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Review paper

Environmental variability, mortality of fish larvae and recruitment

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*Over the past few decades, larval fish studies have been successful in relating certain aspects of recruitment to environmental factors, but without any convincing predictive capability. For example, in a SARP project on sardine (*Sardina pilchardus*) off the Atlantic coast of Spain, although there was some relationship between food availability and potential larval survival, as measured by a range of condition indices, ultimately it was advection of larvae into relatively unproductive deep water that was the main determinant of recruitment success. Similarly, more detailed studies on anchovy (*Engraulis encrasicolus*) in the northern Adriatic have shown how wind mixing can affect feeding conditions for the larvae, but their adaptation to spawning in the well stratified waters of the River Po outflow counteracts any simple relationship between food availability and the detrimental effects of adverse weather.*

*The potential of simulation modelling for investigations of larval survival and recruitment is described in relation to studies on blue whiting (*Micromesistius poutassou*) and mackerel (*Scomber scombrus*) in the eastern North Atlantic. The blue whiting transport model addressed the variability of advection of the planktonic stages under different wind regimes, while for the mackerel various additional biological attributes are incorporated in a bio-physical transport model, these being principally growth and mortality in relation to the biological and physical environment.*

Key words: Recruitment, modelling, sardine, anchovy, blue whiting, mackerel

INTRODUCTION

Variability in the size and sustainability of fish stocks is a perennial concern. It is recognised that fishing pressure exerts a major influence on stock size (e.g. DRAGESUND *et al.*, 1997) but there is also considerable evidence that natural environmental factors can play a significant role (e.g. ANDERSON, 1988). There are strong arguments, and a reasonable body of supportive observations, that the influence of environmental variability on fish stocks is most pronounced during the larval stages (PEPIN, 1991) although the importance of the later pre-recruits and the interactions among all stages should be recognised (BRADFORD and CABANA, 1997).

The traditional approach to understanding the environmental impact on larval survival and fish recruitment is by observational field ecology (e.g. LOUGH *et al.*, 1996) and correlation techniques (e.g. BORJA *et al.*, 1998). These have provided a fundamental body of knowledge and a range of conclusions implicating environmental factors to varying degrees. More recently, mathematical modelling techniques have allowed the representation and simulation of both physical and biological oceanographic processes (HEATH and GALLEGO, 1997); this offers the possibility of extensive examination of a range of different scenarios.

In the present paper, examples and limitations of field investigations of the recruitment process are given, together with an outline of a modelling scheme.

INTRA-SEASONAL SARP STUDIES

Field investigations of variations in fish stock recruitment often include morphometric, histological or biochemical assessments of the nutritional condition of fish larvae (see FERRON and LEGGETT, 1994). Some of these techniques, such as gut enzyme activity (e.g. UEBERSCHÄR, 1995), are indicative of patterns of relatively short-term feeding activity, whereas others, such as lipid levels (e.g. HÅKANSON *et al.*, 1994), represent energy accumulation over a longer period.

Such condition indices have been used in investigations of the influence of food availability on the survival of the larval stages (e.g. BUCKLEY and LOUGH, 1987), whether directly by starvation due to low food availability (e.g. FORTIER *et al.*, 1995), or indirectly through a decrease in the growth rate (e.g. WESTERNHAGEN *et al.*, 1998) thereby prolonging the period of vulnerability of the early development stages to predation (BAILEY and HOUDE, 1989). The estimates of larval condition are taken as indices of incipient starvation and are then used in empirical correlations with various measures of plankton abundance and hydrography (e.g. HÅKANSON *et al.*, 1994; THEILACKER *et al.*, 1996).

The development of techniques for ageing fish larvae within a season, using otolith daily growth rings (BROTHERS *et al.*, 1976), has allowed an extension of such studies to intra-seasonal events (e.g. CAMPANA, 1996), whereby the condition indices obtained for the larvae through the spawning season are compared with the birth-date distribution of the surviving juveniles; this approach being encompassed in a series of Sardine/Anchovy Recruitment Projects (SARP; IOC, 1989).

Sardine (*Sardina pilchardus*) off the north coast of Spain

As part of a European SARP study, a series of cruises were undertaken in 1991 and 1992 to investigate the survival of larvae of sardine (*Sardina pilchardus*) off the north and north-west coasts of Spain (LÓPEZ-JAMAR *et al.*, 1995). On these cruises, various condition assessments were carried out on the larvae through the spawning season from March to July, including histological, enzyme, RNA:DNA and elemental analysis (LÓPEZ-JAMAR *et al.*, 1995; McFADZEN *et al.*, 1997; CHÍCHARO *et al.*, 1998; COOMBS *et al.*, 1999).

