

# Use of satellite data for modelling food availability and survival of marine fish larvae

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## Abstract

A modelling scheme is described which uses satellite retrieved sea-surface temperature and chlorophyll-a to derive monthly zooplankton biomass estimates in the eastern North Atlantic; this forms part of a bio-physical model of inter-annual variations in the growth and survival of larvae and post-larvae of mackerel (*Scomber scombrus*). The temperature and chlorophyll data are incorporated first to model copepod (*Calanus*) egg production rates. Egg production is then converted to available food using distribution data from the Continuous Plankton Recorder (CPR) Survey, observed population biomass per unit daily egg production and the proportion of the larval mackerel diet comprising *Calanus*. Results are validated in comparison with field observations of zooplankton biomass. The principal benefit of the modelling scheme is the ability to use the combination of broad scale coverage and fine scale temporal and spatial variability of satellite data as driving forces in the model; weaknesses are the simplicity of the egg production model and the broad-scale generalizations assumed in the raising factors to convert egg production to biomass.

## 1. Introduction

The scientific basis of fisheries management is often criticised due to the evident failure of many fisheries world-wide. In part, this stems from a limited ability to predict the effects of environmental variability on the marine ecosystem and, in particular, on year-to-year changes in recruitment to the fish stocks. In recent years, mathematical modelling techniques have advanced our ability to represent and simulate various physical and biological oceanographic processes, and hence move towards a more predictive capability. A number of modelling studies have shown the important role of the physical environment, for example, of ocean currents in transporting the planktonic stages to potentially favourable environments (e.g. Kasai et al., 1992; Bartsch and Coombs, 1997). However, there are relatively few examples of modelling studies that have explicitly incorporated biological attributes such as feeding and growth (e.g. Hermann et al., 1996; Werner et al., 1996).

Against this background, an EU funded program (SEAMAR – Shelf Edge Advection, Mortality and Recruitment; [www.ieo.es/seamar/seamar.htm](http://www.ieo.es/seamar/seamar.htm)) was initiated to model growth and mortality of the early life-stages of mackerel (*Scomber scombrus*) in the eastern North Atlantic (figure 1). The aim was to develop an Individual-Based Model (IBM) for the eggs, larvae and post-larvae (subsequently referred to collectively as “larvae”) and to use the model simulations for prediction of year-to-year survival during these early life-history stages, and hence annual recruitment to the adult stock. Details of the model formulation are given in Bartsch and Coombs (2001; in press, a) and of results compared with field observations in Bartsch et al. (in press, b).

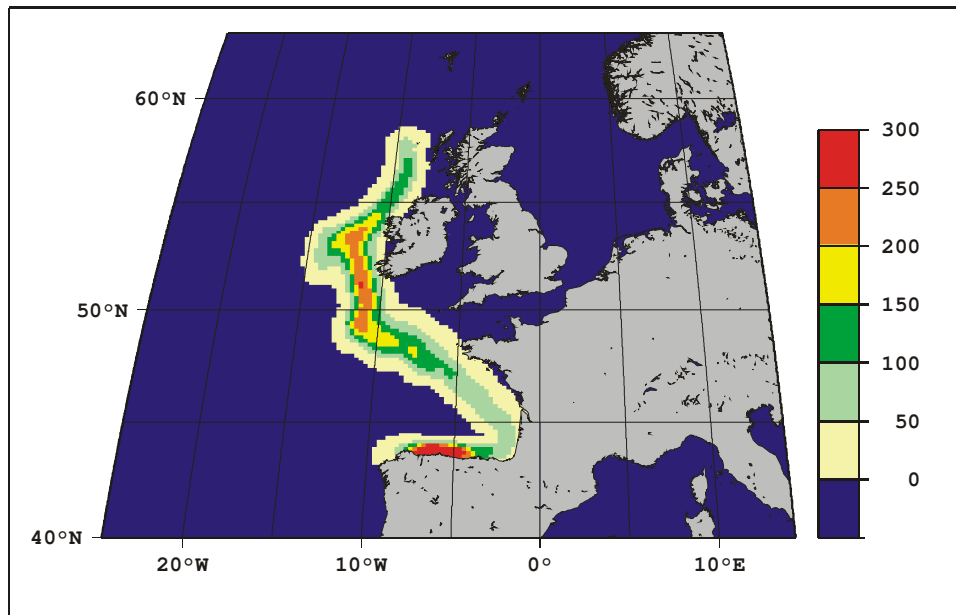


Figure 1. SEAMAR model area and mackerel spawning distribution (numbers of eggs/m<sup>2</sup>) for the main spawning period of 12 March–3 June 1998 (based on data in Anon., 1999).

