

MODELLING THE DYNAMICS OF THE NORTH SEA'S MESOZOOPLANKTON

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ABSTRACT

A simple biomass-only zooplankton submodel is presented, describing the dynamics of copepods and carnivorous zooplankton in the North Sea. This submodel together with the other process-oriented submodels (*viz.* phytoplankton dynamics, the microbial food web, benthic processes, fish dynamics and large-scale advective transport) forms a spatially resolved simulation model of the North Sea ecosystem, the European Regional Seas Ecosystem Model (ERSEM). A large set of field measurements of zooplankton abundance has been assembled against which to compare the ERSEM's performance. These data are not only internally consistent, but have also been gathered at the large spatial scales appropriate to the ERSEM. In addition to the spatially resolved, monthly estimates of zooplankton abundance, several instantaneous, *in situ* estimates of the carbon fluxes between different components of the planktonic web in the northern North Sea are presented. Simulated dynamics are in good agreement with the data only during the mid-summer to mid-winter period. During the latter part of the winter and throughout the spring period zooplankton abundance is under-predicted and the simulated zooplankton growth rate is overpredicted during spring. The excessive decline of mesozooplankton biomass during winter may be caused by failing to capture many of the behavioural/physiological changes which zooplankton manifest during winter. It is suggested that the excessive spring growth is a consequence of a. a failure to properly distinguish between somatic and population growth, b. an inadequate representation of the small scale processes which influence feeding success, and c. an excessive spring phytoplankton bloom. The large phytoplankton bloom is, in part at least, a consequence of the excessively low simulated standing crop of omnivorous zooplankton in spring.

1. INTRODUCTION

The ERSEM (European Regional Seas Ecosystem Model) project has aimed to produce a spatially resolved ecosystem model of the North Sea. The spatial resolution of the model (Fig. 1) is based upon the North Sea's hydrographic characteristics (ICES 1983). In the deeper regions of the North Sea the water column is resolved into surface boxes 1-5, and lower boxes 11-15 which extend to the sea floor. The surface box is 30 m deep, which is the typical depth at which the water column stratifies during the summer in these regions. This spatial resolution is obviously insufficient to enable us to explicitly represent the minute-to-minute, or even day-to-day heterogeneities encountered by an individual zooplankter as a consequence of its movement relative to the local

water mass. Nonetheless, it is frequently suggested that hydrographic conditions can influence local zooplankton dynamics and we might hope to find characteristic differences in the predicted zooplankton dynamics of the various regions of the North Sea arising out of the underlying hydrographic conditions.

The planktonic food web is assumed to have the structure shown in Fig. 2. A suite of submodels was developed to represent the nutrient-phytoplankton-zooplankton dynamics of this food web. This suite is applied to each ERSEM box in turn, and the boxes are coupled through the hydrodynamic forcing which transports planktonic organisms together with suspended and dissolved material. A conceptually similar suite of submodels is used to represent biological and chemical processes which occur in the sediments of the sea floor.

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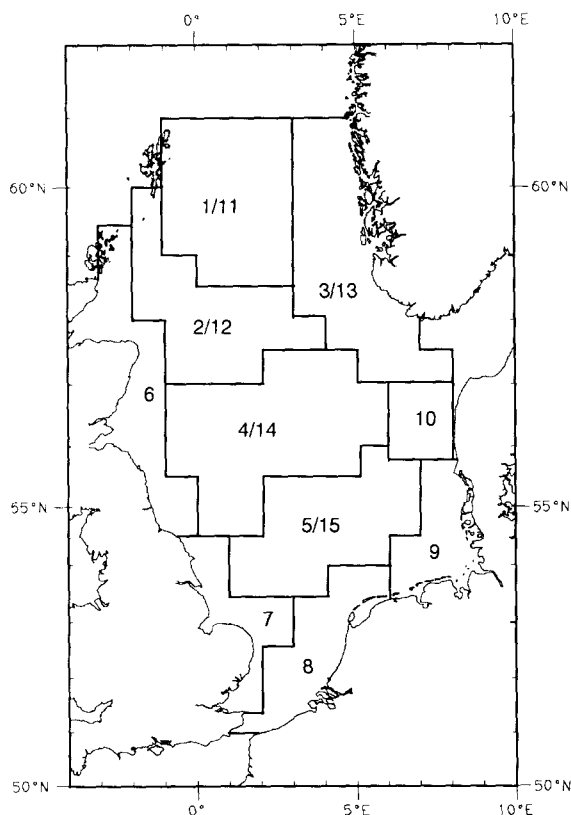


Fig. 1. The spatial structure incorporated in the ERSEM.

In this paper we focus upon the performance of the generic mesozooplankton model. Beside describing the model and the dynamics which it predicts, we pay close attention to deriving a body of test-data which represent zooplankton dynamics at the very coarse spatial scale which the model is designed to represent.

Within the ERSEM context, we define mesozooplankton to be any permanent member of the zooplankton community which is between 200 μm and 3 to 4 cm long as an adult. This definition embraces many species which, as juveniles, are traditionally considered part of the microzooplankton. This slight modification of the traditional, strictly size-based, classification is necessary since not all of the traditional microzooplankton mature into mesozooplankton. On the grounds of an individual's developmental continuity we must treat life-time and transient members of the (traditional) microzooplankton separately. In this paper we barely touch upon microzooplankton (species which are less than 200 μm long as adults). There is increasing evidence that these species consume a substantial fraction of the primary production (Burkill *et al.*, 1993), and for this reason, microzoo-

plankton do form a component of the ERSEM model. The reader is referred to Baretta-Bekker *et al.* (1995) for a full description of the microzooplankton module.

Marine ecosystem models have a comparatively long pedigree which is thoroughly reviewed in Fransz *et al.* (1991b). Similarly, Fransz *et al.* (1991a) review the field studies of zooplankton in the North Sea.

Most models have concentrated upon nutrient primary production questions rather than focusing on the zooplankton community. In such models, only the magnitude of the grazing pressure is important. Consequently, the description of the higher trophic levels can be crude in comparison with that for the autotrophs and abiological processes. In the simplest formulation, grazing upon phytoplankton is represented as a constant or density-dependent proportionate mortality. A more realistic approach involves using experimental observations to derive forcing functions in place of a dynamic representation of grazing mortality (Radach, 1983; Fransz & Verhagen, 1985). The limitation of this approach is that the system is assumed to be in a quasi-equilibrium; it is therefore inadequate where one is seeking to answer questions about the long-term impact of progressive disturbance (*e.g.* eutrophication), particularly if any of the interactions between phytoplankton and zooplankton are non-linear. With this limitation in mind, several fully dynamic phytoplankton-zooplankton models have been developed (*e.g.* Kremer & Nixon, 1978; Ross *et al.*, 1993; Baretta & Ruardij, 1988). These all make some attempt to develop a mechanistic description of the relationship between food abundance and the rates at which zooplankton consume the food, grow and recycle nutrients.

There are two distinct categories of zooplankton models: individually based and biomass models. Individually based models aim to derive a description of the community dynamics based upon descriptions of the behaviour of the (average) individual zooplankton. Frequently, they include some description of the population's age-structure as well as individual abundance (Steele & Frost, 1977; Fransz, 1981). These models have the merit of being based upon a biologically tangible representation. Unfortunately, most zooplankton communities are composed of many species. If these are to be described using an individually based model, then there are three possible approaches. Firstly one could introduce separate equation sets for each species. Secondly one could argue that the community is dominated by just one species and choose to model only this species. Thirdly, one could use a single equation set with parameters derived from some weighted average of the parameters appropriate to each species in the community. At first glance, this latter approach is attractive. However, we have no idea what form the weighting function should take, and more importantly, community-averaged parameters typically yield a physiologically unrealistic composite individual.

In contrast, biomass models make little attempt to relate dynamics to the behaviour of an individual. They adopt a phenomenological approach in which feeding rates *etc.* are expressed per unit of mass rather than per individual and thus can more readily be parameterized from field studies of community consumption rates *etc.* Within the context of ERSEM they have an additional advantage. In common with the general approach adopted within ERSEM the mesozooplankton submodel aims to describe the standing crops of mesozooplankton and the fluxes into and out of the mesozooplankton as measured over large volumes. Thus, the most appropriate data against which to compare the results of the model will be those derived from large volume net hauls, the data from which are usually expressed in terms of biomass.

Biomass models are open to criticism on a number of grounds, notably because a given biomass may be composed of many small individuals or rather fewer large individuals. Under some circumstances this distinction becomes crucial; for example because both per capita consumption and metabolism rates are non-linear functions of weight (Huntley & Boyd, 1984). Nonetheless, biomass models have successfully been used to reproduce the quantitative dynamics of zooplankton in enclosed water columns (Anderson *et al.*, 1987) and in several hydrodynamically very different sea-lochs (Ross *et al.*, 1993a, 1993b, 1994).

Two further points constrained our choice of zooplankton model. Firstly, because of the great overall complexity of the ERSEM, we were aware of the risk that in an overly complex zooplankton model it would be extremely difficult to disentangle cause and effect when it came to interpreting the model's predictions. Perhaps more importantly, similar reasoning had dictated that the representation of the phytoplankton be extremely coarse (functionally, all members of the phytoplankton are considered to be representable as either an archetypical flagellate, or an archetypical diatom). Since the representation of the phytoplankton community is so coarse and the spatial structure of the model so crude, any attempt to build a more finely resolved zooplankton model would require that we introduce mechanisms other than food limitation if we are to avoid one class excluding others through competition. There is little convincing evidence for such mechanisms (at least at the spatial scale we are considering) and we therefore chose to subdivide all members of the mesozooplankton community into one of two classes: omnivore or carnivore. We represent each class using a biomass-only model. This 'hides' the problem associated with parameterizing an individually based model when the species composition is so complex and differs so greatly between the various regions of the North Sea. We chose an omnivore/carnivore classification for two reasons: firstly, we feel that it is probably the most important distinc-

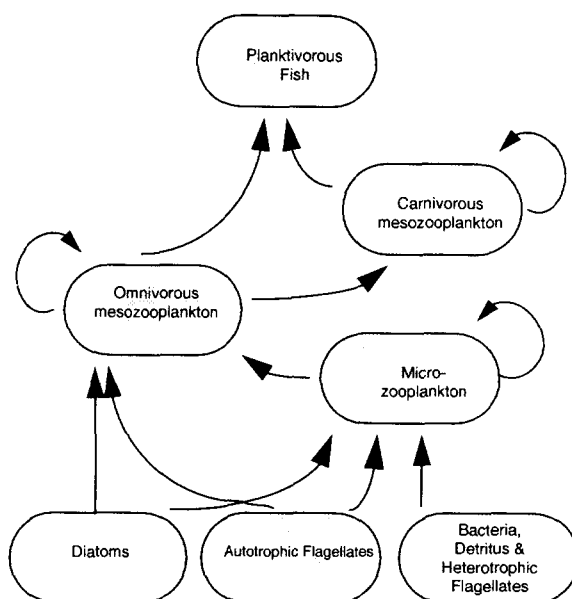


Fig. 2. A schematic representation of the planktonic food web assumed within the ERSEM.

tion between the many constituent species of the mesozooplankton in so far as dynamics are concerned. Secondly, since the carnivorous species are larger than the omnivorous ones, this partitioning of the community also captures some aspects the community's inherent size structure.

In structure, the zooplankton model is similar to that used by Ross *et al.* (1993a, 1993b), but like Anderson *et al.* (1987) we assume the zooplankton to have fixed internal elemental quotas. Copepods are the dominant constituent of the omnivorous group but the carnivorous group is less easy to characterize. The dominant taxon in this group is very much more variable in both time and space. The carnivorous guild includes copepods such as *Pareuchaeta*, annelids such as *Tomopteris*, and gelatinous zooplankton such as chaetognaths and cnidarians.