The results (summarised in LÓPEZ-JAMAR *et al.*, 1995) showed some agreement in that the carbon, histological and enzyme assessments all identified larvae from the May 1992 cruise as being in the poorest condition (for example, Fig. 1) Furthermore, the lowest food availability for larvae was also noted for that same month. However, the subsequent juvenile surveys showed that there was negligible survival of larvae spawned in any of the months from March to June 1992 (Fig. 2; LÓPEZ-JAMAR *et al.*, 1995; ÁLVAREZ and ALEMANY, 1997). Thus, despite being in potentially better condition, the larval populations sampled during the March, March/April and May/June 1992 cruises ultimately fared no better than the May 1992 larvae. One possibility, suggested by LÓPEZ-JAMAR *et al.*, (1995), is that offshore transport associated with upwelling in the Finisterre to Cape Ortegal region (and indicated by the offshore directed tail of the larval distribution, Fig. 3) resulted in loss of the larvae to deep water and away from their habitual nursery grounds. Thus, in 1992, the ultimate survival of larvae through to the

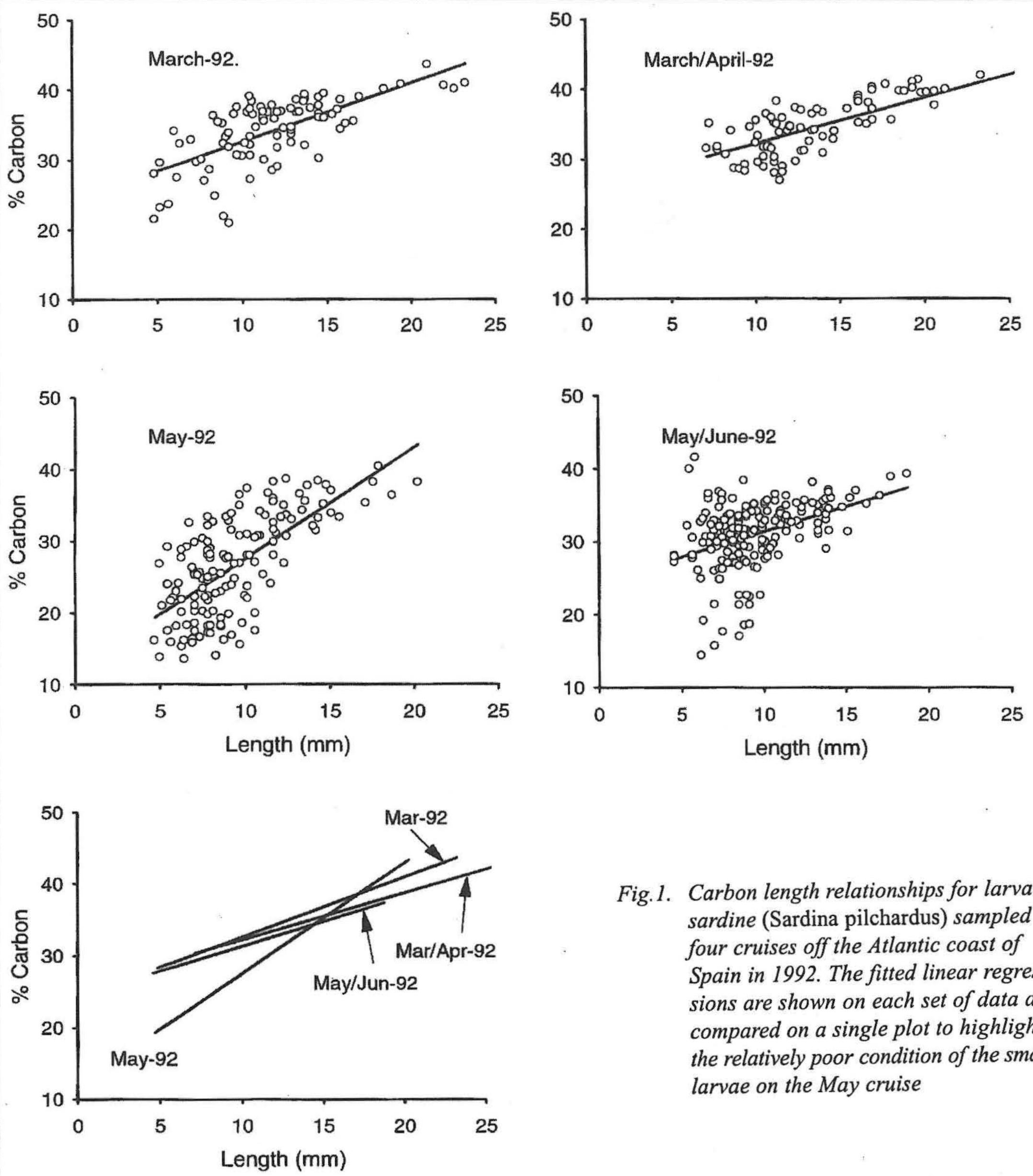

Fig. 1. Carbon length relationships for larvae of sardine (Sardina pilchardus) *sampled on four cruises off the Atlantic coast of Spain in 1992. The fitted linear regressions are shown on each set of data and compared on a single plot to highlight the relatively poor condition of the smaller larvae on the May cruise*

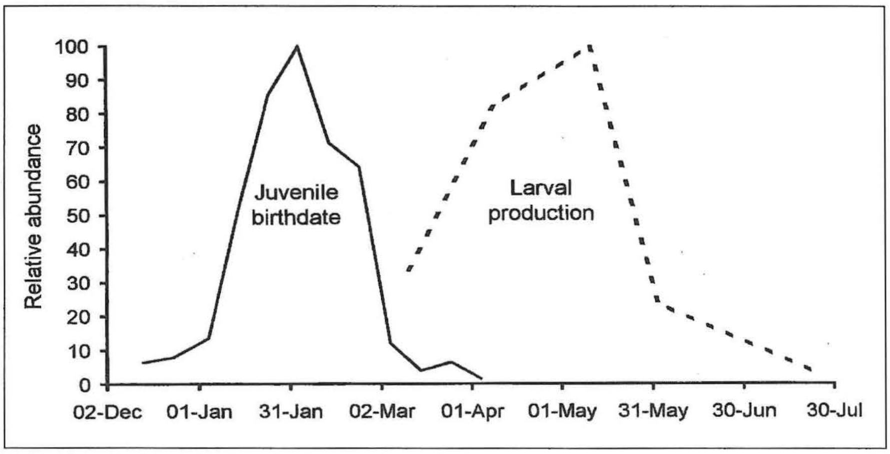

Fig. 2. A comparison of the larval production curve for sardine (Sardina pilchardus) *off the Atlantic coast of Spain in 1992 compared with the back-calculated birth-date from otolith readings of the surviving juveniles. Redrawn from ÁLVAREZ and ALEMANY (1997)*

