nearly 18% larger than that predicted for the latter case. Instead of a simple polarized effect on size structure (Fig. 7.1 b&c), the assumption of non-uniform predation on the large stages results in a "squeezing" in the relative abundance of the intermediate (CI to CV) stages: the relative abundance of the adults converges to the steady state value, but the relative abundance of the naupliar stages is increased by almost 20% (Fig. 7.1d).

The effects on zooplankton populations of both "top-down" and "bottom-up" processes are thus not simple, and there is a growing consensus that these effects are modified by complex indirect interactions (Leibold 1989, Novales-Flamarique *et al.* 1993). Planktivorous fish may affect zooplankton directly from above through predation, possibly from below if local nutrient enrichment through excretion occurs (DeAngelis & Rose 1990), and indirectly by modulating competition or predation effects within the plankton (Novales-Flamarique *et al.* 1993). Body size is considered the chief determinant of a marine pelagic organism's position in the food chain (Sheldon *et al.* 1972). Consideration of body size relationships is highlighted here not only because it pertains to trophodynamic predictions made using single-predator single-prey model systems, but also because it relates more generally to multispecies assemblages in the field. The present modelling efforts synthesized and evaluated some of the processes modulating the transfer of pulses of primary

production into harvestable fish biomass, using a single representative mesozooplankton species and a single planktivorous fish species as indicators of two major functional groups in the southern Benguela region. Species specific differences and indirect interactions were largely ignored, and instead the emphasis was placed on quantifying the effects of spatial and temporal patchiness on the trophic transfer process. Model analyses of processes which potentially modify patterns of zooplankton productivity support the growing realization that heterogeneity at all trophic levels plays a critical role in modulating the relative importance of "bottom-up" and "top-down" processes in determining population change and community structure (Hunter & Price 1992). Future extensions of the present modelling efforts will benefit more from attempts to isolate the critical interactions between different size-class assemblages, than from attempts to resolve individual species differences. Field and experimental studies could complement modelling studies by, for example, elucidating the role of zooplankton groups such as the microzooplankton and macrozooplankton, and by quantifying the magnitude and nature of size-class assemblage shifts which occur in the system.

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APPENDIX I

DOCUMENTATION OF PROGRAM PLANKTON.PAS

A PROGRAM TO SIMULATE THE GROWTH OF THE COPEPOD *Calanoides Carinatus* ALONG THE WEST COAST REGION OF SOUTH AFRICA

This program forms the basic skeleton of all simulations conducted during the course of this study. The program predicts the growth of a model *C. carinatus* population as a function of a minimal number of parameters (see chapter 2). The chief driving variables, chlorophyll *a* concentration and sea surface temperature, are read in to the program from external files. The user is asked to select one of three different data input options:

- i) Daily chlorophyll *a* concentration and sea surface temperature data are read in order to run the model over the summer upwelling season;
- ii) Input data are read for every fourth day (the interval may be changed) and the program interpolates between data points. This scenario is designed for use with satellite-derived estimates of the input parameters, as satellite-derived estimates may not be available on a daily basis;
- iii) Mean monthly averages are read from external files and are used to generate longer data input series, for use eg. in running the annual version of the model (discussed in chapter six).

Input to the program can be changed by either editing the appropriate data file, substituting a new data file name, or, in case (iii), by altering the frequency and intensity of upwelling cycles permitted.

The model described in chapter six is essentially an extension of the basic model developed in chapter two. However, modifications deemed necessary to simulate annual growth trends are only effective from May onwards in the program, and hence do not interfere with short-term model runs over the summer upwelling season.

Information needed to initialise a model *C. carinatus* population includes an initial abundance estimate (no.m^{-3}), which the user is prompted to input, as well as age distribution (proportional composition) and sex ratio (proportion females) parameters, which are easily changed in the variable declaration section at the top of the program listing. The initial ratio of ripe:unripe females can similarly be altered. The only additional information which needs to be input is the number of runs required.

The program is written in Turbo Pascal 6 for use on IBM-compatible computers. The program is divided into a number of procedures which are called from either the main program body or from within another procedure. The construction is such that it is relatively simple to make alterations to one of the program procedures to test the effect on model predictions. Only the basic program skeleton is presented here, and the various minor alterations made to the program, for example, during the sensitivity analysis (chapter three) are not listed for reasons of austerity.

All output from the program is written to external files, which can be imported into spreadsheet packages for further analysis, or output can simply be read using a text editor. When repeating model runs, important output such as daily estimates of Tbiom (the biomass of the copepodite and adult stage individuals) are written sequentially to data files, from where they are input to a second program (BIOM_MEAN.PAS, Appendix II) which calculates the mean and standard deviation of the daily estimates.

The maximum dimensions of all arrays and matrices are declared in the variable declaration sections, and can thus easily be changed. However, because of computer memory limitations, results from large numbers of runs are best written to external data files and analysed separately. The program may be improved by making it more interactive and user-friendly.

LISTING OF PROGRAM PLANKTON.PAS

PROGRAM Plankton;

```
{ The model is a depth-independent model of a time-dependent zooplankton }
{ population in a horizontally homogeneous volume of water.           }
{ The key variables controlling rates of growth, fecundity and       }
{ development are temperature and food supply.                       }
{ The model simulates the population dynamics of the copepod        }
{ Calanoides carinatus in the southern Benguela upwelling region.   }
```

```
{$M 36384, 0, 655360} {Extending stacksize allocated to program}
```

USES

CRT;

CONST

FCRIT = 3; {Threshold feeding concentration}

{Anchor station starting parameters}

AN = 0.305; {Age distribution parameters}

AC1 = 0.440;

AC2 = 0.130;

AA = 0.125;

SEX_RATIO = 0.90; {Ratio of no. of females:males}

Prop_unripe = 0.0384;

TYPE

pstarve = 1 .. 10;

pfeed = 1 ..10;

StarveMatrix = ARRAY[pfeed,pstarve] OF REAL;

Ary = ARRAY[1..365] OF REAL;

VAR

M : StarveMatrix; {% offspring starving after }
{ various food cycles }

start,fin, {Length of data series}

run,ITS,RNUM, {No. of runs}

S,F, {Counters for starving & feeding}

Sa,

SUMUPW, {No. of upwelling cycles}

i,j,k : INTEGER;

BIOM, {Initial population size}

NOS : REAL;

SIa, {Adult starvation index }

SI, {Starvation Index}

FH : ARRAY[1..365] OF INTEGER; {Feeding History}

CHL, {Total chlorophyll}

NET, {Chlorophyll > 10 μ m}

FN,FEC, {Fecundity parameters}

TEMP, {Sea surface temperature}

REC, {Recruits - egg hatch time=24hr}

NAUP, {Naupliar stages}

COP1, {Copepodite stages 1-4}
 COP2, {Copepodite stage 5}
 AD, {Adult *Calanoides carinatus*}
 Fu, {Unripe adult females}
 Fr, {Ripe/egg-laying females}
 MALES,
 TBIOM, {Total biomass of cops. & adults}
 MEGG, {Egg mortality}
 MNAUP,MCOP1,MCOP2,MAD, {Mortality est. for diff. stages}
 Dev1, {Dev. from naupliar - copepodite}
 Dev2, { copepodite 1 - C5 }
 Dev3, { C5 - adult }
 M50,

Starvn,starvc : ARRAY[1..365] OF REAL;

Feed : ARRAY[1..365] OF CHAR; {Intermittent/continuous feeding}

Data_type : SHORTINT;

X : Ary;

No : INTEGER;

sigma,

average,

RANDG,

Mean,

Std_Dev : REAL;

Supw : ARRAY[1..30] OF INTEGER;

PROCEDURE Inputdata;

VAR

 Indata,

 Intemp : TEXT; {Data input file}

BEGIN

 ASSIGN(Indata, 'C:\EVA\Ch130.INP');

 RESET(Indata);

 READLN(Indata);

 CLRSCR;

 {Reading in DAILY chlorophyll concentrations}

 i := start;

 WHILE i <= fin DO

 BEGIN

 READLN(Indata, CHL[i]);

 i := i + 1;

 END;

 CLOSE(Indata);

 ASSIGN(Intemp, 'C:\EVA\Temp30.INP');

 RESET(Intemp);

 READLN(Intemp);

 {Reading in DAILY sea surface temperature}

 i := start;

 WHILE i <= fin DO

 BEGIN

 READLN(Intemp, TEMP[i]);

 i := i + 1;

```

END;
CLOSE(Intemp);
FOR i := 1 TO fin DO
BEGIN
  IF temp[i] > 15 THEN
  BEGIN
    chl[i] := 1.0;
    END;    {Shift to flagellate-dominated community}
  END;
END; {inputdata}

PROCEDURE RANDinp;

VAR
  num   : INTEGER;
  sum   : REAL;

BEGIN
  RANDOMIZE;
  sum:=0;
  FOR num := 1 TO 12 DO
  BEGIN
    sum := sum + (RANDOM(100))/100;
    Randg := (sum-6) * sigma + average;
    IF Randg <= 0 THEN
    BEGIN
      Randg := 0.1;
    END;
  END;
END; {FN Randg}

PROCEDURE Inputrand;

VAR
  Totdays,
  count,
  Daysleft,

  h       : INTEGER;
  CHLUPW,
  CHLLEFT,
  AVELEFT,
  MONCHL  : REAL;
  UpwDATA,
  Outdata,
  Indata,
  Intemp  : TEXT;    {Data input file}
  NEWTEMP,
  NEWCHL  : ARRAY[1..7] OF REAL;
  UPW,
  DAYS    : ARRAY[1..12] OF INTEGER;

BEGIN
  ASSIGN(Indata, 'C:\EVA\CAVE.INP');
  RESET(Indata);
  READLN(Indata);
  CLRSCR;
  {*** NOTE 1972 = LEAP YEAR ***}

```

```

DAYS[1] := 31; DAYS[2] := 28; DAYS[3] := 31; DAYS[4] := 30;
DAYS[5] := 31; DAYS[6] := 30; DAYS[7] := 31; DAYS[8] := 31;
DAYS[9] := 30; DAYS[10] := 31; DAYS[11] := 30; DAYS[12] := 31;

```

```

RANDOMIZE;
SUMUPW := 0;
h := 1;
WHILE h <= 12 DO
BEGIN
  IF (h < 5) OR (h > 8) THEN
  BEGIN
    UPW[h] := RANDOM(3) + 1;
  END ELSE
  BEGIN
    UPW[h] := RANDOM(2);
  END;
  SUMUPW := SUMUPW + UPW[h];
  h := h + 1;
END;
Totdays := 0;
count := 1;
h := 1;
WHILE h <= 12 DO
BEGIN
  IF UPW[h] >= 1 THEN
  BEGIN
    k := 1;
    WHILE k <= UPW[h] DO
    BEGIN
      Supw[count] := RANDOM(DAYS[h]) + Totdays;

      count := count + 1;
      k := k + 1;
    END;
  END;
  Totdays := Totdays + DAYS[h];
  { WRITELN(' h = 'h,' TOTDAYS='TOTDAYS); }
  { READLN; }
  h := h + 1;
END;
count := 2;
WHILE count <= SUMUPW DO
BEGIN
  IF Supw[count] - Supw[count-1] < 2 THEN
  BEGIN
    Supw[count] := Supw[count] + 3;
  END;
  count := count + 1;
END;
ASSIGN(UpwDATA, 'C:\EVA\UPW.OUT');
REWRITE(UpwDATA);
WRITELN(UpwDATA, '*** UPWELLING DATA ***');
WRITELN(UpwDATA);
WRITELN(UpwDATA, ' TOTAL NO. OF UPW = ',SUMUPW);
WRITELN(UpwDATA);
WRITELN(UpwDATA, ' NO. OF UPW. PER MONTH');
WRITELN(UpwDATA);

```

```

FOR h := 1 TO 12 DO
BEGIN
  WRITELN(UpwDATA, H, ' ',UPW[h]);
END;
WRITELN(UpwDATA);
WRITELN(UpwDATA, ' STARTING DAY FOR EACH...');
WRITELN(UpwDATA);
FOR count := 1 TO SUMUPW DO
BEGIN
  WRITELN(UpwDATA, count, ' ',Supw[count]);
END;
CLOSE(UpwDATA);
{Reading in MONTHLY AVERAGE chlorophyll concentrations}
Totdays := 0;
h := 1;
WHILE h <= 12 DO
BEGIN
  READLN(Indata, MONCHL);
  CHLUPW := UPW[h] * 33.5;
  DAYSLEFT := DAYS[h] - UPW[h] * 7;
  CHLLEFT := MONCHL * DAYS[h] - CHLUPW;
  AVELEFT := CHLLEFT / DAYSLEFT;
  IF AVELEFT < 0.1 THEN
  BEGIN
    AVELEFT := 0.1;
  END;
  i := Totdays + 1;
  WHILE i <= Totdays + DAYS[h] DO
  BEGIN
    AVERAGE := AVELEFT;
    { USING OBSERVED STD VALUES }
    { Alternative program versions use SIGMA = 0.25*monchl}
    IF (h < 4) OR (h > 10) THEN
    BEGIN
      SIGMA := 5.6; {SUMMER}
    END ELSE
    BEGIN
      IF h < 6 THEN
      BEGIN
        SIGMA := 7.8; {AUTUMN}
      END ELSE
      BEGIN
        IF h < 9 THEN
        BEGIN
          SIGMA := 2.8; {WINTER}
        END ELSE
        BEGIN
          SIGMA := 7.7; {SPRING}
        END;
      END;
    END;
  END;
  RANDINP;
  CHL[i] := Randg;
  i := i + 1;
END;
Totdays := Totdays + DAYS[h];
h := h + 1;

```

```

END;
CLOSE(Indata);
{Upwelling pulses on days starting Supw ... }
NEWCHL[1] := 4; NEWCHL[2] := 7.9; NEWCHL[3] := 11.2; NEWCHL[4] := 5;
NEWCHL[5] := 2; NEWCHL[6] := 1.9; NEWCHL[7] := 1.5;
count := 1;
WHILE count <= SUMUPW DO
BEGIN
  k := 1;
  h := Supw[count];
  WHILE h <= (Supw[count] + 6) DO
  BEGIN
    CHL[h] := NEWCHL[k];
    k := k + 1;
    h := h + 1;
  END;
  count := count + 1;
END;
WRITELN(' SUMUPW = ',SUMUPW);
WRITELN;

ASSIGN(Intemp, 'C:\EVA\TAVE.INP');
RESET(Intemp);
READLN(Intemp);
{Reading in MONTHLY AVERAGE sea surface temperature at station 1}
Totdays := 0;
h := 1;
WHILE h <= 12 DO
BEGIN
  READLN(Intemp, MONCHL);
  CHLUPW := UPW[h] * 80; {SAME VARS USED BUT THEY ARE FOR TEMP}
  DAYSLEFT := DAYS[h] - UPW[h] * 7;
  CHLLEFT := MONCHL * DAYS[h] - CHLUPW;
  AVELEFT := CHLLEFT / DAYSLEFT;
  IF AVELEFT < 8 THEN
  BEGIN
    AVELEFT := 8;
  END;
  i := Totdays + 1;
  WHILE i <= Totdays + DAYS[h] DO
  BEGIN
    AVERAGE := AVELEFT;
    SIGMA := 2;
    RANDINP;
    TEMP[i] := Randg;
    i := i + 1;
  END;
  Totdays := Totdays + DAYS[h];
h := h + 1;
END;
CLOSE(Intemp);
{Upwelling pulses on days starting Supw ... }
NEWTEMP[1] := 9; NEWTEMP[2] := 10; NEWTEMP[3] := 11; NEWTEMP[4] := 12;
NEWTEMP[5] := 12; NEWTEMP[6] := 13; NEWTEMP[7] := 13;
count := 1;
WHILE count <= SUMUPW DO
BEGIN
  k := 1;

```

```

h := Supw[count];
WHILE h <= (Supw[count] + 6) DO
BEGIN
    TEMP[h] := NEWTEMP[k];
    k := k + 1;
    h := h + 1;
END;
count := count + 1;
END;

FOR i := 1 TO fin DO
BEGIN
    IF temp[i] > 15 THEN
    BEGIN
        chl[i] := 1.0;
    END;    {Shift to flagellate-dominated community}
    IF TEMP[i] < 8 THEN
    BEGIN
        TEMP[i] := 8;
    END;
END;

ASSIGN(Outdata, 'C:\EVA\Annlist.OUT');
IF run = 1 THEN
BEGIN
    REWRITE(Outdata);
END ELSE
BEGIN
    APPEND(Outdata);
    WRITELN(Outdata);
END;
i := start;
WHILE i <= fin DO
BEGIN
    { WRITELN(i, 'CHL[i]:2:1, ',TEMP[i]:2:1); }
    { REPEAT UNTIL KEYPRESSED;          }
    WRITELN(Outdata, i:3, 'CHL[i]:2:1, ',TEMP[i]:2:1);

    i := i + 1;
END;
CLOSE(Outdata);
END; {inputrand}

PROCEDURE Pause;

BEGIN
    WRITELN('    Press any key ...');
    READLN;
END;

PROCEDURE Meanstd;

VAR
    q      : INTEGER;
    Sum_X, Sum_Sq : REAL;

BEGIN

```

```

Sum_X := 0;
Sum_Sq := 0;
FOR q := 1 TO No DO
BEGIN
    Sum_X := Sum_X + X[q];
    Sum_Sq := Sum_Sq + X[q] * X[q];
END;
Mean := Sum_X / No;
IF (Sum_Sq - SQR(Sum_X)/No) <= 0 THEN
BEGIN
    WRITELN(' ERROR...DIF = ',Sum_Sq - SQR(Sum_X)/No,' No= ',No);
    WRITELN(' X[1] = ',X[1],' Sum_X = ',Sum_X,' Sum_Sq= ',Sum_Sq);
    PAUSE;
    Std_Dev := 0;
END ELSE
BEGIN
    Std_Dev := SQRT((Sum_Sq - SQR(Sum_X) / No ) / (No - 1));

END;

END; {Procedure MeanStd}

PROCEDURE SAT_data;

VAR
    Indata    : TEXT;    {Data input file - CTdata.DAT}

BEGIN
    ASSIGN(Indata, 'C:\MSDOC\Anchor.DAT');
    RESET(Indata);
    CLRSCR;
    Textcolor(Red);
    Textbackground(Lightgray);
    {Reading in chlorophyll concentrations for every fourth day}
    READLN(Indata);
    i := start;
    WHILE i <= fin DO
    BEGIN
        READ(Indata, CHL[i]);
        i := i + 4 ;
    END;
    {Reading in sea surface temperature for every fourth day}
    READLN(Indata);
    READLN(Indata);
    i := start;
    WHILE i <= fin DO
    BEGIN
        READ(Indata, TEMP[i]);
        i := i + 4 ;
    END;
    CLOSE(Indata);
END; {inputdata}

PROCEDURE initialise;

VAR
    Datalist : TEXT;

```

```

BEGIN
  ASSIGN(Datalist, 'C:\EVA\Datalist.OUT');
  REWRITE(Datalist);
  CLRSCR;
  i := start;
  WHILE i <= (fin-4) DO
  BEGIN
    k := 0;
    FOR j := i TO i+3 DO
      BEGIN
        k := k + 1;
        CHL[j] := 0.25*(CHL[i+4]-CHL[i])*k+1.25*CHL[i]-0.25*CHL[i+4];
        TEMP[j] := 0.25*(TEMP[i+4]-TEMP[i])*k+1.25*TEMP[i]-0.25*TEMP[i+4];
      END;    {linear interpolation of observed values}
    i := i + 4;
  END;
  FOR j := fin TO fin+3 DO
  BEGIN
    CHL[j] := CHL[fin];
    TEMP[j] := TEMP[fin];
  END;
  FOR i := 1 TO fin+3 DO
  BEGIN
    IF TEMP[i] > 15 THEN
      BEGIN
        CHL[i] := 2.9;
      END;    {Shift to flagellate-dominated community}
  END;
  WRITELN(Datalist, ' DAY', ' CHLOROPHYLL', ' TEMPERATURE');
  FOR j := 1 TO fin+3 DO
  BEGIN
    WRITELN(Datalist, j:02, ' ', CHL[j]:03:02, ' ', TEMP[j]:04:02);
  END;
  GOTOXY(2,4);
  WRITELN(' Doing simulations ... ');
END; {of initialise}

PROCEDURE feedhistory;

VAR
  History : TEXT;

BEGIN
  ASSIGN(History, 'C:\EVA\His.OUT');
  REWRITE(History);
  i := start;
  WHILE i <= (fin) DO
  BEGIN
    IF (S > 0) AND (CHL[i] > FCRIT) THEN {End of starvation period}
    BEGIN
      SI[i] := S;    {No. of days starved}
      S := 0;
    END ELSE BEGIN
      SI[i] := 0;
    END;
    IF CHL[i] > FCRIT THEN
    BEGIN
      F := F + 1;
    END;
  END;

```

```

    FH[i] := 0;

END ELSE {Chlorophyll concentration <= Fcrit}
BEGIN
    FH[i] := F; {No. of days fed}
    F := 0;
    S := S + 1;

END;
IF S >= 3 THEN
BEGIN
    Feed[i] := 'I'; {Intermittent feeding}
END ELSE
BEGIN
    Feed[i] := 'C'; {Continuous feeding}
END;

    WRITELN(History, ' Feeding and starvation history');
    WRITELN(History, ' day..', i);
    WRITELN(History, ' feeding..', F);
    WRITELN(History, ' starving.. ', S);
    WRITELN(History, ' SI .. ', SI[i]);
    WRITELN(History, ' FH .. ', FH[i]);
    WRITELN;
    IF SI[i] > 0 THEN
    BEGIN
        WRITELN( ' Starvation index and Feeding history');
        WRITELN;
        WRITELN(' Day ...', i);
        WRITELN(' Starvation index ...', SI[i]);
        WRITELN(' Feeding history ...', FH[(i-SI[i])]);
        WRITELN;

    END;
    i := i + 1;
END;
CLOSE(History);

END; {of feedhistory}

PROCEDURE Netchlor;

VAR
    Netchla : TEXT;

    Fmax : REAL; {Chl. conc. at which egg prodn. rates saturate}
BEGIN
    ASSIGN(Netchla, 'C:\EVA\Net.OUT');
    REWRITE(Netchla);
    WRITELN(Netchla, ' Net chlorophyll and corresponding fecundity values..');
    Fmax := 40;
    i := start;
    WHILE i <= (fin) DO
    BEGIN
        IF CHL[i] >= FMAX THEN
        BEGIN
            CHL[i] := FMAX; {Chl.conc. at which fecundity plateaus}
        END;
    END;