2. VALIDATION DATA

To validate the performance of the ERSEM with respect to its predictions of zooplankton dynamics we must compare the model's output with field observations of standing stocks of zooplankton, daily production *etc.* Ideally, we require contemporaneous, and continuous measurements of zooplankton abundance *etc.* throughout the North Sea. We are aware of only two data sets which span the entire North Sea: data from the Continuous Plankton Recorder surveys (CPR) and data provided by Krause & Martens (1990). Unfortunately, this latter set provide one-off

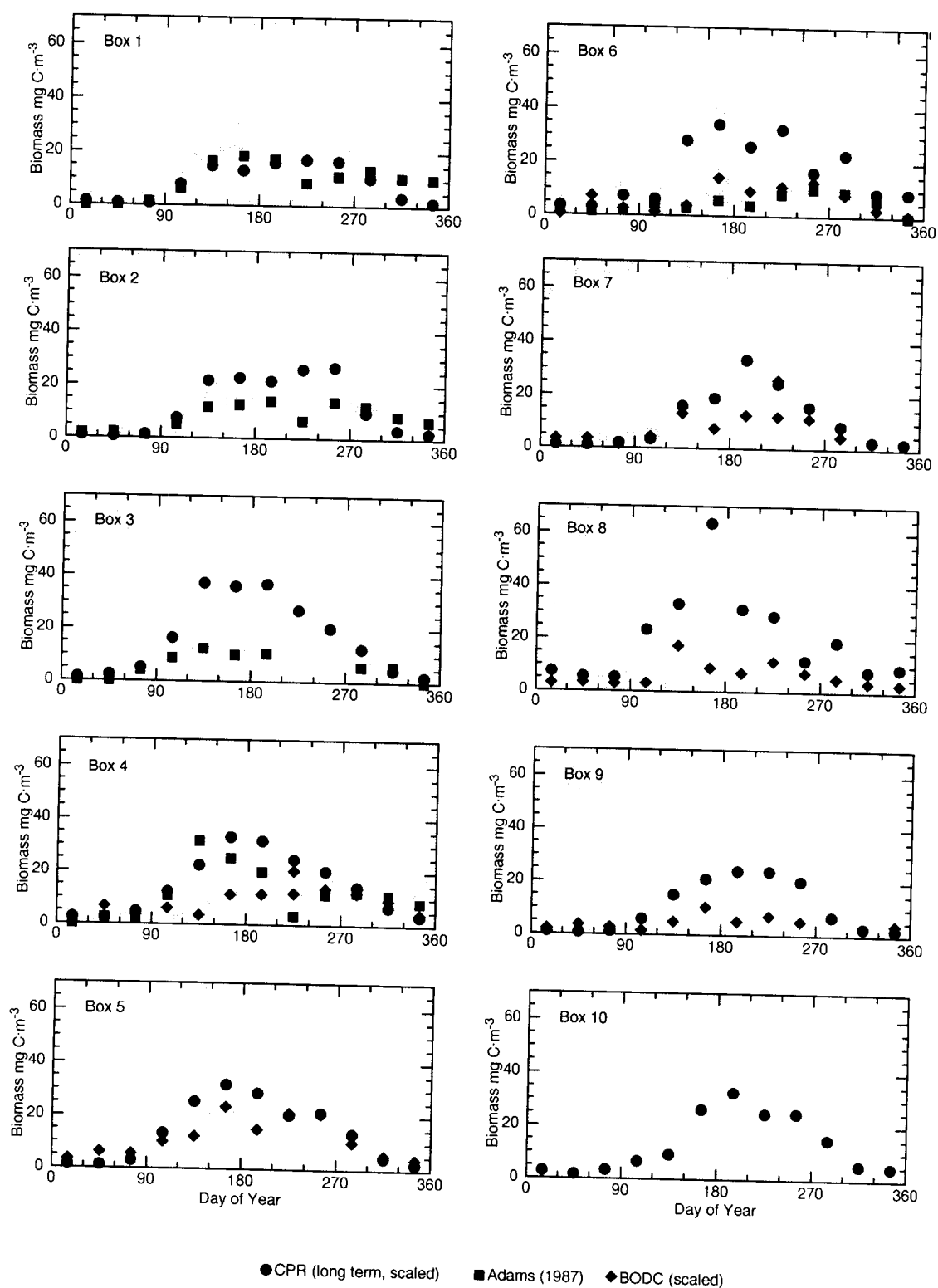


Fig. 3a. Observed seasonal abundance patterns for omnivorous mesozooplankton.

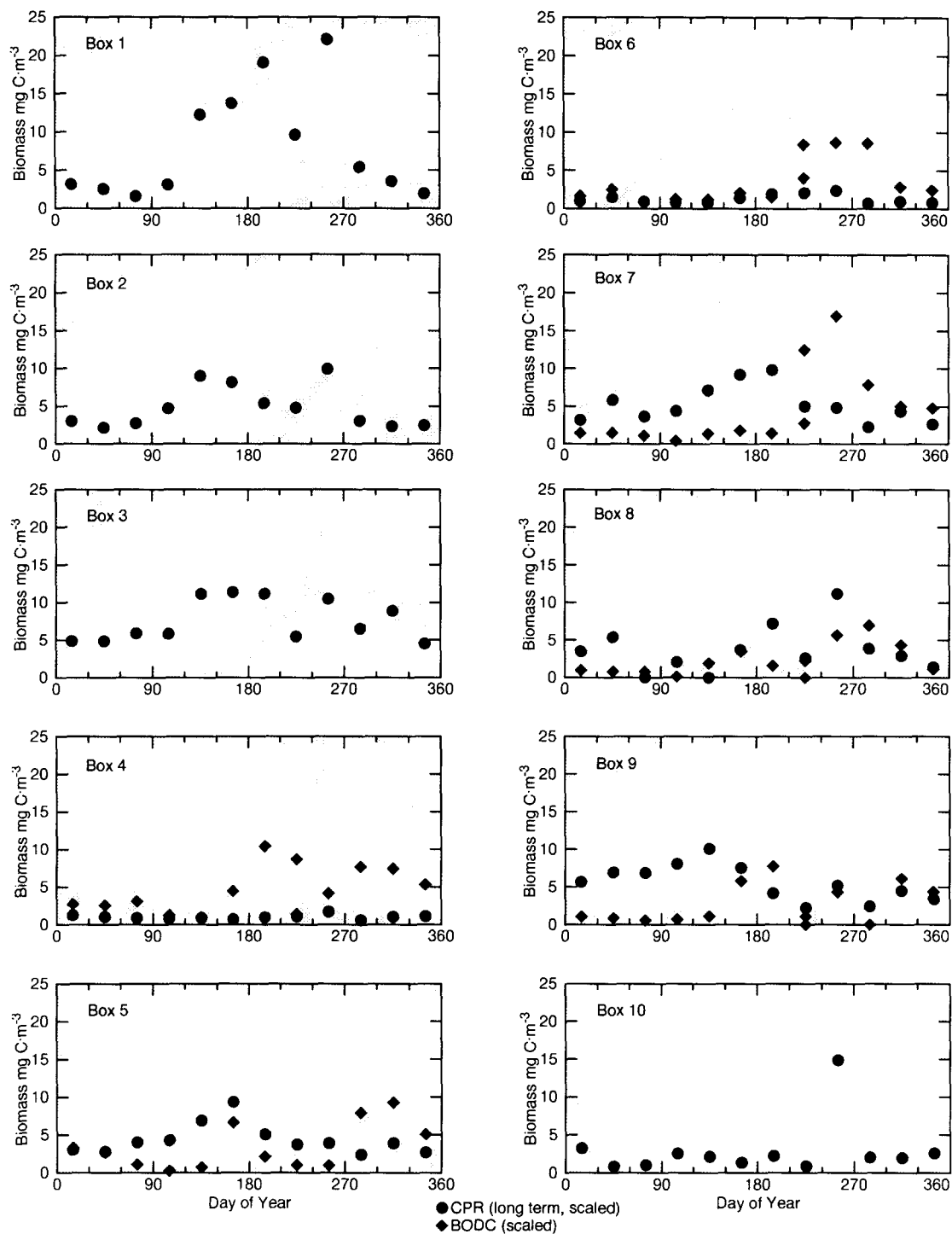


Fig. 3b. Observed seasonal abundance patterns of carnivorous mesozooplankton.

'snap shot' measurements in the spring of 1986 and the winter of 1987 only and we do not consider them further.

The CPR data are frequently criticized on a variety of grounds: particularly inappropriate mesh size and sampling depth. It is often argued that the CPR provides good estimates of the relative abundances of certain taxa but that it cannot be used as a direct quantitative measure of zooplankton abundance. It is certainly true that the CPR is biased towards catching only comparatively large zooplankters, but the degree by which it undersamples the smaller plankton is surprisingly consistent. A comparison of the zooplankton-biomass estimates from several detailed studies (FLEX 76: Krause & Radach, 1980; Williams & Lindley, 1980a, 1980b; REFLEX 83: Fransz & Diel, 1984; ACE: Hay *et al.*, 1991 and the Oyster ground area: Fransz *et al.*, 1984) with those predicted from the appropriate CPR data indicates that the CPR catches approximately 25% of the omnivore biomass and about 60% of the carnivore biomass. These figures are consistent with the detailed analyses of the sampling efficiency of the CPR mesh for different zooplankton size fractions (Robertson, 1968). Thus, it seems that CPR data can be used to derive accurate reconstructions of the zooplankton's seasonal biomass dynamics. The CPR data were used to derive mean monthly counts of the dominant planktonic organisms in each ERSEM box between 1953 and 1990. The data are approximately log-normally distributed and, in addition the underlying population dynamic processes of reproduction, mortality and emigration are multiplicative (though immigration is additive). Therefore it is appropriate to log transform the data though this requires that zeros be excluded. All analyses were based upon these (natural) log-transformed counts.

Reliable seasonal and trend estimates may be derived only if missing and zero values are randomly distributed throughout the year. This is not always the case, particularly for the rarer taxa (G-test, 5% significance level). To minimize the bias introduced by this seasonality we adopted an iterative method to estimate the trend and seasonality. Trend was first estimated using a 12-month moving average smoother. This trend was subtracted from the log counts, and the average value in each month calculated. Ideally, these should sum to zero, but because of seasonality in the distribution of zeroes, and missing values, and imperfect detrending this was not always the case. The difference between the twelve-monthly sum and zero was calculated and divided by 12 to yield a 'mean monthly deviation'. This was subtracted from each monthly factor and added back onto the trend values. This provided a first estimate of the seasonal component in each time series. The original time series was de-seasonalized by subtracting this first estimate of the seasonality from it. After this first step we re-estimated a long-term trend by applying a

LOWESS (locally weighted, linear smoothing) filter to the de-seasonalized data. The filter window was 15% of the data, which corresponds to approximately six years where there are no missing values. Seasonal components were recomputed by subtracting the LOWESS trend estimates from the original log-transformed counts and calculating monthly averages, again with the zero sum constraint. In general, this iterative technique converged after two or three passes. The 'typical' monthly abundance of each taxon in each region was then derived by exponentiating the sum of the average value of the trend curve and the corresponding average monthly deviation from this. This approach yields a count which approximates the geometric average monthly abundance. In conjunction with estimates of the weight of individual zooplankters in each taxa (Appendix 1), these numbers were used to derive zooplankton biomass estimates which were rescaled by the factors described earlier to account for the sampling bias of the CPR mesh.

In addition to these whole North Sea data sets, Adams (1987) provides long-term average, depth integrated bi-weekly mesozooplankton biomass estimates for several areas of the northern North Sea. Zooplankton counts for the dominant copepod species and chaetognaths in the southern North Sea between August 1988 and August 1989 are also available and have been used to derive biomass estimates (NERC North Sea data base (BODC)).

In Fig. 3 we plot the (re-scaled) CPR estimates of zooplankton biomass together with the results from Adams (1987) and the (re-scaled) BODC data. Though these biomass estimates are accompanied by substantial (but unknown) uncertainty, some differences between the seasonal patterns in the various boxes are apparent.

The relative and seasonal abundance patterns for the omnivorous zooplankton appear similar throughout the North Sea. There is some evidence that the spring increase occurs earlier, and the autumn decline later in northern waters, and that both are more rapid there. The peak abundance occurs one to three months later in northern waters (July to September, compared with June to August in southern waters).

In contrast, the latitudinal variations in the dynamics of those carnivorous species which the CPR samples are very striking. Most obviously, the carnivore biomass is five to ten times greater in the northern waters of the North Sea than in the southern waters. In addition, whilst there appears to be a marked seasonal cycle of abundance in boxes 1 and 2 (northern North Sea), there is less of a seasonal cycle elsewhere. In all regions what seasonality there is, is driven by seasonal changes in the weight of individuals, rather than changes in the population density. This should not be too surprising since many of the carnivores are long-lived. In addition, the CPR

grossly undersamples the gelatinous carnivores, the dynamics of which do appear to be more tightly linked to the omnivorous zooplankton (Möller, 1979). Indeed, in both the CPR and the similar BODC data, the chaetognath dynamics are closely coupled with those of the omnivorous zooplankton.