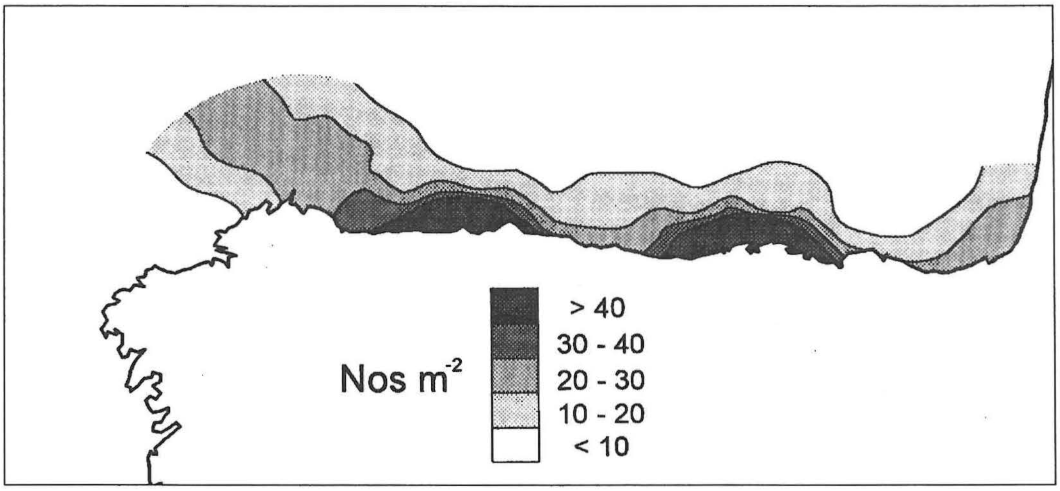

Fig. 3. The combined distribution and abundance of larvae of sardine (Sardina pilchardus) *sampled on four cruises off the Atlantic coast of Spain in 1992*

juvenile stage may be ascribed to the overriding influence of advective loss rather than to intra-seasonal variations in food availability.

PHYSICAL CONTROLS OF FOOD AVAILABILITY

Links between food availability and larval survival can be investigated in terms of overall levels of food abundance (for example, the above SARP study) but these do not generally allow for small-scale local patchiness and persistence of food particles (e.g. LOCHMANN *et al.*, 1997). The importance of vertical structure in the formation of aggregations of food particles and their influence on larval survival was highlighted by LASKER (1975), such vertical structuring of the zooplankton being related to wind mixing and water column stability (e.g. PETERMAN and BRADFORD, 1987; LAGADEUC *et al.*, 1997).

Wind mixing also affects larval feeding through its influence on predator/prey contact rates (SUNDBY, 1997; DOWER *et al.*, 1997) and consequent larval feeding success (ROTHSCHILD and OSBORN, 1988).

Anchovy (*Engraulis encrasicolus*) in the northern Adriatic

Within the above context, a fine-scale study was carried out in June/July 1996 to investigate the survival of anchovy larvae (*Engraulis encrasicolus*) in relation to changing hydrometeorological conditions and food availability (ALICE programme; COOMBS *et al.*, in press, a). The selected study area around the outflow of the River Po in the northern Adriatic provided a relatively well-defined spawning area (PICCINETTI *et al.*, 1980) which is subject to an intermittent and intense north-easterly katabatic wind (the "Bora"). This offered the possibility for a natural experiment to study larval mortality and food availability in relation to wind mixing and changes in the physical environment.

Sampling was carried out on two grid surveys, one after a period of low winds and settled weather and the other after an intervening period of strong winds which resulted in a general decrease in water column stratification (Fig. 4). In both surveys the spawning areas of anchovy and the larval distributions were associated with the river outflow plume (Fig. 4). Elsewhere, a similar selection of river outflow regions for anchovy spawning has been noted by SABATES (1990) in the Mediterranean and by MOTOS *et al.* (1996) and KOUTSIKOPOULOS and LE CANN (1996) in the Bay of Biscay.

Potential food particles for anchovy larvae, primarily copepod nauplii and copepodite stages (CONWAY *et al.*, 1998), were also concentrated in the area of the river outflow, although there was a nearly 50% reduction in the mean water column abundance of potential food between