```

```

NET[i] := 0.98 * CHL[i] - 1.2;           {Chl. a > 10 µm}
NET[i] := 10 * NET[i];                 {Convert to biomass}
NET[start-1] := NET[start];
IF (NET[i-1]<=0) OR (NET[i]<=0) THEN
BEGIN
  FN[i] := 0;
END ELSE
BEGIN
  FN[i] := EXP(0.430 * LN(NET[i]) + 0.447 * LN(NET[i-1])) - 1.278;
END;
WRITELN(Netchla, ' Day ..',i);
WRITELN(Netchla, ' Net chl.a = ',NET[i]:08:02, ' Fecundity = ',FN[i]:15:02);
WRITELN;
i := i + 1;
END;
CLOSE(Netchla);

END; {of Netchlor}

PROCEDURE Fecundity;

VAR
  FS,           {Normal fecundity value}
  NEWF : REAL;  {Fecundity modified according to feeding history}
  Fecund : TEXT;
BEGIN
  ASSIGN(Fecund, 'C:\EVA\Fec.OUT');
  REWRITE(Fecund);
  i := start;
  WHILE i <= (fin) DO
  BEGIN
    IF (SI[i] > 0) AND (CHL[i] > FCRIT) THEN {End of starvation period}
    BEGIN
      IF NET[i] <= 3 THEN
      BEGIN
        NET[i] := 1;
      END;
      IF NET[i+1] <= 0 THEN
      BEGIN
        NET[i+1] := NET[i];
      END;
      FS := EXP(0.430 * LN(NET[i+1]) + 0.447 * LN(NET[i]))-1.278;
      NEWF := 5 * FS * EXP(-0.176 * SI[i]);
      j := i;
      FOR k := 1 TO 4 DO
      BEGIN
        FEC[j] := (k-1)/6 * (NEWF - FS); {Linear increase in egg prodn.}
        j := j + 1;
      END;
      FEC[i+4] := FS; {5 days recovery period to average egg prodn.}
      i := i + 5;
    END ELSE
    BEGIN
      IF CHL[i] < FCRIT THEN
      BEGIN
        FEC[i] := 0; {Food limitation of chlorophyll prodn.}
        IF CHL[i] > 1 THEN
        BEGIN

```

```

        IF CHL[i] > 2 THEN
        BEGIN
            FEC[i] := 5;
        END ELSE
        BEGIN
            FEC[i] := 1;
        END;
    END;
END ELSE
BEGIN
    FEC[i] := FN[i];
END;
i := i + 1;
END;
END;
WRITELN(Fecund, ' Modified fecundity values..');
FOR i := start TO (fin) DO
BEGIN
    WRITELN;
    WRITELN(Fecund, ' Day = ',i);
    WRITELN(Fecund, ' Fecundity = ',FEC[i]);
END;
CLOSE(Fecund);

END; {of Fecundity}

PROCEDURE Development;

VAR
    Feeding    : CHAR;
    TDev       : REAL;
    Dev        : TEXT;
BEGIN
    ASSIGN(Dev, 'C:\EVA\Dev.OUT');
    REWRITE(Dev);
    i := start;
    WHILE i <= (fin) DO
    BEGIN
        {Intermittent feeding causes dev. times to approx. double}
        IF TEMP[i] <= 8 THEN
        BEGIN
            TEMP[i] := 8;
        END;
        Feeding := Feed[i];
        CASE Feeding OF
        'C' : BEGIN      {Continuous feeding}
            TDev := 1469.2 * (1/(EXP(1.665*LN(TEMP[i]-1.5))));
            WRITELN(Dev, ' Day = ',i, ' ',Feeding = continuous');
        END;
        'T' : BEGIN      {Intermittent feeding}
            TDev := 2938.4 * (1/(EXP(1.665*LN(TEMP[i]-1.5))));
            WRITELN(Dev, ' Day = ',i, ' ',Feeding = intermittent');
        END;
        END; {of case}

        {Development indices(in days) based on temperature & feeding regime}
        Dev1[i] := 1 / (0.295 * TDev);  {From naupliar to copepodite}
    END;
END;

```

```

Dev2[i] := 1 / (0.481 * TDev); {From copepodite I to C5 }
Dev3[i] := 1 / (0.169 * TDev); {From C5 to adult }
WRITELN(Dev, TDev, ' ', 'DEV1[i]', ' ', 'DEV2[i]', ' ', 'DEV3[i]');
WRITELN(Dev);

i := i + 1;
END;
CLOSE(Dev);

END; {of Development}

PROCEDURE StarvingMortality;

{ Matrix values taken from Borchers & Hutchings (1986) give the }
{ % of C. carinatus offspring starving after various food cycles at 18°C }

VAR
Smat : TEXT;
row,col : INTEGER; {Pointers to locate feeding cycle}
Feedcycle, {Base case matrix value of % offspring starved}
ATEMP : REAL; {Average temperature over a starvation period}
BEGIN
ASSIGN(Smat, 'C:\EVA\Matrix.OUT');
REWRITE(Smat);
FOR i := 1 TO 10 DO
BEGIN
FOR j := 1 TO 2 DO
BEGIN
M[i,j] := 0;
END;
END;
FOR i := 1 TO 2 DO
BEGIN
FOR j := 1 TO 10 DO
BEGIN
M[i,j] := 0;
END;
END;
FOR i := 3 TO 10 DO
BEGIN
FOR j := 3 TO 10 DO
BEGIN
IF j > i THEN
BEGIN
M[i,j] := 1;
END;
END;
END;
M[3,3]:=0.67;
M[4,3]:=0.50; M[4,4]:=0.75;
M[5,3]:=0.40; M[5,4]:=0.60; M[5,5]:=0.80;
M[6,3]:=0.33; M[6,4]:=0.50; M[6,5]:=0.67; M[6,6]:=0.83; M[6,7]:=0.83;
M[7,3]:=0.29; M[7,4]:=0.43; M[7,5]:=0.57; M[7,6]:=0.71; M[7,7]:=0.71;
M[7,8]:=0.86;
M[8,3]:=0.25; M[8,4]:=0.38; M[8,5]:=0.50; M[8,6]:=0.63; M[8,7]:=0.63;
M[8,8]:=0.75; M[8,9]:=0.88;
M[9,3]:=0.22; M[9,4]:=0.33; M[9,5]:=0.44; M[9,6]:=0.56; M[9,7]:=0.56;
M[9,8]:=0.67; M[9,9]:=0.78; M[9,10]:=0.89;

```

```

M[10,3]:=0.2; M[10,4]:=0.3; M[10,5]:=0.4; M[10,6]:=0.5; M[10,7]:=0.5;
M[10,8]:=0.6; M[10,9]:=0.7; M[10,10]:=0.8;
WRITE(Smat, ' Percentage offspring starving after various');
WRITELN(Smat, 'food cycles at Temp. = 18');
WRITELN(Smat);
WRITELN(Smat, ' ROW = Period of feeding ; COL = Period of starvation');
WRITELN(Smat);
FOR i := 1 TO 10 DO
BEGIN
  FOR j := 1 TO 10 DO
  BEGIN
    WRITE(Smat, M[i,j]:4:2, ' ');
  END;
  WRITELN(Smat);
END;
WRITELN(Smat);
WRITELN(Smat, '% offspring starving after various food & temp. cycles');
WRITELN(Smat);
i := start;
WHILE i <= (fin) DO
BEGIN
  IF SI[i] > 0 THEN      {End of starvation period}
  BEGIN
    ATEMP := 0;
    IF SI[i] = 10 THEN
    BEGIN
      row := 10;
    END ELSE
    BEGIN
      row := FH[(i-SI[i]); {Previous period of feeding (days)}
    END;
    col := SI[i];      {Period of starvation (days)}
    IF (row < 1) THEN
    BEGIN
      row := 1;
      { WRITELN(' ROW & COL = ',ROW, ' ',COL); }
      { PAUSE; }
    END;
    IF (row >= 10) OR (col >= 10) THEN {Max. days starvation}
    BEGIN
      IF col >= 10 THEN
      BEGIN
        col := 10;
      END;
      IF row >= 10 THEN
      BEGIN
        row := 10;
      END;
    END;
    Feedcycle := M[row,col];
    {Calculating average temperature over starvation period}
    FOR j := (i-col) TO (i-1) DO
    BEGIN
      ATEMP := ATEMP + TEMP[j];
    END;
    ATEMP := ATEMP / COL;
    {Modifying starvation tolerance as a linearly decreasing }
    { function of temperature. }
  END;
  i := i + 1;
END;

```

```

STARVN[i] := 0.67*ATEMP / 18 * Feedcycle;
STARVC[i] := 0.33*ATEMP / 18 * Feedcycle;

M50[i] := 18 / ATEMP * 12; {Adult & CV starv.tolerance limit}
{ WRITELN(' STARVE =',i,' ',FEEDCYCLE,' ',STARVE[i],' ',M50[i]);}
{ PAUSE; }
END ELSE
BEGIN
STARVN[i] := 0; {No offspring starve}
STARVC[i] := 0;
M50[i] := 1000;
ATEMP := TEMP[i];
END;
WRITE(Smat,'DAY =',i,' STARVN =',STARVN[i]:10:02);
WRITELN(Smat,' AVE. TEMP =',ATEMP:20:02);
i := i + 1;
END;
CLOSE(Smat);
END; {of StarvingMortality}

PROCEDURE Population;

CONST
Eggmort = 0.9;

VAR
Age,
Eggs,
Popln,      {Lotus file to present output}
Popn       : TEXT;
ADVECT,
ADVECT2,
count      : INTEGER;
ToT,
ToTEgg,
CV,
NAGE, C1AGE,
C2AGE, ADAGE,
pmortn,pmortc1,  {Mortality due to predators}
pmortc2,pmorta,
fmortn,fmortc1,  {Mortality due to starvation}
fmortc2,fmorta   : REAL; {Constant mortality percentages}
BEGIN
ASSIGN(Popn,'C:\EVA\Pop.OUT');
REWRITE(Popn);
ASSIGN(Popln,'C:\LOTUS\EVA\Popln.WK1');
REWRITE(Popln);
REC[start] := (BIOM/6 * FEC[start])/10; {assumes 90% mortality of eggs}
{ Mortality as a linearly increasing function of density }
{ Includes mortality due to predation, cannibalism etc. }
pmortn := 0.10;
pmortc1 := 0.10;
pmortc2 := 0.10;
pmorta := 0.10;

i := start;

```

```

WHILE i <= (fin) DO
BEGIN
  {Egg-laying population taken as the no. of ripe adult females(Fr), }
  { assuming newly developed females (Fu) take three days before   }
  { laying eggs. }
  Fu[i] := 0;
  IF i <= (start+1) THEN
  BEGIN
    Fu[i] := Prop_unripe * BIOM;
  END ELSE
  BEGIN
    FOR j := i-2 TO i DO
    BEGIN
      Fu[i] := Fu[i] + (1-pmorta) * (Dev3[j] * COP2[j]);
    END;
  END;
  IF Fu[i] < 0 THEN
  BEGIN
    Fu[i] := 0;
  END ELSE
  BEGIN
    Fu[i] := ROUND(Fu[i]);
  END;
  { **** Assume a female:male sex ratio of 9:1 **** }
  Fr[i] := (AD[i] - Fu[i]) * Sex_Ratio;
  MALES[i] := (1-Sex_Ratio) * AD[i];
  {Population recruitment}
  IF FEC[i] = 0 THEN
  BEGIN
    REC[i+1] := 0;  {Prevents negative recruitment!}
  END ELSE
  BEGIN
    REC[i+1] := ROUND(Fr[i]) * FEC[i];
  END;
  MEGG[i+1] := Eggmort * REC[i+1];
  REC[i+1] := ROUND(REC[i+1] - MEGG[i+1]);
  {Population growth equations}
  NAUP[i+1] := (1-Dev1[i]) * NAUP[i] + REC[i+1];
  COP1[i+1] := (1-Dev2[i]) * COP1[i] + Dev1[i] * NAUP[i];
  COP2[i+1] := (1-Dev3[i]) * COP2[i] + Dev2[i] * COP1[i];
  AD[i+1] := AD[i] + Dev3[i] * COP2[i];
  {Mortality (starvation) estimates for copepod stages}
  IF STARVC[i+1] > 0 THEN
  BEGIN
    {Percentage of offspring die due to starvation }
    {Adults are less susceptible to starvation due to }
    { lipid food reserves & carnivorous feeding. }
    { However their egg prodn. is assumed very }
    { sensitive to food supply. }
    fmortn := STARVN[i+1]; {Starvation tolerance of NAUPs}
    fmortc1 := STARVC[i+1]; {LESS than copepodites }
  END ELSE
  BEGIN
    fmortn := 0;
    fmortc1 := 0;
  END;
  {M50 is the no. of days of starvation required }
  { to induce 50% adult & pre-adult starvation }

```

```

IF Sla[i+1] > M50[i] THEN
BEGIN
  fmortc2 := 0.5;  {starvation tolerance of CV cops}
  fmorta := 0.5;  {          adults }
END ELSE
BEGIN
  fmortc2 := 0;
  fmorta := 0;
END;
{ MORTALITY OF OLDER STAGES DUE TO ANCHOVY RECRUITS }
IF (i > 120) AND (i < 275) THEN
BEGIN
  pmorta := 0.15;
  pmortc2 := 0.15;
END ELSE
BEGIN
  pmorta := 0.10;
  pmortc2 := 0.10;
END;
MNAUP[i+1] := (pmortn + fmortn) * NAUP[i+1];
MCOP1[i+1] := (pmortc1 + fmortc1) * COP1[i+1];
MCOP2[i+1] := (pmortc2 + fmortc2) * COP2[i+1];
MAD[i+1] := (pmorta + fmorta) * AD[i+1];
{Net population growth assuming mortality estimates above}
COP2[i+1] := ROUND(COP2[i+1] - MCOP2[i+1]);
AD[i+1] := ROUND(AD[i+1] - MAD[i+1]);
IF REC[i+1] < 0 THEN
BEGIN
  REC[i+1] := 0;
END;
IF NAUP[i+1] < 0 THEN
BEGIN
  NAUP[i+1] := 0;
END;
IF COP1[i+1] < 0 THEN
BEGIN
  COP1[i+1] := 0;
END;
IF COP2[i+1] < 0 THEN
BEGIN
  COP2[i+1] := 0;
END;
{RANDOM ADVECTION OF C5.s INTO THE AREA DURING WINTER&SPRING}
ADVECT := 0;
ADVECT2 := 0;
IF (i > 151) AND (i < 275) THEN
BEGIN
  RANDOMIZE;
  count := 1;
  WHILE count <= SUMUPW DO
  BEGIN
    IF i = Supw[count] THEN
    BEGIN
      ADVECT := RANDOM(27) + 26;
      ADVECT2 := RANDOM(11) + 10;
      count := SUMUPW;
    END ELSE
    BEGIN

```

```

        count := count + 1;
    END;
END;
END;
COP2[i+1] := COP2[i+1] + ADVECT;
AD[i+1] := AD[i] + ADVECT2;
IF (i > 120) AND (i < 306) THEN
BEGIN
WRITELN(Popn, i, ' ADVECT=' ,ADVECT, ' ,ADVECT2,' ,COP2[i+1]);
WRITELN(Popn);
END;
WRITELN;
WRITELN(Popn, ' Day .. ',i);
WRITELN(Popn, 'Recruits =' ,REC[i]:06:0, ' ',Naups =' ,NAUP[i]:15:0);
WRITELN(Popn, 'Copepodites=' ,COP1[i]:04:0, ' ', C5 =' ,COP2[i]:15:0);
WRITELN(Popn, 'Adults =' ,AD[i]:08:0);
WRITELN(Popn);
WRITE(Popln, i:02, ' ,REC[i]:03:0, ' ,NAUP[i]:04:0);
WRITE(Popln, COP1[i]:05:0, ' ,COP2[i]:06:0, ' ,AD[i]:7:0);
WRITELN(Popln, ' ,Fu[i]:04:0, ' ,Fr[i]:04:0, ' ,MALES[i]:4:0);
    i := i + 1;
END;
CLOSE(Popn);
CLOSE(Popln);
ToTEgg := 0;
i := start;
WHILE i <= fin DO
BEGIN
    ToTEgg := ToTEgg + REC[i];
    X[i] := REC[i];
    i := i + 1;
END;
No := fin;
Meanstd;
CV := Std_Dev / Mean;
ASSIGN(Eggs, 'C:\EVA\EGGS.SEN');
IF run = 1 THEN
BEGIN
    REWRITE(Eggs);
    WRITELN(Eggs, 'Tot & Mean EGGs, STD, CV // Mean Eggs/ADs, STD, CV');
    WRITELN(Eggs);
END ELSE
BEGIN
    APPEND(Eggs);
END;
WRITE(Eggs, run, ' ,ToTEgg:5:1, ' ,Mean:5:1, ' ,Std_Dev:5:1);
WRITE(Eggs, ' ,CV:3:2);
i := start;
WHILE i <= fin DO
BEGIN
    IF Fr[i] > 0 THEN
    BEGIN
        X[i] := REC[i] / (Fr[i]);
    END ELSE
    BEGIN
        X[i] := 0;
    END;
    i := i + 1;

```

```

END;
No := fin;
Meanstd;
CV := Std_Dev / Mean;
WRITELN(Eggs, ' ',Mean:5:2,' ',Std_Dev:5:1,' ',CV:3:2);
CLOSE(Eggs);
{ *** AGE STRUCTURE **** }
ToT := NAUP[fin] + COP1[fin] + COP2[fin] + AD[fin];
WRITELN(' TOT = ',TOT,' BIOM= ',BIOM);

ASSIGN(Age, 'C:\EVA\AGE.OUT');
IF run = 1 THEN
BEGIN
    REWRITE(Age);
    WRITELN(Age, '*** AGE.OUT ***');
    WRITELN(Age, 'Initial & Final: Prop. N; C1-C4; C5; AD; MALE; Fr');
    WRITELN(Age);
END ELSE
BEGIN
    APPEND(Age);
END;
WRITE(Age, run, ' ',AN:1:3,' ',AC1:1:3,' ');
WRITE(Age, AC2:1:3,' ',AA:1:3,' ');
WRITELN(Age, MALES[start]/BIOM:1:3,' ',Fr[start]/BIOM:1:3,' ');
WRITE(Age, run+1, ' ',NAUP[fin]/ToT:1:3,' ',COP1[fin]/ToT:1:3,' ');
WRITE(Age, COP2[fin]/ToT:1:3,' ',AD[fin]/ToT:1:3,' ');
WRITELN(Age, MALES[fin]/ToT:1:3,' ',Fr[fin]/ToT:1:3,' ');
WRITELN(Age);
WRITELN(Age, ' MONTHLY AVERAGES FOR MARCH, JUNE, OCT. & DEC. ');
WRITELN(Age);
NAGE := 0;
C1AGE := 0;
C2AGE := 0;
ADAGE := 0;
i := 60;    { AVE. AGE STRUCTURE IN MARCH }
WHILE i <= 90 DO
BEGIN
    NAGE := NAGE + NAUP[i];
    C1AGE := C1AGE + COP1[i];
    C2AGE := C2AGE + COP2[i];
    ADAGE := ADAGE + AD[i];
    i := i + 1;
END;
ToT := NAGE + C1AGE + C2AGE + ADAGE;
WRITE(Age, 'MARCH ',NAGE/ToT:1:3,' ',C1AGE/ToT:1:3,' ');
WRITELN(Age, C2AGE/ToT:1:3,' ',ADAGE/ToT:1:3,' ');
ToT := C1AGE + C2AGE + ADAGE;
WRITE(Age, ' ',C1AGE/ToT:1:3,' ');
WRITELN(Age, C2AGE/ToT:1:3,' ',ADAGE/ToT:1:3,' ');
WRITELN(Age);
NAGE := 0;
C1AGE := 0;
C2AGE := 0;
ADAGE := 0;
i := 152;    { JUNE }
WHILE i <= 181 DO
BEGIN
    NAGE := NAGE + NAUP[i];

```

```

    C1AGE := C1AGE + COP1[i];
    C2AGE := C2AGE + COP2[i];
    ADAGE := ADAGE + AD[i];
    i:=i+1;
END;
ToT := NAGE + C1AGE + C2AGE + ADAGE;
WRITE(Age, ' JUNE ',NAGE/ToT:1:3, ' ,C1AGE/ToT:1:3, ' );
WRITELN(Age, C2AGE/ToT:1:3, ' ,ADAGE/ToT:1:3, ' );
ToT := C1AGE + C2AGE + ADAGE;
WRITE(Age, ' ',C1AGE/ToT:1:3, ' ');
WRITELN(Age, C2AGE/ToT:1:3, ' ,ADAGE/ToT:1:3, ' );
WRITELN(Age);
NAGE := 0;
C1AGE := 0;
C2AGE := 0;
ADAGE := 0;
i := 273;          { OCTOBER }
WHILE i <= 303 DO
BEGIN
    NAGE := NAGE + NAUP[i];
    C1AGE := C1AGE + COP1[i];
    C2AGE := C2AGE + COP2[i];
    ADAGE := ADAGE + AD[i];
    i:=i+1;
END;
ToT := NAGE + C1AGE + C2AGE + ADAGE;
WRITE(Age, ' OCTOBER ',NAGE/ToT:1:3, ' ,C1AGE/ToT:1:3, ' );
WRITELN(Age, C2AGE/ToT:1:3, ' ,ADAGE/ToT:1:3, ' );
ToT := C1AGE + C2AGE + ADAGE;
WRITE(Age, ' ',C1AGE/ToT:1:3, ' ');
WRITELN(Age, C2AGE/ToT:1:3, ' ,ADAGE/ToT:1:3, ' );
WRITELN(Age);
NAGE := 0;
C1AGE := 0;
C2AGE := 0;
ADAGE := 0;
i := 334;          { DECEMBER }
WHILE i <= 365 DO
BEGIN
    NAGE := NAGE + NAUP[i];
    C1AGE := C1AGE + COP1[i];
    C2AGE := C2AGE + COP2[i];
    ADAGE := ADAGE + AD[i];
    i:=i+1;
END;
ToT := NAGE + C1AGE + C2AGE + ADAGE;
WRITE(Age, ' DECEMBER ',NAGE/ToT:1:3, ' ,C1AGE/ToT:1:3, ' );
WRITELN(Age, C2AGE/ToT:1:3, ' ,ADAGE/ToT:1:3, ' );
ToT := C1AGE + C2AGE + ADAGE;
WRITE(Age, ' ',C1AGE/ToT:1:3, ' ');
WRITELN(Age, C2AGE/ToT:1:3, ' ,ADAGE/ToT:1:3, ' );
WRITELN(Age);
CLOSE(Age);

END; {of Population}

PROCEDURE Production;