None of the data show evidence of a spring zooplankton bloom at the very large spatial scale we are considering here. This does not appear to be a consequence of any 'smearing' arising from averaging across years (Broekhuizen & McKenzie, 1995). Rather, the raw data upon which Adams (1987) bases his figures indicate that the bloom is a very small-scale phenomenon. In spring, particularly, the distribution of biomass estimates is very skewed (Marine Laboratory Aberdeen - MLA, unpubl. data). At any time, most of the sea harbours a relatively low biomass of zooplankton; only a few, comparatively small areas are 'in bloom'. In contrast, during summer, though the local maximum densities may be lower than those observed in spring, these are superimposed upon a much higher background level. The CPR mesh is too coarse to catch the naupliar stages of most copepod species and we cannot rule out the possibility of a large-scale spring naupliar bloom which we fail to account for by using a time-independent 'rescaling' factor. If a naupliar bloom does occur, it must be accompanied by correspondingly elevated naupliar per-capita mortality rates, or it would also be manifest in the later developmental stages which the CPR samples more reliably.

If the ERSEM is to provide a suitable tool to understanding the North Sea ecosystem, then it must be able to mirror these very coarse-scale differences in the dynamics of the omnivorous and carnivorous mesozooplankton.

Comparison of model predictions with spatially resolved time series data on the biomass of biological constituents in the North Sea provides one test of the model's performance. A further, and possibly, more powerful, test is provided by making comparisons of the predicted and measured fluxes between various of the system's dynamical units.

Though many measurements of photosynthesis, zooplankton feeding and growth rates have been carried out in the North Sea, only rarely have a wide-ranging suite of such measurements been carried out simultaneously such that a coherent subset of the biological fluxes in ERSEM can be assembled for a particular site. Two such investigations were carried out during the 1988/1989 period selected for evaluation of the ERSEM (Heath *et al.*, unpublished data).

In an as yet unpublished investigation of the northern North Sea, M.R. Heath and co-workers from MLA made simultaneous measurements of the carbon biomass of all the ERSEM phytoplankton and zooplankton categories over the period 12 to 24 June 1988.

Phytoplankton biomass at 20 m and 40 m was estimated from microscopic analysis of water samples

and cell volume:carbon weight conversions. Chlorophyll was measured by *in situ* fluorescence and spectrophotometric analysis of pigments extracted in 90% acetone. Production of soluble and particulate matter by phytoplankton was estimated by incubation experiments with radio-labelled carbon.

Zooplankton biomass was measured by a combination of techniques. Larger plankton were sampled using a Gulf III towed sampler with a 200 μm mesh. Vertical distributions of meso- and microzooplankton were determined by filtering 30 dm^3 of pumped water through a 30 μm mesh at each sampling depth. Sub-samples of the Gulf III material and all of the pumped material were identified to species and stage. Carbon biomass was determined from length-weight relations. Nanozooplankton were enumerated together with the phytoplankton in sedimented samples.

Copepod ammonia and egg production rates were estimated using incubation experiments. Zooplankton consumption rates were estimated using gut contents analyses and a gut evacuation model.

Using these data Heath has calculated the *in situ* fluxes between the phytoplankton, microzooplankton and mesozooplankton groups. The study in June 1988 included five sites in areas 1 and 2 of the ERSEM. In addition to these data, unpublished results were available from a similar investigation carried out by the Marine Laboratory Aberdeen during the period 1 to 15 April 1989. Methods were identical to those used in June 1988, and six sites were investigated in ERSEM boxes 4, 6 and 10. We will compare the model's predictions of standing crop, daily production, and intercompartment flux with these data.

3. THE MODEL

A formal mathematical description of the zooplankton model is presented in Appendix 2. Here we present a verbal description of the model, together with the assumptions which underlie it.

For conceptual clarity, we discuss biomass changes which emerge from events occurring at the physiological level (*i.e.* individual growth/starvation) and those which occur at the demographic level (*i.e.* birth, death) separately. Additionally, in a spatially resolved, open system such as the North Sea model, we must account for biomass changes resulting from net immigration/emigration.

We consider the mesozooplankton as passive passengers within the water masses. The rate of immigration/emigration is determined by the net rate of water exchange between adjacent boxes. Lenhart *et al.* (1995) describe the manner in which water exchanges are calculated for the ERSEM simulations. Given the spatial resolution of the ERSEM it is reasonable to assume the zooplankton to be passengers upon the horizontal water currents. It is less realistic to assume that the zooplankton make no vertical

movement independent of the vertical water movements. Many species of zooplankton exhibit marked diurnal vertical migrations, but they occur at a finer time scale than that at which the model is designed to operate; secondly, though the migration often results in temporary aggregation upon highly localized maxima in the phytoplankton vertical profile, these occur at a finer spatial scale than the model represents. Finally, since transport across box boundaries is calculated on a daily basis, it would be an extremely complex problem to ensure that the appropriate quantities of zooplankton were transported between boxes if the model zooplankton were to exhibit diurnal vertical movement. This is unfortunate since vertical migrations, together with depth dependent horizontal water flows may, in reality, have a major influence upon the horizontal transport of zooplankton populations.

The omnivore and carnivore modules differ in two respects only: the composition of each guild's diet and the parameterization of the various functions in the model. Since we assume the carnivores to feed primarily upon omnivores, we expect to find their predicted dynamics to be strongly coupled to those of their prey which contrasts with the weak coupling observed in the CPR data.

3.1. FEEDING AND ASSIMILATION

Omnivores are considered to be filter feeders. Their diet consists of diatoms, flagellates, microzooplankton and smaller members of their own guild. We will refer to this latter component as cannibalism, but this should not be understood to imply that all adult omnivorous mesozooplankton indulge in cannibalism *sensu stricto*.

The carnivorous guild cannot be so easily characterized. Some of its members are filter feeders, others are raptorial, some actively pursue their prey while others adopt a sit and wait strategy. Their primary food source is omnivorous zooplankton, but we consider that the carnivores will also indulge in 'cannibalism'.

We assume that neither the omnivores, nor the carnivores exhibit any fixed or dynamic preference for one prey taxon over any other. Each prey taxon is consumed in proportion to its instantaneous relative abundance in the local environment. One consequence of this assumption is that a consumer can be maintained at very high abundances by one food source and, by virtue of its high abundance, inflict a comparatively high mortality upon other, rarer members of its diet. In view of the diversity of species in both the consumer and prey classes, we felt it would be unrealistic to introduce any switching behaviour.

We assume that an individual belonging to trophic group X has a (carbon) consumption rate $I_{X,C}$ ($\text{mg}\cdot\text{d}^{-1}$) which is given by a type II functional response (Holling, 1959) to the total food concentration meas-

ured in units of carbon. Both the search volume and the handling time (inverse of the maximum consumption rate) have been assumed to be independent of prey type so the loss of material from prey group Y to a particular predator group is given by the product of the predator group's total ingestion rate and the fractional (carbon) biomass in the predator group's diet represented by prey group Y.

We are attempting to model growth and feeding rates averaged across very large areas, effectively ignoring local heterogeneities and though several authors have reported evidence for feeding thresholds, or other less extreme examples of type III functional responses (e.g. Frost, 1975; Reeve & Walter, 1977), these are phenomena which arise at the small scale and it is not clear how such behaviour could properly be incorporated into our large scale model. In addition, we note that other authors have found no evidence that a type III response provides a better description of the functional response than does the type II model (e.g. Corner *et al.*, 1976; Ambler & Frost, 1974; Libourel-Houde & Roman, 1987). Finally, though the assumption that search volume is prey independent may be adequate for filter feeders, it is more questionable in the case of raptorial feeders.

A substantial fraction of the material which is consumed is not incorporated into body tissues. Much of it is lost as faeces. Additional losses are likely to occur because we have assumed the zooplankton to have fixed internal nutrient quotas. The ratio of nitrogen and phosphorus to carbon in the food which crosses the gut wall is unlikely to match the ratio within the zooplankton, and the excess of the two non-limiting elements in the ingested food must be excreted if the zooplankton is to maintain its internal nutrient quota.

In determining the assimilation rates for carbon, nitrogen, phosphorus and silicon we make the following assumptions. We define a zooplankton's activity costs to be those associated with processing ingested food and therefore, proportional to the rate at which it ingests carbon. We assume that the zooplankton meets these costs out of the carbon it has just ingested, but prior to it being incorporated into tissues. In effect, the assimilation efficiency for nitrogen and phosphorus is higher than that for carbon. The costs associated with gathering the food are subsumed within 'basal' metabolism (see below). We justify this on the grounds that filtering activity is often closely associated with other 'background' activity such as swimming. We assume that a fixed proportion (f) of the ingested material is lost to faeces. This proportion is the same for carbon, nitrogen and phosphorus and equal to one for silicon.

3.2. RESPIRATION AND MORTALITY

An individual's metabolic rate is usually found to be a geometric function of its weight, with an exponent

between 0.7 and 0.8 (e.g. Peters, 1983; Huntley & Boyd, 1984); however, in a pure biomass model such as this one, we have no knowledge of the population's weight distribution. Thus, the only defensible assumption is that the population's basal metabolic rate is proportional to its biomass. Additionally, in order to simplify the calculations associated with ensuring that the zooplankter's internal nutrient quota remains constant we choose to assume that basal metabolism accounts for the same fractional loss for each of carbon, nitrogen and phosphorus.

A zooplankter may die as a result of any one of many causes: senescence, infection, predation by invertebrates or fish, *etc.* The manner in which fish predation is implemented is described in Bryant *et al.* (1995). Here we discuss our implementation of mortality from causes other than predation by fish. An individual zooplankter may succumb to predation by a fellow member of the mesozooplankton. Individual omnivores may succumb to cannibalism or predation by a carnivore. A carnivore can succumb only to cannibalism. Cannibalism introduces a density (biomass) dependent mortality, but this is unlikely to be dynamically significant since the ratio of 'self' to 'other' in the diet is usually small.

In addition to this predation mortality we have implemented a mortality term to cover death from other causes, such as senescence. Most of these are likely to be density independent, and this mortality is represented as a fixed proportionate loss from each of the mesozooplankton groups. Material lost through this latter mortality is deposited into the pelagic detritus.

3.3. TEMPERATURE DEPENDENCE

Up until this point, we have talked as if the coefficients governing metabolism and mortality were temperature independent. In practice this is rarely the case (Peters, 1983; Huntley & Boyd, 1984). There are

a variety of models of the influence of temperature upon feeding rate, metabolism *etc.* most of which yield similar results over the temperature range found in the North Sea. Consequently, we have adopted the standard geometric model (Appendix 1, Eq. 3) with a Q10 of 2. Fortunately, the seasonal and spatial temperature range in the North Sea is comparatively narrow; thus, even if this assumption is incorrect it is unlikely to make any substantial difference to the quantitative predictions of the model.

3.4. PARAMETERIZATION

We have already touched upon the principal problem associated with parameterizing a model of this type: that of deciding how to represent the function of a behaviourally and physiologically diverse community in just one state variable. We concluded that, even if the data were available, it would be misleading to work with rate parameters derived from 'weighted estimates' derived from the corresponding rates for individual members of the community. Rather, one must choose either to develop explicit representations for each component, or to represent just one component explicitly, hiding the impact of the remaining components in a forcing function, or ignoring them altogether.

As far as possible we have chosen to adopt the latter approach; there are, however, comparatively few data sets from which parameter estimates may be drawn. Thus, subjective judgements become an inevitable integral part of the process.

There are ten parameters associated with each of the two mesozooplankton groups. Of these, two differ between the two groups and eight are common to both guilds (Table 1).