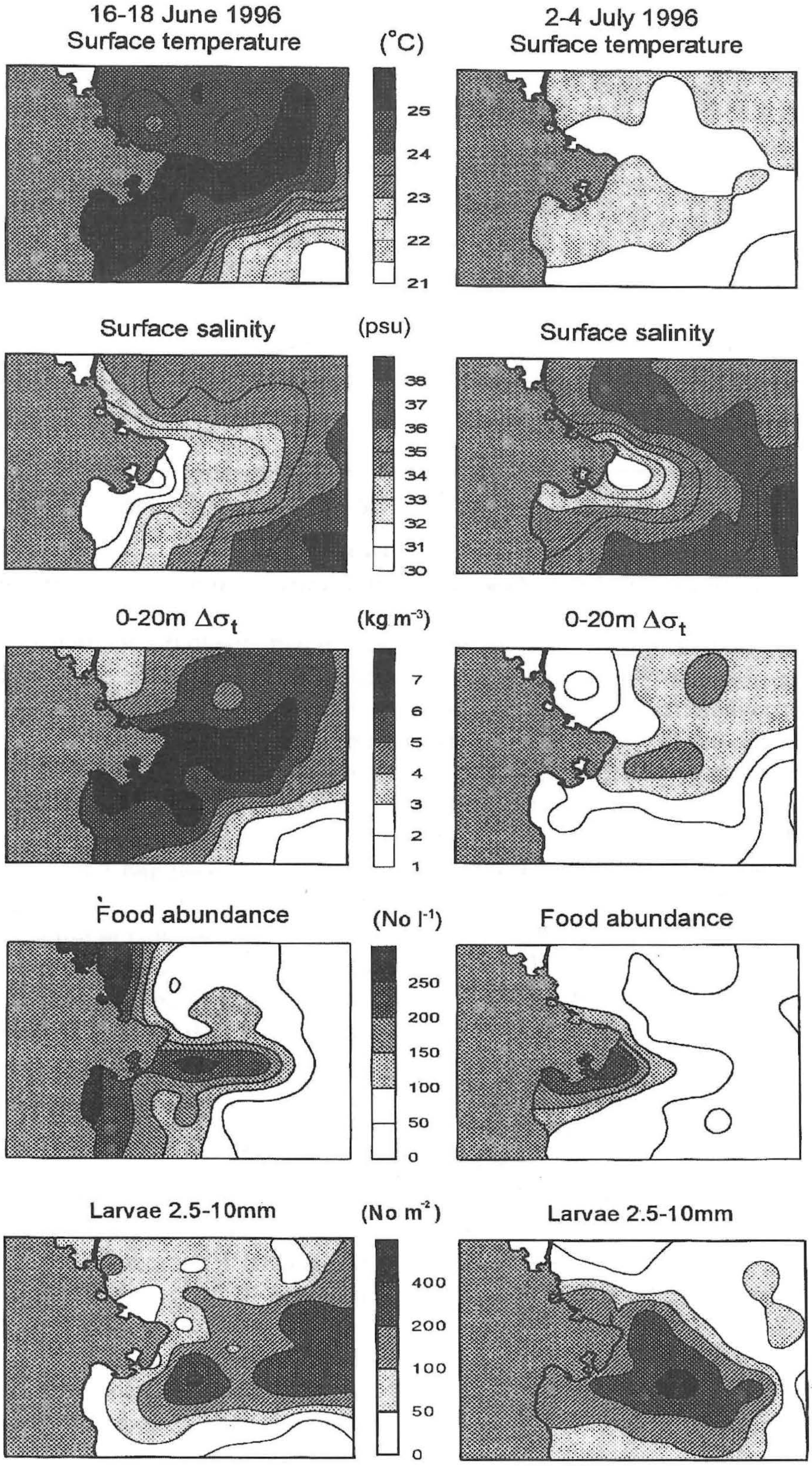

*Fig. 4. Contour plots of temperature, salinity, stratification, food abundance and distribution of larvae of anchovy (*Engraulis encrasicolus*) on two cruises in the outflow region of the River Po in the northern Adriatic. Sampling in the period 16-18 June was preceded by an extended period of fine settled weather whereas there was unsettled weather with strong winds before the sampling in the period 2-4 July*

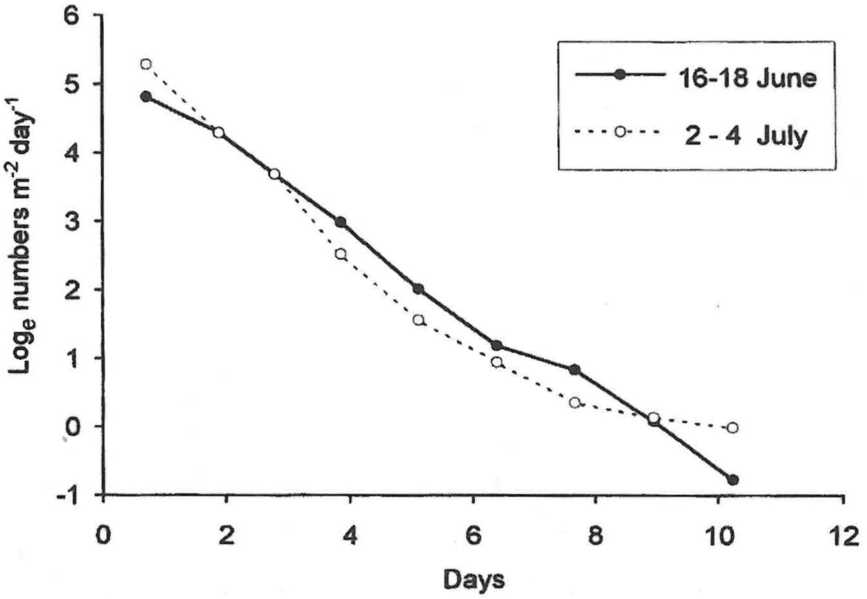

*Fig. 5. Survival curves for eggs and larvae of anchovy (*Engraulis encrasicolus*) from the two sampling grids in the northern Adriatic*

the two survey grids (Fig. 4). Despite this change in overall food abundance, there was no significant change in mortality of anchovy eggs and larvae between the two grids (Fig. 5); the exponential decline in numbers of eggs and larvae to 10 mm in length being equivalent to mortality rates of 43.2% per day on the first survey and 44.7% per day on the second; these rates being comparable with previous mortality estimates for the planktonic stages of anchovy in the Adriatic (PICCINETTI *et al.*, 1982; DULČIĆ, 1995) and in the Mediterranean (PALOMERA and LLEONART, 1989).