Mackerel spawn along the European shelf edge from the Iberian peninsula to west of Scotland (figure 1). Spawning starts in January/February in the south and moves progressively northwards following the seasonal warming, ending around July to the west of Scotland (Lockwood et al., 1981). Eggs take about one week to hatch into larvae about 3.0 mm in length. The duration of the larval and early post-larval stages extends to 50–100 days, when the post-larvae may reach up to 80 mm in length. Eggs, larvae and early post-larvae are essentially planktonic, but become increasingly mobile and able to have directed swimming activity as they increase in size. The initial larval diet consists of copepod eggs and nauplii, and by the post-larval stage, gradually switches to larger food items such as copepodites and adult copepods (Conway et al., 1999).

The SEAMAR modelling scheme is formulated on the basis that larval and post-larval growth rate is dependent on water temperature and food availability, and that mortality is inversely related to growth rate i.e. faster growing individuals have better survival (e.g. Anderson, 1988); thus, the two main determinants of survival are temperature and food availability, and for modelling purposes these two parameters are required over the entire model area at the model grid resolution (18.6 km at the centre of the model area) with real inter-annual and seasonal variability. The most straightforward method of providing estimates of food biomass, would be to use direct measures from field plankton sampling surveys; however, the resolution and coverage of all existing field data are too sparse and incomplete for this purpose.

One solution is to use satellite remote sensing, which can provide high resolution charts of sea-surface temperature (SST, from AVHRR – Advanced Very High Resolution Radiometer) and ocean bio-optical properties (from SeaWiFS - Sea-viewing Wide Field-of-view Sensor). Using reflectance band ratios, SeaWiFS imagery can be used to quantify properties such as surface chlorophyll-a concentration (O'Reilly et al., 1998) and hence to estimate phytoplankton primary production (Joint and Groom, 2000). Although both of these provide some index of

marine productivity, they cannot be used directly in the model parameterizations of larval growth energetics, which is based on secondary (zooplankton) biomass.

The method adopted, and described in the present paper, was to apply the copepod egg production model of Prestidge et al. (1995), originally developed for use in the Irish Sea, for the entire SEAMAR model area. Satellite data are used for input of temperature and chlorophyll-a values to estimate copepod egg production. Copepod egg production is then converted to biomass of available food for mackerel larvae, to modify their growth and mortality functions. In the SEAMAR model, this methodology was applied for representative small (*Acartia*) and large (*Calanus*) copepods, but is described here for *Calanus* only, which represents more than ten times the food biomass of *Acartia*.

## 2. Methods

An outline of the modelling scheme is shown in figure 2. All data were processed as monthly means and subsequently interpolated to weekly values for application in the SEAMAR model.

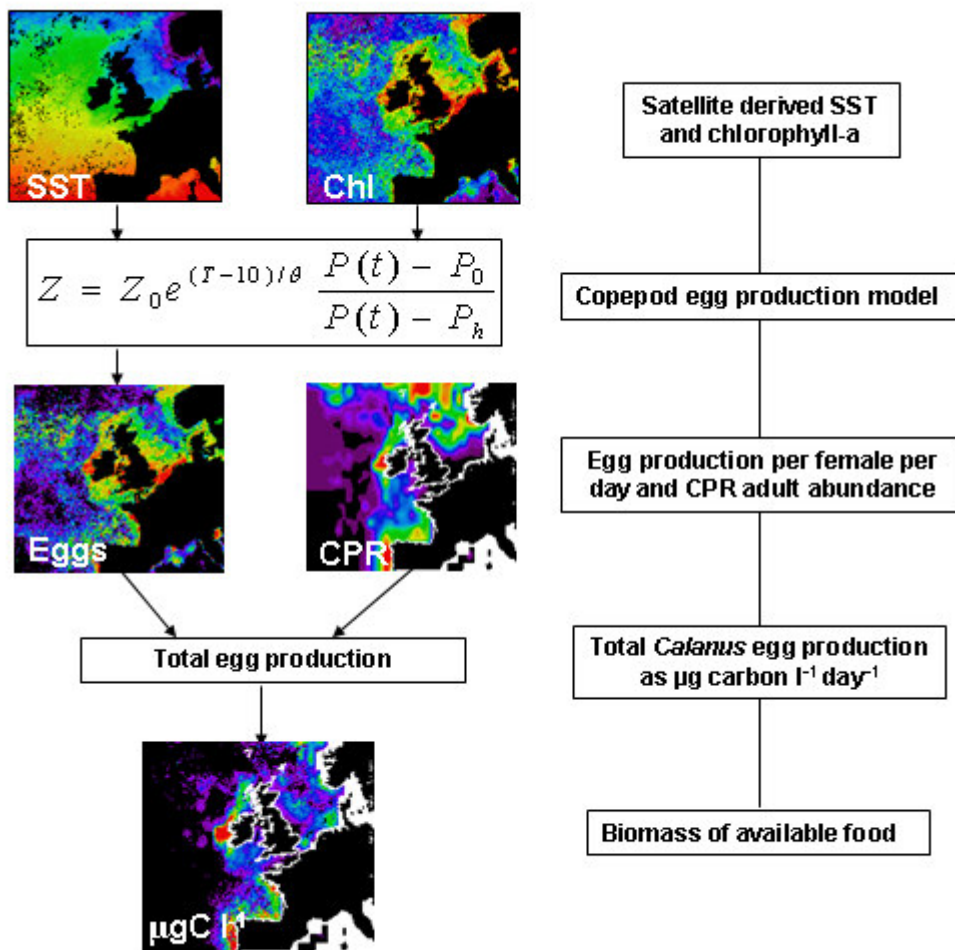


Figure 2.