The most difficult parameters to estimate are those associated with feeding: the search volume and the handling time. These can be estimated from standard experiments on consumption rate *versus* food con-

TABLE 1
Parameter estimates for the mesozooplankton.

parameter	symbol	units	value		source
			omnivores (Zi=Z4)	carnivores (Zi=Z3)	
search volume	V_{zi}	$\text{m}^3 \cdot \text{mg C}^{-1} \cdot \text{d}^{-1}$	0.006	0.008	Fitted
handling time	τ_{zi}	$\text{d} \cdot \text{mg C} \cdot \text{mg C}^{-1}$	0.5	0.5	Fransz <i>et al.</i> (1991a)
activity respiration	r_{zi}	$\text{mg C} \cdot \text{mg C}^{-1}$	0.05	0.05	Kjørboe <i>et al.</i> (1985)
faeces production	f_{zi}	$\text{mg C} \cdot \text{mg C}^{-1}$	0.35	0.35	Kjørboe <i>et al.</i> (1985)
basal metabolism	b_{zi}	$\text{mg C} \cdot \text{mg C}^{-1} \cdot \text{d}^{-1}$	0.02	0.02	Huntley & Boyd (1984)
background mortality	m_{zi}	$\text{mg C} \cdot \text{g C}^{-1} \cdot \text{d}^{-1}$	0.02	0.01	Corkett & MacLaren (1979)
N:C ratio	κ_n	$\text{mmol N} \cdot \text{mg C}^{-1}$	0.015	0.015	Båmstedt (1986)
P:C ratio	κ_p	$\text{mmol P} \cdot \text{mg C}^{-1}$	0.00167	0.00167	Båmstedt (1986)
coefficient of temp. function	Q	-	2	2	Huntley & Boyd (1984)
exponent of temp. function	ϕ	-	0.1	0.1	Huntley & Boyd (1984)

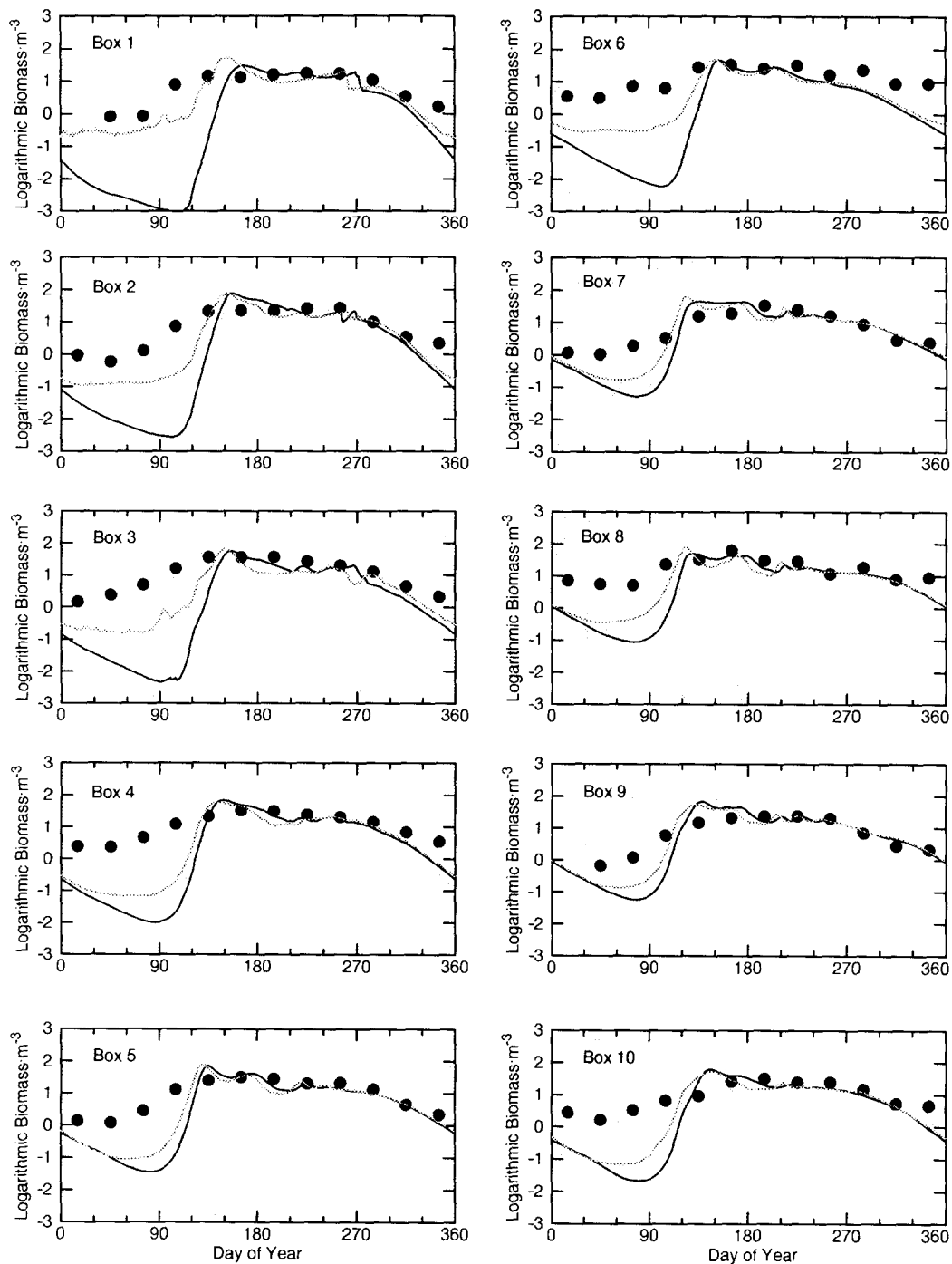


Fig. 4a. CPR-measured $^{10}\log$ seasonal abundance (mg C m^{-3} ; circles) of omnivorous mesozooplankton together with predictions of omnivore abundance in the presence of static fish loadings. solid line: reflecting boundary conditions; dashed line: explicit boundary conditions.

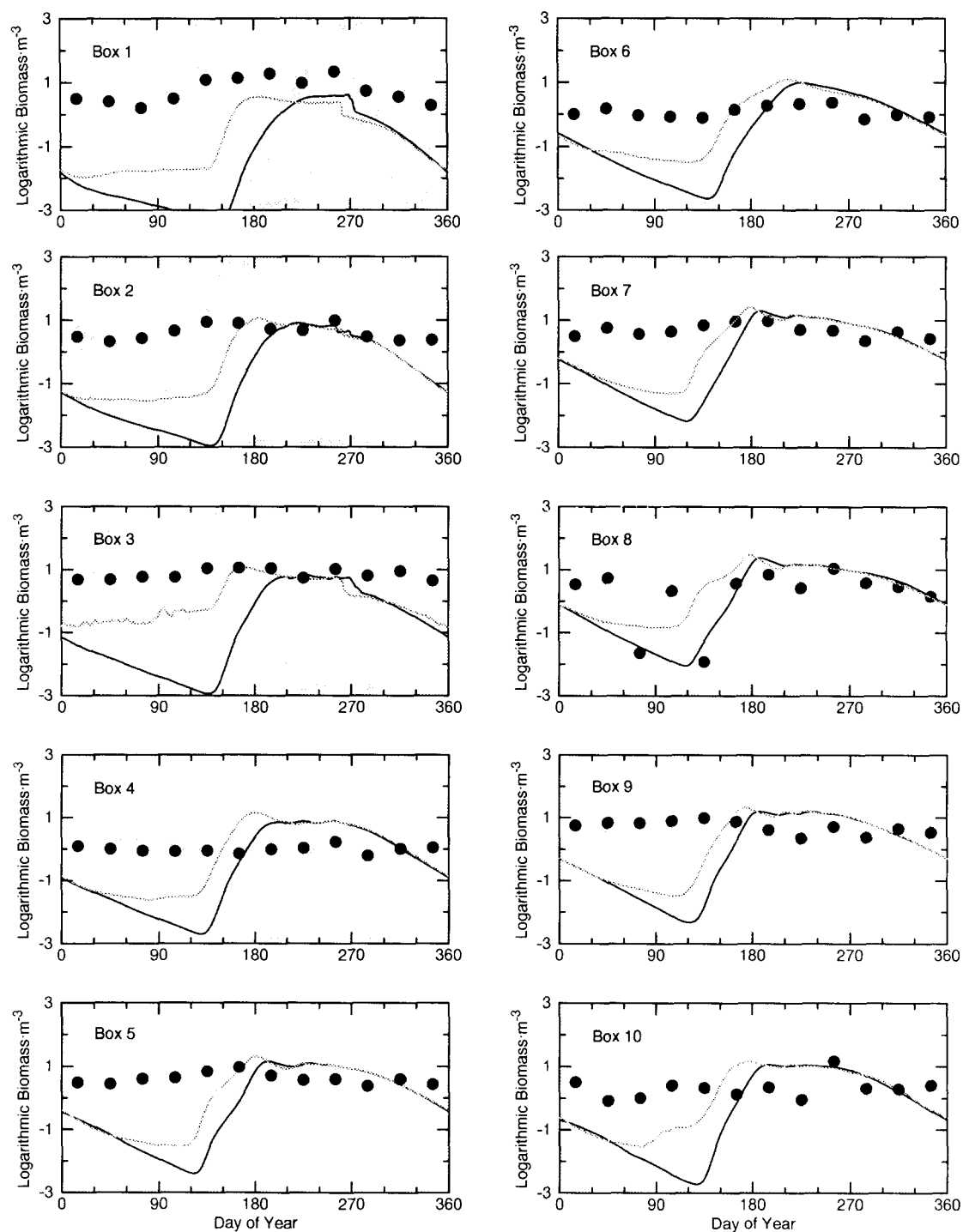


Fig. 4b. CPR-measured $^{10}\log$ seasonal abundance ($\text{mg C} \cdot \text{m}^{-3}$; circles) of carnivorous mesozooplankton together with predictions of carnivore abundance under static fish loadings. solid line: reflecting boundary conditions; dashed line: explicit boundary conditions.

centration; unfortunately, the results of such experiments are notoriously variable. Only a small part of this variation is attributable to the different experimental methods. More importantly, it seems that individual feeding rates also appear to depend upon food quality, past feeding success and time of day (Gamble, 1978; Daro, 1980, 1986).

Based upon a review of experimental data for a wide variety of zooplankton species, Huntley & Boyd (1984) conclude that search volume scales with (carbon) weight raised to the power 0.68 with a scaling coefficient of approximately 0.001. Whether this value is relevant to the natural situation is unclear: random search in a heterogeneous environment reduces the apparent search volume (Ruxton *et al.*, 1995). On the other hand, if the zooplankton are able to hold station within microhabitats harbouring a high prey density, their effective search volume is increased. The scaling coefficient quoted above, is approximately 70% of that derived from data for *Calanus finmarchicus* and *Temora longicornis* from data presented in Fransz *et al.* (1991a).

The data of Fransz *et al.* (1991a) suggest that maximum uptake ($\text{mg C} \cdot \text{individual}^{-1} \cdot \text{d}^{-1}$) scales with (carbon) weight raised to the power 0.66. This value is a little higher than that quoted for the freshwater cladoceran *Daphnia pulex* (Gurney *et al.*, 1990). The scaling coefficient for *C. finmarchicus* is approximately twice that for *T. longicornis*. We have used an intermediate value of 0.008.

A wide variety of authors have attempted to relate metabolic expenditure and size. Unfortunately, these data are often difficult to relate to one another because of differences in experimental procedure: fed *versus* unfed individuals, temperature *etc.* In the ensuing calculations we have adopted the parameter values proposed by Huntley & Boyd (1984), which are similar to those quoted by most authors. Huntley & Boyd (*op. cit.*) suggest that individual costs ($\text{mg C} \cdot \text{d}^{-1}$) scale with (carbon weight) raised to the power 0.8 with a scaling coefficient of around 0.03.

Having decided how search volume, handling time and metabolism scale with individual size, we must now derive parameters which can be related to population biomass. This requires that we make some assumptions about the size structure of the community. Data of this sort are still more difficult to come by, but a very rough measure could be derived by assuming the population stage structure to be static and using stage specific mortality rates (*e.g.* those from the Loch Ewe bag experiments; Gamble *et al.*, 1977) to estimate what the relative frequencies of the differing stage classes should be and subsequently to associate some (fixed) individual weight with each developmental stage. Note, however, that extrapolating mortality rates from bag experiments to the field situation is fraught with danger. For example, Hay *et al.* (1988) suggest that the larval herring population in their bags was unnaturally high, and therefore imposed an unnaturally high mortality upon the plankton community. Nonetheless, 'population' search volume, handling time, respiration and mortality rates and hence, rates per unit biomass have been estimated in this manner. We emphasize that the assumptions about the underlying population size structure play a key role in determining the eventual parameter estimates. Though the estimates derived in this manner provide a useful guide to the likely realistic range for each parameter, drawing a single value from this realistic range is the most subjective step in the parameterisation process.