The resilience of larval survival under potentially less favourable feeding conditions, after the period of wind mixing, was ascribed to the maintenance of local water column stratification by the superficial low salinity input from the River Po. This stratification in the immediate outflow area was associated with the presence of concentrated layers of potential food particles (typically >50 particles l^{-1} and 1.5 to 2.8 times the mean water column abundance) in the upper 10 m of the water column (Fig. 6) in a similar depth range as the peak concentrations of anchovy larvae.

The conclusions of this study were that the region around the mouth of the River Po is favourable for the survival of anchovy larvae, at least in part, due to the additional water column stability conferred by the superficial low salinity river outflow. This helps maintain water column stratification and consequent vertical aggregations of food particles which might otherwise be dispersed by wind mixing.

Thus, a simple mechanistic relationship between wind speed and food availability cannot be assumed, although it is recognised that there are a range of other non-linear interactions such as predator/prey contact rates (SUNDBY, 1997) or enhancement of production by water column mixing (BAKUN, 1996) which were not considered in this study.

TRANSPORT MODELLING

The SEFOS project (Shelf-Edge Fisheries and Oceanography Studies, 1994-1996) was a multi-national EU funded investigation of the Shelf-Edge Current (SEC) extending from Portugal, via Biscay and the west of the British Isles, to the Norwegian Sea. Biological studies of the fish stocks associated with the shelf-edge were included in the programme, with particular emphasis on their interaction with the SEC and on how changes in the current might affect different aspects of their life-history. The egg and larval stages of fish species which spawn at the

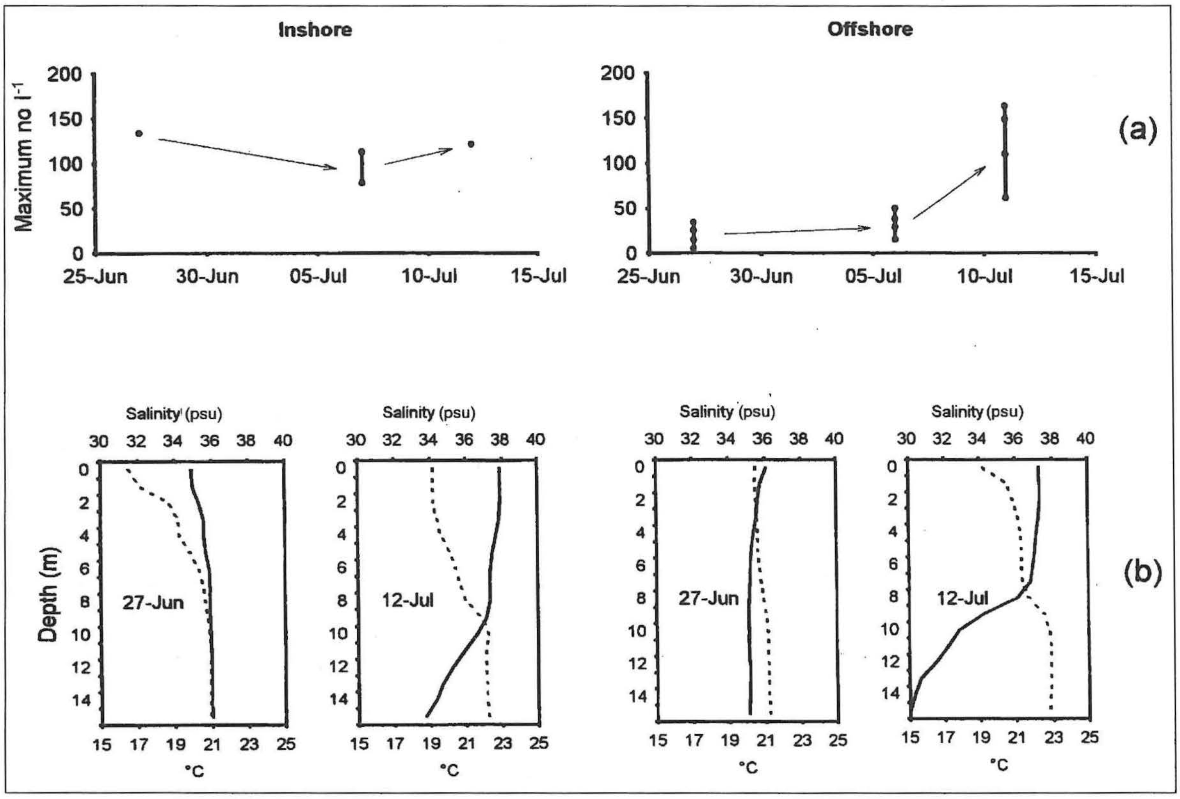

*Fig. 6. (a) Changes in food abundance for larvae of anchovy (*Engraulis encrasicolus*) and (b) temperature and salinity profiles at inshore and offshore sampling locations in the outflow region of the River Po in the northern Adriatic to show the contrasting conditions following strong wind mixing (27 June) and after a return to more settled weather (12 July)*

shelf-edge were of particular interest since these planktonic stages are especially vulnerable to advection to areas of unsuitable larval food supply, increased predation risk or to inappropriate nursery grounds.