*Schematic outline of the food availability model (April 1998).*

### 2.1 Egg production model

In the copepod egg production model (Prestidge et al., 1995), copepod egg production rate (EP) is exponentially dependent on temperature and has a Michaelis-Menten relationship with chlorophyll concentration:

$$EP = \begin{cases} Z_0 \exp\{(T - 10)/\theta\} \cdot \frac{P(t) - P_0}{P(t) + P_h} & \text{when } P(t) > P_0 \\ 0.0 & \text{otherwise} \end{cases} \quad (1)$$

where  $Z_0$ =maximum egg production rate at 10°C  
 $T$ =sea-surface temperature  
 $\theta$ =temperature coefficient  
 $P$ =surface phytoplankton concentration (at time  $t$ )  
 $P_0$ =threshold phytoplankton concentration  
and  $P_h$  = half-saturation phytoplankton concentration.

Parameter values for  $Z_0$ ,  $\theta$ ,  $P_0$ , and  $P_h$  for running the model for *Calanus helgolandicus* are provided in Prestidge et al. (1995); the same values are also used as a first approximation for *C. finmarchicus*, which progressively replaces *C. helgolandicus* from west of the British Isles northwards. NASA Pathfinder AVHRR data were used for input of  $T$  (SST) and SeaWiFS data to give  $P$  (surface chlorophyll-a). Both data sets have an equal angle resolution of 9 km which was resized to the SEAMAR model grid resolution of ~18 km.

## 2.2. Conversion to population egg production

Egg production per female was converted to total egg production for the entire population, using a raising factor to allow for the number of females present (as numbers  $l^{-1}$ ) in each model grid box. This was derived from Continuous Plankton Recorder (CPR) long-term (1948-1999) monthly mean abundance data for *Calanus* (e.g. see figure 7 of Colebrook, 1982) by standard CPR rectangles of 1° x 2° latitude by longitude interpolated onto the SEAMAR model grid (figure 2). Allowances were incorporated to allow for the CPR sample size of 3m<sup>3</sup> and for the proportion of the CPR category “*Calanus* stages V and VI” which are mature females (25%), based on more detailed analysis of plankton samples taken throughout the model area. Missing data were interpolated from adjacent sampled rectangles and by reference to results from plankton time-series stations along the north coast of Spain (RADIALES project) and off Plymouth.

## 2.3. Conversion to biomass

The production to biomass conversion uses an empirical relationship from Lynch *et al.* (2001; Table 2), where the total standing stock biomass of all *Calanus* eggs, nauplii and copepodite stages at quasi-steady-state is 3174 µg at an egg production rate of 52.08 eggs/female/day at 5°C.

Hence, for the SEAMAR model area at a mean temperature 15°C, the standing stock biomass in carbon units is 8.05 µg carbon per unit egg production obtained using a  $Q_{10}$  of 3 (Huntley and Lopez, 1992; Kiørboe and Sabatini, 1995) for temperature adjusted development time and a carbon content of 40% (Lindley et al., 1997).

## 2.4. Conversion to available food

A final raising factor was applied to give total available food biomass (figure 2) for mackerel larvae, by raising the biomass estimates of *Calanus* proportionately to the observed proportion (12.5%) represented by *Calanus* in the gut contents of mackerel larvae and post-larvae (Conway et al., 1999).

## 3. Results

Results from the model for February and March, show relatively low biomass (mostly <5 µg C  $l^{-1}$ ) confined along the coastal margins of the Iberian peninsula, around the Bay of Biscay and in

the southern and eastern North Sea (figure 3). In late spring and early summer, April/May, biomass levels increase (often  $5-10 \mu\text{g C l}^{-1}$  and sometimes to  $20 \mu\text{g C l}^{-1}$ ) and extend into offshore waters while progressing northwards with the seasonal warming. From June to September, the main biomass concentrations ( $10-25 \mu\text{g C l}^{-1}$ ) remain to the west and northwest of the British Isles. Over the same period, an extensive area of low biomass extends over deep water areas of the Bay of Biscay and the adjacent Celtic Sea shelf margin.