We have assumed that the assimilation efficiency (activity respiration and absorption efficiency) is size independent. There is broad agreement that assimilation efficiency is in the region of 50% to 80% (*e.g.* Kiørboe *et al.*, 1985). We assume that 65% of ingested phosphorus and nitrogen is assimilated, and that the remainder is lost as faeces. Since we subtract an additional loss term (activity respiration) from the ingested carbon, only 60% of carbon is assimilated. Activity respiration is difficult to estimate, and this value (5% of ingested carbon) has been indirectly

TABLE 2

Characterizations of the observed (long-term CPR) and predicted omnivorous mesozooplankton dynamics in the presence of static fish loadings.

box	winter crop (mg C m^{-3})		summer crop (mg C m^{-3})		ratio		onset		summer maximum	
	obs.	pred.	obs.	pred.	obs.	pred.	obs.	pred.	obs.	pred.
1	1.27	0.05	15.51	18.93	12.21	378.60	April	May	August	June
2	1.26	0.08	23.46	36.94	18.62	461.75	April	May	September	June
3	2.03	0.10	33.36	26.07	16.43	260.70	April	May	May	June
4	2.79	0.20	29.82	30.57	10.68	152.85	April	May	June	June
5	1.63	0.44	26.18	23.94	16.06	54.41	April	May	June	May
6	5.12	0.17	30.85	24.31	6.03	133.00	May	May	June	June
7	1.52	0.51	25.67	26.34	1.69	47.66	May	May	July	June
8	7.30	0.82	41.20	26.49	5.64	32.30	April	May	June	May
9	1.27	0.63	23.10	27.75	18.19	44.05	April	April	July	May
10	3.05	0.56	27.92	27.71	8.56	49.48	May	May	July	June

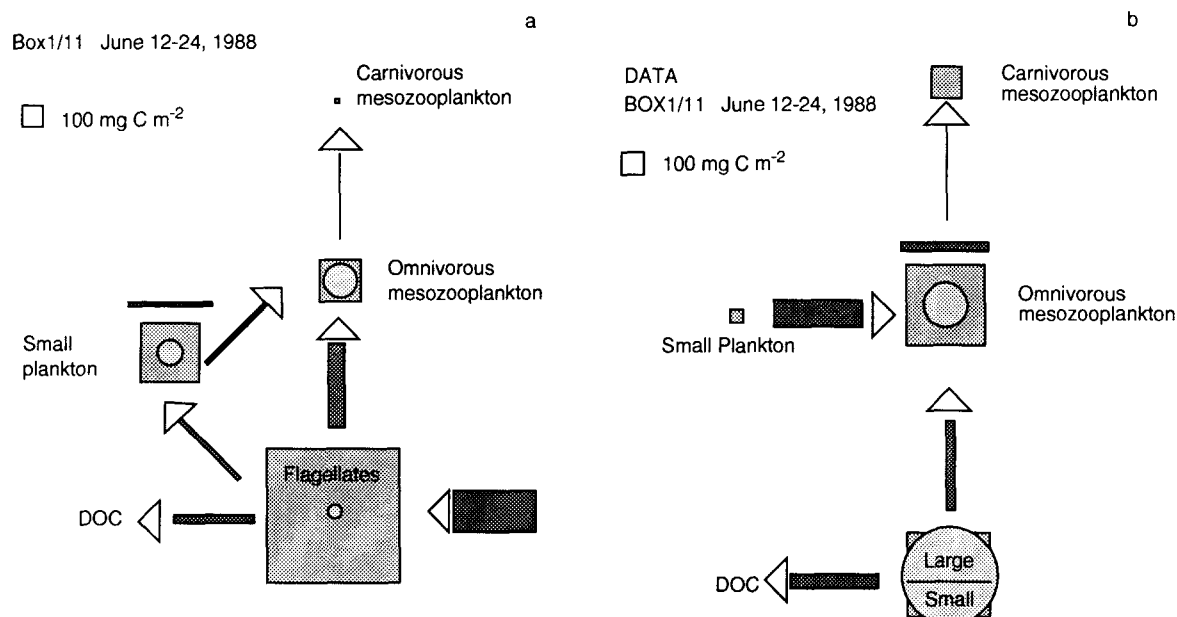


Fig. 5. a. Predicted and b. observed abundance (squares, mg C m⁻²), production (circles, mg C m⁻² d⁻¹) and inter-group fluxes (arrows, mg C m⁻² d⁻¹) in box 1, between June 12 and 24, 1988. Horizontal bars above boxes indicate the magnitude of the cannibalism flux.

estimated. It approximates the difference between the metabolic rates of actively feeding and unfed copepods.

An individual zooplankton may succumb to one of a variety of agents of mortality. In the model we deal explicitly with two sources: predation by another zooplankton and predation by fish (see Bryant *et al.*, 1995). All other agents of mortality are lumped together and represented as a temperature dependent fractional loss. Mortality rates are notoriously difficult to estimate. Hay *et al.* (1988) estimate that naupliar and copepodite death rates amounted to

25% and 3% per day, respectively, but comment that much of this mortality resulted from the unnaturally high herring larval densities in their enclosures. Using these death rates, daily mortality amounts to 10-20% of biomass per day. These are exceptionally high values. More often, mortality is estimated to amount to about 5% of biomass per day (Corkett & MacLaren, 1979). Since we are representing fish predation explicitly, we use a rather lower figure of just 2% per day. This is lower than the population average derived from the stage-specific mortality rates, weighted by stage specific abundance, used in deriv-

TABLE 3

Characterizations of the observed (long-term CPR) and predicted carnivorous mesozooplankton dynamics in the presence of static fish loadings.

box	winter crop (mg C m ⁻³)		summer crop (mg C m ⁻³)		ratio		onset		summer maximum	
	obs.	pred.	obs.	pred.	obs.	pred.	obs.	pred.	obs.	pred.
1	2.56	0.01	14.13	1.12	5.52	112.00	May	July	June	September
2	2.57	0.04	6.11	3.66	2.38	91.5	-	June	June	August
3	4.76	0.05	9.34	3.36	1.96	67.2	-	June	May	August
4	1.13	0.09	0.93	4.53	0.82	50.33	-	June	June	August
5	2.86	0.27	6.03	8.31	2.11	30.78	June	June	December	July
6	1.11	0.17	1.79	3.74	1.61	22.00	-	July	June	August
7	3.88	0.39	8.02	10.99	2.07	28.18	-	June	July	July
8	3.46	0.54	4.51	12.76	1.30	23.63	October	June	February	July
9	5.33	0.35	4.64	10.90	0.87	31.14	-	June	September	August
10	2.23	0.16	1.49	7.46	2.62	46.63	October	June	September	August

ing the metabolic and feeding parameters. Recall, however, that Gamble *et al.* (1977) argued that the zooplankton mortality rates were unnaturally high as a result of the excessive numbers of herring larvae within their enclosures.

4. RESULTS

The zooplankton model, as described above forms one part of the standard ERSEM (version 5.2) and we will start by describing the (zooplankton) dynamics which this model predicts.

Complex models of the ERSEM type can have very long transients, particularly when the initial conditions are not well known, as is the case here. To reduce the transient behaviour, initial conditions were taken from the end values of a forty-year simulation which used the same annual forcing functions and transport year after year.

Fig. 4a presents the predicted omnivorous mesozooplankton dynamics under two scenarios: firstly assuming reflecting boundary conditions for the mesozooplankton at the external borders of the North Sea (solid line) and secondly, using explicit boundary conditions derived from CPR data for these areas. Fig. 4b presents the corresponding results for the carnivorous mesozooplankton. Quadratic interpolation was used to estimate daily biomass values from the monthly CPR values. The CPR data do not give any information regarding the abundance of zooplankton in the deeper layers of water and for simplicity we

have assumed that they were equally abundant throughout the water column. In each figure we also plot the corresponding biomass estimates derived from the long-term CPR data. We have chosen to focus our attention upon the long-term CPR data for three reasons: the data span the entire North Sea, a standard sampling technique has been applied throughout the North Sea, and these data come from large-volume, space-averaged samples and should correspond most closely with the spatial scales the ERSEM model aims to represent.

To focus discussion further, we have chosen several key features of the North Sea's zooplankton dynamics which we believe the model ought to be able to reproduce. These are: mean winter standing crop, mean summer standing crop, the ratio of summer to winter standing crops, and timing of the onset of population growth in the spring and month in which the average abundances is greatest. We define 'winter' to be December to February inclusive and 'summer' to be June to August inclusive. The month of the 'onset of spring growth' is defined to be the first month in which the monthly average abundance exceeds three times the mean winter crop. Tables 2 and 3 present comparisons of the observed and predicted values for each of these features when the model is run with static fish loadings.

The most obvious deviation between model predictions and observation is during the late winter months. Predicted winter standing crops of omnivores in northern waters are about 5% of the observed lev-

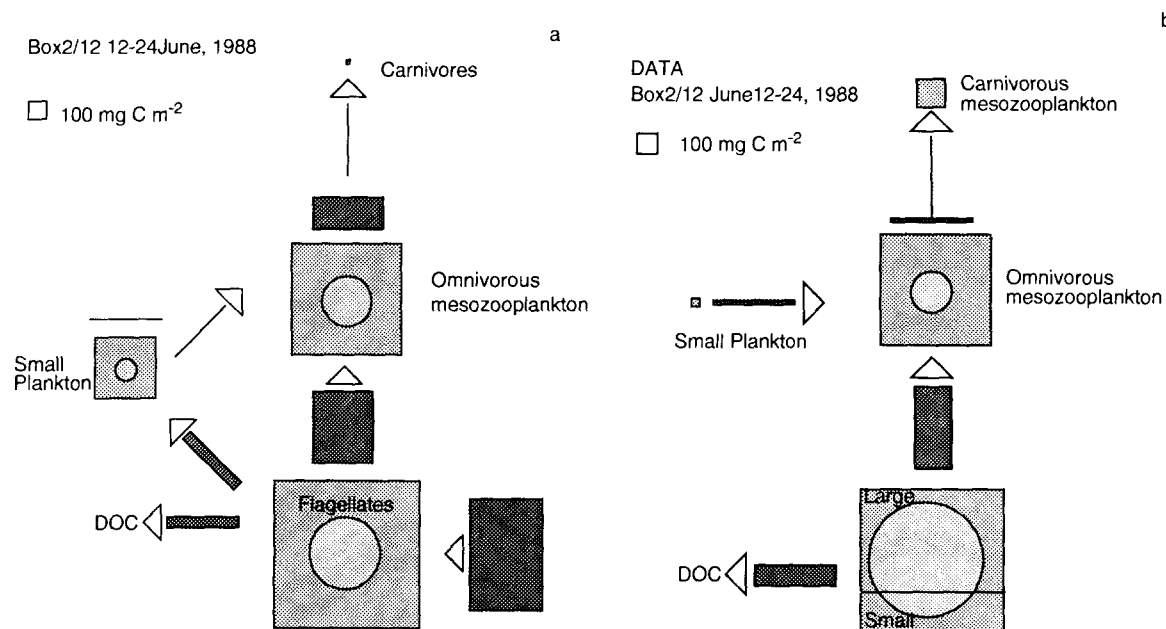


Fig. 6. a. Predicted, and b. observed abundance (squares, mg C m^{-2}), production (circles, $\text{mg C m}^{-2} \text{d}^{-1}$) and inter-group fluxes (arrows, $\text{mg C m}^{-2} \text{d}^{-1}$) in box 2, between June 12 and 24, 1988. Horizontal bars above boxes indicate the magnitude of the cannibalism flux.