An important feature of the work was the formulation of a numerical circulation and transport model system of the SEFOS area (Figs. 7 and 8) to investigate the effects of actual or long-term climatological wind patterns on the dispersion of the planktonic stages. Similar modelling work has been carried out in studies of a number of other fish species, for example, on walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska in which it was shown that the broad-scale features of the modelled and observed larval distributions were related to meteorological conditions (HERMANN *et al.*, 1996). Similarly, BARTSCH (1993) compared simulated tracer distributions of herring (*Clupea harengus*) in the North Sea with observed sequential distributions of the larvae and

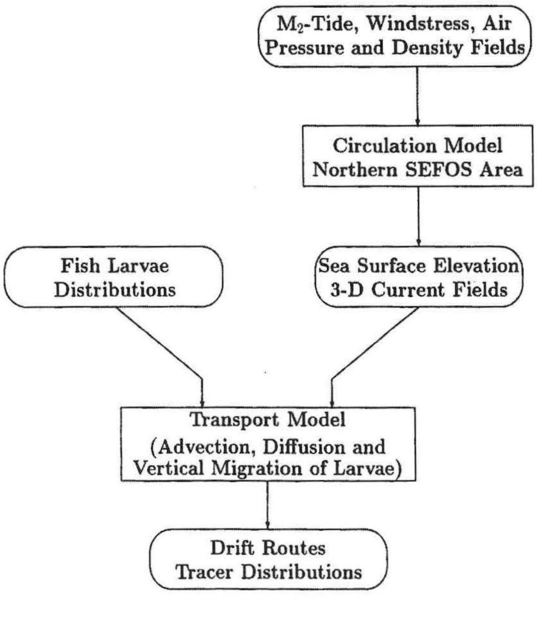

Fig. 7. Schematic of the transport model system

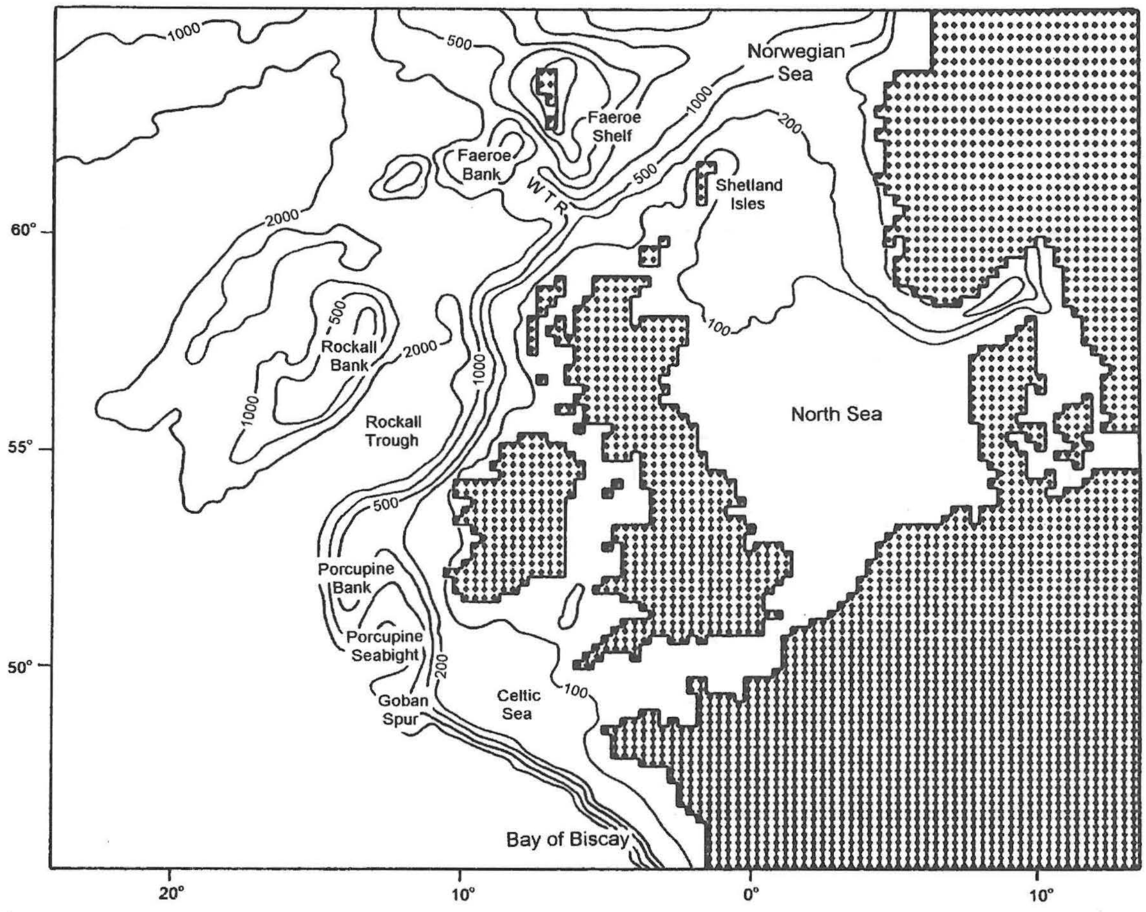

Fig. 8. Model area with depths given in metres

demonstrated the predictive hindcast ability of the transport model.