```

```

VAR
  Bio,
  Biop,
  Prod  : TEXT;
  WEGG,      {Mean wt (ugC) of Calanoides egg      }
  WCOP1,     {Mean body wt (ugC) for Copepodites I - IV  }
  WCOP2,     {Body wt. for CV                      }
  WMALE,     {Body wt. for adult male and female C.carinatus}
  WFEM      : REAL;  { assuming equal sex distribution  }
  BCOP1,BCOP2,BCOP, {Biomass of copepodite stages  }
  BMALE,     { " " adult male copepods }
  BFEMALE,
  BFu,BFr    { " " unripe & ripe females}
            : ARRAY[1..365] OF REAL;
BEGIN

  {Calculating Biomass}
  ASSIGN(Bio, 'C:\LOTUS\EVA\Bio.WK1');
  REWRITE(Bio);
  WCOP1 := 8.9720;
  WCOP2 := 31.569;
  WMALE := 35.721;
  WFEM := 56.81;

  COP1[1] := BIOM*AC1;
  COP2[1] := BIOM*AC2;
  AD[1] := BIOM*AA;
  ASSIGN(Biop, 'C:\EVA\Biop.SEN');
  IF run = 1 THEN
  BEGIN
    REWRITE(Biop);
  END ELSE
  BEGIN
    APPEND(Biop);
  END;
  i := start;
  WHILE i <= (fin) DO
  BEGIN
    BCOP1[i] := WCOP1 * COP1[i];
    BCOP2[i] := WCOP2 * COP2[i];
    BCOP[i] := BCOP1[i] + BCOP2[i];
    BMALE[i] := WMALE * MALES[i];
    BFr[i] := WFEM * Fr[i];
    BFu[i] := WFEM * (AD[i]*Sex_Ratio - Fr[i]);
    BFEMALE[i] := WFEM * AD[i] * Sex_Ratio;
    TBIOM[i] := BCOP[i] + BMALE[i] + BFEMALE[i];
    WRITE(Bio, i:02,',',TBIOM[i]:03:0,',',BCOP[i]:04:0);
    WRITELN(Bio, ',',BMALE[i]:05:0,',',BFr[i]:06:0,',',BFu[i]:07:0);
    { WRITE(i:02,',',TBIOM[i]:03:0,',',BCOP[i]:04:0); }
    { WRITELN(' ',BMALE[i]:05:0,',',BFr[i]:06:0,',',BFu[i]:07:0); }
    { PAUSE; }
    IF i = start THEN
    BEGIN
      WRITELN(Biop);
      WRITELN(Biop, run);
      WRITELN(Biop);
    END;
    WRITELN(Biop, TBIOM[i]:02:0);
  END;

```

```

        i := i + 1;
    END;
    CLOSE(Bio);
    CLOSE(Biop);

END; {of Production}

PROCEDURE Sensitivity;

VAR
    ANC,
    MODEL,
    BAss,
    Bss    : TEXT;
    Bcomp  : File OF REAL;
    SS,
    Plus,
    CV,
    Banc   : REAL;
BEGIN
    ASSIGN(ANC, 'C:\EVA\ANCBIO.INP');
    RESET(ANC);
    READLN(ANC);
    SS := 0; {Diff between model run's biomass of cops&ads and ANCHOR DATA}

    Plus := 0; {Checks whether runs results are above or below mean}
    i := start;
    WHILE i <= fin DO
    BEGIN
        READLN(ANC, Banc);
        X[i] := SQRT((TBIOM[i] - Banc)*(TBIOM[i] - Banc));
        SS := SS + X[i];
        IF Banc > TBIOM[i] THEN
        BEGIN
            Plus := Plus + 1;
        END;
        i := i + 1;
    END;
    CLOSE(ANC);
    Plus := Plus / fin; {proportion of time above}
    No := fin;
    Meanstd;
    CV := Std_Dev / Mean;
    ASSIGN(Bss, 'C:\EVA\BIOSS.SEN');
    IF run = 1 THEN
    BEGIN
        REWRITE(Bss);
        WRITELN(Bss);
        WRITELN(Bss, 'BIOSS.SEN: SS - MODEL vs ANC STATION Tbiom ');
        WRITELN(Bss);
        WRITELN(Bss, 'RUN - TOTss - MEAN SS - STD - CV - PROP. VAL. ABOVE');
        WRITELN(Bss);
    END ELSE
    BEGIN
        APPEND(Bss);
    END;
    WRITE(Bss, run, ' ', 'SS:10:0, ', 'MEAN:5:0, ', 'STD_DEV:4:1);
    WRITELN(Bss, ' ', 'CV:1:2, ', 'PLUS:1:2);

```

```

WRITELN(Bss);
CLOSE(Bss);

ASSIGN(MODEL, 'C:\EVA\MODBIO.INP');
RESET(MODEL);
READLN(MODEL);
SS := 0; {Diff between model run's biomass of cops&ads and BASE CASE}
Plus := 0; {Checks whether runs results are above or below mean}
i := start;
WHILE i <= fin DO
BEGIN
  READLN(MODEL, Banc);
  X[i] := SQRT((TBIOM[i] - Banc)*(TBIOM[i] - Banc));
  SS := SS + X[i];
  IF Banc > TBIOM[i] THEN
  BEGIN
    Plus := Plus + 1;
  END;
  i := i + 1;
END;
CLOSE(MODEL);
Plus := Plus / fin; {proportion of time above}
No := fin;
Meanstd;
CV := Std_Dev / Mean;
ASSIGN(BAss, 'C:\EVA\BASESS.SEN');
IF run = 1 THEN
BEGIN
  REWRITE(BAss);
  WRITELN(BAss);
  WRITELN(BAss, 'BASESS.SEN: SS - MODEL vs BASE CASE Tbiom ');
  WRITELN(BAss);
  WRITELN(BAss, 'RUN- TOTss - MEAN SS - STD - CV - PROP. VAL. ABOVE');
  WRITELN(BAss);
END ELSE
BEGIN
  APPEND(BAss);
END;
WRITE(BAss, run, ' ', SS:10:0, ' ', MEAN:5:0, ' ', STD_DEV:4:1);
WRITELN(BAss, ' ', CV:1:2, ' ', PLUS:1:2);
WRITELN(BAss);
CLOSE(BAss);

END; {of Sensitivity}

PROCEDURE Sens2;

CONST
  AD_base = 60;
  C5_base = 31;
  Cop_base = 74;
  Naup_base = 16;
  Biom_base = 4925;

VAR
  PCOMP,
  Finval,
  PBase : TEXT;

```

```

BNum,
Plus,
CV,
C1,C2,C3,
C4,C5    : REAL;

BEGIN
  ASSIGN(Finval, 'C:\EVA\FINVAL.SEN');
  IF run = 1 THEN
    BEGIN
      REWRITE(Finval);
      WRITELN(Finval, '***** FINVAL.SEN *****');
      WRITELN(Finval, ' Ratio of final run values to base case values');
      WRITELN(Finval);
      WRITELN(Finval, ' NAUPS - C1 to C4 - C5 - ADULT - TBIOM');
      WRITELN(Finval);
    END ELSE
    BEGIN
      APPEND(Finval);
    END;
    C1 := NAUP[fin] / Naup_base;
    C2 := COP1[fin] / Cop_base;
    C3 := COP2[fin] / C5_base;
    C4 := AD[fin] / AD_base;
    C5 := TBIom[fin] / Biom_base;
    WRITE(Finval, run, ' ', C1:5:3, ' ', C2:5:3, ' ', C3:5:3, ' ');
    WRITELN(Finval, C4:5:3, ' ', C5:8:3);
    CLOSE(Finval);

  END;
  BEGIN {Main Program}
    CLRSCR;
    WRITELN('**PROGRAM TO ESTIMATE ZOOPLANKTON PRODUCTION**');
    WRITELN;
    WRITE(' How many days data do you want to enter ? ');
    WRITELN(' Please give starting and last day ...');
    READLN(start,fin);
    WRITELN;
    WRITELN(' INPUT NO. OF RUNS');
    READLN(RNUM);
    WRITELN;
    WRITELN(' Please input starting biomass (no./m3) ...');
    READLN(NOS);
    run := 1;
    ITS := 1;
    WHILE ITS <= RNUM DO
      BEGIN
        BIOM := NOS;

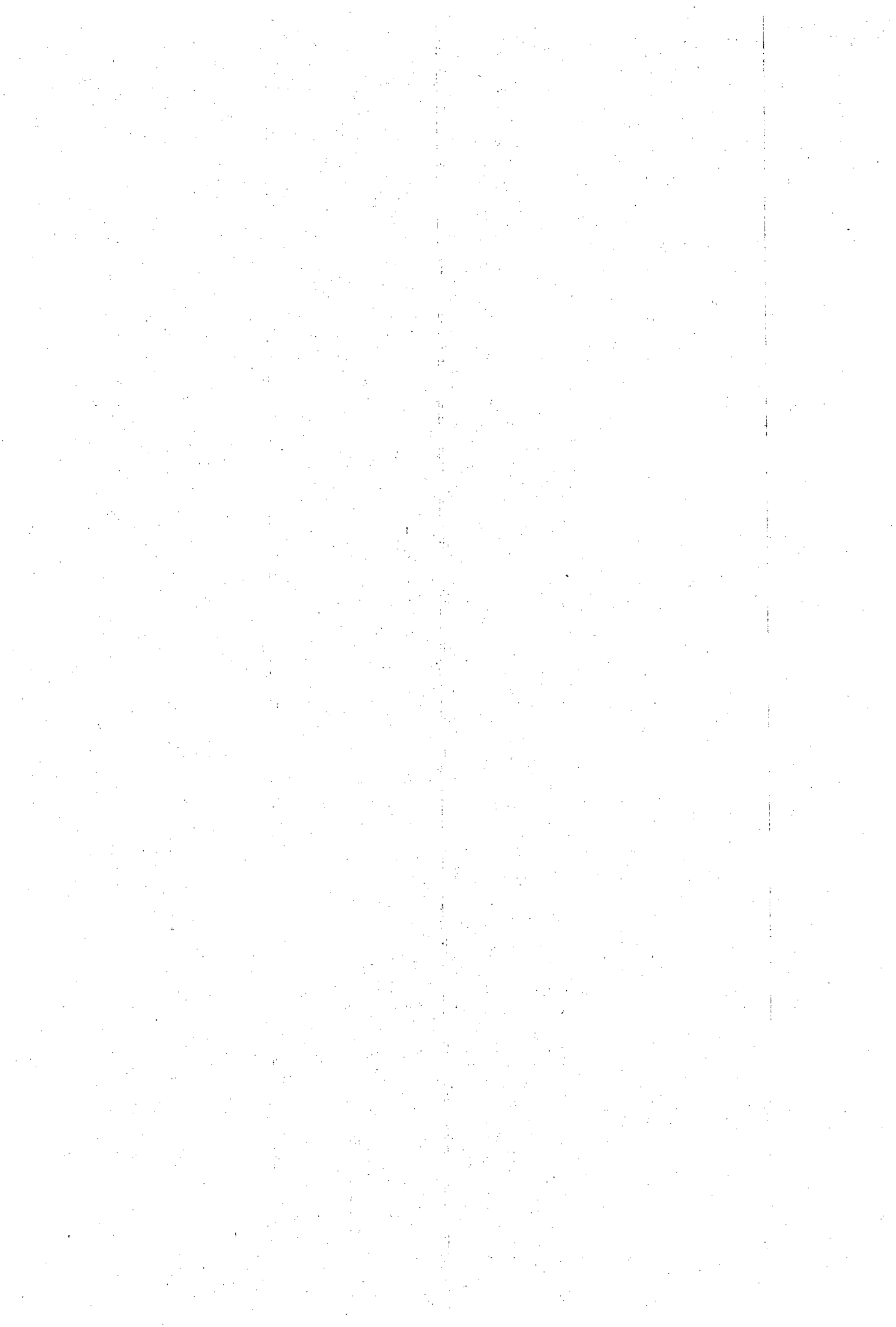
        WRITELN;
        IF start = 1 THEN
          BEGIN
            S := 0;
            F := 0;
            Sa := 0;
            SI[start] := 0;
            SIa[start] := 0;
          END; {Initialise variables}

```

```

NAUP[start] := BIOM*AN;    {Assume an even initial age distribution}
COP1[start] := BIOM*AC1;  {      "      }
COP2[start] := BIOM*AC2;  {      "      }
AD[start] := BIOM*AA;     {      "      }
WRITELN;
WRITELN;
WRITELN(' Press 1 to run the model over the upwelling season; or');
WRITE(' Press 2 to interpolate between data points available for ');
WRITELN('every fourth day; or');
WRITELN(' Press 3 to run the annual version of the model!');
READLN(Data_type);
WRITELN;
IF Data_type = 1 THEN
BEGIN
    Inputdata;
END ELSE
BEGIN
    IF Data_type = 2 THEN
    BEGIN
        SAT_DATA;
        INITIALISE;
    END ELSE
    BEGIN
        Inputrand;
    END;
END;
FEEDHISTORY;
NETCHLOR;
FECUNDITY;
DEVELOPMENT;
STARVINGMORTALITY;
POPULATION;
PRODUCTION;
{ Drawings; }
{ Sensitivity; }
{ Sens2; }
run := run + 1;
ITS := ITS + 1;
END;
WRITELN;
GOTOXY(2,6);
WRITELN(' *** Program successful ! ***');
WRITELN;
REPEAT UNTIL KEYPRESSED;
END.

```



APPENDIX II



DOCUMENTATION AND LISTING OF PROGRAM BIOM_MEAN.PAS

A listing follows of the program used to calculate the means and standard deviations of model estimates. Biomass or other data read into external files during simulations described in this thesis are read by programs similar to that listed below, and statistics are then performed on the data according to the required specifications. Slightly different versions of the program below are used, for example, in reading from data files with different formats, or for calculating eg. daily means versus overall means.

```
PROGRAM MEANBIOP;

USES
  CRT;

TYPE
  Ary = ARRAY[1..1000] OF REAL;

VAR
  time,
  No,
  run,
  i   : INTEGER;
  Mean,
  Std_Dev  : REAL;
  X       : Ary;

PROCEDURE Meanstd;

VAR
  Check,
  Sum_X, Sum_Sq : REAL;

BEGIN
  Sum_X := 0;
  Sum_Sq := 0;
  FOR i := 1 TO No DO
    BEGIN
      Sum_X := Sum_X + X[i];
      Sum_Sq := Sum_Sq + X[i] * X[i];
    END;
  Mean := Sum_X / No;
  Std_Dev := SQRT((Sum_Sq - SQR(Sum_X) / No) / (No - 1));
END; {Procedure MeanStd}

PROCEDURE BioMean;
```

```

VAR
  MBIOP,
  InDATA   : TEXT;
  count,
  j        : INTEGER;
  ALLAVG,
  LOW,
  HIGH,
  Biom     : REAL;
  CV,
  BSTD,
  DAY      : ARRAY[1..365] OF REAL;

BEGIN
  count := 1;
  time := 4;
  ASSIGN(InDATA, 'C:\EVA\ALLDAYS.OUT');
  WHILE count <= time DO
  BEGIN
    RESET(InDATA);
    IF count > 1 THEN
    BEGIN
      j := 1;
      WHILE j <= (count-1) DO
      BEGIN
        READLN(InDATA);
        j := j + 1;
      END;
    END;
    i := 1;
    WHILE i <= run DO
    BEGIN
      READLN(InDATA, Biom);
      X[i] := Biom;
      j := 1;
      WHILE j <= (time-1) DO
      BEGIN
        READLN(InDATA);
        j := j + 1;
      END;
    END;
    i := i + 1;
  END;
  No := run;
  Meanstd;
  DAY[count] := MEAN;
  BSTD[count] := STD_DEV;
  IF Mean > 0 THEN
  BEGIN
    CV[count] := Std_Dev/Mean;
  END ELSE
  BEGIN
    CV[count] := 0;
  END;
  WRITELN('MEAN ON DAY',count+1,' = ',MEAN,' ',STD_DEV);
  count := count + 1;
END;
CLOSE(InDATA);
ALLAVG := 0;

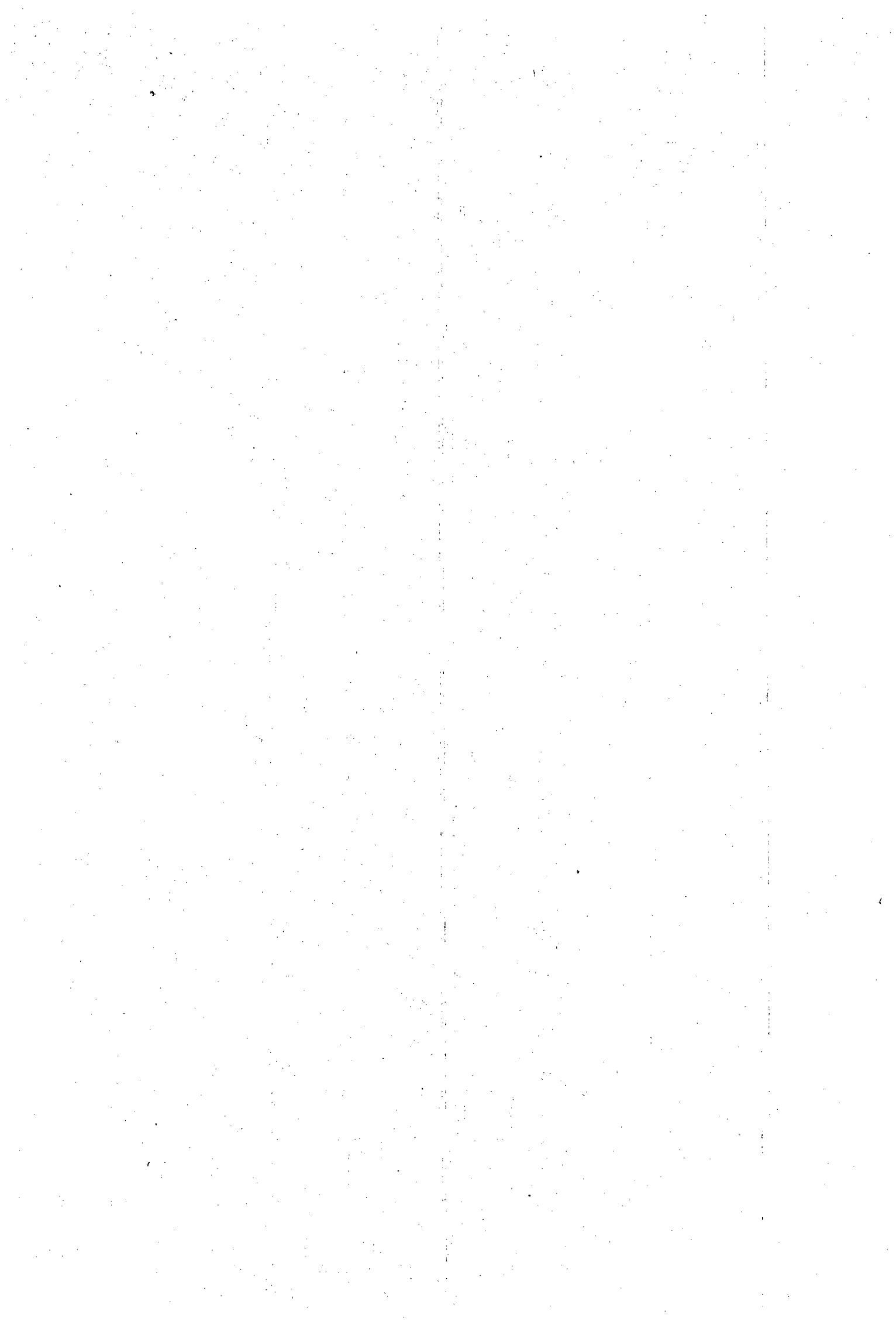
```

```

count := 1;
WHILE count <= TIME DO
BEGIN
    ALLAVG := ALLAVG + DAY[count];
    count := count + 1;
END;
WRITELN;
WRITELN('AVERAGE MORTALITY = ',ALLAVG/TIME);
ASSIGN(MBIOP, 'C:\EVA\DMORT.SEN');
REWRITE(MBIOP);
WRITELN(MBIOP, '*** MBIOP.SEN *** : MEAN OF ',run, ' RUNS');
WRITELN(MBIOP, ' MEAN - STD - CV - MEAN-STD - MEAN+STD ');
WRITELN(MBIOP);
count := 1;
WHILE count <= time DO
BEGIN
    LOW := DAY[count]-BSTD[count];
    HIGH := DAY[count]+BSTD[count];
    WRITELN(MBIOP, DAY[count]:1:2, ' ',BSTD[count]:1:2, ',CV[count]:3:2);
    count := count + 1;
END;
CLOSE(MBIOP);
END;

BEGIN {MAIN}
    CLRSCR;
    WRITELN(' INPUT NO.OF RUNS...');
    READLN(run);
    BIOMEAN;
    REPEAT
    UNTIL KEYPRESSED;
END.

```



APPENDIX III

DOCUMENTATION AND PARTIAL LISTING OF PROGRAM PATCHY.PAS

A PROGRAM TO SIMULATE THE EFFECT OF SPATIAL PATCHINESS IN CHLOROPHYLL *a* CONCENTRATION ON THE GROWTH OF THE COPEPOD *Calanoides carinatus*

A partial listing follows of the program used to generate the output presented in chapter four of this thesis. The program is basically an extension of the program PLANKTON.PAS (Appendix I): the major program extension involves adding a spatial dimension to simulate copepods feeding in a spatially heterogeneous environment. As most of the program is therefore similar to that presented in Appendix I, only the new and relevant sections are listed below.