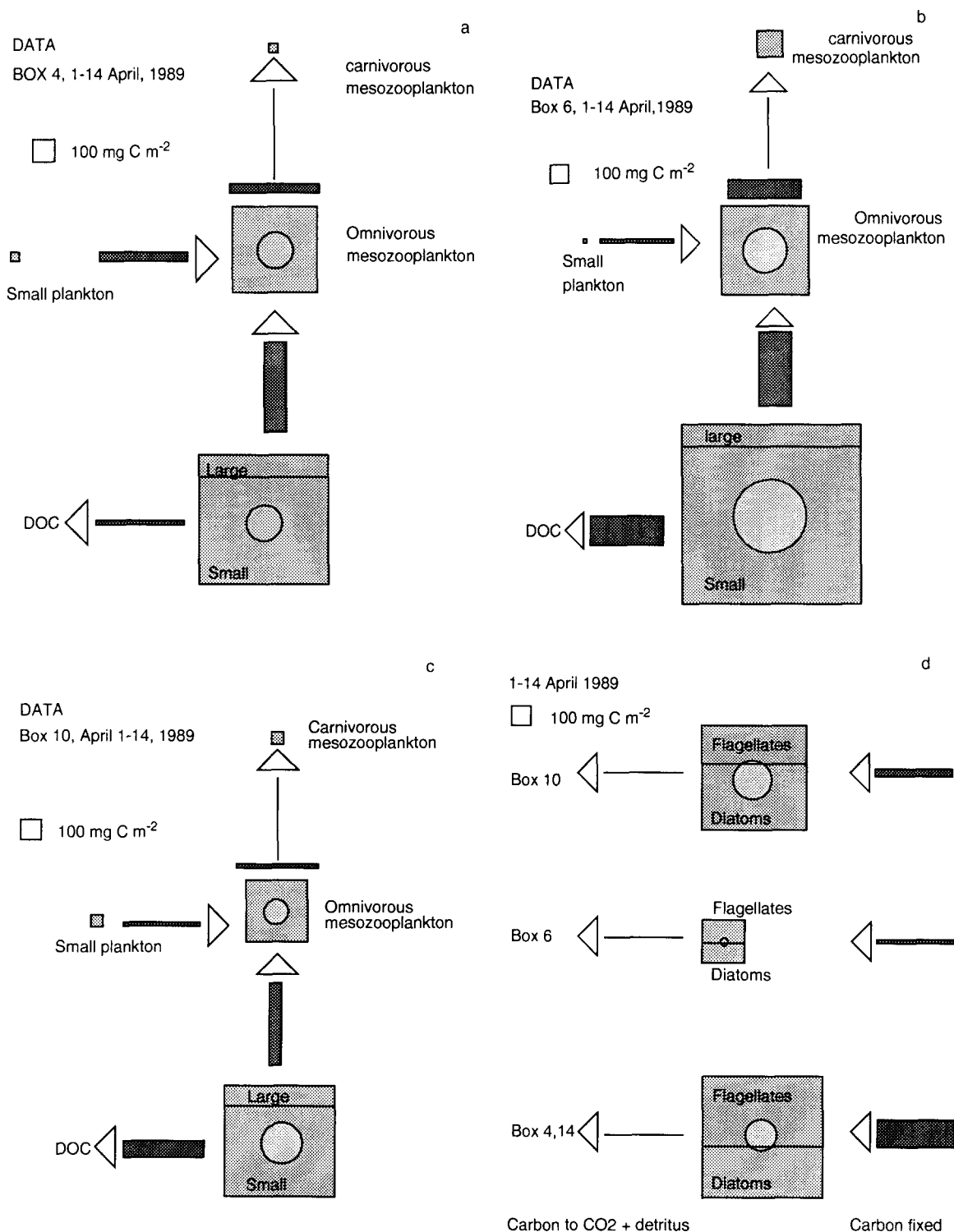


Fig. 7. a. b. c. Observed and d. predicted abundance (squares, mg C m^{-2}), production (circles, $\text{mg C m}^{-2} \text{d}^{-1}$) and inter-group fluxes (arrows, $\text{mg C m}^{-2} \text{d}^{-1}$) in boxes 4, 6 and 10, between April 1 and 14, 1989. Horizontal bars above boxes indicate the magnitude of the cannibalism flux.

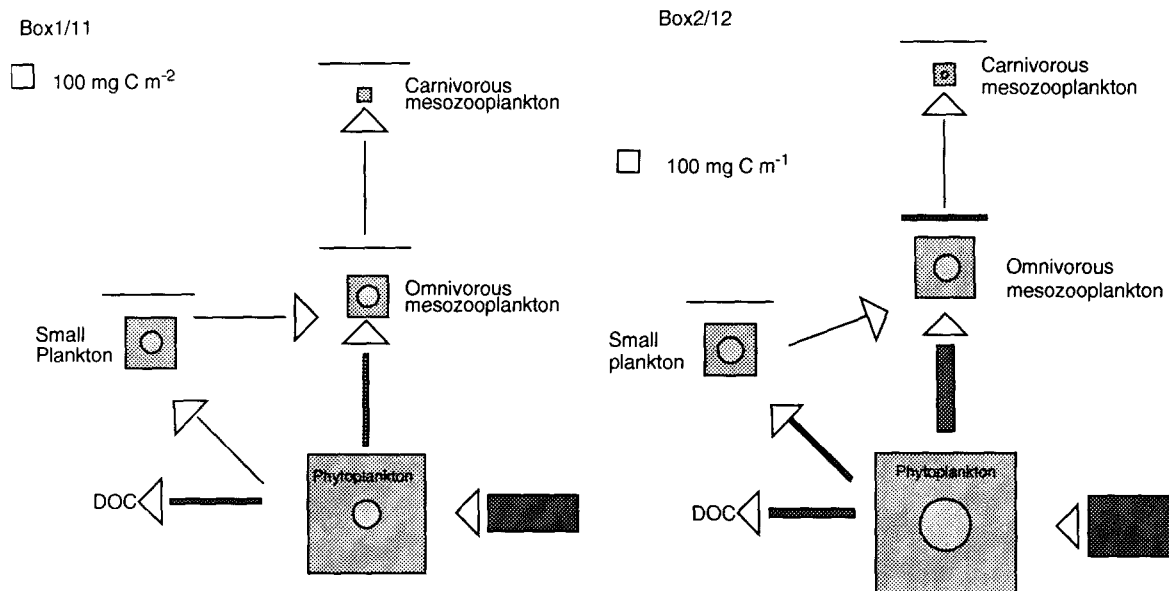


Fig. 8. Predicted mean annual abundance (squares, mg C m⁻²), daily production (circles, mg C m⁻² d⁻¹) and inter-group fluxes (arrows, mg C m⁻² d⁻¹) in Boxes 1 and 2 during 1988. Horizontal bars above boxes indicate the magnitude of the cannibalism flux.

els; in more southerly waters they are nearer 20% of observed levels. The data suggest that the spring rise in omnivore abundance starts around April in northern and western waters and in May in south-eastern waters of the North Sea. The model predicts the reverse pattern. The predicted spring increase is also far too rapid and the predicted maximum is consistently too high, particularly in southern waters. The very high omnivore biomass declines rapidly during June and July, until it reaches levels which are in close agreement with those derived from the field data. From mid-summer to early winter the standing crops predicted by the model are in good agreement with those indicated by the data. The rapid changes in biomass predicted in many of the boxes around day 270 are associated with the mixing of zooplankton populations (and other material) between the surface and sub-surface boxes as stratification breaks down.

According to the data, the carnivores should be five to ten times more abundant in the northern waters of the North sea than in southern waters. The model predicts the reverse pattern. Similarly, though not surprisingly given the structure of the model, the carnivores are predicted to show a marked seasonal cycle in response to the omnivore dynamics, yet the data show little, if any seasonality.

The addition of explicit boundary conditions makes very little difference to the dynamics of either omni-

vores or carnivores in the second half of the year but increases winter standing crops by an order of magnitude or more. Not surprisingly, this effect is most notable in those boxes where import from the external seas is greatest. When explicit boundary conditions are used the spring increase in omnivore biomass is predicted to begin two to four weeks earlier, and to be a little more gradual than otherwise. The carnivore rise is brought forward still further, but the rate of increase is little changed.

The model reproduces the standing crops of the omnivores relatively well in the latter part of the year, but performs poorly early on. This comparative failure in the early part of the year is manifest in the comparison between the field measurements of production, and intercompartment fluxes, *etc.* of Heath *et al.* (pers. comm.) and the corresponding model predictions (Figs 5-8).

In June 1988, the standing crop of phytoplankton is predicted to be approximately 130% too high in box 1, but the daily production is predicted to be close to zero when field measurements indicate it to have been approximately equal to the standing crop. The model predicts the 'small plankton' (microzooplankton and heterotrophic flagellates) to be higher than measured in the field (note, however, that Heath *et al.* (pers. comm.) believe that they may have undersampled this group). The predicted standing crops of mesozooplankton are about 30% of those measured

in the field. Carnivores are also underpredicted. The relative magnitude of the flux from phytoplankton into omnivorous mesozooplankton is approximately correct, but the flux of material from the small plankton to omnivores is predicted to be almost zero though field measurements indicate it to be substantial. This reflects the predicted dominance of heterotrophic flagellates (which the model omnivores do not graze upon) over microzooplankton.

In box 2 the predicted standing crop of phytoplankton is approximately 20% too high, but the predicted production is only about 50% of that measured in the field. Once again, the abundance of small zooplankton (*i.e.* microzooplankton and heterotrophic flagellates) is overpredicted. Omnivore standing crops are predicted to be about 20% too high (reflecting the overly abundant phytoplankton) but the P:B ratio is correctly predicted. The carnivores are predicted to be too rare. The flux from phytoplankton into omnivores is approximately 40% too high, but much of this overprediction is a consequence of the overprediction of the standing crops. The flux from microzooplankton into omnivores is near zero, in contrast to field measurements. Again this reflects the predicted rarity of microzooplankton (upon which the model omnivores do feed) in comparison with heterotrophic flagellates (which the model omnivores do not feed on).

The situation is much worse in the spring of 1989. In boxes 4/14 and especially box 6, the model underpredicts the standing crop of phytoplankton and in all regions the model predicts all of the heterotrophic plankton groups to be all but absent, in marked contrast with field observations.

5. DISCUSSION

5.1. OVERVIEW

The model successfully reproduces the summer and autumn standing stocks of omnivorous mesozooplankton throughout the North Sea but consistently underpredicts their abundance during winter and early spring. For carnivores, the correspondence between observation and prediction is extremely poor throughout the North Sea.

Structurally similar zooplankton models have successfully reproduced the quantitative biomass dynamics of a variety of zooplankton communities, ranging from those of enclosed water columns (*e.g.* CEPEX: Anderson *et al.*, 1987) to those of sea lochs (Ross *et al.*, 1993a, 1993b, 1994). Examination of the structural differences between these systems and the North Sea may help to explain the comparative failure of our model.

Even the smallest spatial box of our North Sea model is much larger than —and hydrographically very different from— a sea loch or mesocosm. This has several implications: firstly, the inherent 'internally well-mixed' assumption of the box modelling

approach is closer to reality in the smaller systems. Inhomogeneities at the scale of centimetres to metres (which may have a crucial influence upon the growth and survival of individuals) are equally poorly represented in all models; however, the spatial scale associated with population structure and development is much closer to that used in the CEPEX and loch models than is the spatial scale which ERSEM is forced to adopt.

Another consequence of the greater spatial extent of the ERSEM boxes is that the species diversity for even one box in the North Sea is greater than those of systems where simple models have been applied in the past. Thus, the parameterization problems which result from the 'functional group' approach are considerably greater, and the resultant approximation to reality very much poorer in the ERSEM than in similar models of less diverse systems.

The second major difference between the North Sea and other systems in which simple, biomass zooplankton models have been used involves boundary conditions. In general, these have been more easily specified in other systems. At the one extreme, CEPEX-type systems are entirely closed to exchange of nutrients and constituents of the biological community. At the other, import of nutrients and import/export of phytoplankton and zooplankton are very large in the loch systems but good hydrographic and nutrient data at the boundaries allowed these exchanges to be accurately quantified. Indeed, Ross *et al.* (1993a) demonstrate that the import of zooplankton during the winter and spring is crucial to determining the summer zooplankton levels and the timing and magnitude of the spring phytoplankton and zooplankton increases in sea loch systems.

Unfortunately, the boundary conditions for the North Sea biota are largely unknown. In the default model, zooplankton abundance in the incoming water is assumed to be the same as that within the box into which the water is being imported. Water entering the northern North Sea is imported from the extremely productive continental shelf region, so this very simple import assumption is likely to be a gross underestimate of the true import and may partially explain the underprediction of winter levels and the erroneous spring dynamics. We have attempted to assess the direct role of zooplankton import by the addition of explicit boundary conditions for the mesozooplankton. Unfortunately, however, ERSEM has not yet succeeded in assembling a complete set of boundary conditions for many of the other state variables in the system. In particular there are no explicit boundary conditions for the phytoplankton and microzooplankton on which the omnivores depend for food and the logic of using reflecting boundary conditions for some biological state variables and explicit boundary conditions for others must be questioned.

With these differences in mind, we must make some attempt to identify the internal processes which

are crucial to determining the system's dynamics.