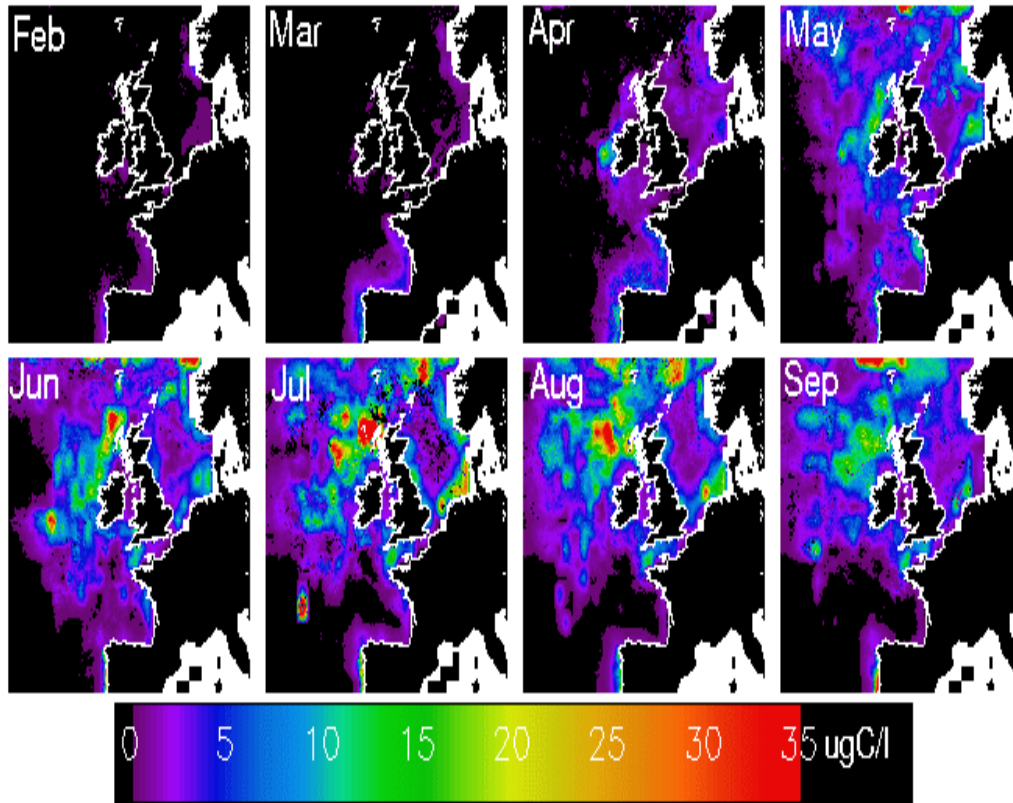


Figure 3. Modelled mean monthly food biomass ( $\mu\text{g C l}^{-1}$ ) for 2000.

There is a clear similarity in the overall pattern of distribution of biomass by years, with differences between years being observed only in the detail. For example, in August the biomass concentration to the west of Scotland (figure 4) varies from being mostly in the range  $5-15 \mu\text{g C l}^{-1}$  in 1998, to  $10-30 \mu\text{g C l}^{-1}$  in 1999 and close to these higher levels in 2000. More subtle details such as variability in the degree of continuity of the low food biomass along the north coast of Spain (e.g. August 1998 cf. 1999 and 2000, figure 4) can have significant effects on the year-to-year pattern of survival of mackerel larvae.

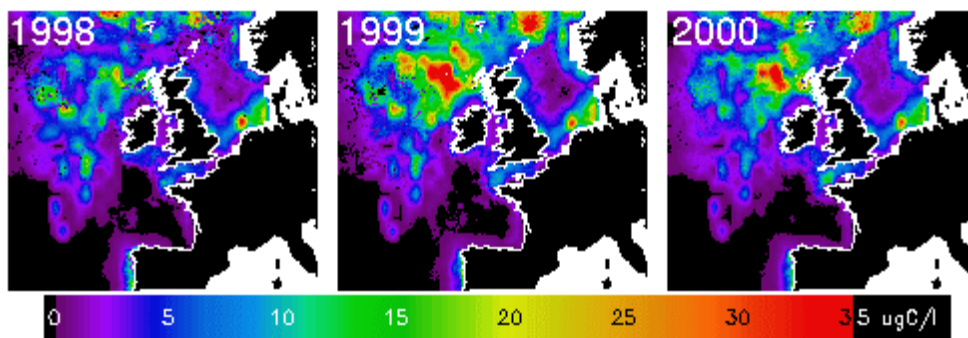


Figure 4. Modelled mean food biomass ( $\mu\text{g C l}^{-1}$ ) for August 1998, 1999 and 2000.

## 4. Validation

### 4.1. Egg production

Although detailed validation of the egg production model is outside the scope of the present paper, some evaluation of the model's performance is required, since the model output forms the basis for the subsequent biomass calculations. Prestidge et al. (1995) had already acknowledged that, at least for the Irish Sea, there was not always a good match between the egg production model and field experiments.