The three dimensional non-linear baroclinic numerical model used in the SEFOS study was based on the HAMburg Shelf Ocean Model (HAMSOM; BACKHAUS, 1985) with a horizontal resolution of around 20 km in 16 vertical layers. In the transport model, the simulations of the drift routes of the eggs and larvae were performed by means of tracers, in essence ''marked'' water particles representing the fish larvae, which were introduced into the model area and pursued in time and space domains.

Blue whiting (*Micromesistius poutassou*) to the west of the British Isles

The above modelling scheme was applied to the egg and larval stages of blue whiting (*Micromesistius poutassou*) which is one of the major fish stocks spawning along the edge of the European continental shelf (COOMBS *et al.*, 1990). The circulation model was run using tidal forcing and climatological density fields as well as both climatological meteorological forcing and actual six-hourly wind stress fields for 1994 and 1995. The results showed that transport from the main spawning areas situated to the west of the British Isles and north of Porcupine Bank was associated with currents along the shelf-edge and in the Rockall Trough (BARTSCH and COOMBS, 1997). Tracers were dispersed either to the north and north-east along the shelf-edge, extending into the northern North Sea and Norwegian Sea, or were retained in the Rockall Gyre and over Porcupine Bank. A less intense southerly flow from Porcupine Bank was observed both under climatological conditions and in the 1995 simulation (Fig. 9), when winds were more variable than in 1994. The results based on the 1995 meteorological conditions showed the most extreme retention of tracers in the Rockall Trough/shelf-edge area west of Scotland and a low penetration of tracers onto the shelf; it being noted that the 1995 year-class of blue whiting is the highest year-class estimate on record.

The above modelling of blue whiting larvae was based on tracking passive particles i.e. with no behaviour, growth or mortality. A more realistic representation can be achieved in a bio-physical transport model which incorporates larval behaviour, such as vertical migration, and growth and mortality rates as functions of the biological and physical environment, for example, in terms of food availability (HEWITT *et al.*, 1985), turbulence (GALLEGO *et al.*, 1996) or temperature (PEPIN, 1991). There are relatively few examples of modelling exercises which have incorporated such biological attributes, one being the coupled model system described by WERNER *et al.,* (1996) which accounts for advective and trophodynamic processes (feeding and growth) for larval cod and haddock on Georges Bank in the eastern North Atlantic; another being described by HERMANN *et al.* (1996) for the growth and drift of walleye pollock on the Alaskan shelf. HEATH and GALLEGO (1997) have summarised the development of IBM models and categorised them according to the extent to which they incorporated biological detail.

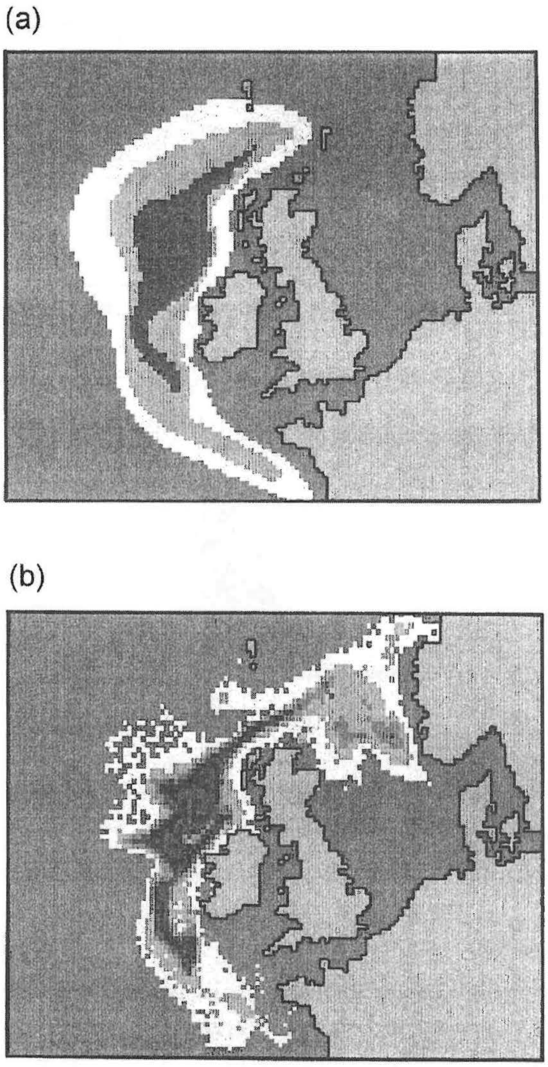

Fig. 9. (a) The initial distribution and (b) the resultant distribution after sixty days transport using 1995 wind forcing for larvae of blue whiting (Micromesistius poutassou)

Mackerel *(Scomber scombrus)* in the north-east Atlantic

The requirement for biological input in modelling studies is being addressed in an ongoing EU funded project for the development and application of a bio-physical transport model of the planktonic stages of mackerel in the north-east Atlantic (SEAMAR - Shelf-Edge Advection, Mortality And Recruitment). This modelling scheme illustrates ways in which biological attributes can be realistically incorporated, principally through Individual-Based Modules of growth and mortality of the larvae and post-larvae during their planktonic drift phase.

These modules are then incorporated in the physical transport model. Initialization data are based on observed egg distributions and the model output validated against the observed distribution and abundance (relative year-class strength) of the recruits.