5.2. OMNIVOROUS ZOOPLANKTON

The model greatly underpredicts the abundance of zooplankton during the winter months, especially in northern waters. This underprediction is important firstly because it suggests that our zooplankton model is overly simplistic and secondly, because the winter zooplankton and phytoplankton levels are crucial in determining the timing and magnitude of the spring growth of the plankton communities. In contrast, despite misrepresenting the spring zooplankton dynamics, the model accurately reproduces the summer dynamics. This might suggest that the spring bloom represents an initial (*i.e.* winter) condition dependent transient on the way to a much more robust summer 'solution'.

The model generally overpredicts the phytoplankton spring bloom (Varela *et al.*, 1995); indeed there is very little evidence of a spring phytoplankton bloom when measured over the large spatial scales we are considering in ERSEM. Incorporation of explicit boundary conditions increases winter/spring omnivore biomasses by about an order of magnitude yet has almost no discernible impact upon the timing and magnitude of the predicted diatom bloom. The maximum of the flagellate bloom is reduced by 25%, and the bloom declines more rapidly when explicit boundary conditions are used. This suggests that (in the model) the diatom bloom is controlled by nutrient and light conditions only, while grazing plays at least some part in regulating the flagellate bloom. It therefore seems unlikely that the phytoplankton bloom would be sufficiently reduced even if the overwintering biomass of omnivores was predicted more correctly.

Given the marked discrepancy between model predictions of zooplankton levels and observations during winter it is not surprising to find that it is in this respect that all of the zooplankton models are crudest. Many species of zooplankton adopt distinct 'overwintering strategies' in order to cope with the period of winter starvation. Our model entirely fails to capture many of the behavioural and physiological adaptations typical of the overwintering individuals. The onset of overwintering manifests itself as a rapid change in the behaviour/physiology of an individual, or a reproductive switch inducing the production of offspring whose behavioural/physiological characteristics are radically different from those of their parents. Features typical of the overwintering state are: 'torpor' and occupation of a habitat which differs from that of the more active individuals. For example, many species are reported to produce 'resting eggs' which sink into the bottom sediments and take considerably longer to hatch than can be accounted for by the standard temperature responses alone (Uye, 1982). Other species, for example *Calanus finmarchi-*

cus overwinter as torpid subadults (Båmstedt & Tande, 1988; Båmstedt *et al.*, 1990). Even this picture may be simplistic. There is evidence that *C. finmarchicus* produces two alternative overwintering morphs: a deep-water, non-feeding, torpid type and a shallow-water, active type. It is not clear whether the two types represent genetically distinct lineages or whether one lineage can exhibit one or the other behaviour in response to environmental triggers (Båmstedt *et al.*, 1990). Our current understanding of the mechanisms which induce overwintering, and break the behaviour/physiology in spring is poor.

The consequences of many overwintering strategies could be represented in a biomass model which incorporated time-dependent parameters but an alternative approach would be to adopt a more mechanistic, physiologically structured modelling approach. Even this latter approach would leave the question of what determines when overwintering is adopted, but it does at least allow a more accurate representation of overwintering, and more satisfactory investigation of the consequences of differing strategies.

When the mesozooplankton biomass does eventually start rising during late spring its growth rate is much greater than that indicated by the data. This is only partly explained by the excessively high densities achieved by the phytoplankton in spring. Aside from the high food abundance three other factors will influence the rate at which the individual zooplankters grow: their maximal consumption rate, their maximal tissue synthesis rate and the distribution of food. Over the short term an individual's rate of weight gain will be determined by its realized consumption rate (loosely, the lesser of food supply rate or maximal consumption rate). In general, however, the maximal tissue synthesis rate will be less than the maximal consumption rate and individuals will often become satiated and cease feeding. Thus, over a slightly longer period, an individual's growth rate will be determined by the lesser of the short-term consumption rate or the maximal tissue synthesis rates. In this model, we have used a maximal consumption rate of twice body carbon per day at 10°C. This corresponds to observed short-term consumption rates. It is tempting to argue that this is too high for the reasons described above and reduce it somewhat to limit the pace of biomass increase during the spring growth phase.

To determine the effect of maximum consumption rate upon the rate of spring increase, we made runs using maximum uptake rates of 1.0 and 0.5 times body C·d⁻¹ (*c.f.* the default of 2.0 times body C·d⁻¹). Throughout the North Sea, the omnivorous mesozooplankton abundance profile becomes much more symmetrical, with a peak around July/August. This peak is around 40 mg C·m⁻³ in southern waters and 20 mg C·m⁻³ in northern waters. Nowhere do they attain appreciable concentrations until May/June but rise extremely rapidly thereafter. The spring phytoplankton bloom is predicted to be a little larger, partic-

ularly in southern waters, and there is a tendency for the phytoplankton to oscillate through the summer. The very low densities of omnivores in spring and early summer are now unable to keep the microzooplankton in check, and they show a rapid response to the phytoplankton bloom, peaking at concentrations of up to $200 \text{ mg C} \cdot \text{m}^{-3}$. The carnivores are not predicted to peak until late summer/early autumn, and are even more rare in northern waters than is the case with the default parameters. Thus, though reducing the maximum consumption rate improves our prediction of the timing of the summer maxima, it does so by delaying the onset of significant growth, rather than greatly slowing the growth rate. It has the unfortunate consequence of worsening the overprediction of the phytoplankton bloom.

Somatic growth depends upon the tissue synthesis rate, and before an individual can commence reproduction, it must complete its somatic growth. In reality, much of the zooplankton biomass increase arises from the subsequent growth of newborn individuals. Thus, if a spring phytoplankton bloom is short-lived, and the zooplankton population's age distribution is initially tight, the lag between the initiation of individual growth, and subsequent reproduction could lead to a situation in which most offspring are growing up in post-bloom conditions in which food is limiting and growth rates are consequently lower. A biomass model cannot distinguish between population (numbers) and somatic growth and is inherently incapable of duplicating this time-lag effect.

We have made some preliminary investigations using a variety of physiologically structured population models. These have ranged from those which assume maturation to be a Poisson process (Van-Sickle, 1977) to more sophisticated models in which an individual's probability of maturation increases as it accumulates reserve tissues. As expected, the population biomass growth rates are somewhat reduced, but the dynamics are extremely sensitive to the timing of reproduction relative to the peak of phytoplankton production. Thus, they require detailed knowledge of the rules which determine when overwintering eggs begin hatching, or torpid juveniles become reactivated. This information is generally lacking.

Aside from age structure effects, we believe that another important reason for the overprediction of growth rate is our inability to represent the consequences of fine-scale patchiness in the food distribution. In general, even if individual zooplankters are able to aggregate on high density phytoplankton patches, the *population* growth rate will tend to be lower than that predicted on the basis of a random encounter model such as ours because of the low growth rates achieved by the majority of individuals who, as a consequence of their limited mobility, must spend much of their time in the large voids between the comparatively few and small high-density food patches (Ruxton *et al.*, 1995). Given sufficient knowl-

edge about the physical and biological characteristics of the system under investigation it might be possible to develop a phenomenological representation of this effect, but as yet such information is not available to us and there are few clues in the theoretical literature to guide our hands.

5.3. CARNIVOROUS

The CPR data indicate that during the summer, the carnivorous mesozooplankton standing crops are higher in the northern North Sea than in the southern North Sea, yet the two omnivorous zooplankton communities appear to have similar standing crops. The model correctly predicts the southern and northern omnivorous zooplankton standing crops to be similar but erroneously predicts the carnivores to be less abundant in northern waters.

Before seeking explanations for this discrepancy we should reiterate the limitations of the data. The biomass estimates are derived from the CPR estimates of individual abundance coupled with corresponding weight estimates for the individuals. The CPR mesh is relatively coarse and undoubtedly undersamples the mesozooplankton community. Of those carnivorous taxa which the CPR does sample, larger species such as *Pareuchaeta* tend to dominate in the north, while in the south, small species such as *Evadne* are dominant (at least in the CPR data). It is therefore probable that the southern community is undersampled to a greater extent than the northern one. In addition, there may well be latitudinal (as well as seasonal) variations in individual weights, but there are no data which comprehensively quantify such variations. Consequently, we have used fixed (latitude-independent) conversion factors to convert from CPR estimates of individual abundance into weight. The CPR also undersamples the gelatinous zooplankton which are a key component of the carnivorous functional group. Data on the distribution of gelatinous zooplankton are comparatively rare, but if anything they appear to be more abundant in northern than southern waters (Hay *et al.*, 1990), further reinforcing the apparent latitudinal abundance pattern in the data. Nonetheless, the deviation between observed and predicted carnivore dynamics may be a consequence of the inadequacies of the data as much as any inadequacies in the model.

If we accept the latitudinal abundance pattern which the data indicate, then we must seek to determine where the model is at fault. We start by emphasizing that were we to predict the winter omnivore biomasses correctly, the prediction of carnivore stocks would also be more correct. Nonetheless, they would probably still be a little low during winter, and the latitudinal gradient would almost certainly continue to be incorrectly predicted.

We have already described the inadequacies of our assumptions regarding the import of material across

the North Sea's boundaries and import may be still more important for the predatory groups than for the omnivores since many seem to overwinter in the deep waters of the Atlantic and be imported into the northern North Sea in spring (e.g. Hay *et al.*, 1990). Another possible explanation for the apparently erroneous prediction of the latitudinal carnivore distribution lies in the marked changes in the structures of both the omnivore and carnivore communities with latitude, none of which are reflected in the model. In northern waters, *Calanus finmarchicus* dominates the omnivore group, in southern waters it is dominated by a variety of smaller copepods. According to the CPR data, nowhere is the carnivorous community dominated by a single taxon, though the relative abundances of each taxa do vary markedly between areas. At present, the carnivores are parameterized as though they are large copepods (e.g. *Pareuchaeta*). In reality, however, this parameterization is only realistic for the north-eastern North Sea. Perhaps the most realistic parameterization would be that appropriate to gelatinous zooplankton, which, though not abundant in terms of carbon biomass, do form a substantial fraction of carnivore numbers and wet weight in many parts of the North Sea. These suffer comparatively little fish predation, in contrast to our current archetype *Pareuchaeta*, but there are very few data either to parameterize the model, or against which to test such a model.

For most of the year, and in most regions the model underpredicts the standing crops of carnivorous zooplankton. Varela *et al.* (1995) conclude that the levels of gross primary production predicted by the ERSEM are a little low throughout the North Sea. In the model, and possibly in reality, the omnivorous and carnivorous zooplankton are subject to very weak internal regulation and it is well established that under these circumstances, any excess production at the base of the food web is rapidly transformed into increased biomass at the top of the food chain with little impact upon intermediate levels. Thus, the low predicted primary production rates may help to explain why the carnivore abundance is generally low despite the correct prediction of omnivore standing crops in summer and autumn.

5.4. GENERAL

It seems clear that further improvements in our ability to reproduce observed zooplankton dynamics will require that we adopt a formulation which allows us to better represent overwintering. Unfortunately, the additional 'degrees of freedom' in such a model will make it still more difficult to disentangle cause and effect.

Several authors have published more realistic (and more complex models) of zooplankton population dynamics. These all represent numbers and age structure explicitly. They range from the simple 'expo-

nentially linked' box models of VanSickle (1977) in which individuals pass from one developmental stage into the next according to a Poisson process, through delay-differential equations (e.g. Bossicart, 1980) through to more realistic, yet extremely complex models such as that of Carlotti & Nival (1992). Even the simplest of these models would greatly increase the computational load in an already complex model.

Models which incorporate physiological structure are relatively simple to formulate and solve for spatially homogenous, closed systems. Unfortunately, in the context of an open, spatially inhomogeneous system, such as ERSEM assumes for the North Sea, these models become more difficult to formulate. As an example: zooplankton populations in adjacent regions are unlikely to be at identical developmental stages. Consequently, transport of zooplankton between adjacent regions will lead to potentially serious problems associated with maintaining developmental continuity unless we fully represent the probability distribution of each population's developmental index (age, weight, accumulated reserves *etc.*). This requires that we solve coupled partial differential equations with all the associated numerical and computational overheads.

Aside from these technical problems, it is important to note that suitable data for establishing boundary conditions and test data sets for these more realistic models are almost entirely absent. Finally, one must question whether it would be logical to increase the physiological / developmental resolution of the zooplankton module without a similar change of resolution in the phytoplankton module. Making both changes will increase the computational complexity of the ERSEM manifold. Inevitably, simulation times will increase still further, so making it more difficult to explore the model's properties fully.

In view of the difficulties outlined above, we are currently developing a biomass-only mesozooplankton model which incorporates time-dependent parameters in order that we may better represent overwintering without an unacceptable increase in the model's complexity, run-time and data requirements.