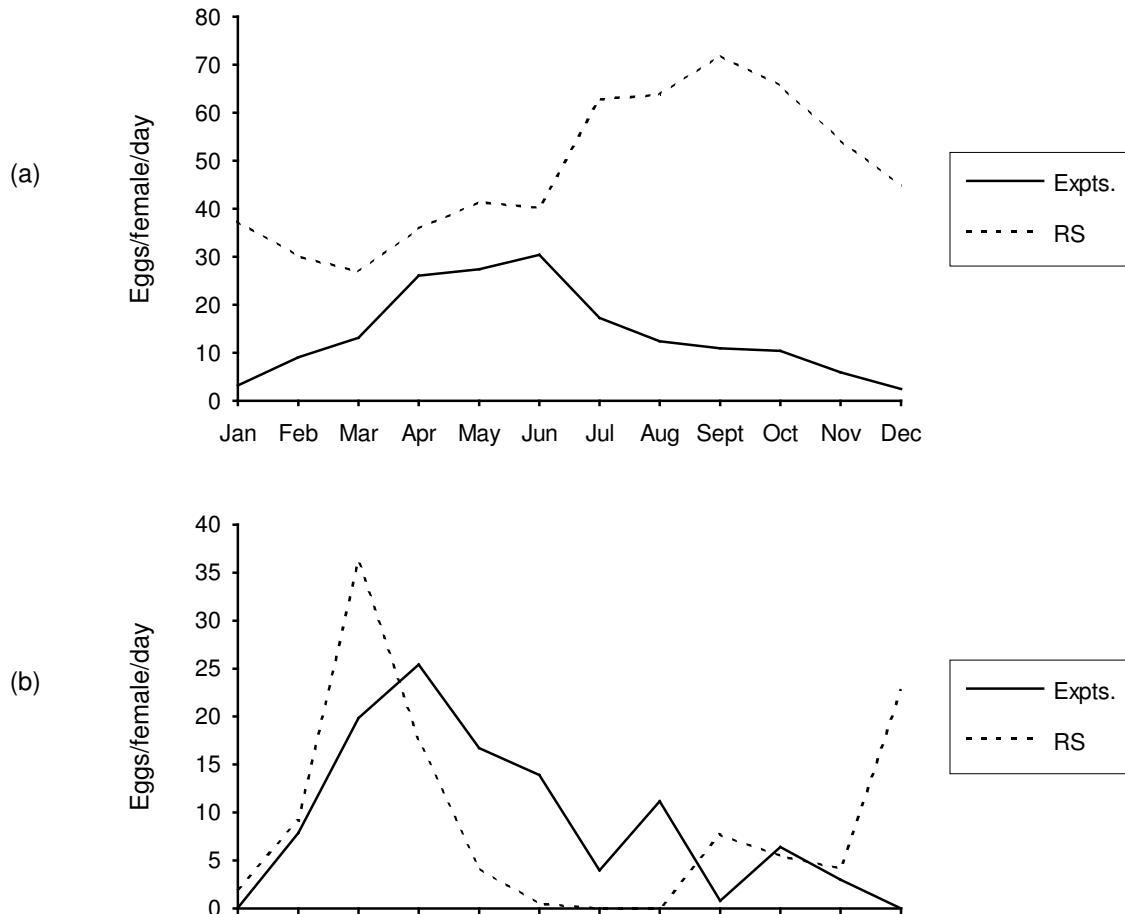


Figure 5. *Calanus* egg production from model output (RS) using satellite data for temperature and chlorophyll-*a*, and results from egg production experiments (Expts.) at (a) station L4 off the south-west of England, 1998–2003 and (b) station E2 off the north coast of Spain, 2000–2002.

Two contrasting sets of data with good seasonal coverage of field egg production experiments were available. The first, at station L4 (50°15'N 04°13'W), is 4 nautical miles off the coast of the south-west of England, with a water depth of 50 m, and is representative of a shelf-sea neritic environment. The other station, E2 (43°42'N 06°09'W), is 9.0 nautical miles off the north coast of Spain and 4 miles from the shelf-edge, over a water depth of 135 m and has a more oceanic influence.

At station L4, the egg production model consistently overestimates egg production compared with the experimental results, particularly in the second half of the year (figure 5a). At station E2, there is a closer correspondence between the two data sets without any consistent bias in the model output (figure 5b).