Growth is the prime biological variable to be incorporated, since it gives both a direct link with the physical environment (as temperature-mediated growth rate) and can act as a proxy for

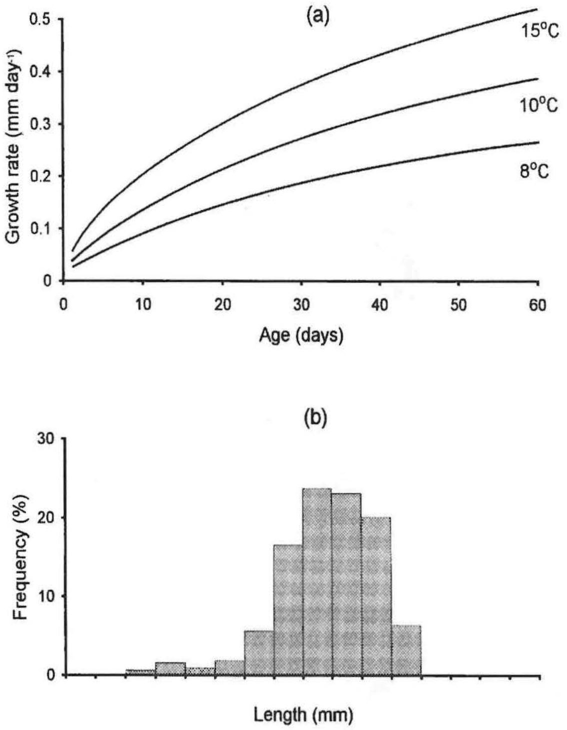

*Fig. 10. Simulations for larvae of mackerel (*Scomber scombrus*) of (a) growth rate in relation to age at different temperatures and (b) the resultant length frequency distribution from 13 mm to 21 mm for a single larval cohort after 60 days transport and dispersion*

survival, it being recognised that size-specific growth rates and mortality interact to determine survivorship in fish populations, survival being directly related to growth rates during the pre-recruit period (ANDERSON, 1988). The key feature is that faster growing larvae remain at the shorter and more vulnerable sizes for less time than slower growing larvae, and hence experience higher survival rates.

A general model supporting the benefits of rapid growth to diminish size-dependent predation is given by COWAN *et al.* (1996).

More specifically, a temperature/size growth model is described by CAMPANA and HURLEY (1989) for cod and haddock. This latter model is being utilised in a modified form in the SEAMAR programme with the growth rate of larvae being parameterised using a power function of age; in a second step the growth rate is modified by a temperature dependent function (Fig. 10; BARTSCH and COOMBS, in press; BARTSCH, in press).

Growth of fish larvae is also dependent on food availability. A knowledge of the diet, and cannibalistic habit, of mackerel larvae and post-larvae is thus required (CONWAY *et al.*, 1999) so that measures of food availability, and hence its influence on growth and mortality, are based on the relevant planktonic components. Measures of food availability can also include gross indices such as zooplankton biomass, as dry weight and carbon equivalent, or as modelled primary production from satellite-derived chlorophyll *a*.

The behaviour of larvae must also be addressed, since mechanisms such as vertical migration (COOMBS *et al.*, in press, b) and shoaling will tend to counteract the natural diffusion based on the simulated variance which is built into the model; previous modelling exercises having shown the sensitivity of the drift pattern to the vertical distribution behaviour of the particles (BARTSCH, 1993; WERNER *et al.*, 1996) and the dependence of mortality rates of pelagic fish eggs and early stage larvae on their spatial patchiness (McGURK 1986).

The progressive inclusion of various biological attributes in a transport model, as outlined above, all build towards a realistic representation of the planktonic early life-history. For this, valid parameterisations are essential, which will entail experimental and field investigations. There is also the requirement for validation data such as recruit distribution and abundance. Thus, although a modelling scheme is ultimately a highly flexible and powerful mathematical tool, it still relies on a body of fundamental research on the chosen species and an ongoing field research commitment.

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Varijabilnost okoliša, smrtnost ribljih ličinki i obnavljanje populacije

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SAŽETAK

U posljednjih nekoliko desetljeća, uspješno je proučavano obnavljanje populacija ribljih ličinki u odnosu na utjecaj čimbenika okoliša, ali bez ikakvih predvidivih prognoza. Na primjer, u SARP projektu o sardini (*Sardina pilchardus*) na atlantskoj obali Španjolske, postojala je veza između dostupnosti hrane i potencijalnog preživljavanja ličinki, označena nizom pokazatelja kondicije. Ipak u posljednje vrijeme kao glavna odrednica uspješnosti obnavljanja populacija je prodor ličinki u relativno neproduktivne dubine. Slično tome, detaljnija proučavanja inćuna (*Engraulis encrasicolus*) u sjevernom Jadranu su pokazala kako miješanje vjetrom može utjecati na uvjete hranjenja ličinki, ali njihova prilagodba razmnožavanju u slojevitoj vodi odljeva rijeke Po protivna je ikakvoj i najjednostavnijoj vezi između raspoložive hrane i pogubnih učinaka nepovoljnog vremena.

Mogući model simulacije pogodan za istraživanje preživjelih ličinki i obnavljanja populacije opisan je u istraživanjima ugotice pučinke (*Micromesistius poutassou*) i skuše (*Scomber scombrus*) u sjevernoistočnom Atlantiku. Transportni model ugotice pučinke upućuje na varijabilnost raspodjele planktonskih stadija pod različitim režimima vjetra, dok su za skušu različiti dodatni biološki atributi uključeni u bio-fizikalni transportni model, a to su posebito rast i smrtnost ličinki u odnosu na biološke i fizikalne čimbenike okoliša.