We do not believe that the ERSEM should be viewed as an end in itself. Rather, we view it in much the same light as a traditional experimental manipulation: our hypotheses of the manner in which the physical environment influences food-web structure and function are put to the test by the construction of the ERSEM and comparison of its predictions with appropriate field data. We have devoted considerable effort to assembling and analysing a large body of field data. In doing so, we have attempted to ensure that the data are not only mutually consistent, but also gathered at, or aggregated to the spatial and temporal scales corresponding to those at which the ERSEM operates. It is undeniable that the mesozooplankton model fails to reproduce the patterns in the data. Nonetheless, as with most experiments, the

mode of failure is instructive. The failure of the zooplankton model is most notable by two characteristics: the overly rapid spring biomass increase and the unnaturally low winter biomasses.

The rapid spring rise arises out of three causes. Firstly, a failure to distinguish between individual growth, and population growth. With due attention to the problems associated with maintaining developmental continuity *etc.* there are a variety of models incorporating both physiological structure and numerical abundance which might be used to alleviate this problem. The two further causes are less easily surmounted because they stem from the enormous difference between the spatial scale which ERSEM explicitly represents, and that which is relevant to the individual zooplankton. An individual zooplankton inhabits an extremely patchy world. At some times its growth rate will be food limited, at other times it will be limited by tissue synthesis rates, and occasionally it will be limited by the maximal consumption rates. While it is possible to develop an individual model which takes explicit account of food level acclimation *etc.* by the individual zooplankton (e.g. Franks *et al.*, 1986) it is not clear how such processes should be approximated when the spatial inhomogeneity which induces such responses are not explicitly described. Similarly, without appropriate data it is impossible to know how to reparameterize the functional response to take account of the fact that predator-prey encounters are not random in time in an inhomogeneous environment.

The primary reason for the model's failure to reproduce the zooplankton winter dynamic is our failure to incorporate overwintering strategies. Most of these strategies could be well approximated even in a biomass model, but there are few quantitative data to indicate what causes a zooplankton to adopt its overwintering strategy in the autumn, and what induces the emergence from overwintering in spring.

That the ERSEM mesozooplankton is inadequate is not in doubt, but it seems clear that without further experimental and field observations to back them, enhancements of the model will be no more than speculation.

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APPENDIX 1

Individual weights used to derive zooplankton biomass estimates from population density data.

TABLE A.1.1

Month specific individual weights used in converting between numbers and biomass. Units are $\mu\text{g C}$ except for euphausiids, which are in mg C . Where only a January figure is given, the same value was used throughout the year. Sources are H. Hunt (Plymouth Marine Laboratory) and S.J. Hay (SOAFD Marine Laboratories).

taxa	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
small copepods	5.52	5.44	6.08	6.08	6.12	5.84	6.08	6.12	5.76	5.80	5.76	5.76
<i>Calanus C5/C6</i>	67.2											
<i>Pareuchaeta</i>	18.0											
<i>Evadne</i> spp.	1.01											
<i>Limacina retroversa</i>	4.09											
<i>Euphausiid</i> spp. (mg C)	1.28	1.29	1.29	1.57	1.74	1.72	2.16	2.08	2.45	0.95	1.26	0.96
<i>Tomopteris</i> spp	200											
<i>Hyperiid</i> spp.	123											
<i>Chaetognath</i> spp	24											

APPENDIX 2

Mathematical specification of the model

In the ensuing description the following notation is used:

TABLE A.2.1

Symbols used to denote state variable classes.

symbol	variable
P1	diatoms
P2	non-diatom autotrophs (flagellates)
Z5	microzooplankton
Z4	omnivorous mesozooplankton
Z3	carnivorous mesozooplankton
R6	detritus
D	dissolved nutrients (phosphorus, nitrogen, silicon)

The ERSEM considers the circulation of four elements: carbon, nitrogen, phosphorus and silicon. Thus, each dynamical unit in the ERSEM is fully specified by a column vector with four elements in which the first, second, third and fourth elements correspond to carbon, nitrogen, phosphorus and silicon contents of the unit, respectively. Similarly, all flows between units are composed of four separate fluxes, one for each of the elements. Individual elements of a matrix will be denoted by subscripts, for example the carbon biomass of omnivores (Z4) will be denoted by $Z4_c$.

An individual in trophic group X perceives a local food concentration ($F_{X,[c,p,n,si]}$), given by:

$$F_{X,[c,n,p,si]} = \begin{cases} P1_{[c,n,p,si]} + P2_{[c,n,p,si]} + Z4_{[c,n,p,si]} + Z5_{[c,n,p,si]}, & \text{if predator is Z4} \\ Z4_{[c,n,p,si]} + Z3_{[c,n,p,si]}, & \text{if predator is Z3} \end{cases} \quad (1)$$

The total carbon consumption ($I_{X,c}$) rate of group X is given by a type II functional response to the concentration of food carbon. P, N and Si are ingested in the appropriate proportions:

$$\begin{bmatrix} I_{X,c} \\ I_{X,n} \\ I_{X,p} \\ I_{X,si} \end{bmatrix} = X_c \cdot \begin{bmatrix} \frac{\theta(T^o) \cdot V \cdot F_{X,c}}{1 + V \cdot \tau \cdot F_{X,c}} \\ I_{X,c} \cdot \frac{F_{X,n}}{F_{X,c}} \\ I_{X,c} \cdot \frac{F_{X,p}}{F_{X,c}} \\ I_{X,c} \cdot \frac{F_{X,si}}{F_{X,c}} \end{bmatrix} \quad (2)$$

X_c denotes the carbon-mass per cubic metre of trophic group X , V denotes the search volume and τ denotes the handling time. $\theta(T^o)$ denotes the temperature dependence of uptake, costs and natural mortality, It is given by:

$$\theta(T^o) = Q^{\phi(T^o - 10)} \quad (3)$$

with Q and ϕ as defined in Table 1.

Of the ingested material, a fraction ϵ is assimilated, a fraction f is lost as faeces and a fraction r is burnt to meet activity costs. Thus ϵ is given by:

$$\begin{bmatrix} \epsilon_{X,c} \\ \epsilon_{X,n} \\ \epsilon_{X,p} \\ \epsilon_{X,si} \end{bmatrix} = \begin{bmatrix} 1 - r_{X,c} - f_{X,c} \\ 1 - r_{X,n} - f_{X,n} \\ 1 - r_{X,p} - f_{X,p} \\ 1 - r_{X,si} - f_{X,si} \end{bmatrix} = \begin{bmatrix} 1 - r_{X,c} - f_{X,c} \\ 1 - f_{X,n} \\ 1 - f_{X,p} \\ 0 \end{bmatrix} \quad (4)$$

Before the ingested material is incorporated into the body tissue the zooplankter must determine the ratios (L) of each element to carbon in the assimilate in order to determine which element limits growth:

$$\begin{bmatrix} L_c \\ L_n \\ L_p \\ L_{si} \end{bmatrix} = \begin{bmatrix} 1 \\ \frac{\epsilon_{X,n} \cdot I_{X,n}}{\epsilon_{X,c} \cdot I_{X,c}} \\ \frac{\epsilon_{X,p} \cdot I_{X,p}}{\epsilon_{X,c} \cdot I_{X,c}} \\ 0 \end{bmatrix} \quad (5)$$

$$Lim = \begin{cases} \text{carbon, if } (L_n > \kappa_n) \text{ and } (L_p > \kappa_p) \\ \text{nitrogen, if } \left(\frac{L_n}{\kappa_n} < \frac{L_p}{\kappa_p} \right) \text{ and } (L_n < \kappa_n) \\ \text{phosphorus, if } \left(\frac{L_p}{\kappa_p} < \frac{L_n}{\kappa_n} \right) \text{ and } (L_p < \kappa_p) \end{cases} \quad (6)$$

where K_p and K_n are the fixed N:C and P:C ratios, respectively.

It then determines what fraction of the two non-limiting elements in the ingestate must be excreted if it is to maintain its fixed internal nutrient quota:

$$\lambda_c = \begin{cases} 0 & \text{if Lim=carbon} \\ \frac{\kappa_n \epsilon_c I_{X,c} - \epsilon_n I_{X,n}}{\kappa_n I_{X,c}} & \text{if Lim=nitrogen} \\ \frac{\kappa_p \epsilon_c I_{X,c} - \epsilon_p I_{X,p}}{\kappa_p I_{X,c}} & \text{if Lim=phosphorus} \end{cases} \quad (7)$$

$$\lambda_n = \begin{cases} \frac{\epsilon_n I_{X,n} - \kappa_n \epsilon_c I_{X,c}}{I_n} & \text{if Lim=carbon} \\ 0 & \text{if Lim=nitrogen} \\ \frac{\epsilon_n I_{X,n} - \kappa_n (\epsilon_c I_{X,c} - \lambda_c I_{X,c})}{I_n} & \text{if Lim=phosphorus} \end{cases} \quad (8)$$

$$\lambda_p = \begin{cases} \frac{\epsilon_p I_{X,p} - \kappa_p \epsilon_c I_{X,c}}{I_p} & \text{if Lim=carbon} \\ \frac{\epsilon_p I_{X,p} - \kappa_p (\epsilon_c I_{X,c} - \lambda_c I_{X,c})}{I_p} & \text{if Lim=nitrogen} \\ 0 & \text{if Lim=phosphorus} \end{cases} \quad (9)$$

$$\lambda_s = 0 \quad (10)$$

The mortality rates from predation by other mesozooplankton are given by:

$$fZ4Z4 = \left(\frac{Z4}{F} \right) I_{Z4} \quad (11)$$

$$fZ4Z3 = \left(\frac{Z4}{F} \right) I_{Z3} \quad (12)$$

$$fZ3Z3 = \left(\frac{Z3}{F} \right) I_{Z3} \quad (13)$$

where $fZ4Z4$ denotes the flux of material into the omnivorous group due to 'cannibalism', $fZ4Z3$ denotes the flux from omnivores into carnivores, and $fZ3Z3$ denotes the flux within the carnivorous group resulting from 'cannibalism'.

Finally, we are now in a position to write down a differential equation for each of the state variables upon which the zooplankton have a direct influence. It should be remembered that these equations are incomplete, each has additional terms to account for transport processes and the operation of other parts of the food web *etc.* For the diatoms (P1) and autotrophic flagellates (P2):

$$\frac{dP1}{dt} = - \left(\frac{P1}{F_{Z4}} \right) \cdot I_{Z4} \quad (14)$$

$$\frac{dP2}{dt} = - \left(\frac{P2}{F_{Z4}} \right) \cdot I_{Z4} \quad (15)$$

For the microzooplankton (Z5), omnivores (Z4) and carnivores (Z3):

$$\frac{dZ5}{dt} = -\left(\frac{Z5}{F_{Z4}}\right) \cdot I_{Z4} \quad (16)$$

$$\frac{dZ4}{dt} = -fZ4Z4 - fZ4Z3 + (\epsilon_{z4} - \lambda_{z4}) \cdot I_{Z4} - Z4 \cdot (b_{z4} + m_{z4}) \cdot \theta(T^p) \quad (17)$$

$$\frac{dZ3}{dt} = -fZ3Z3 + (\epsilon_{z3} - \lambda_{z3}) \cdot I_{Z3} - Z3 \cdot (b_{z3} + m_{z3}) \cdot \theta(T^p) \quad (18)$$

and for the dissolved materials (D) and detritus (R6):

$$\frac{dD}{dt} = (b_{z3} \cdot Z3 + b_{z4} \cdot Z4) \cdot \theta(T^p) + (U \cdot E) \cdot (\lambda_{z3} \cdot I_{z3} + \lambda_{z4} \cdot I_{z4}) \quad (19)$$

$$\frac{dR6}{dt} = (m_{z3} \cdot Z3 + m_{z4} \cdot Z4) \cdot \theta(T^p) + (f_{z3} + E \cdot \lambda_{z3}) \cdot I_{z3} + (f_{z4} + E \cdot \lambda_{z4}) \cdot I_{z4} \quad (20)$$

with b , m and f as defined in Table 1.

The dissolved materials are: CO₂, nitrogen (as ammonia), phosphorus (as phosphate) and silicon (as silicate). The vector E in equations 19 and 20 is used to determine whether ingested elements which are in excess to requirements are excreted in detrital form (corresponding element of E takes the value 1) or in solution (corresponding element of E takes the value 0). The vector U is filled with ones.