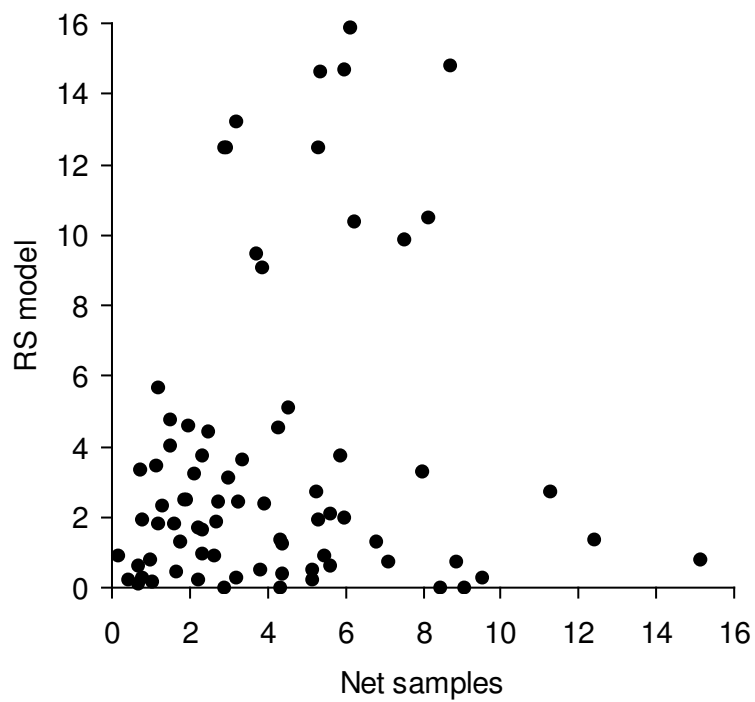
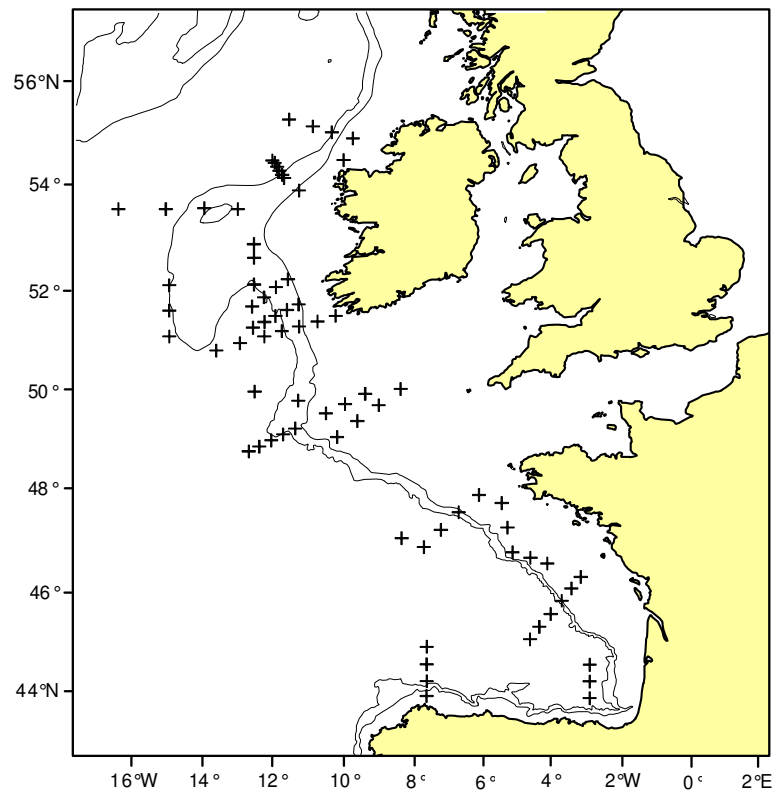


Figure 6.(a) Position of net sampling stations (0–100 m depth, 200  $\mu\text{m}$  mesh net) in June/July 1999 and (b) comparison of these net measures of plankton biomass (Net samples, 200–1000  $\mu\text{m}$  size fraction) against modelled food availability (RS model); both sets of data as  $\mu\text{g C l}^{-1}$ .

#### 4.2. Biomass

Mackerel larvae are predatory carnivores and, considering specimens from 5–50 mm in length, will prey on the majority of zooplankton (Conway et al., 1999). The predicted biomass of available food to mackerel larvae is therefore expected to be close to total zooplankton biomass.

In general terms, the levels of food availability predicted from the model in the main feeding months (April–August) and distributional areas of mackerel larvae west of the British Isles, range from low values around  $2 \mu\text{g C l}^{-1}$  in more peripheral areas, to  $>10 \mu\text{g C l}^{-1}$  and often as high as  $30 \mu\text{g C l}^{-1}$  to the west of Scotland (figure 3). Results from field sampling have tended to give biomass levels towards the lower end of the model range, for example Batten et al. (1999), Head et al. (1999) and Joint et al. (2001) all gave figures of  $2\text{--}12 \mu\text{g C l}^{-1}$  for sampling in May–August at various locations west of the British Isles; however, their use of 200–280  $\mu\text{m}$  sized net mesh would have under-sampled a significant proportion of relevant smaller sized zooplankton.

Specific comparisons were also made between modelled food availability and measures from plankton sampling (200–1000  $\mu\text{m}$  size fraction from 0–100 m depth tows with 200  $\mu\text{m}$  mesh net) taken at 76 stations in June/July 1999 over a wide area in the eastern North Atlantic and adjacent shelf (figure 6a). While there was no significant correlation between the two datasets, the two sets of values are, at least, in a similar range ( $0\text{--}16 \mu\text{g C l}^{-1}$ ) and the higher model estimates tend to relate to field measurements in the middle of that range (figure 6b); the most evident failing is the number of higher measures of net biomass when corresponding modelled values are low. Furthermore, including the biomass of the 53–200  $\mu\text{m}$  size fraction, which was measured at a number of the 1999 stations at a mean of 95.6% of the 200–1000  $\mu\text{m}$  biomass, will nearly double the net measures of biomass and tend to result in the comparative modelled values being underestimates by around 50% or more.