Briefly, the model area is partitioned into 50x50 independent model cells, each containing a local copepod population. The grid reference of each cell is depicted using the row and column co-ordinates (r,c). At the start of each model run, the user is required to enter the total number of food patches *p*, which are distributed throughout the model area. The position of each of the *p* patches is generated randomly, along with an index describing the size (*Patchsize*) and intensity (*P_Intensity*) (relative to the base-case input value) of the patch. The latter two variables are either held constant in model runs, or generated randomly within a prespecified range. Because some patches have a spatial extent greater than one model cell, the total number of patch cells (*Patcells*) is greater than the total number of discrete patches *p* in the model area. Patches larger than one model cell in extent are modelled by randomly selecting *Patchsize* minus one surrounding cells.

The classification of each of the *r x c* model cells as patch or background cells is determined in the procedure **Patchiness**. The procedure **Patconcentration** is then called from within a loop which sequentially simulates the dynamics of each of the *r x c* local copepod populations, as a function of their daily spatial position relative to the various food patches. Chlorophyll *a* concentration is used as an index of food availability. For copepods situated in a patch, food availability *PCHL* is synonymous with intra-patch chlorophyll *a* concentration. For copepods which are assumed

to start each day's foraging episodes one model cell or further away from the nearest food patch, food availability *PCHL* is modelled using equation 4.1 (see chapter 4). Briefly, the chlorophyll *a* concentration used to drive the dynamics of a particular copepod aggregation is calculated each day as a function of the proximity to, and number, size and intensity of, surrounding "active" patches. For a particular copepod aggregation, "active" patches refer to all patches less than twice the distance of the closest patch, but no further than five model cells distant. The program uses the Pythagorean theorem to calculate the distance (in units of cells) between a cell [r,c] and the various patch cells. Predicted growth trends for each of the 2500 copepod aggregations are calculated separately, for each of days one to *fin*. The mean predicted copepodite biomass is then used as an estimate of zooplankton production in a heterogeneous environment. Results are compared with those obtained for a homogeneous analog of the system, which consists simply of a single model run based on daily chlorophyll *a* concentration inputs equal to the mean daily *PCHL* value integrated over all r x c model cells. Model output is read to external files, and synthesized using a program of the form listed in Appendix II.

PARTIAL LISTING OF PATCHY.PAS

Relevant global variables:

CONST

numcells = 2500;

VAR

start,fin, {Length of time series}
P, {No. of patches }
r,c, {Row & column grid reference }
count,
sim, {Simulation no. - runs from cell 1 to cell 2500 }
i,j,k : INTEGER;

rpat,cpat, {Grid refs. of patch centres}
P_intensity,
Patchsize,
Patcontribs : ARRAY[1..1000] OF INTEGER;
 {Grid refs of patch extensions}
rpatext,
cpatext : ARRAY[1..2000] OF INTEGER;

```

PROCEDURE Patchiness;

VAR
  ran          : INTEGER;

  cellindex,
  patcells    : REAL;

BEGIN
  RANDOMIZE;
  {Random selection of patch centres and patch sizes}
  FOR i := 1 TO P DO
  BEGIN
    rpat[i] := 1+RANDOM(50);
    cpat[i] := 1+RANDOM(50);
    Patchsize[i] := 1+RANDOM(4);
    P_intensity[j] := 1+RANDOM(4);
  END;
  {Loop to ensure that the same patches are not chosen twice}
  i := 1;
  WHILE i <= P DO
  BEGIN
    j := i + 1;
    WHILE j <= P DO
    BEGIN
      IF (rpat[i] = rpat[j]) AND (cpat[i] = cpat[j]) THEN
      BEGIN
        rpat[j] := 1+RANDOM(50);
        cpat[j] := 1+RANDOM(50);
        Patchsize[j] := 1+RANDOM(4);
        P_intensity[j] := 1+RANDOM(4);
        i := 0;
        j := P;
      END ELSE
      BEGIN
        j := j + 1;
      END;
    END;
    i := i + 1;
  END;
  FOR i := 1 TO P DO
  BEGIN
    WRITELN(i, ',rpat[i], ',cpat[i], ',Patchsize[i]);
    Pause;
  END;

  count := 1;   {counts no. of model cells comprising patches because }
                {of the spatial dimensions of a chosen patch centre}
  PATCELLS := 0; {total no. of patch model cells}
  FOR i := 1 TO P DO
  BEGIN
    { Ran describes the number of model cells covered by patch i }
    { The calculations below need to be modified to deal with patch }
    { sizes > 4 model cells }
    RAN := PATCHSIZE[i];

    { The total number of model cells classified as patch cells is PATCELLS}
    { However, some of these patch cells belong to the same patch ie. they }

```

```

{ are part of a large patch with a spatial dimension > 1 }
{ Values in the array PATCONTRIBS are used to mark the RAN-1 }
{ adjoining cells which are the spatial extension of patch i }
{ This is so that the model system essentially contains only p patches }
{ (albeit of different sizes) and not PATCELLS patches, and also to }
{ enable calculation of the shortest distance from a particular cell }
{ to a patch }
IF i = 1 THEN
BEGIN
  PATCONTRIBS[1] := 1;
END ELSE
BEGIN
  PATCONTRIBS[i] := count;
END;
PATCELLS := PATCELLS + RAN;
IF RAN > 1 THEN
BEGIN
  IF (RPAT[i] = 1) AND (CPAT[i] = 1) THEN
  BEGIN
    IF RAN < 4 THEN
    BEGIN
      CELLINDEX := 1 + RANDOM(3);
      IF CELLINDEX = 1 THEN
      BEGIN
        RPATEXT[count] := 1;
        CPATEXT[count] := 2;
      END ELSE
      BEGIN
        IF CELLINDEX = 2 THEN
        BEGIN
          RPATEXT[count] := 2;
          CPATEXT[count] := 2;
        END ELSE
        BEGIN
          RPATEXT[count] := 2;
          CPATEXT[count] := 1;
        END;
      END;
      count := count + 1;
    END;
    IF RAN = 3 THEN
    BEGIN
      IF CELLINDEX = 1 THEN
      BEGIN
        RPATEXT[count] := 2;
        CELLINDEX := 1 + RANDOM(2);
        IF CELLINDEX = 1 THEN
        BEGIN
          CPATEXT[count] := 1;
        END ELSE
        BEGIN
          CPATEXT[count] := 2;
        END;
      END ELSE
      BEGIN
        IF CELLINDEX = 2 THEN
        BEGIN
          CELLINDEX := 1 + RANDOM(2);

```



```

Pe      : INTEGER;      {No. of 'active' patches (closer than mindist)}

mindistance,
H      : REAL          {Used to calculate chl.concentration }
                        {coefficient which determines the chl.}
                        {conc. available to the popln. in   }
                        {block [r,c].                       }
ACHL   : ARRAY[1..100] of REAL; {Mean chl.a conc. for days 1 - 100 }
                        {= daily average integrated over all cells}

dist,      {Distance of block [r,c] to the various patch centres}
dist2     : ARRAY[1..3000] of REAL; {Used to calc. min. distance}

```

```

BEGIN
RANDOMIZE;
ASSIGN(Patch, 'C:\PATCH\Patconc.OUT');
IF sim = 1 THEN
BEGIN
REWRITE(Patch);
END ELSE
BEGIN
APPEND(Patch);
END;
ASSIGN(Avechl, 'C:\LOTUS\Ave.wk1');
REWRITE(Avechl);
mindistance := 50000;
pat := 0;
FOR i := 1 TO P DO
BEGIN
IF (r = rpat[i]) AND (c = cpat[i]) THEN
BEGIN
pat := 1;  {Identifies block [r,c] as a patch centre}
END;
END;
FOR i := 1 TO count DO
BEGIN
IF (r = rpatext[i]) AND (c = cpatext[i]) THEN
BEGIN
pat := 1;  {Identifies block [r,c] as part of a patch}
END;
END;
END;

FOR i := 1 TO P DO
BEGIN
IF pat = 0 THEN
BEGIN

{ Calculating the distance from cell [r,c] to each of the patch centres}

dist[i] := SQRT(((r-rpat[i])*(r-rpat[i]))+((c-cpat[i])*(c-cpat[i])));

{ Calculating the distance from cell [r,c] to all the cells comprising }
{ patch i, and then setting the distance from [r,c] to patch i as the }
{ shortest distance to the patch }
IF PATCHSIZE[i] > 1 THEN
BEGIN
count1 := PATCONTRIBS[i];
count2 := PATCONTRIBS[i] + PATCHSIZE[i] - 2;

```

```

FOR j := count1 TO count2 DO
BEGIN
  dist2[j] := SQRT(((r-rpatext[j])*(r-rpatext[j]))+((c-cpatext[j])*(c-
cpatext[j]))));
  IF dist2[j] < dist[i] THEN
  BEGIN
    dist[i] := dist2[j];
  END;
END;
END;

{Calculating the distance to the nearest patch ie. the overall}
{minimum distance from cell [r,c] to one of the p patches }
IF dist[j] < mindistance THEN
BEGIN
  mindistance := dist[i];
END;
END ELSE
BEGIN
  dist[i] := 0;    {the cell is part of a patch}
END;
END;

{Only patches closer than twice the distance of the closest patch to }
{block [r,c] are included as affecting block [r,c]      }

Pe := P;
FOR i := 1 TO P DO
BEGIN
  IF (dist[i] > (2 * mindistance)) OR (dist[i] >= 5) THEN
  BEGIN
    FOR j := i+1 TO P DO
    BEGIN
      dist[j-1] := dist[j];
      Patchsize[j-1] := Patchsize[j];
      P_intensity[j-1] := P_intensity[j];
    END;
    Pe := Pe - 1;
  END;
END;

j := start;
WHILE j <= fin DO
BEGIN
  H := 0;
  IF pat = 0 THEN    {Non-patch cells}
  BEGIN
    IF Pe = 0 THEN    {No 'active' patch cells in the vicinity - }
      {chl. a conc. < Fcrit and copepods starve }
    BEGIN
      PCHL[j] := 0.1;
    END ELSE
    BEGIN
      FOR i := 1 TO Pe DO
      BEGIN
        {Calculating chl. conc. as a function of the distance }
        {from all 'active' patch centres & the size of the }
        {various patch centres. See eqn 4.1      }

```

```

        H := H + EXP(Pe*LN((SQRT(Patchsize[i])*P_intensity[i])/dist[i]));
    END;
    PCHL[j] := EXP((1/Pe)*LN(H)) * CHL[j];
    PCHL[j] := ROUND(PCHL[j]*100)/100;

    { writeln(' pchl = ',i,' ',j,' ',PCHL[j]); }

    END;
END ELSE
BEGIN
    PCHL[j] := CHL[j];
END;
j := j + 1;
END;

j := start;
WHILE j <= fin DO
BEGIN
    IF sim = 1 THEN
    BEGIN
        ACHL[j] := PCHL[j];
    END ELSE
    BEGIN
        ACHL[j] := (ACHL[j]+PCHL[j]);
    END;
    j := j + 1;
END;
IF sim = numcells THEN
BEGIN
    j := start;
    WHILE j <= fin DO
    BEGIN
        ACHL[j] := ACHL[j] / numcells;
        WRITELN(Avechl, j:02, ', ', ACHL[j]:03:02);
        j := j + 1;
    END;
END;
WRITE(Patch, r:02, ' ', c:03);
j := start;
WHILE j <= fin DO
BEGIN
    WRITE(Patch, ' ', PCHL[j]:j+3);
    j := j + 1;
END;
WRITELN(Patch);
CLOSE(Patch);
CLOSE(Avechl);
END;

BEGIN {Main Program}

CLRSCR;
WRITELN('**SPATIAL PATCHINESS PROGRAM**');
WRITELN;
WRITE(' How many days data do you want to enter ? ');
WRITELN(' Please give starting and last day ...');
READLN(start,fin);

```

```

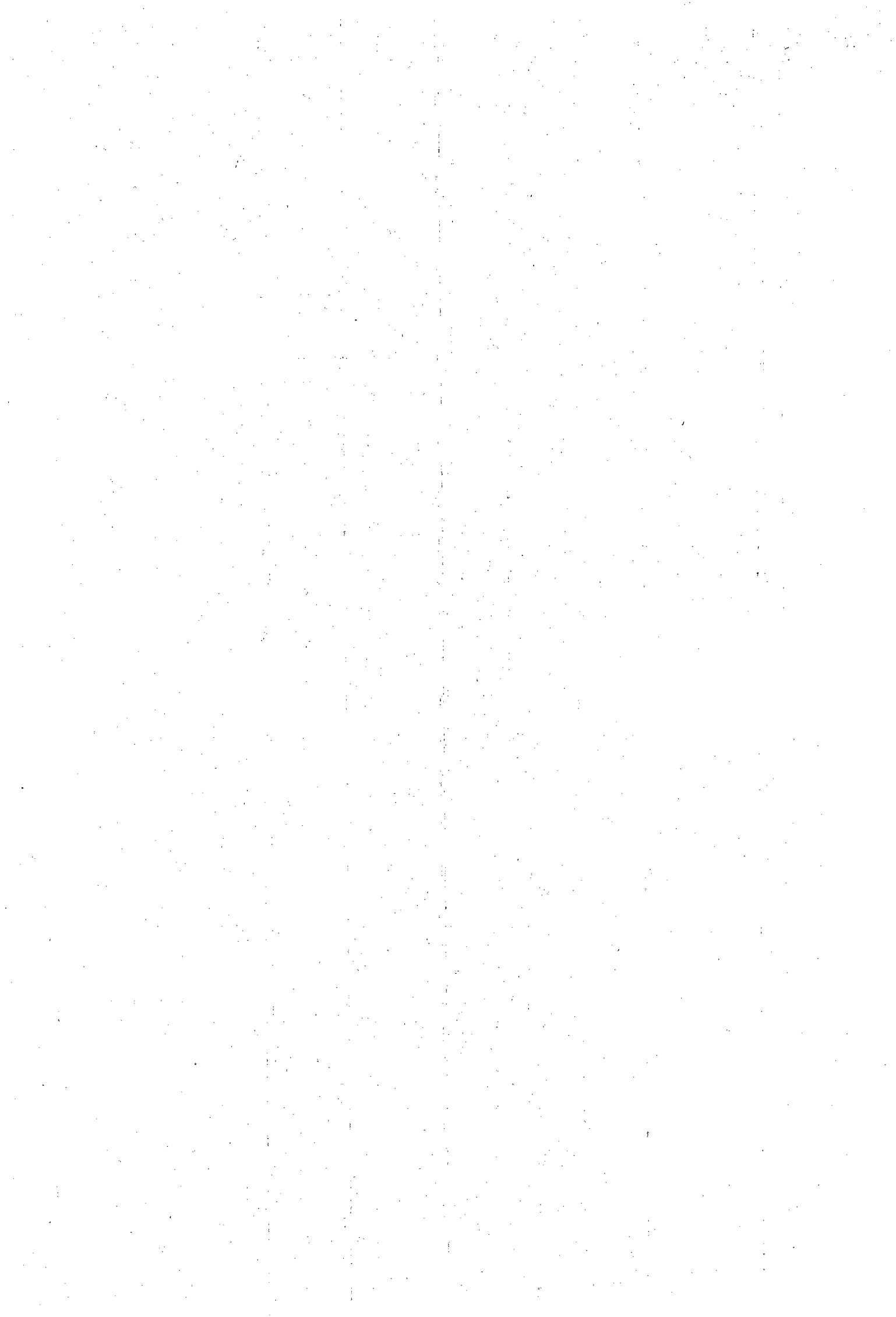
WRITELN;
WRITELN;
WRITE(' INPUT NO. OF PATCHES...');
READLN(P);
IF P > 1000 THEN
BEGIN
  WRITE(' For more than 1000 patches it is necessary to increase ');
  WRITELN(' the array size of the variables rpat, cpat & Patchsize');
  WRITE(' accordingly, under the global var. declaration section,');
  WRITELN(' and of dist in the PATCONCENTRATION procedure. ');
  P := 1000;
END;
WRITELN;
{Initialise with same starting biomass (Bint) for all quadrats}
{Other program versions may either randomise Bint or choose }
{ specific values for each block }
WRITELN(' Please input starting biomass (no./m3)');
READLN(BIOM);
{Initializing age structure}
AN := 0.305;
AC1 := 0.44;
AC2 := 0.13;
AA := 0.125;
sim := 1;
INPUTDATA;
PATCHINESS;

r := 1;
WHILE r <= 50 DO {Spatial area divided into 50x50 cells }
BEGIN { each referenced by row r and column c }
c := 1;
WHILE c <= 50 DO
BEGIN

PATCONCENTRATION;
FEEDHISTORY;
NETCHLOR;
FECUNDITY;
DEVELOPMENT;
STARVINGMORTALITY;
POPULATION;
PRODUCTION;

sim := sim + 1;
c := c + 1;
END;
r := r + 1;
END;
WRITELN;
GOTOXY(2,6);
WRITELN(' *** Program successful ! ***');
WRITELN;
REPEAT UNTIL KEYPRESSED;
END.

```



APPENDIX IV

DOCUMENTATION OF PROGRAM PREDATION.PAS

A PROGRAM TO SIMULATE JUVENILE ANCHOVY SHOALS FEEDING ON HETEROGENEOUSLY DISTRIBUTED AGGREGATIONS OF THE COPEPOD *Calanoides carinatus*

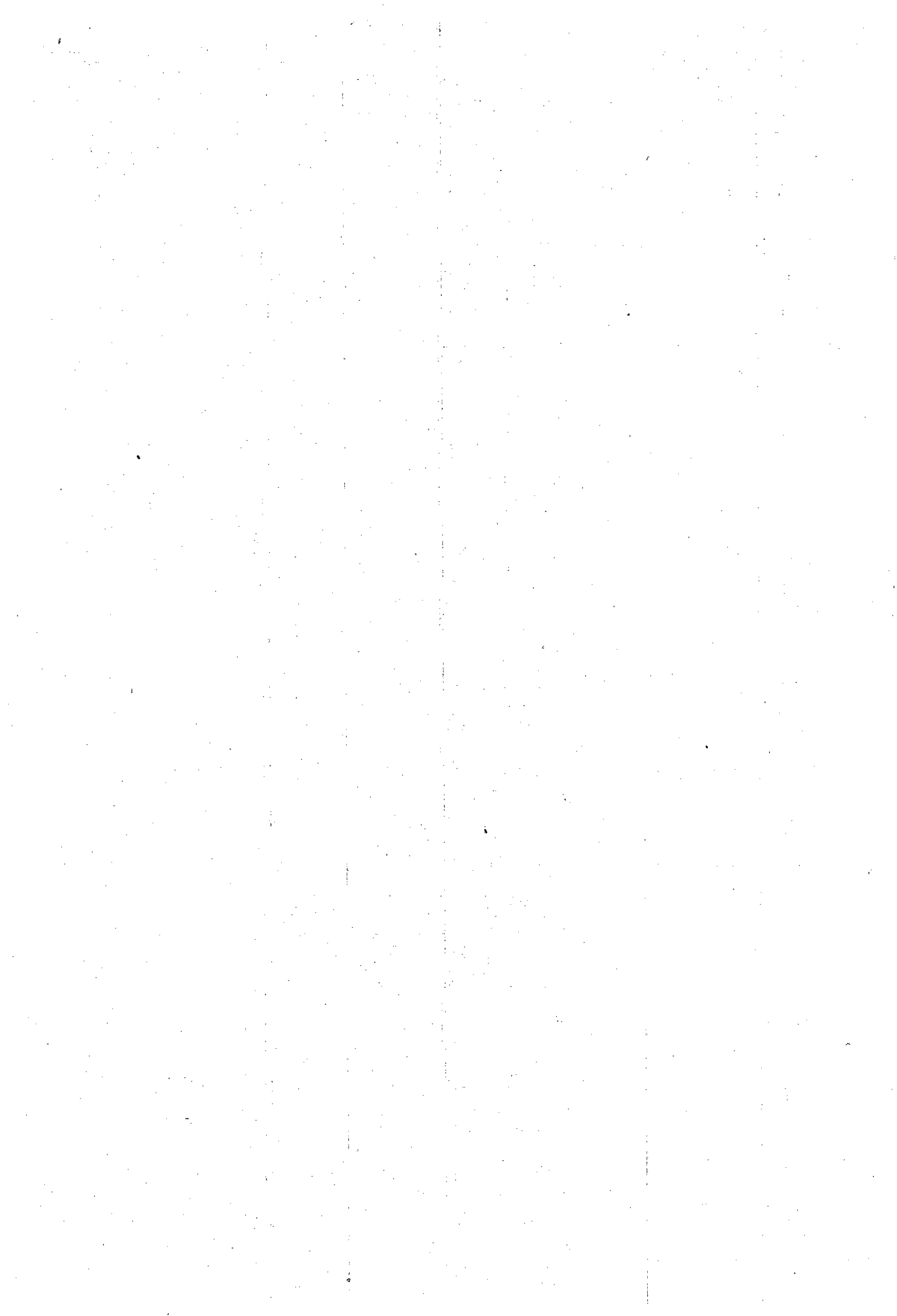
Aspects of this program are similar to that listed in Appendix I because the same methods are used to simulate the population dynamics of *C. carinatus*, except that predation on copepodite stages CIV to CVI (referred to as prey) is modelled explicitly. The model area is divided into $rmax \times cmax$ independent cells, each containing a local copepod population. The base-case model area measures 100 km² and comprises cells measuring 0.5 km x 0.5 km. Copepod population size in each cell is initialised using either a uniform initial abundance estimate *Biom* input by the user, or by randomly generating starting values within a range (*Biom1* - *Biom2*) prespecified by the user. The user is also required to input the length of the time series (days 1 to *fin*), and the month of the year (which determines the age of fish in the model). For each of runs 1 to *Numruns*, the program records changes in the size of local copepod populations 1 to $rmax \times cmax$, on each of days 1 to *fin*. During each model run, daily averages integrated over the whole model area are calculated and written to external files. The average of estimates calculated thus for each of runs 1 to *Numruns* (usually set at 100) is then calculated using a program of the form listed in Appendix II.

The number of discrete juvenile anchovy shoals entering the model area each day, along with the size (tons) of each shoal is either entered individually by the user, set as constants, or generated within prespecified random ranges. Each shoal *j* is assigned a random point of entry along the northern edge of the model area, and a randomly determined feeding path describes the route to be followed in search of food, and the furthest point that may be reached on day *i* by shoal *j*.

The growth of each local copepod aggregation is calculated in a similar fashion to that described in chapter two. A mean prey (CIV - CVI) background concentration level *background* (the moving threshold - see chapter five) is then calculated for each day *i* as the average of the no. prey.m⁻³ in all cells with a prey density less than the threshold feeding concentration *patconc*. The procedure **Predation** is then called to determine which model cells lie on the feeding paths (termed 'hit' cells) of each of the shoals present in the model area on day *i*. Prey concentrations in all 'hit' cells with a prey density > *patconc* are depleted to the *background* level.

The procedure **Fishes** collates information on total daily absolute and *per capita* rates of consumption by shoal *j* on day *i*, as well as each shoal's total time spent feeding and in search of food. Consumption values are used to calculate the average daily proportion of prey biomass removed by the fish.

The procedure **Energy** calculates a net energy budget for each shoal *j*, based on the shoal's cumulative daily energetic gains from particulate feeding, minus the energetic costs incurred from the feeding process itself, and whilst travelling between food patches. Net energetic values *Enet* are used to predict the daily growth in caudal length of individual fish.



LISTING OF PROGRAM PREDATION.PAS

PROGRAM Predation;

```
{ This model investigates the effect of variable predator-prey encounters }
{ on both the prey and the predator populations. }
{ The key variables controlling rates of growth, fecundity and }
{ development in the prey population, are temperature and food supply. }
{ The model simulates the population dynamics of the copepod }
{ Calanoides carinatus in each of a number of independent cells }
{ measuring 0.5 km x 0.5 km and assumed situated }
{ off the West Coast of South Africa }
{ Predators move from cell to cell in this model area along stochastically }
{ determined feeding trajectories and deplete the prey concentration in }
{ each cell encountered according to the manner described in the text. }

{ NB!! Throughout the model: }
{ PREY refers to the CIV - CVI stages of Calanoides carinatus }
{ PREDATOR/FISH refers to the anchovy Engraulis capensis }

{$M 65000, 0, 655360} {Extending stacksize allocated to program}
{$N+,E+} {Links with the full 8087 emulator to allow the use of eg.extended}
{ real variables. This format allows the .EXE file to be run on }
{ any machine since if an 8087 numeric coprocessor is present, the }
{ program will use it;otherwise, the run-time library emulates it. }
```

USES

CRT;

CONST

```
AN = 0.305; {Age distribution parameters to initialize }
AC1 = 0.27; { starting biomass in each age class }
AC2 = 0.17;
AC3 = 0.13;
AA = 0.125;
FCRIT = 3; {Threshold feeding concentration}
rmax = 20; {Maximum row & column co-ord }
cmax = 20;
DWrat = 7.143; {Dry to Wet Weight conversion ratio for copepods}
Stdshoal = 10; {Size (tons) of a standard shoal of fish to simplify calcs}
patconc = 6; { Prey density which defines a patch = threshold feeding concnetration}
Ttotal = 720; {Total available foraging time (mins)}
maxdist = 15; { Sets the max. distance travelled by an anchovy }
{ in one day. Real distance travelled will depend }
{ on the concentrations of food encountered along }
{ the way and the size of the shoal }
NumRuns = 100;
```

TYPE

```
pstarve = 1 .. 10;
pfeed = 1 .. 10;
StarveMatrix = ARRAY[pfeed,pstarve] OF REAL;
Ary = ARRAY[1..101] OF REAL;
```

VAR

```
M : StarveMatrix; {% offspring starving after }
{ various food cycles }
S,F, {Counters for starving & feeding - copepods}
```



```

REC,                {Recruits - egg hatch time=24hr}
Fu,                 {Unripe adult females}
Fr,                 {Ripe/egg-laying females}
MEGG,               {Egg mortality}
MNAUP,MCOP1,
MCOP2,MCOP3,MAD,   {Mortality est. for diff. stages}
Dev1,               {Dev. from naupliar - copepodite}
Dev2,               {  copepodite 1 - CIV   }
Dev3,               {      CIV - C5    }
Dev4,               {      C5 - adult   }
M50,
Starve      : ARRAY[1..100] OF REAL;

TotAve,TotFP,
AvNAUP,AvCOP1,
AvCOP2,AvCOP3,AvAD,
FPNAUP,FPCOP1,
FPCOP2,FPCOP3,FPAD : ARRAY[1..30] OF REAL;

NAUP,               {Naupliar stages}
COP1,               {Copepodite stages 1-3}
COP2,               {Copepodite stage 4}
COP3,               {Copepodite stage 5}
AD      : ARRAY[1..101] OF REAL; {Adult Calanoides}

Feed      : ARRAY[1..100] OF CHAR; {Intermittent/continuous feeding}

X      : Ary;

{SI MEANSTD.PAS}

PROCEDURE Inputdata;

VAR
  Indata,
  Intemp  : TEXT;   {Data input file}

BEGIN
  ASSIGN(Indata, 'C:\EVA\Ch12.INP');
  RESET(Indata);
  READLN(Indata);
  CLRSCR;
  {Reading in DAILY chlorophyll concentrations}
  i := start;
  WHILE i <= fin DO
  BEGIN
    READLN(Indata, CHL[i]);
    i := i + 1;
  END;
  CLOSE(Indata);
  ASSIGN(Intemp, 'C:\EVA\Temp.INP');
  RESET(Intemp);
  READLN(Intemp);
  {Reading in DAILY sea surface temperature}
  i := start;
  WHILE i <= fin DO
  BEGIN
    READLN(Intemp, TEMP[i]);
  
```

```

    i := i + 1;
END;
CLOSE(Intemp);
FOR i := 1 TO fin DO
BEGIN
    IF temp[i] > 15 THEN
        BEGIN
            chl[i] := 1.0;
            END;    {Shift to flagellate-dominated community}
        END;
END;

END; {inputdata}

PROCEDURE Pause;

BEGIN
    WRITELN('    Press any key ...');
    READLN;
END;

PROCEDURE Shoals;

VAR
    Mass,
    TMass,AMass,    {Total shoal biomass;ave. daily shoal biomass}
    Index      : REAL;  {Index of predator pulsing rate}
    RS1,RS2,
    ss,
    Choice      : INTEGER;
    Res2       : TEXT;
    Ent        : File OF INTEGER;
    SHbiom     : File OF REAL;
    ENTER      : ARRAY[1..200] OF INTEGER;
    {Total mass of fish (tons) entering area on day i}
    Dmass      : ARRAY[1..30] OF REAL;
BEGIN
    RANDOMIZE;
    k := 0;    {Counter for shoal no.}
    schools[start] := 0; {No point in modelling predation on copepods }
        { on the 1st day, as starting values may simply be}
        { considered net popn. values at the end of day 1}

    Dmass[start] := 0;
    ASSIGN(SHbiom, 'C:\EVA\SHOALsize.DAT');
    REWRITE(SHbiom);
    ASSIGN(Ent, 'C:\EVA\Enterday.DAT');
    REWRITE(Ent);
    IF NumRuns = 1 THEN
        BEGIN
            WRITELN(' Enter 1 to manually enter shoals or 2 for automatic ....');
            READLN(choice);
        END ELSE
        BEGIN
            choice := 2;
        END;
    i := start+1;
    WHILE i <= (fin) DO
        BEGIN
            IF choice = 1 THEN

```

```

BEGIN
  WRITELN(' How many shoals on day ',i,' ');
  READLN(schools[i]);
END ELSE
BEGIN
{The number of fish shoals passing through the model area each day }
{ can be set to any desired level, an example follows }
  schools[i] := 0;
  IF i = 2 THEN
  BEGIN
    schools[i] := 8;
  END;
  IF i = 3 THEN
  BEGIN
    schools[i] := 8;
  END;
  IF i = 8 THEN
  BEGIN
    schools[i] := 8;
  END;
  IF i = 9 THEN
  BEGIN
    schools[i] := 8;
  END;
END;
IF schools[i] > 0 THEN
BEGIN
  Mass := 0;
  FOR j := 1 TO schools[i] DO
  BEGIN
    k := k + 1;    {k = total no. of shoals}
    WRITELN('K = ',K);
    IF Choice = 1 THEN
    BEGIN
      WRITELN(' Size of shoal (tons) ',j,' ');
      READLN(SHOAL[k]);
    END ELSE
    BEGIN
      SHOAL[k] := 2500 / SCHOOLS[i];
    END;
    ENTER[k] := i;
    Mass := Mass + SHOAL[k];
  END;
  Dmass[i] := Mass;
END ELSE
BEGIN
  Dmass[i] := 0;
END;
i := i + 1;
END;
CLRSCR;
WRITELN(' Doing simulations - Please wait ..... !!!');
WRITELN;
Totalshoals := k;
ASSIGN(Res2, 'C:\EVA\Result2.OUT');
REWRITE(Res2);
WRITELN(Res2, '*** Result2.OUT ***');
WRITELN(Res2);

```

```

WRITELN(Res2);
WRITELN(Res2, ' SHOAL NO. - RELATIVE SIZE - DAY ENTERS');
WRITELN(Res2);
CLRSCR;

FOR j := 1 TO k DO
BEGIN
    SHOAL[j] := SHOAL[j]/stdshoal;
    WRITELN('J,K,SHOAL ',j,' ',K,' ',SHOAL[j]);
    WRITE(SHbiom, SHOAL[j]);
    WRITELN(Res2, 'j:02,' ',SHOAL[j]:03:02,' ',ENTER[j]);
    WRITE(Ent, ENTER[j]);
END;
TMass := 0;
FOR i := 2 TO fin DO
BEGIN
    TMass := TMass + DMass[i];
END;
AMass := TMass / (fin-1);
FOR i := 2 TO fin DO
BEGIN
    Index := ABS(DMass[i] - AMass);
END;
Index := Index / (fin-1);
WRITELN(Res2);
WRITELN(Res2);
WRITELN(Res2, ' Total tonnage of fish entering model area on day i..');
WRITELN(Res2);
WRITELN(Res2, ' DAY - TOTAL MASS (tons) - NO. OF FISH SCHOOLS');
WRITELN(Res2);
FOR i := 1 TO fin DO
BEGIN
    WRITELN(Res2, 'i:02,' ',Dmass[i]:06,' ',Schools[i]);
END;
WRITELN(Res2);
WRITELN(Res2);
WRITELN(Res2, 'Total fish mass - Ave. daily mass - Pulsing Index');
WRITELN(Res2);
WRITELN(Res2, TMass:05:0,' ',AMass:05:0,' ',Index:05:02);
WRITELN(Res2);
WRITELN(Res2);
WRITELN(Res2);
WRITELN(Res2);
CLOSE(Res2);
CLOSE(SHbiom);
CLOSE(Ent);
{Will now assign a random starting point to each shoal - all shoals }
{enter the block along the northerly edge and move southwards, hence }
{only the column co-ord needs to be determined (ie. starting row =1) }
RANDOMIZE;
FOR i := 1 TO k DO
BEGIN
    cpat[i] := RANDOM(20) + 1; {Random no. from 1 to 20 - changed }
    {as required for more than 20 cols. etc.}
    rpat[i] := 1;
END;
END;

```

```

PROCEDURE RANDGAUSS;

BEGIN
  RANDOMIZE;
  IF Randg = 0 THEN
  BEGIN
    Randg := RANDOM(5) + 1;
  END ELSE
  BEGIN
    IF (Randg = 1) OR (Randg = 5) THEN
    BEGIN
      IF Randg = 1 THEN
      BEGIN
        Randg := RANDOM(4) + 1;
      END ELSE
      BEGIN
        Randg := RANDOM(4) + 2;
      END;
    END ELSE
    BEGIN
      Randg := RANDOM(5) + 1;
    END;
  END;
  IF cpat[j] = cmax THEN
  BEGIN
    Randg := RANDOM(2) + 2;
  END;
  IF cpat[j] = 1 THEN
  BEGIN
    Randg := RANDOM(2) + 3;
  END;
  IF (Randg = 1) OR (Randg = 5) THEN
  BEGIN
    Rowmove := 0;
  END ELSE
  BEGIN
    Rowmove := 1;
  END;
  IF (Randg = 1) OR (Randg = 2) THEN
  BEGIN
    Colmove := -1;
  END;
  IF (Randg = 4) OR (Randg = 5) THEN
  BEGIN
    Colmove := 1;
  END;
  IF Randg = 3 THEN
  BEGIN
    Colmove := 0;
  END;
END; {FN Randg}

```

```

PROCEDURE Trajectories;

```

```

VAR
  Turns,
  Hits : TEXT;
  Distance : REAL;

```

```

h,
row      : INTEGER;
BEGIN
i := day;
{Loop 1 - executed only at the start of each day, to define the }
{ feeding trajectories for each fish shoal ...                }
IF Traj = 1 THEN
BEGIN
IF schools[i] > 0 THEN      {Loop only executed if new shoals enter}
BEGIN
IF firstsch = 0 THEN
BEGIN
firstsch := i;  {Day on which first fish schools enter area}
END;
v := u + schools[i];  {v is the total no. of shoals that have }
                    { entered the model area up to day i   }
                    {u is the no. of shoals up to day i-1, }
                    { some of which have left already     }
                    {k (elsewhere) is total no. up to day fin}
WRITELN('FIRST V =',V);
END;
IF i > firstsch THEN
BEGIN
FOR j := 1 TO u DO      { Old shoals }
BEGIN
IF rpat[j] >= 10 THEN {Fish leave model area- change for r>10}
BEGIN
IF SHOAL[j] > 0 THEN
BEGIN
WRITELN(' Shoal no. ',j,' exits model area on day ',day-1);
LEAVE[j] := day-1;
END;
SHOAL[j] := 0;
END;
END;
END;
END; {of loop checking old shoals exist on day i}
ASSIGN(Turns, 'C:\EVA\Angle.OUT');
IF a = 0 THEN
BEGIN
REWRITE(Turns);
WRITELN(Turns, 'DAY - SHOAL - U - V');
WRITELN(Turns);
a := 1
END ELSE
BEGIN
APPEND(Turns);
END;
FOR j := 1 TO v DO
BEGIN
WRITELN(Turns, i, 'j, ',u, ',v);
END;
WRITELN(Turns);
CLOSE(Turns);
u := v;  {u is max no. of fish schools in area on day i }
        {schools which have already left have shoal size = 0}

Traj := 2;
{Returns to procedure PREDATION}

```

```

END ELSE
BEGIN
{Loop 2 - (Traj = 2), executed each day, for each fish shoal in the area,}
{ to determine which cells lie on a feeding trajectory ... }
  j := shoalnumber;
  hit := 0;    {counts the no. of hits by shoal j}
  {Shoals entering the model area on day i label one of the cells in the }
  { first row as a target, whereas old shoals have rpat[j] = the last }
  { cell reached on the previous day's foraging efforts, and hence cells }
  { labelled as targets on day i should not include this last cell }
  { reached on day i-1 }
  IF rpat[j] = 1 THEN
  BEGIN
    row := rpat[j];
  END ELSE
  BEGIN
    row := rpat[j] + 1;
  END;
  Randg := 0;
  distance := 0.707;
  WHILE distance <= maxdist DO
  BEGIN
    hit := hit + 1;
    Randgauss;
    cpat[j] := cpat[j] + colmove;
    rpat[j] := rpat[j] + rowmove;
    row := rpat[j];
    IF row = 1 THEN
    BEGIN
      Target[hit] := cpat[j];
    END ELSE
    BEGIN
      Target[hit] := row*20 + cpat[j] - 20;
    END;
    distance := distance + 0.707;
    IF row = rmax THEN
    BEGIN
      distance := maxdist;
    END;
  END;
  ASSIGN(Hits, 'C:\EVA\Cellhit.OUT');
  IF (i = firstsch) AND (j = 1) THEN
  BEGIN
    REWRITE(Hits);
    WRITELN(Hits, 'DAY - SHOAL - HIT - CELL NO. ');
    WRITELN(Hits);
  END ELSE
  BEGIN
    APPEND(Hits);
  END;
  FOR h := 1 TO hit DO
  BEGIN
    WRITELN(Hits, i, 'j, ', h, ', ', Target[h]);
  END;
  WRITELN(Hits);
  CLOSE(Hits);
  END; {of loop 2, returns to PREDATION to assess effect of fish shoal j}
END; {of Trajectories}

```

```

PROCEDURE Fishes(var Totaleaten, Feedtime, M1, M2, M3 : REAL);
TYPE
  {Variables need to be integers or structure too large for memory}
  days = 1..30;
  shoalnos = 1..200;
  FishMatrix = ARRAY[days,shoalnos] OF INTEGER;
VAR
  VISITS,
  FTIME,
  CONSUMP      : FishMatrix;
  Alldays,
  MSim,
  Res,
  OutV, OutC, OutF : TEXT;
  Prey,
  Ent          : File OF INTEGER;
  SHbiom       : File OF REAL;

  Enters,      {day each shoal entered model area}
  INdays,
  sh,dy,sh2,sh3, {counters}
  mats,        {no. of matrices to be printed}
  Beforepred,
  Totalconsump : INTEGER;
  AM1,AM2,AM3,
  Aconsump,
  STconsump,
  Predmort,    {Average daily prey mortality rate due to predators}
  Avemort,    {Average prey mortality rate for entire time period}
  test        : REAL; {counters for printouts}
  Gross       : LONGINT;
  SCONSUMP    : ARRAY[1..200] OF INTEGER;
  DCONSUMP    : ARRAY[1..30] OF INTEGER;
  APREY       : ARRAY[1..30] OF REAL;
BEGIN
  i := day;
  j := shoalnumber;
  VISITS[i,j] := Finds;
  CONSUMP[i,j] := ROUND(Totaleaten);
  IF Feedtime >= 1 THEN
  BEGIN
    FTIME[i,j] := ROUND(Feedtime);
  END ELSE
  BEGIN
    FTIME[i,j] := 0;
  END;
  {Shoals not yet in the area have all the above parameters = 0 on day i :}
  FOR sh := j+1 TO Totalshoals DO
  BEGIN
    VISITS[i,sh] := 0;
    CONSUMP[i,sh] := 0;
    FTIME[i,sh] := 0;
  END;
  IF j = 1 THEN {Loop only executed at the start of each day}
  BEGIN
    ASSIGN(Prey, 'C:\EVA\Preyconc.DAT');
    RESET(Prey);
  
```

```

{Calculates total no. of CV & ADULTS present on day i, BEFORE predation}
Gross := 0;
FOR l := 1 TO 400 DO
BEGIN
  READ(Prey, Beforepred);
  Gross := Gross + ROUND(Beforepred);
END;
{Calculating average no. of prey per m3 per day, BEFORE predation}
APREY[i] := Gross/(rmax*cmax);
CLOSE(Prey);
END;
IF (M1 > 0) OR (M2 > 0) THEN {Loop only executed when shoalno. = last }
BEGIN { shoal for day i, ie. j = v }
  ASSIGN(Res, 'C:\EVA\Results.OUT');
  IF i = firstsch THEN
  BEGIN
    REWRITE(Res);
    WRITELN(Res);
    WRITELN(Res, 'DAY - CV MORTALITY RATE - ADULT MORTALITY RATE ');
    WRITELN(Res);
    AM1 := 0;
    AM2 := 0;
  END ELSE
  BEGIN
    APPEND(Res);
  END;
  {Printing the average daily rate of mortality of CIV,CV & ADULT }
  { copepods due to predation by fish = M1, M2 & M3 respectively }
  WRITELN(Res, i:2, ' ',M1:1:3, ' ',M2:1:3, ' ',M3:1:3);
  AM1 := AM1 + M1;
  AM2 := AM2 + M2;
  AM3 := AM3 + M3;
  IF i = fin THEN
  BEGIN
    {Calc. an AVERAGE PRED MORT for all days for CIV (AM1) }
    { CV (AM2) & ADULT (AM3)}
    AM1 := AM1 / (fin-1);
    AM2 := AM2 / (fin-1);
    AM3 := AM3 / (fin-1);
    WRITELN(Res);
    WRITELN(Res);
    WRITE(Res, 'Average PRED MORT RATE for CIV for ',fin-1);
    WRITELN(Res, ' days = ',AM1:1:3);
    WRITELN(Res);
    WRITELN(Res);
    WRITE(Res, 'Average PRED MORT RATE for CV for ',fin-1);
    WRITELN(Res, ' days = ',AM2:1:3);
    WRITELN(Res);
    WRITE(Res, 'Average PRED MORT RATE for ADULTS for ',fin-1);
    WRITELN(Res, ' days = ',AM3:1:3);
    WRITELN(Res);
    WRITELN(Res);
    WRITELN(Res);
  END;
  CLOSE(Res);
END;
IF (i = fin) AND (j = u) THEN {Last shoal, last day}
BEGIN

```

```

CLRSCR;
WRITELN(' Printing Results to files ....');
WRITELN;
{For shoals still in area on the final day, the no. of days }
{ over which performance is estimated is simply (fin-entry day) }
FOR sh := 1 TO u DO
BEGIN
  IF SHOAL[sh] > 0 THEN
  BEGIN
    LEAVE[sh] := fin;
  END;
END;
ASSIGN(SHbiom, 'C:\EVA\SHOALsize.DAT');
RESET(SHbiom);
{Shoal sizes read from initial file as these values were changed }
{ to zero whenever a shoal left the area. }
sh := 1;
WHILE sh <= u DO
BEGIN
  READ(SHbiom, SHOAL[sh]);
  sh := sh + 1;
END;
CLOSE(SHbiom);
ASSIGN(Res, 'C:\EVA\Results.OUT');
APPEND(Res);
{On day 1 (when all values = 0 for fish), these values instead set}
{as the shoal no. for printing purposes}
FOR sh := 1 TO u DO
BEGIN
  VISITS[1,sh] := sh;
  CONSUMP[1,sh] := sh;
  FTIME[1,sh] := sh;
END;
{Calculating total consumption of each shoal over entire time period}
FOR sh := 1 TO u DO
BEGIN
  SCONSUMP[sh] := 0;
  FOR dy := 2 TO fin DO
  BEGIN
    SCONSUMP[sh] := SCONSUMP[sh] + CONSUMP[dy,sh];
  END;
END;
ASSIGN(Ent, 'C:\EVA\Enterday.DAT');
RESET(Ent);
WRITELN(Res);
WRITE(Res, 'SHOAL - SIZE - DAYS - TOT.CONSUMP -');
WRITELN(Res, ' AVE. CONSUMP - STANDARD CONSUMP. ');
WRITELN(Res);
WRITELN(Res, ' Consumption values are no.prey x 375 x 10^4. ');
WRITELN(Res);
FOR sh := 1 TO u DO
BEGIN
  {Calculating total no. of days spent in model area by each shoal}
  READ(Ent, Enters);
  INdays := (LEAVE[sh] - Enters) + 1;
  {Calc. average daily consumption by each shoal while in the area}
  Aconsump := SCONSUMP[sh] / INdays;
  {Calc. standardized consumption=ave. daily consump. per ton of fish}