### 5. Discussion

In modelling growth and survival of marine fish larvae, some representation of food availability is essential, as this is a prime determinant of their viability. A complex, population dynamic/ecosystem model such as in Carlotti and Wolf (1998) could be used to model zooplankton abundance, but rapidly becomes computational intractable at the scale of the present application. One option, as used by Heath and Gallego (1996), is to treat temperature as a proxy for a range of environmental factors, implicitly including feeding variability, which influence larval growth. Another possibility is for chlorophyll-a to be used as an index of (primary) production, although this still needs to be related to zooplankton biomass (the main component of fish larval diet) and is not readily applied in energetics equations defining growth and survival of fish larvae. The modelling scheme adopted in the present paper is driven largely by chlorophyll-a, temperature being a relatively conservative property, but follows biological linkages to derive secondary (zooplankton) production and biomass. This is essentially an analytical method (see Guisan and Zimmermann, 2000) where the main potential weakness is the adequacy of the parameterizations, as discussed below. The contrasting approach is statistical (i.e. regression and derivatives) where an empirical relationship is used to predict biomass directly from observed variables (e.g. Woodd-Walker et al., 2001). Although there are at present insufficient field data to develop such a statistical model at the scale of the SEAMAR study, this is potentially a viable alternative which could incorporate the benefits of using satellite retrieved data as the forcing fields.

#### 5.1. Satellite data

As used in the present model, the overwhelming advantages in using satellite observations to drive the egg production model are the broad spatial coverage and ability to incorporate seasonal and inter-annual variability. The main disadvantage is that both the SST and chlorophyll satellite



retrievals are representative of the surface, rather than being indicative of the water column. For chlorophyll-a, there will often be a sub-surface peak, particularly when the water column is stratified; hence, chlorophyll may be under-estimated, with a consequent reduction in the egg production and biomass estimates. The surface temperature measurement is less problematical, since even under stratified conditions it will remain fairly representative of the upper water column, where most copepods are located. Other problems in use of the satellite data are: (1) inadequacies of the reflectance band ratio to chlorophyll-a conversion algorithms, particularly in coastal areas with high terrigenous loadings (IOCCG, 2000), and (2) the monthly averaging required to remove cloud contaminated pixels to ensure comprehensive coverage.

### 5.2. Egg production model

Performance of the egg production model is a key feature in the overall modelling scheme. Results from the validations suggest that the model is either unduly influenced by the temperature cycle (figure 5a) or has only a rather general relationship with field observations (figures. 5b and 6b). There has been some controversy over whether copepod egg production is regulated principally by temperature (e.g. Huntley and Lopez, 1992), or by food availability (see Kleppel et al., 1996). It has become clear that both factors are important and when food is abundant, i.e. above the limit of satiation, then temperature will be the dominant variable (e.g. in high production nearshore environments), whereas in more oligotrophic oceanic waters it is more likely to be food availability that dominates. There have been a number of field observations showing a linear relationship between chlorophyll and copepod egg production (e.g. Peterson, 1986), however, this is not consistent, for example, Hay (1995) found no correlation between copepod production and chlorophyll in the North Sea. Additionally, the influence of other factors such as storage reserves or changes in food quality (Kiørboe, 1989; Kleppel et al., 1996; Pond et al., 1996; Richardson et al., 1999; Irigoien and Harris, 2003) are not incorporated in the egg production model used here.

Thus, there is an acknowledged simplicity in the egg production model, which is applied universally, irrespective of physiological status of the population, timing in the seasonal production cycle or distributional location. Although not inconsiderable, these limitations could be addressed with improved parameterization of the egg production model.

### 5.3. Conversion factors

A number of factors are used to convert egg production per female copepod, first to population production, which is raised to population biomass, and then to total zooplankton biomass as available food to mackerel larvae. Each of these stages has a level of uncertainty.

The conversion to population production uses a raising factor based on abundance of *Calanus* in CPR distributional data. Firstly, while the CPR data are extensive, there was still a certain amount of subjective interpolation and estimation to create values in unsampled areas, albeit by reference to other datasets (e.g. time-series stations and cruise sampling results). Secondly, while Batten et al. (1999) gave some credence to the absolute levels of mesozooplankton abundance represented by the CPR data, in a more extensive set of comparisons, Clark et al. (2001) indicated considerable under-sampling by the CPR, which samples at ~7m depth, compared to conventional vertically-integrating net hauls (*Calanus* being 2.8 times more abundant in net samples compared to the CPR). The computed biomass using the CPR data might then be underestimated by a similar amount. Other variables in using the CPR data include estimation of the proportion of mature adults and percentage of females; these factors have some reliability in that they were derived from detailed analysis of both CPR and other net samples, but their application as universal constants does not account for any spatial and seasonal variation.