```

```

STconsump := Aconsump / (Stdshoal * SHOAL[sh]);
WRITE(Res, sh:3, ' ', SHOAL[sh]:3:2, ' ', INdays:2, ' ');
WRITELN(Res, SCONSUMP[sh]:5, ' ', Aconsump:5, ' ', STconsump:4);
END;
CLOSE(Ent);
WRITELN(Res);
WRITELN(Res);
WRITELN(Res);
{Calculating total consumption by ALL shoals for each day }
FOR dy := 2 TO fin DO
BEGIN
DCONSUMP[dy] := 0;
FOR sh := 1 TO u DO
BEGIN
DCONSUMP[dy] := DCONSUMP[dy] + CONSUMP[dy,sh];
END;
END;
{Calculating total consumption by all shoals over all days}
Totalconsump := 0;
FOR dy := 2 TO fin DO
BEGIN
Totalconsump := Totalconsump + DCONSUMP[dy];
END;
{Need above / total biomass / total feeding days = ave performance}
WRITELN(Res);
WRITE(Res, 'DAY - PREY PRESENT(P) - DAILY CONSUMPTION(D) ');
WRITELN(Res, ' - PRED MORTALITY RATE (D/P)');
WRITELN(Res);
{Calculating the average rate of mortality of PREY copepods due }
{ to predation by fish = PRED MORT }
{ PRED MORT (day i) = AVERAGE CONSUMPTION PER m3 (day i) / }
{ AVERAGE NO. PREY PER m3 PRESENT BEFORE PREDATION (day i) }
ASSIGN(Alldays, 'C:\EVA\ALLDAYS.OUT');
IF runs = 1 THEN
BEGIN
REWRITE(Alldays);
END ELSE
BEGIN
APPEND(Alldays);
END;
Avemort := 0;
FOR dy := 2 TO fin DO
BEGIN
DCONSUMP[dy] := ROUND(DCONSUMP[dy] / (rmax*cmax));
Predmort := DCONSUMP[dy] / APREY[dy];
WRITE(Res, dy:2, ' ', APREY[dy]:4:0, ' ');
WRITELN(Res, DCONSUMP[dy]:4, ' ', Predmort:1:3);
WRITELN(Alldays, Predmort:1:3);
Avemort := Avemort + Predmort;
END;
CLOSE(Alldays);
{Calculating an AVERAGE PRED MORT for all days }
Avemort := Avemort / (fin-1);
WRITELN(Res);
WRITELN(Res);
WRITELN(Res, 'Average PRED MORT for ', fin-1, ' days = ', Avemort:1:3);
WRITELN(Res);
WRITELN(Res);

```

```

CLOSE(Res);
ASSIGN(MSIM, 'C:\EVA\MSIM.OUT');
IF runs = 1 THEN
BEGIN
    REWRITE(MSIM);
END ELSE
BEGIN
    APPEND(MSIM);
END;
WRITELN(MSIM, Avemort:1:3);
CLOSE(MSIM);
{Printing out values for VISITS, CONSUMP & FTIME}
{Calculating the no. of matrices required to print above values}
test := u/14;
IF test < 1 THEN
BEGIN
    mats := 1;
END ELSE
BEGIN
    test := u MOD 14;
    IF test = 0 THEN
    BEGIN
        mats := TRUNC(u/14);
    END ELSE
    BEGIN
        mats := TRUNC(u/14) + 1;
    END;
END;
ASSIGN(OutV, 'C:\EVA\Visit.OUT');
REWRITE(OutV);
WRITELN(OutV);
WRITELN(OutV, ' No. of cells encountered by a shoal on day i ');
WRITELN(OutV);
WRITELN(OutV, ' ROW = day  ; COL = shoal no. ');
WRITELN(OutV);
ASSIGN(OutC, 'C:\EVA\Consump.OUT');
REWRITE(OutC);
WRITELN(OutC);
WRITELN(OutC, ' No. of prey per m2 eaten by a shoal on day i ');
WRITELN(OutC);
WRITELN(OutC, ' ROW = day  ; COL = shoal no. ');
WRITELN(OutC);
ASSIGN(OutF, 'C:\EVA\Times.OUT');
REWRITE(OutF);
WRITELN(OutF);
WRITELN(OutF, ' Total time spent feeding on day i by shoal j ');
WRITELN(OutF);
WRITELN(OutF, ' ROW = day  ; COL = shoal no. ');
WRITELN(OutF);
sh2 := 0;
sh3 := 0;
FOR k := 1 TO mats DO
BEGIN
    IF mats = 1 THEN
    BEGIN
        sh2 := u;
    END ELSE
    BEGIN

```

```

l := TRUNC(u/14)*14;
IF test = 0 THEN
BEGIN
    l := l - 14;
END;
IF sh2 = l THEN
BEGIN
    sh2 := u;
END ELSE
BEGIN
    sh2 := sh2 + 14;
END;
END;
sh3 := sh3 + 1;
FOR dy := 1 TO fin DO
BEGIN
    IF dy = 1 THEN
    BEGIN
        WRITE(OutV, ' ');
        WRITE(OutC, ' ');
        WRITE(OutF, ' ');
    END ELSE
    BEGIN
        WRITE(OutV, dy:2, ' ');
        WRITE(OutC, dy:2, ' ');
        WRITE(OutF, dy:2, ' ');
    END;
    FOR sh := sh3 TO sh2 DO
    BEGIN
        WRITE(OutV, VISITS[dy,sh]:2, ' ');
        WRITE(OutC, CONSUMP[dy,sh]:4, ' ');
        WRITE(OutF, FTIME[dy,sh]:3, ' ');
    END;
    WRITELN(OutV);
    WRITELN(OutC);
    WRITELN(OutF);
    IF dy = 1 THEN
    BEGIN
        WRITELN(OutV);
        WRITELN(OutC);
        WRITELN(OutF);
    END;
END;
END;
CLOSE(OutC);
CLOSE(OutF);
ASSIGN(Ent, 'C:\EVA\Enterday.DAT');
RESET(Ent);
WRITELN(OutV);
WRITELN(OutV);
WRITELN(OutV);
WRITELN(OutV, 'SHOAL - DAY ENTERS - DAY LEAVES');
WRITELN(OutV);
FOR sh := 1 TO u DO
BEGIN
    READ(Ent, Enters);
    WRITELN(OutV, sh, 'Enters, ', LEAVE[sh]);
END;

```

```

        CLOSE(Ent);
        CLOSE(OutV);
    END;
END; {of Fishes}

PROCEDURE Energy(var Bcheck, Feedtime : REAL);

VAR
    EN1,EN2,EN3,
    BW1,BW2,BW3,
    ESim,
    Res2,
    Res3      : TEXT;
    Growth,
    AEnergy   : REAL;
BEGIN
    i := day;
    j := shoalnumber;
    ASSIGN(Res2, 'C:\EVA\Result2.OUT');
    APPEND(Res2);
    IF (i = firstsch) AND (j = 1) THEN
        BEGIN
            shoaldays := 0;
            TEnergy := 0;
            Maint := 0;
            AveBW := 0;
            AveSUP := 0;
            WRITELN(Res2);
            WRITELN(Res2);
            WRITELN(Res2, ' From PROCEDURE ENERGY....');
            WRITELN(Res2);
            WRITE(Res2, ' (i) Calculating consumption (kg.wet wt/day) as a');
            WRITELN(Res2, ' % body weight (kg.wet wt) ');
            WRITELN(Res2);
            WRITE(Res2, ' (ii) Calculating Rate of Supply = % Body wt. ');
            WRITELN(Res2, ' gained per hour whilst feeding. ');
            WRITELN(Res2, ' for each shoal ');
            WRITELN(Res2);
            WRITELN(Res2, ' DAY - SHOAL - %BW - SUPPLY RATE ');
            WRITELN(Res2);
        END;
    IF j = 1 THEN
        BEGIN
            WRITELN(Res2);
        END;
    {Rem : Bcheck is total biomass consumed (in kg.wet mass), }
    {  Feedtime is total time spent feeding (mins),      }
    { & Finds is total no. of cells encountered,        }
    { All above are on day i, by shoal j }
    IF Bcheck > 0 THEN {Only for shoals still in area}
        BEGIN
            {Calculating consumption (kg.wet wt/day) as a % body weight (kg.wet wt)}
            BWPER := (Bcheck / (SHOAL[j] * Stdshoal * 1000)) * 100;
            {Calc. Rate of Supply = % Body wt. per hour on day i, for shoal j }
            SUPPLY := BWPER * (Feedtime / 60);
            WRITELN(Res2, i:02, ' j:02, ' ,BWPER:03:02, ' ,SUPPLY:03:02);
            {Calc. Average values over the entire model time period}
            AveBW := AveBW + BWPER;
        END;
    END;
END;

```

```

    AveSUP := AveSUP + SUPPLY;
    shoaldays := shoaldays + 1;
END;
CLOSE(Res2);
{Output files are changed depending on how average body wt. estimates }
{are to be calculated }
IF i = 2 THEN
BEGIN
    ASSIGN(BW1, 'C:\EVA\BW1.SEN');
    IF runs = 1 THEN
    BEGIN
        REWRITE(BW1);
    END ELSE
    BEGIN
        APPEND(BW1);
    END;
    WRITELN(BW1, BWPER:03:02);
    CLOSE(BW1);
END;
IF i = 3 THEN
BEGIN
    ASSIGN(BW2, 'C:\EVA\BW2.SEN');
    IF runs = 1 THEN
    BEGIN
        REWRITE(BW2);
    END ELSE
    BEGIN
        APPEND(BW2);
    END;
    WRITELN(BW2, BWPER:03:02);
    CLOSE(BW2);
END;
IF (i = 8) OR (i = 9) THEN
BEGIN
    ASSIGN(BW3, 'C:\EVA\BW3.SEN');
    IF runs = 1 THEN
    BEGIN
        REWRITE(BW3);
    END ELSE
    BEGIN
        APPEND(BW3);
    END;
    WRITELN(BW3, BWPER:03:02);
    CLOSE(BW3);
END;
IF i = firstsch THEN
BEGIN
{Calculating average age (years) & caudal length (mm) of anchovy }
{ in the month selected }
{ From refs, average birthdate set at October (can be changed!) }
    Age := (month+2) / 12;      {Estimating length at age from Von Bertalanffy curve}
                                { in Waldron et al.1989}
{ CLength := 148 * (1 - EXP((-1.367 * (Age + 0.032))))); }
{ CLength := CLength / 10;   {Convert to cm }           }
{ In base-case simulations length set at 8.42 cm (Fweight = 3.46g }
    CLength := 8.42;
    FWeight := 0.0034 * EXP(3.25*LN(CLength));
{ Calculating Average Swim speed (in cm) = 1.695 BL/s & }

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```

{Average swim speed during particulate feeding = 2.412 BL/s (J & F 1989) }
Vswim := 1.695 * CLength;
Vfeed := 2.412 * CLength;
{ Calculating energy expenditure whilst feeding and swimming: }
{ Values used (from James 1989) are Active: 0.282mgO2/g.wet.wt/hr & }
{ Particulate feeding: 0.414 mgO2/g.wet.wt/hr }
{ These values converted to J/Fweight/hr using 1mgO2=3.42cal & 1cal=4.184J}
Mswim := 4.03 * FWeight;
Mfeed := 5.92 * FWeight;
END; {of calculations for first day}
If Finds > 0 THEN
BEGIN
{ Calculating Total travelling time (hours) for shoal j on day i }
{ This excludes all time spent resting, filter feeding etc. as the }
{ simplified energy budget presented here assumes that net energy = 0 }
{ from all these processes & considers only gains from particulate feeding}
Mindist := Finds * 0.707;
Travel := Finds * 49;
TimeFeed := (Feedtime - Travel) / 60; {Convert to hrs}
Travel := Travel / 60;
{ Calculating energy expenditure (in Joules) }
ENERs := Travel * Mswim;
ENERf := TimeFeed * Mfeed;
{ Calculating energy gain using energy value for copepod prey = }
{ 2.87 * 10^6 J/kg wet mass }
{ Assuming an assimilation efficiency of 71.35%, (after James 1989), }
{ this is 2.048*10^3 kJ/kg }
{ Total energetic gain is divided by no. of fish }
FWeight := Stdshoal/FWeight;
Egain := (Bcheck * 2.048) / FWeight;
{ WRITELN(i, 'j, ENERGY GAIN = ',Egain); }
{ Pause; }
{ Calc. net energetic gain from particulate feeding process }
Enet := Egain - (ENERs + ENERf);
{ Calc. % of the time shoals are above their maintenance ration }
IF Enet >= 0 THEN
BEGIN
Maint := Maint + 1;
END;
{ Calc. predicted growth in caudal length, after Nonacs et al. 1994}
{Eqn. is for a base-case recruit with initial length 8.42 }
Growth := EXP((1/3.195)*LN((23276+Enet)/25.736)) - 8.42;
ASSIGN(Res3, 'C:\EVA\Energy.OUT');
IF (i = firstsch) AND (j = 1) THEN
BEGIN
REWRITE(Res3);
WRITELN(Res3, ' *** ENERGY.OUT *** ');
WRITELN(Res3);
WRITELN(Res3, ' Estimated age of average anchovy = ',age,' mo');
WRITELN(Res3);
WRITELN(Res3, ' Estimated caudal length = ',Clength:03:01,' cm');
WRITELN(Res3);
WRITELN(Res3, ' Average swimming speeds of this model anchovy :');
WRITE(Res3, ' Travelling speed = ',Vswim:02:01,' cm/sec ');
WRITELN(Res3, ' Speed while feeding = ',Vfeed:02:01,'cm/sec');
WRITELN(Res3);
WRITELN(Res3, ' Swimming Metabolism for this anchovy : ');
WRITE(Res3, ' Travelling = ',Mswim:04:01,' J/hr ');

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WRITELN(Res3, ' Feeding = ',Mfeed:04:01,' J/hr');
WRITELN(Res3);
WRITELN(Res3);
WRITE(Res3, 'DAY-SHOAL-DIST(km)-TRAVEL TIME(h)');
WRITELN(Res3, '-FEED TIME(h)-Eswim-Efeed-Eeat-NET ENERGY(J)-
Growth(cm.d-1)');
WRITELN(Res3);
WRITELN(Res3);
END ELSE
BEGIN
  APPEND(Res3);
END;
WRITE(Res3, i:02,' ',j:03,' ');
WRITE(Res3, Mindist:02:02,' ',Travel:01:02,' ',Timefeed:01:02);
WRITE(Res3, ' ',ENERs:10:01,' ',ENERf:10:01,' ',Egain:10:01);
WRITELN(Res3, ' ',Enet:10:01,' ',Growth:1:03);
TEnergy := TEnergy + ENet;
IF j = Totalshoals THEN
BEGIN
  AEnergy := TEnergy / shoaldays;
  Maint := Maint / shoaldays;
  TMAINT := TMAINT + MAINT;
  WRITELN(Res3);
  WRITELN(Res3);
  WRITELN(Res3, 'Ave net energy(per shoal/day) = ',AEnergy:06:01);
  WRITELN(Res3);
  WRITELN(Res3);
  WRITELN(Res3, '% of time above maintenance = ',Maint:02:02);
  WRITELN(Res3);
END;
CLOSE(Res3);
ASSIGN(Esim, 'C:\EVA\ESIM.OUT');
IF runs = 1 THEN
BEGIN
  REWRITE(Esim);
END ELSE
BEGIN
  APPEND(Esim);
END;
WRITELN(Esim, j, ',AEnergy:06:01);
CLOSE(Esim);
IF i = 2 THEN
BEGIN
  ASSIGN(EN1, 'C:\EVA\EN1.OUT');
  IF runs = 1 THEN
  BEGIN
    REWRITE(EN1);
  END ELSE
  BEGIN
    APPEND(EN1);
  END;
  WRITELN(EN1, ENET:06:01);
  CLOSE(EN1);
END;
IF i = 3 THEN
BEGIN
  ASSIGN(EN2, 'C:\EVA\EN2.OUT');
  IF runs = 1 THEN

```

```

BEGIN
  REWRITE(EN2);
END ELSE
BEGIN
  APPEND(EN2);
END;
WRITELN(EN2, ENET:06:01);
CLOSE(EN2);
END;
IF (i = 8) OR (i = 9) THEN
BEGIN
  ASSIGN(EN3, 'C:\EVA\EN3.OUT');
  IF runs = 1. THEN
  BEGIN
    REWRITE(EN3);
  END ELSE
  BEGIN
    APPEND(EN3);
  END;
  WRITELN(EN3, ENET:06:01);
  CLOSE(EN3);
END;
END;
IF (i = fin) AND (j = u) THEN
BEGIN
  AveBW := AveBW / shoaldays;
  AveSUP := AveSUP / shoaldays;
  APPEND(Res2);
  WRITELN(Res2);
  WRITELN(Res2, '*** CALCULATING AVERAGES OVER ENTIRE TIME
PERIOD');
  WRITELN(Res2);
  WRITELN(Res2, ' Total no. of shoal days = ',shoaldays);
  WRITELN(Res2);
  WRITELN(Res2, '(i) Average % BW = ',AveBW:03:02);
  WRITELN(Res2);
  WRITELN(Res2, '(ii) Average Supply Rate = ',AveSUP:03:02);
  WRITELN(Res2);
  WRITELN(Res2);
  CLOSE(Res2);
END;
END; {of Energy}

PROCEDURE Predation;
CONST
  FR = 5.24; {Feeding rate constant}

VAR
  CIVS,
  Out3, Out4 : File OF REAL;

  Fish : TEXT;
  MHIT, {Mortality rate in a 'hit' cell}
  Amounteaten,
  Totaleaten,
  ICOP2, ICOP3,
  IAD, {Initial concentrations}
  MRcop2, MRcop3,

```

```

MRad,      {Mortality values}
M1,M2,M3,  {Ave. daily mort. rate for CIV, CV & ADULTS respect.}
BCOP2,BCOP3,BAD,  {Biomass values}
Btotal,Bcheck,
Sate,
BWPER,AveBW,  {Passing parameters}
Feedtime,
Feedingrate : REAL;
h,
Depletes  {Total no. 'patch' cells depleted by ALL shoals on day i }
          : INTEGER;
Ontraj    : ARRAY[1..100] OF INTEGER;
Totalprey,
Time      : ARRAY[1..200] OF REAL;
BEGIN
  i := day;
  ASSIGN(CIVS, 'C:\EVA\Cops2.DAT');
  RESET(CIVS);
  ASSIGN(Out3, 'C:\EVA\Cops3.DAT');
  RESET(Out3);
  ASSIGN(Out4, 'C:\EVA\Adults.DAT');
  RESET(Out4);
  FOR k := 1 TO (rmax*cmax+1) DO
  BEGIN
    READ(CIVS, COP2[k]);
    READ(Out3, COP3[k]);
    READ(Out4, AD[k]);
    Totalprey[k] := COP2[k] + COP3[k] + AD[k];
    Ontraj[k] := 0; {Checks if model cell lies on a feeding trajectory}
                  {If so, Ontraj will take value 1 later on.}
  END;
  CLOSE(CIVS);
  CLOSE(Out3);
  CLOSE(Out4);
  ASSIGN(Fish, 'C:\EVA\Fishes.OUT');
  IF i = 2 THEN
  BEGIN
    REWRITE(Fish);
  END ELSE
  BEGIN
    APPEND(Fish);
  END;
  WRITELN;
  WRITELN(' Calling Trajectories - ...');
  WRITELN;
  Trajectories;
  IF firstsch > 0 THEN
  BEGIN
    Depletes := 0; {Total no. of 'patch' cells hit by all shoals on day i}
    MRcop2 := 0; {Cumulative CIV mortality rate on day i}
    MRcop3 := 0; {Cumulative CV mortality rate on day i}
    MRad := 0; {Cumulative ADULT mortality rate on day i}
    FOR j := 1 TO v DO {Loop executed for each shoal}
    BEGIN
      shoalnumber := j;
      hit := 0;
      Time[j] := 0;
      Finds := 0;
    END;
  END;

```

```

Totaleaten := 0;
Btotal := 0;
Bcheck := 0;
{10% max. satiation level (in kg) calculated as : }
{ 0.1 * shoal biomass(tons) (=shoal[j]*stdshoal) * 1000 }
Sateiate := shoal[j] * stdshoal * 1000;
IF shoal[j] > 0 THEN
BEGIN
  Trajectories;
END;
IF hit > 0 THEN {Loop only executed for shoals still in model area}
BEGIN
  r := 1; {Associating a r-c grid ref. with each cell no.}
  c := 0;
  k := 1;
  WHILE k <= 400 DO
  BEGIN
    IF c = cmax THEN
    BEGIN
      c := 1;
      r := r + 1;
    END ELSE
    BEGIN
      c := c + 1;
      r := r;
    END;
    h := 1;
    WHILE h <= hit DO
    BEGIN
      IF k = Target[h] THEN
      BEGIN
        Finds := Finds + 1; {Counts no. of 'hit' cells located}
        {Fish deplete the prey in a cell only if: }
        {a). the cell lies on their feeding trajectory }
        {b). the cell has not already been 'hit' by another shoal}
        {c). & prey conc. is above the threshold level }
        IF (Totalprey[k] >= patconc) AND (Ontraj[k] = 0) THEN
        BEGIN
          Depletes := Depletes + 1;
          {Initial concentrations}
          ICOP2 := COP2[k];
          ICOP3 := COP3[k];
          IAD := AD[k];
          {Prey conc. depleted to background level - model }
          {assumes prey encountered sequentially according to}
          {its relative abundance }
          COP2[k] := ROUND(COP2[k]/Totalprey[k] * Background);
          COP3[k] := ROUND(COP3[k]/Totalprey[k] * Background);
          AD[k] := ROUND(AD[k]/Totalprey[k] * Background);
          WRITELN('MORTALITY IN HIT CELLS');
          {Calculating biomass consumed - max. satiation level}
          { is 10% of fish biomass. }
          {*** Dry wt. of CIV = 28.1 ug }
          {*** Dry wt. of CV = 61.9 ug }
          {*** Average dry wt. of ADULT = 98.2 ug }
          BCOP2 := (ICOP2 - COP2[k]) * 28.1;
          BCOP3 := (ICOP3 - COP3[k]) * 61.9;
          BAD := (IAD - AD[k]) * 98.2;
        END;
      END;
      h := h + 1;
    END;
    k := k + 1;
  END;
END;