Perhaps the biggest limitation of the CPR data is in having to use the same long-term monthly means as raising factors for each of the modelled years. This is because the CPR data

are too sparse to give any useful year-to-year variation in distribution and abundance at anything near the model resolution. This will tend to remove potential differences between years in the modelled biomass, the yearly variation being driven solely by temperature and chlorophyll, and may partially account for the similarities in the distribution of available food between years.

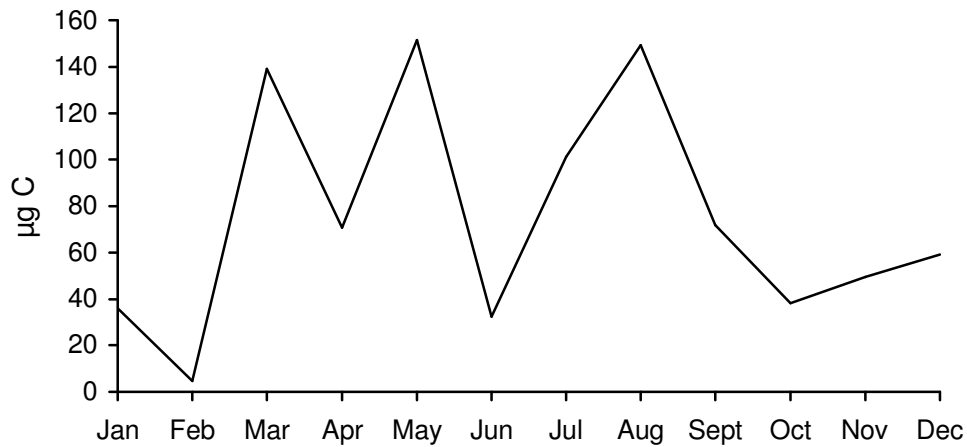


Figure 7. Variations in standing stock biomass of all development stages of *C. helgolandicus* per unit daily egg production at station L4 off the south-west of England in 2003.

The conversion to population biomass assumes a constant relationship between egg production and the numbers and stage structure of the *Calanus* population (8.05 µg carbon per unit egg production) and is based on an age/weight structure for *C. finmarchicus* from the western North Atlantic (from Lynch et al., 2001). Therefore, no allowance has been made for inter-specific, geographical or changes in *Calanus* population stage structure through the season. More recent results for 2003 from station L4 off the south-west coast of England, show a mean level of *C. helgolandicus* population biomass (combined for all naupliar and copepodite stages in net sampling) per unit daily egg production (from experimental results) nearly an order of magnitude higher (figure 7) than used in the model, and hence under-estimation of biomass in the model; however, there was no systematic seasonal variation in the biomass/egg production ratio (figure 7).

The final stage in the conversion routines is to raise the estimates of *Calanus* biomass in relation to the proportion of the mackerel larval diet which it represents. This has the benefit of being a straightforward and direct method, but using a single value (12.5% of the diet being *Calanus* stages) does not allow for regional or seasonal variation. For example, the annual mean proportion that *Calanus* comprises of total zooplankton biomass off the south-west of England is 37.7% (200µm net) compared with 7.3% (250µm net) at a mid-shelf station off Santander on the north coast of Spain; there are also wide seasonal variations, with lower proportions of *Calanus* in the winter (typically one-tenth the proportion in the spring/early summer) and variations in seasonal cycles (e.g. a sharper spring peak in the proportion of *Calanus* off Spain, tending to give model under-estimates of biomass in the summer in that area, compared to the more extended summer peak off Plymouth). It is unlikely that these differences in the representation of *Calanus* in total zooplankton biomass will not be reflected to some extent in the larval diet.

In the modelled sequence from chlorophyll-a via egg production to zooplankton biomass, a certain amount of time should be allowed for the delay in biological response. Peterson (1986) showed a 3-4 day delay before an increase in phytoplankton was expressed as an increase in copepod egg production; from egg to adult is then likely to take from about 1-4 weeks, depending on species and temperature (Henderson and Steele, 1995). Radach et al., (1998) found a modelled delay of about four weeks between the spring bloom of phytoplankton and zooplankton in the North Sea. Rather than incorporating delays in the production model, this was applied in the growth and survival modules of the SEAMAR models by using food availability

values displaced forwards 4 weeks in time (e.g. mid-May food calculations were used in the growth and survival modules for mid-June).

## 6. Conclusions

The modelling scheme described in the present paper was intended as a pragmatic solution to broad-scale modelling of food availability at a tractable level of complexity for a module within the overall SEAMAR bio-physical transport model. The advantages of using satellite-derived data for model forcing are the wide geographical coverage and fine scale temporal and spatial resolution. It is recognised that some broad generalisations have been made in implementation of the model and that refinements in the parameterizations would enhance the reality of the biomass predictions.

## 7. Acknowledgements

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