```

```

Btotal := Btotal + BCOP2 + BCOP3 + BAD;
{Bcheck is the total biomass consumed (in kg wet wt),}
{ when totalled over the 3.75 * 106 cubic metre }
{ subcells comprising each cell -          }
{ 1 cell has area = 500*500 m2 and prey concentration}
{ averaged over a 15m range in depth      }
Bcheck := Bcheck + ((3.75 * Btotal * DWrat) / 1000);
Ontraj[k] := 1;
{Calculation of time (mins) for a shoal of relative}
{ size (shoal[j]) to deplete prey patch to }
{ background prey concentration level.   }
{Time to travel between patches is 49 min. }
{Maximum time available for foraging on copepods}
{ is 12 hours, which includes travel time  }
Amounteaten := Totalprey[k]-Background;
Feedingrate := (((Amounteaten*500*500*15)*Fweight) / (Shoal[j] *
Stdshoal)) * (FR/60);
Time[j] := Time[j] + (Feedingrate + 49);
Totaleaten := Totaleaten + Amounteaten;
{Calculating daily mortality rates for CV & ADULTS..}
{...calculations continued below }
IF ICOP2 < 1 THEN
BEGIN
    ICOP2 := 1;
END;
IF ICOP3 < 1 THEN
BEGIN
    ICOP3 := 1;
END;
IF IAD < 1 THEN
BEGIN
    IAD := 1;
END;
MRcop2 := MRcop2 + ((ICOP2 - COP2[k]) / ICOP2);
MRcop3 := MRcop3 + ((ICOP3 - COP3[k]) / ICOP3);
MRad := MRad + ((IAD - AD[k]) / IAD);
END ELSE
BEGIN
    Time[j] := Time[j] + 49; {Travel time}
    COP2[k] := COP2[k];
    COP3[k] := COP3[k];
    AD[k] := AD[k];
END;
IF (Time[j] >= Ttotal) OR (Finds = hit) THEN
BEGIN
    k := rmax*cmax; {Shoal j reached furthest cell}
    IF Time[j] > Ttotal THEN
    BEGIN
        Time_counter := Time_counter + 1;
    END;
    IF Finds = hit THEN
    BEGIN
        Hit_counter := Hit_counter + 1;
    END;
END;
IF Bcheck >= Satiatate THEN
BEGIN
    k := rmax * cmax; {Shoal fed to satiation level}

```

```

        Feed_counter := Feed_counter + 1;
    END;
    h := hit+1;
END ELSE
BEGIN
    COP2[k] := COP2[k];
    COP3[k] := COP3[k];
    AD[k] := AD[k];
    h := h + 1;
END;
END; {of loop for each 'hit' made by a shoal}
k := k + 1;
END; {of loop checking each cell for a 'hit'}
rpat[j] := r;
cpat[j] := c;
END ELSE {of loop for shoals still in area}
BEGIN
    rpat[j] := rmax;
    cpat[j] := cmax;
END;
WRITELN(Fish);
WRITE(Fish, 'Day=', i, ', ', 'Shoal=', j, ', ', '10% MAX = ', Sateiate);
WRITELN(Fish, ' ', 'BIOM CONSUMED = ', Bcheck, ' PER M^3', Btotal);
WRITELN(Fish);
Feedtime := Time[j];
IF (j = v) AND (Depletes > 0) THEN
BEGIN
    {Mortality rate is averaged over all 'patch' cells depleted }
    M1 := MRcop2 / Depletes;
    M2 := MRcop3 / Depletes;
    M3 := MRad / Depletes;
    {Mort. rate in all other cells, (where no. of cells = total cells }
    { minus depleted cells), is zero, thus ave. mort. rate is less... }
    M1 := (Depletes / (rmax*cmax)) * M1;
    M2 := (Depletes / (rmax*cmax)) * M2;
    M3 := (Depletes / (rmax*cmax)) * M3;
END ELSE
BEGIN
    M1 := 0;
    M2 := 0;
    M3 := 0;
END;
CLRSCR;
GOTOXY(2,6);
WRITELN(' Calling Fishes... ');
Fishes (Totaleaten, Feedtime, M1, M2, M3);
WRITELN;
WRITELN;
WRITELN(' Calling Energy... ');
WRITELN;
Energy (Bcheck, Feedtime);
END; {of loop for all shoals on day i}
REWRITE(Out3);
REWRITE(Out4);
REWRITE(CIVS);
FOR k := 1 TO (rmax*cmax+1) DO
BEGIN
    WRITE(CIVS, COP2[k]);

```

```

        WRITE(Out3, COP3[k]);
        WRITE(Out4, AD[k]);
    END;
    WRITELN(Fish);
    WRITELN(Fish, 'Day= ',i);
    WRITELN(Fish);
    FOR j := 1 TO v DO
    BEGIN
        WRITE(Fish, 'Shoal ',j, ' Size ',SHOAL[j], ' r= ',rpat[j]);
        WRITELN(Fish, ' c= ',cpat[j], ' T=',Time[j]:05:0);
    END;
    CLOSE(CIVS);
    CLOSE(Out3);
    CLOSE(Out4);
    CLOSE(Fish);
END ELSE {of loop executed only if at least 1 shoal has entered area}
BEGIN
    CLOSE(Fish);
END;
END; {Predation}

```

```

PROCEDURE AveragePopn(var Abiom : REAL);

```

```

VAR
    Out1,Out2,CIVS;
    Out3,Out4    : File OF REAL;
    Aprey,
    Cops,
    Nnp,
    Apop        : TEXT;
    CV, MIN, MAX,
    P1,P2,P3,P4,P5,
    Naups,Cops1,
    Cops2,Cops3,Ads : REAL;

```

```

BEGIN
    i := day;
    IF i = (start+1) THEN
    BEGIN
        AvNAUP[1] := ABIOM*AN;
        AvCOP1[1] := ABIOM*AC1;
        AvCOP2[1] := ABIOM*AC2;
        AvCOP3[1] := ABIOM*AC3;
        AvAD[1] := ABIOM*AA;
        FPNAUP[1] := ABIOM*AN;
        FPCOP1[1] := ABIOM*AC1;
        FPCOP2[1] := ABIOM*AC2;
        FPCOP3[1] := ABIOM*AC3;
        FPAD[1] := ABIOM*AA;
        TotAve[1] := ABIOM;
        TotFP[1] := ABIOM;
    END;
    ASSIGN(Out1, 'C:\EVA\Naupliar.DAT');
    ASSIGN(Out2, 'C:\EVA\Cops1.DAT');
    ASSIGN(CIVS, 'C:\EVA\Cops2.DAT');
    ASSIGN(Out3, 'C:\EVA\Cops3.DAT');
    ASSIGN(Out4, 'C:\EVA\Adults.DAT');
    RESET(Out1);

```

```

RESET(Out2);
RESET(CIVS);
RESET(Out3);
RESET(Out4);
P1 := 0;
P2 := 0;
P3 := 0;
P4 := 0;
P5 := 0;
MIN := 10000;
MAX := 0;
FOR j := 1 TO (rmax*cmax+1) DO
BEGIN
  READ(Out1, Naups);
  READ(Out2, Cops1);
  READ(CIVS, Cops2);
  READ(Out3, Cops3);
  READ(Out4, Ads);
  { Calc. the mean and std dev. of the no. of prey per cell over model area}
  X[j] := Cops2 + Cops3 + Ads;
  { Calc. the range }
  IF X[j] < MIN THEN
  BEGIN
    MIN := X[j];
  END;
  IF X[j] > MAX THEN
  BEGIN
    MAX := X[j];
  END;
  IF j < (rmax*cmax+1) THEN
  BEGIN
    P1 := P1 + Naups;
    P2 := P2 + Cops1;
    P3 := P3 + Cops2;
    P4 := P4 + Cops3;
    P5 := P5 + Ads;
  END ELSE
  BEGIN
    FPNAUP[i] := Naups;
    FPCOP1[i] := Cops1;
    FPCOP2[i] := Cops2;
    FPCOP3[i] := Cops3;
    FPAD[i] := Ads;
  END;
END;
CLOSE(Out1);
CLOSE(Out2);
CLOSE(CIVS);
CLOSE(Out3);
CLOSE(Out4);
AvNAUP[i] := P1 / (rmax*cmax);
AvCOP1[i] := P2 / (rmax*cmax);
AvCOP2[i] := P3 / (rmax*cmax);
AvCOP3[i] := P4 / (rmax*cmax);
AvAD[i] := P5 / (rmax*cmax);
P1 := AvNAUP[i];
P2 := AvCOP1[i];
P3 := AvCOP2[i];

```

```

P4 := AvCOP3[i];
P5 := AvAD[i];
TotAve[i] := AvNAUP[i] + AvCOP1[i] + AvCOP2[i] + AvCOP3[i]+AvAD[i];
TotFP[i] := FPNAUP[i] + FPCOP1[i] + FPCOP2[i] + FPCOP3[i]+FPAD[i];
{ Mean & Std Dev. of no.of prey }
No := rmax * cmax;
MeanStd(X, No, Mean, Std_Dev);
CV := Std_Dev / Mean;
ASSIGN(APrey, 'C:\EVA\PREY.OUT');
IF RUNS = 1 THEN
BEGIN
REWRITE(APrey);
WRITELN(APrey, ' **** PREY.OUT ***** ');
WRITELN(APrey, ' No. of prey (= CIV, CV & AD) per m3 ');
WRITELN(APrey);
WRITELN(APrey, ' Mean, Std_Dev, CV, Min, Max');
WRITELN(APrey);
END ELSE
BEGIN
APPEND(APrey);
END;
WRITELN(APrey, MEAN:5:1);
CLOSE(APrey);
IF i = fin THEN
BEGIN
ASSIGN(APop, 'C:\EVA\AvePop.OUT');
REWRITE(APop);
WRITELN(APop, ' *** APop.OUT *** ');
WRITELN(APop);
WRITELN(APop);
WRITE(APop, 'Average Popn. No.s (no.m^3) with variable ');
WRITELN(APop, 'predation pressure. (VP)');
WRITELN(APop);
WRITELN(APop, 'DAY - NAUP - COP1 - CIV - CV - ADULTS - TOTAL');
WRITELN(APop);
FOR j := 1 TO fin DO
BEGIN
WRITE(APop, j:2, ',AvNAUP[j]:4,',AvCOP1[j]:4,');
WRITE(APop, AvCOP2[j]:4,',AvCOP3[j]:4,',AvAD[j]:4);
WRITELN(APop, ' ',TotAve[j]:4);
END;
WRITELN(APop);
WRITELN(APop);
WRITELN(APop);
WRITE(APop, 'Average Popn. No.s (no.m^3) with fixed ');
WRITELN(APop, 'predator mortality rate = 0.1.(FP) ');
WRITELN(APop);
WRITELN(APop, 'DAY - NAUP - COP1 - C4 - C5 - ADULTS - TOTAL');
WRITELN(APop);
FOR j := 1 TO fin DO
BEGIN
WRITE(APop, j:2, ',FPNAUP[j]:4,',FPCOP1[j]:4,');
WRITE(APop, FPCOP2[j]:4,',FPCOP3[j]:4,',FPAD[j]:4);
WRITELN(APop, ' ',TotFP[j]:4);
END;
{Calculating population age structure as % total no. }
{Note arrays AvNAUP - AvAD are re-used to print values & }
{thus from this point they no longer store the ave.popn. values}

```

```

WRITELN(APop);
WRITELN(APop);
WRITELN(APop, '**INITIAL & FINAL POPULATION AGE STRUCTURE...');
WRITELN(APop, '      ( % total number ) ');
WRITELN(APop);
WRITELN(APop, '      NAUP - COP1 - C4 - C5 - ADULTS');
WRITELN(APop);
{Initial popn. age structure - same for variable pred & FP }
AvNAUP[1] := AvNAUP[1] / TotAve[1];
AvCOP1[1] := AvCOP1[1] / TotAve[1];
AvCOP2[1] := AvCOP2[1] / TotAve[1];
AvCOP3[1] := AvCOP3[1] / TotAve[1];
AvAD[1] := AvAD[1] / TotAve[1];
{Final age structure for variable predation (VP) run}
AvNAUP[2] := AvNAUP[fin] / TotAve[fin];
AvCOP1[2] := AvCOP1[fin] / TotAve[fin];
AvCOP2[2] := AvCOP2[fin] / TotAve[fin];
AvCOP3[2] := AvCOP3[fin] / TotAve[fin];
AvAD[2] := AvAD[fin] / TotAve[fin];
{Final age structure for fixed predation (FP) run}
AvNAUP[3] := FPNAUP[fin] / TotFP[fin];
AvCOP1[3] := FPCOP1[fin] / TotFP[fin];
AvCOP2[3] := FPCOP2[fin] / TotFP[fin];
AvCOP3[3] := FPCOP3[fin] / TotFP[fin];
AvAD[3] := FPAD[fin] / TotFP[fin];
FOR j := 1 TO 3 DO
BEGIN
  IF j = 1 THEN
  BEGIN
    WRITE(APop, 'INITIAL  : ');
  END;
  IF j = 2 THEN
  BEGIN
    WRITE(APop, 'FINAL (VP): ');
  END;
  IF j = 3 THEN
  BEGIN
    WRITE(APop, 'FINAL (FP): ');
  END;
  WRITE(APop, AvNAUP[j]:01:02, ' ', AvCOP1[j]:01:02, ' ');
  WRITE(APop, AvCOP2[j]:01:02, ' ', AvCOP3[j]:01:02);
  WRITELN(APop, ' ', AvAD[j]:01:02);
  WRITELN(APop);
END;
CLOSE(APop);
ASSIGN(Cops, 'C:\EVA\COPS.SEN');
IF runs = 1 THEN
BEGIN
  REWRITE(Cops);
END ELSE
BEGIN
  APPEND(Cops);
END;
FOR j := 1 TO fin DO
BEGIN
  WRITELN(Cops, AvCOP1[j] + AvCOP2[j] + AvCOP3[j] + AvAD[j]:4);
END;
CLOSE(Cops);

```

```

    ASSIGN(Nnp, 'C:\EVA\Numnaup.SEN');
    IF runs = 1 THEN
    BEGIN
        REWRITE(Nnp);
    END ELSE
    BEGIN
        APPEND(Nnp);
    END;
    FOR j := 1 TO fin DO
    BEGIN
        WRITELN(Nnp, AvNAUP[j]:4);
    END;
    CLOSE(Nnp);
END; {of AveragePopn}

PROCEDURE feedhistory;

VAR
    History : TEXT;

BEGIN
    ASSIGN(History, 'C:\EVA\His.OUT');
    IF sim = 1 THEN
    BEGIN
        REWRITE(History);
    END ELSE
    BEGIN
        APPEND(History);
    END;

    IF start = 1 THEN
    BEGIN
        S := 0;
        F := 0;
        SI[start] := 0;
    END; {Initialise variables}
    i := start;
    WHILE i <= (fin) DO
    BEGIN
        IF (S > 0) AND (CHL[i] > FCRIT) THEN {End of starvation period}
        BEGIN
            SI[i] := S; {No. of days starved}
            S := 0;
        END ELSE BEGIN
            SI[i] := 0;
        END;
        IF CHL[i] > FCRIT THEN
        BEGIN
            F := F + 1;
            FH[i] := 0;
        END ELSE {Chlorophyll concentration <= Fcrit}
        BEGIN
            FH[i] := F; {No. of days fed}
            F := 0;
            S := S + 1;
        END;
    END;
    IF S >= 3 THEN

```

```

BEGIN
  Feed[i] := 'I'; {Intermittent feeding}
END ELSE
BEGIN
  Feed[i] := 'C'; {Continuous feeding}
END;
WRITELN(History, ' Feeding and starvation history');
WRITELN(History, ' day..', i);
WRITELN(History, ' feeding..', F);
WRITELN(History, ' starving.. ', S);
WRITELN(History, ' SI .. ', SI[i]);
WRITELN(History, ' FH .. ', FH[i]);
WRITELN;
IF SI[i] > 0 THEN
BEGIN
  WRITELN(' Starvation index and Feeding history');
  WRITELN;
  WRITELN(' Day ...', i);
  WRITELN(' Starvation index ...', SI[i]);
  WRITELN(' Feeding history ...', FH[(i-SI[i])]);
  WRITELN;
END;
i := i + 1;

END;
CLOSE(History);
END; {of feedhistory}

PROCEDURE Netchlor;

VAR
  Netchla : TEXT;
  Fmax : REAL; {Chl. conc. at which egg prodn. rates saturate}
BEGIN
  ASSIGN(Netchla, 'C:\EVA\Net.OUT');
  REWRITE(Netchla);
  WRITELN(Netchla, ' Net chlorophyll and corresponding fecundity values..');
  Fmax := 40;
  i := start;
  WHILE i <= (fin) DO
  BEGIN
    IF CHL[i] >= FMAX THEN
    BEGIN
      CHL[i] := FMAX; {Chl.conc. at which fecundity plateaus}
    END;
    NET[i] := 0.98 * CHL[i] - 1.2; {Chl. a > 10 µm}
    NET[i] := 10 * NET[i]; {Convert to biomass}
    NET[start-1] := NET[start];
    IF (NET[i-1] <= 0) OR (NET[i] <= 0) THEN
    BEGIN
      FN[i] := 0;
    END ELSE
    BEGIN
      FN[i] := EXP(0.430 * LN(NET[i]) + 0.447 * LN(NET[i-1])) - 1.278;
    END;
    WRITELN(Netchla, ' Day ..', i);
    WRITELN(Netchla, ' Net chl.a = ', NET[i]:08:02, ' Fecundity = ', FN[i]:15:02);
    WRITELN;
  END;
END;

```

```

    i := i + 1;
  END;
  CLOSE(Netchla);
END; {of Netchlor}

PROCEDURE Fecundity;

VAR
  FS,      {Normal fecundity value}
  NEWF : REAL; {Fecundity modified according to feeding history}
  Fecund : TEXT;
BEGIN
  ASSIGN(Fecund, 'C:\EVA\Fec.OUT');
  IF sim = 1 THEN
    BEGIN
      REWRITE(Fecund);
    END ELSE
    BEGIN
      APPEND(Fecund);
    END;
  i := start;
  WHILE i <= (fin) DO
    BEGIN
      IF (SI[i] > 0) AND (CHL[i] > FCRIT) THEN {End of starvation period}
        BEGIN
          IF NET[i] <= 3 THEN
            BEGIN
              NET[i] := 1;
            END;
          IF NET[i+1] <= 0 THEN
            BEGIN
              NET[i+1] := NET[i];
            END;
          FS := EXP(0.430 * LN(NET[i+1]) + 0.447 * LN(NET[i])) - 1.278;
          NEWF := 5 * FS * EXP(-0.176 * SI[i]);
          j := i;
          FOR k := 1 TO 4 DO
            BEGIN
              FEC[j] := (k-1)/6 * (NEWF - FS); {Linear increase in egg prodn.}
              j := j + 1;
            END;
          FEC[i+4] := FS; {5 days recovery period to average egg prodn.}
          i := i + 5;
        END ELSE
        BEGIN
          IF CHL[i] < FCRIT THEN
            BEGIN
              FEC[i] := 0; {Food limitation of chlorophyll prodn.}
              IF CHL[i] > 1 THEN
                BEGIN
                  IF CHL[i] > 2 THEN
                    BEGIN
                      FEC[i] := 5;
                    END ELSE
                    BEGIN
                      FEC[i] := 1;
                    END;
                END;
            END;
          END;
        END;
    END;
  END;

```

```

        END ELSE
        BEGIN
            FEC[i] := FN[i];

            END;
            i := i + 1;
        END;
    END;
    WRITELN(Fecund, ' Modified fecundity values..');
    FOR i := start TO (fin) DO
    BEGIN
        WRITELN;
        WRITELN(Fecund, ' Day = ',i);
        WRITELN(Fecund, ' Fecundity = ',FEC[i]);
    END;
    CLOSE(Fecund);

END; {of Fecundity}

PROCEDURE Development;

VAR

    Feeding    : CHAR;
    TDev       : REAL;
    Dev        : TEXT;
BEGIN
    ASSIGN(Dev, 'C:\EVA\Dev.OUT');
    IF sim = 1 THEN
    BEGIN
        REWRITE(Dev);
    END ELSE
    BEGIN
        APPEND(Dev);
    END;
    WRITELN(Dev);

    i := start;
    WHILE i <= (fin) DO
    BEGIN
        Feeding := Feed[i];
        CASE Feeding OF
            'C' : BEGIN      {Continuous feeding}
                    TDev := 1469.2 * (1/(EXP(1.665*LN(TEMP[i]-1.5))));
                    WRITELN(Dev, ' Day = ',i, ' ', 'Feeding = continuous');
                END;
            'I' : BEGIN      {Intermittent feeding}
                    TDev := 2938.4 * (1/(EXP(1.665*LN(TEMP[i]-1.5))));
                    WRITELN(Dev, ' Day = ',i, ' ', 'Feeding = intermittent');
                END;
        END; {of case}
        {Development indices(in days) based on temperature & feeding regime}
        Dev1[i] := 1 / (0.295 * TDev); {From naupliar to copepodite}
        Dev2[i] := 1 / (0.361 * TDev); {From copepodite I to CIV  }
        Dev3[i] := 1 / (0.120 * TDev); {From CIV - C5          }
        Dev4[i] := 1 / (0.169 * TDev); {From C5 to adult      }
        WRITE(Dev, TDev, '  DEV1 = ',DEV1[i], ' ', 'DEV2 = ',DEV2[i]);
        WRITELN(Dev, '  DEV3 = ',DEV3[i], ' ', 'DEV4 = ',DEV4[i]);
    END;
END;

```

```

        WRITELN(Dev);
        i := i + 1;
    END;
    CLOSE(Dev);
END; {of Development}

```

```

PROCEDURE StarvingMortality;

```

```

{ Matrix values taken from Borchers & Hutchings (1986) give the }
{ % of C. carinatus offspring starving after various food cycles at 18°C }

```

```

VAR

```

```

    Smat      : TEXT;
    row,col   : INTEGER; {Pointers to locate feeding cycle}
    Feedcycle, {Base case matrix value of % offspring starved}
    ATEMP     : REAL; {Average temperature over a starvation period}
BEGIN
    ASSIGN(Smat, 'C:\EVA\Matrix.OUT');
    REWRITE(Smat);
    FOR i := 1 TO 10 DO
        BEGIN
            FOR j := 1 TO 2 DO
                BEGIN
                    M[i,j] := 0;
                END;
            END;
            FOR i := 1 TO 2 DO
                BEGIN
                    FOR j := 1 TO 10 DO
                        BEGIN
                            M[i,j] := 0;
                        END;
                    END;
                END;
            FOR i := 3 TO 10 DO
                BEGIN
                    FOR j := 3 TO 10 DO
                        BEGIN
                            IF j > i THEN
                                BEGIN
                                    M[i,j] := 1;
                                END;
                            END;
                        END;
                    END;
                END;
            END;
            M[3,3]:=0.67;
            M[4,3]:=0.50; M[4,4]:=0.75;
            M[5,3]:=0.40; M[5,4]:=0.60; M[5,5]:=0.80;
            M[6,3]:=0.33; M[6,4]:=0.50; M[6,5]:=0.67; M[6,6]:=0.83; M[6,7]:=0.83;
            M[7,3]:=0.29; M[7,4]:=0.43; M[7,5]:=0.57; M[7,6]:=0.71; M[7,7]:=0.71;
            M[7,8]:=0.86;
            M[8,3]:=0.25; M[8,4]:=0.38; M[8,5]:=0.50; M[8,6]:=0.63; M[8,7]:=0.63;
            M[8,8]:=0.75; M[8,9]:=0.88;
            M[9,3]:=0.22; M[9,4]:=0.33; M[9,5]:=0.44; M[9,6]:=0.56; M[9,7]:=0.56;
            M[9,8]:=0.67; M[9,9]:=0.78; M[9,10]:=0.89;
            M[10,3]:=0.2; M[10,4]:=0.3; M[10,5]:=0.4; M[10,6]:=0.5; M[10,7]:=0.5;
            M[10,8]:=0.6; M[10,9]:=0.7; M[10,10]:=0.8;
            WRITE(Smat, 'Percentage offspring starving after various');
            WRITELN(Smat, 'food cycles at Temp. = 18');
            WRITELN(Smat);
        END;
    END;

```

```

WRITELN(Smat, ' ROW = Period of feeding ; COL = Period of starvation');
WRITELN(Smat);
FOR i := 1 TO 10 DO
BEGIN
  FOR j := 1 TO 10 DO
  BEGIN
    WRITE(Smat, M[i,j]:4:2, ' ');
  END;
  WRITELN(Smat);
END;
WRITELN(Smat);
WRITELN(Smat, '% offspring starving after various food & temp. cycles');
WRITELN(Smat);
i := start;
WHILE i <= (fin) DO
BEGIN
  IF SI[i] > 0 THEN      {End of starvation period}
  BEGIN
    ATEMP := 0;
    row := FH[(i-SI[i]); {Previous period of feeding (days)}
    col := SI[i];      {Period of starvation (days)}
    IF (row >= 10) OR (col >= 10) THEN {Max. days starvation}
    BEGIN
      IF col >= 10 THEN
      BEGIN
        col := 10;
      END;
      IF row >= 10 THEN
      BEGIN
        row := 10;
      END;
    END;
    Feedcycle := M[row,col];
    {Calculating average temperature over starvation period}
    FOR j := (i-col) TO (i-1) DO
    BEGIN
      ATEMP := ATEMP + TEMP[j];
    END;
    ATEMP := ATEMP / COL;
    {Modifying starvation tolerance as a linearly decreasing }
    {      function of temperature.      }
    STARVE[i] := ATEMP / 18 * Feedcycle;
    M50[i] := 18 / ATEMP * 12; {Adult & CV starv.tolerance limit}
  END ELSE
  BEGIN
    STARVE[i] := 0; {No offspring starve}
    M50[i] := 1000;
    ATEMP := temp[i];
  END;
  WRITE(Smat, 'DAY =',i, ' STARVE =',STARVE[i]:10:02);
  WRITELN(Smat, ' AVE. TEMP =',ATEMP:20:02);
  i := i + 1;
END;
CLOSE(Smat);
END; {of StarvingMortality}

PROCEDURE Population;

```

```

CONST
  { Predation Mortality as a linearly increasing function of density }
  { pmortc2 & pmorta apply only to the control cell which has a }
  { fixed predation mortality }
  pmortn = 0.1;
  pmortc1 = 0.1;
  pmortc2 = 0.1;
  pmorta = 0.1;
  { Background mortality rates }
  bmortc2 = 0.05;
  bmorta = 0.05;
VAR
  Popln,          {Lotus file to present output}
  Popn           : TEXT;
  {Typed files to modify popn. no.s according to predation pressure}
  Out1,Out2,CIVS,
  Out3,Out4      : File OF REAL;
  Prey,
  Bran          : File OF INTEGER;
  f             : LONGINT;
  fmortn,fmortc1, {Mortality due to starvation}
  fmortc2,fmorta, {Constant mortality percentages}
  Abiom         : REAL;
  ONAUP, OCOP1,
  OCOP2, OCOP3, OAD,
  PREYNUM       : ARRAY[1..101] OF INTEGER;
BEGIN
  ASSIGN(Popn, 'C:\EVA\Pop.OUT');
  ASSIGN(Popln, 'C:\EVA\Popln.OUT');
  IF sim = 1 THEN
  BEGIN
    REWRITE(Popn);
    REWRITE(Popln);
  END ELSE
  BEGIN
    APPEND(Popn);
    APPEND(Popln);
  END;
  ASSIGN(Out1, 'C:\EVA\Naupliar.DAT');
  ASSIGN(Out2, 'C:\EVA\Cops1.DAT');
  ASSIGN(CIVS, 'C:\EVA\Cops2.DAT');
  ASSIGN(Out3, 'C:\EVA\Cops3.DAT');
  ASSIGN(Out4, 'C:\EVA\Adults.DAT');
  ASSIGN(Prey, 'C:\EVA\Preyconc.DAT');

  WRITELN(Popn);
  Abiom := 0; {Used to calculate average starting biomass }
  IF StartBiomass = 1 THEN
  BEGIN
    REC[start] := (BIOM/6 * FEC[start])/10; {assumes 90% mortality of eggs}
    NAUP[start] := BIOM*AN; {Assume an even initial age distribution}
    COP1[start] := BIOM*AC1; { " }
    COP2[start] := BIOM*AC2; { " }
    COP3[start] := BIOM*AC3; { " }
    AD[start] := BIOM*AA; { " }
    Abiom := BIOM;
  END;

```

```

i := start;
WHILE i <= (fin) DO
BEGIN
  cell := 0;
  sim := 1;
  IF i > 1 THEN
  BEGIN
    RESET(Out1);
    RESET(Out2);
    RESET(Out3);
    RESET(CIVS);
    RESET(Out4);
    FOR j := 1 TO (rmax*cmax+1) DO
    BEGIN
      {Memory saving method of storing popn values for each cell}
      READ(Out1, NAUP[j]);
      ONAUP[j] := ROUND(NAUP[j]);
      READ(Out2, COP1[j]);
      OCOP1[j] := ROUND(COP1[j]);
      READ(CIVS, COP2[j]);
      OCOP2[j] := ROUND(COP2[j]);
      READ(Out3, COP3[j]);
      OCOP3[j] := ROUND(COP3[j]);
      READ(Out4, AD[j]);
      OAD[j] := ROUND(AD[j]);
    END;
    CLOSE(Out1);
    CLOSE(Out2);
    CLOSE(Out3);
    CLOSE(CIVS);
    CLOSE(Out4);
  END;
  day := i;
  IF i > 1 THEN
  BEGIN
    AveragePopn(Abiom);
  END;
  IF sim = 1 THEN
  BEGIN
    REWRITE(Out1);
    REWRITE(Out2);
    REWRITE(Out3);
    REWRITE(CIVS);
    REWRITE(Out4);
  END;
  REWRITE(Prey);
  {Process repeated for each of the rmax*cmax cells - the extra cell }
  {is the 'baseline cell' which has a fixed predation (FP) pressure }
  r := 1;
  WHILE r <= (rmax+1) DO
  BEGIN
    c := 1;
    WHILE c <= cmax DO
    BEGIN
      cell := cell + 1;
      IF r = (rmax+1) THEN {Baseline cell has imaginary co-ords }
      BEGIN { / (rmax+1,cmax) }
        c := cmax;

```

```

END;
IF (StartBiomass <> 1) AND (i = start) THEN
BEGIN
  ASSIGN(Bran, 'C:\EVA\ABiomass.DAT');
  IF (r = 1) AND (c = 1) THEN
  BEGIN
    REWRITE(Bran);
  END ELSE
  BEGIN
    RESET(Bran);
    Seek(Bran,f);

    END;
    {Chooses a random starting biomass between BIOM1 & BIOM2 for cell}
    { number cell!                }

    RANDOMIZE;
    BIOM := RANDOM(BIOM2 - BIOM1) + BIOM1;
    WRITE(Bran, BIOM);
    f := FileSize(Bran);

    CLOSE(Bran);
    {Starting biomass for baseline cell is average biomass ###}

    IF r = (rmax + 1) THEN
    BEGIN
      RESET(Bran);
      FOR k := 1 TO (rmax*cmax) DO
      BEGIN
        READ(Bran, BIOM);
        ABiom := ABiom + BIOM;
      END;
      CLOSE(Bran);
      ABiom := ABiom / (rmax*cmax);
      BIOM := ROUND(ABiom);          { ### }
    END;
    REC[start] := (BIOM/6 * FEC[start])/10;
    NAUP[start] := BIOM*AN;
    COP1[start] := BIOM*AC1;
    COP2[start] := BIOM*AC2;
    COP3[start] := BIOM*AC3;
    AD[start] := BIOM*AA;

    END;
    IF i > 1 THEN
    BEGIN
      NAUP[i] := ONAUP[cell];
      COP1[i] := OCOP1[cell];
      COP2[i] := OCOP2[cell];
      COP3[i] := OCOP3[cell];
      AD[i] := OAD[cell];
    END;
    {Egg-laying population taken as the no. of ripe adult females(Fr), }
    { assuming newly developed females (Fu) take three days before  }
    { laying eggs.                }
    Fu[i] := 0;
    IF i <= (start+1) THEN
    BEGIN

```

```

    Fu[i] := 0.0384 * BIOM;
END ELSE
BEGIN
    Fu[i] := (1-pmorta) * (Dev4[i] * COP3[i])/3;
END;
IF Fu[i] < 0 THEN
BEGIN
    Fu[i] := 0;
END ELSE
BEGIN
    Fu[i] := ROUND(Fu[i]);
END;
Fr[i] := (AD[i] - Fu[i]) / 2;
{Population recruitment}
IF FEC[i] = 0 THEN
BEGIN
    REC[i+1] := 0;    {Prevents negative recruitment!}
END ELSE
BEGIN
    REC[i+1] := ROUND(Fr[i] * FEC[i];
    MEGG[i+1] := 0.9 * REC[i+1];
    REC[i+1] := ROUND(REC[i+1] - MEGG[i+1]);
END;

{Population growth equations}
NAUP[i+1] := (1-Dev1[i]) * NAUP[i] + REC[i+1];
COP1[i+1] := (1-Dev2[i]) * COP1[i] + Dev1[i] * NAUP[i];
COP2[i+1] := (1-Dev3[i]) * COP2[i] + Dev2[i] * COP1[i];
COP3[i+1] := (1-Dev4[i]) * COP3[i] + Dev3[i] * COP2[i];
AD[i+1] := AD[i] + Dev4[i] * COP3[i];
{Mortality (starvation) estimates for copepod stages}
IF STARVE[i+1] > 0 THEN
BEGIN
    {Percentage of offspring die due to starvation }
    {Adults are less susceptible to starvation due to }
    { lipid food reserves & carnivorous feeding. }
    { However their egg prodn. is assumed very }
    { sensitive to food supply. }
    fmortn := 0.67 * STARVE[i+1]; {Starvation tolerance of NAUPs}
    fmortc1 := 0.33 * STARVE[i+1]; {twice that of copepodites }
END ELSE
BEGIN
    fmortn := 0;
    fmortc1 := 0;
END;
{M50 is the no. of days of starvation required }
{ to induce 50% adult & pre-adult starvation }
IF SI[i+1] > M50[i] THEN
BEGIN
    fmortc2 := 0.5;    {starvation tolerance of CV cops}
    fmorta := 0.5;    { adults }
END ELSE
BEGIN
    fmortc2 := 0;
    fmorta := 0;
END;
MNAUP[i+1] := (pmortn + fmortn) * NAUP[i+1];
MCOPI[i+1] := (pmortc1 + fmortc1) * COP1[i+1];

```

```

IF r = (rmax + 1) THEN {p = pred.mort. ; b = background mort }
BEGIN
  MCOP2[i+1] := (pmortc1 + fmortc1) * COP2[i+1];
  MCOP3[i+1] := (pmortc2 + fmortc2) * COP3[i+1];
  MAD[i+1] := (pmorta + fmorta) * AD[i+1];
END ELSE
BEGIN
  MCOP2[i+1] := (bmortc2 + fmortc1) * COP2[i+1];
  MCOP3[i+1] := (bmortc2 + fmortc2) * COP3[i+1];
  MAD[i+1] := (bmorta + fmorta) * AD[i+1];
END;
{Net population growth assuming mortality estimates above}
NAUP[i+1] := (NAUP[i+1] - MNAUP[i+1]);
COP1[i+1] := (COP1[i+1] - MCOP1[i+1]);
COP2[i+1] := (COP2[i+1] - MCOP2[i+1]);
COP3[i+1] := (COP3[i+1] - MCOP3[i+1]);
AD[i+1] := (AD[i+1] - MAD[i+1]);
IF REC[i+1] < 0 THEN
BEGIN
  REC[i+1] := 0;
END;
IF NAUP[i+1] < 0 THEN
BEGIN
  NAUP[i+1] := 0;
END;
IF COP1[i+1] < 0 THEN
BEGIN
  COP1[i+1] := 0;
END;
IF COP2[i+1] < 0 THEN
BEGIN
  COP2[i+1] := 0;
END;
IF COP3[i+1] < 0 THEN
BEGIN
  COP3[i+1] := 0;
END;
IF i = fin THEN
BEGIN
  WRITELN;
  WRITELN(Popn, 'R= ',r,' C= ',c,' Day .. ',i);
  WRITELN(Popn, 'Recs =',REC[i+1]:06:0,' ', 'Naups =',NAUP[i]:15:0);
  WRITELN(Popn, 'Copepodites=',COP1[i]:04:0,' ', 'C4 =',COP2[i]:15:0);
  WRITELN(Popn, ' C5 =',COP3[i]:15:0,' ', 'Adults =',AD[i]:08:0);
  WRITELN(Popn);
END;
WRITE(Popln, i:02,' ',cell:03,' ',REC[i+1]:04:0,' ',NAUP[i]:05:0);
WRITE(Popln, COP1[i]:06:0,' ',COP2[i]:07:0,' ',COP3[i]:08:0);
WRITELN(Popln, ' ',AD[i]:09:0);
WRITE(Out1, NAUP[i+1]);
WRITE(Out2, COP1[i+1]);
WRITE(CIVS, COP2[i+1]);
WRITE(Out3, COP3[i+1]);
WRITE(Out4, AD[i+1]);
PREYNUM[sim] := ROUND(COP2[i+1] + COP3[i+1] + AD[i+1]);
WRITE(Prey, PREYNUM[sim]);
sim := sim + 1;
c := c + 1;

```

```

END;
r := r + 1;
END;
WRITELN(PopIn);
CLOSE(Out1);
CLOSE(Out2);
CLOSE(Out3);
CLOSE(CIVS);
CLOSE(Out4);
CLOSE(Prey);
RESET(Prey);
background := 0;
k := 0;
FOR j := 1 TO (rmax*cmax) DO
BEGIN
  READ(Prey, PREYNUM[j]);
  {Calculation of daily background prey concentration using all}
  {cells with less prey than the threshold feeding concentration}
  { which is 6 prey individuals.m-3 }
  IF PREYNUM[j] < patconc THEN
  BEGIN
    background := background + PREYNUM[j];
    k := k + 1;
  END;
  IF j = RMAX*CMAX THEN
  BEGIN
    IF (k > 1) THEN
    BEGIN
      background := background/k;
      IF (background < 1) THEN
      BEGIN
        background := 1;
      END;
    END ELSE
    BEGIN
      background := patconc;
    END;
  END;
END;
CLOSE(Prey);

{The procedure PREDATION is now called to determine which model }
{cells are hit by fish shoals, whether or not the prey concentration}
{is depleted to the background level(only if prey conc. is above the}
{threshold feeding concentration) and to calculate mortality rates. }
day := i+1;
Traj := 1;
WRITELN;
WRITELN(' Calling Predation ...');
WRITELN;
IF day <= fin THEN
BEGIN
  Predation;
END;
i := day - 1;
WRITELN('COMPLETED DAY = ',i+1);
i := i + 1;

```

```

END;
CLOSE(Popn);
CLOSE(PopIn);

END; {of Population}

PROCEDURE RunsAverage;

VAR
  Msim,
  Aruns   : TEXT;
  Morts,
  CV,
  MIN,MAX : REAL;

BEGIN

  ASSIGN(MSim, 'C:\EVA\MSim.OUT');
  RESET(MSim);

  FOR j := 1 TO NumRuns DO
  BEGIN
    READ(MSim, Morts);

    { Calc. the mean and std dev. of the MORTALITY RATE }
    X[j] := Morts;
    { Calc. the range }
    IF X[j] < MIN THEN
    BEGIN
      MIN := X[j];
    END;
    IF X[j] > MAX THEN
    BEGIN
      MAX := X[j];
    END;
  END;
  CLOSE(MSim);
  { Mean & Std Dev. of mortality values }
  No := NumRuns;
  MeanStd(X, No, Mean, Std_Dev);
  CV := Std_Dev / Mean;
  ASSIGN(ARuns, 'C:\EVA\ARUNS.OUT');
  REWRITE(ARuns);
  WRITELN(ARuns);
  WRITELN(ARuns, ' *** ARUNS.OUT ***');
  WRITELN(ARuns);
  WRITELN(ARuns, ' Average Mortality Rate over ',NumRuns,' runs');
  WRITELN(ARuns);
  WRITELN(ARuns, ' Mean, Std_Dev, CV, Min, Max');
  WRITELN(ARuns);

  WRITE(ARuns, MEAN:1:2,' ',STD_DEV:1:2,' ',CV:3:2);
  WRITELN(ARuns, ' ',MIN:1:2,' ',MAX:1:2);
  CLOSE(ARuns);
END;

BEGIN {Main Program}

```

```

CLRSCR;
WRITELN( '**PREDATOR - PREY SIMULATION PROGRAM **');
WRITELN;
WRITE( ' This model investigates the effect of variable ');
WRITELN( 'predator-prey encounters ');
WRITELN( ' on both the prey and the predator populations. ');
WRITELN;
WRITELN( ' Please give starting and last day ... ');
READLN(start,fin);
WRITELN;
WRITELN( ' Please input the month, as an integer from 1 to 12... ');
READLN(month);
WRITELN;
WRITELN;
WRITELN( ' Do you want to run the program with : ');
WRITELN( ' (1). the same starting biomass in all cells, or ');
WRITELN( ' (2). a randomly chosen starting biomass in each cell ? ');
WRITELN( ' Type the number of your choice... ');
READLN(StartBiomass);
IF StartBiomass = 1 THEN
BEGIN
{Initialise with same starting biomass (Bint) for all quadrats}
{Other program versions may either randomise Bint or choose }
{ specific values for each block }
WRITELN( ' Please input starting biomass (no./m3) - integers only! ');
READLN(BIOM);
END ELSE
BEGIN
WRITELN;
WRITE( ' Please input a minimum and maximum starting biomass - ');
WRITELN( ' INTEGERS ONLY ! ');
WRITELN;
WRITELN( ' Minimum ... ');
READLN(BIOM1);
WRITELN;
WRITELN( ' Maximum ... ');
READLN(BIOM2);
WRITELN;
END;
Time_counter := 0;
Feed_counter := 0;
Hit_counter := 0;
runs := 1;
WHILE runs <= NumRuns DO
BEGIN
sim := 1;
a := 0;
u := 0; {counter for shoal number}
firstsch := 0; {check for first day shoals enter area}
INPUTDATA;
SHOALS;
FEEDHISTORY;
NETCHLOR;
FECUNDITY;
DEVELOPMENT;
STARVINGMORTALITY;
POPULATION;

```

```

runs := runs + 1;
END;
IF NumRuns > 1 THEN
BEGIN
    RunsAverage;
END;
WRITELN('Ave. % of time shoals above maint = ',Tmaint/numruns:3:2);
WRITELN;
WRITELN;
WRITE('Time, Hits and Feed counters ',Time_counter,' ',Hit_counter);
WRITELN(' ',Feed_counter);
READLN;
WRITELN;
GOTOXY(2,6);
CLRSCR;
WRITELN(' *** Program successful ! ***');
WRITELN;
END.

```

```

PROCEDURE Meanstd ( X : Ary; No : INTEGER;
    VAR Mean, Std_Dev : REAL);

```

```

VAR
    Std : TEXT;

```

```

    i : INTEGER;

```

```

    Check,
    Sum_X, Sum_Sq : REAL;

```

```

BEGIN
    ASSIGN(Std, 'C:\EVA\STD.OUT');
    REWRITE(Std);
    FOR i := 1 TO No DO
    BEGIN
        Check := X[i];
        WRITELN(Std, Check, No);
    END;
    CLOSE(Std);
    Sum_X := 0;
    Sum_Sq := 0;
    FOR i := 1 TO No DO
    BEGIN
        Sum_X := Sum_X + X[i];
        Sum_Sq := Sum_Sq + X[i] * X[i];
    END;
    Mean := Sum_X / No;
    Std_Dev := SQR((Sum_Sq - SQR(Sum_X) / No) / (No - 1));
END; {Procedure MeanStd}
The END at last!

```

" *These are hairy but reasonable assumptions. The assumptions are yak-like on a scale from mole-rats to yaks!*"

" *It is through no fault of the authoress that the SEAWiFs satellite failed to be launched during the extended duration of this thesis.*"

" ... go on, ignore my comments!"

Larry Hutchings

THAT'S THE WHOLE PROBLEM WITH
SCIENCE. YOU'VE GOT A BUNCH OF
EMPIRICISTS TRYING TO DESCRIBE
THINGS OF UNIMAGINABLE WONDER.

