

**Chapter 13. DIAGNOSIS AND PREDICTION OF
VARIABILITY IN SECONDARY PRODUCTION AND FISH
RECRUITMENT PROCESSES: DEVELOPMENTS IN
PHYSICAL-BIOLOGICAL MODELING**

JEFFREY A. RUNGE

University of New Hampshire

PETER J. S. FRANKS

University of California, San Diego

WENDY C. GENTLEMAN

Dalhousie University

BERNARD A. MEGREY

Alaska Fisheries Science Center

KENNETH A. ROSE

Louisiana State University

FRANCISCO E. WERNER

University of North Carolina, Chapel Hill

BRUNO ZAKARDJIAN

Université du Québec

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1. Introduction

The use of coupled 3-D physical-biological models has been envisaged as an essential component, combined with observations of ecological processes at sea, for the development of quantitative diagnostic and predictive understanding of recruitment in fish populations (e.g., Cushing, 1996). Such models could provide integrated, "holistic" simulations of impacts on ecosystems and recruitment processes of interannual and decadal scale variability in climate forcing.

The convergence of scientific advancement in several domains of coastal ocean research has now made application of 3-D, coupled physical-biological models more feasible. Increased emphasis in observing long-term changes within ocean systems has fostered the development of coastal ocean observing programs around the world. Impressive advances have been made in the application of operational oceanography to provide synoptic visualization of characteristics of the ocean state. (e.g. Schofield et al., 2002). At the same time, advances in mathematical models for coastal marine ecosystems (e.g. Hofmann and Lascara, 1998), data assimilation methodology (e.g. Robinson et al., 1998; Robinson and Lermusiaux, 2002) and developments in computer technology are leading to the interpretative, diagnostic and forecast model systems for coastal climate-ocean processes. The challenge is to integrate models of different types across trophic levels, embed them into representations of the physics of the coastal ocean, and devise approaches to incorporating uncertainty into simulation projections (de Young et al., 2004).

Much of the emphasis in data acquisition systems and interpretative/predictive physical-biological modeling has been on the characterization of the physical ocean state and biological conditions at the lower trophic level, i.e. primary production (Hofmann and Friedrichs, 2002). Many pressing, real-world questions, including the conservation and management of the coastal fisheries, also require understanding of the physical-biological interactions controlling dynamics of the heterotrophic plankton, i.e. secondary production and recruitment into the exploited populations (e.g., Harrison and Parsons, 2000). Increasing knowledge of the dynamics and interactions determining the distribution and abundance of zooplankton and ichthyoplankton, combined with the developments in physical circulation modeling and computational capacity, is also leading to improved understanding of variation at these higher trophic levels. Understanding in this context implies the ability to diagnose sources and mechanisms of observed variation and the capability to make predictions of change in the future.

In this chapter, we review progress in the development of coupled physical-biological models and in their contribution to the understanding of secondary production and recruitment processes. In the context here, the term *coupled* denotes the embedding of a biological model describing the dynamics of components of pelagic marine ecosystems in time-varying flow and temperature fields provided by a physical circulation model of the region and time period of interest. The two models need not be dynamically coupled, i.e. run at the same time; the currents and hydrographic output from the physical simulation can be stored and used to force the biological model. We describe the recent advances; identify gaps and weaknesses in the approach and outline a vision as to where the coupled models

are going and how they might be applied to fisheries and other management issues in coastal and shelf seas.

In Sections 2–4, we examine approaches to the coupled modeling of key processes controlling the dynamics and interactions of heterotrophic populations in the coastal and shelf oceans. No single model or modeling approach can include all relevant processes; a hierarchy of models needs to be developed and applied according to the region or regions and particular questions under consideration (deYoung et al., 2004). The nature of real-world problems is such that consideration of individual species becomes more important at higher trophic levels. This introduces a complexity that can be dealt with by taking a “middle out” approach, in which the dynamics of species or species groups of interest are described in detail and the linked state variables at trophic levels above and below the targeted species are more coarsely resolved or are supplied from other models (e.g. Fig. 13.1).

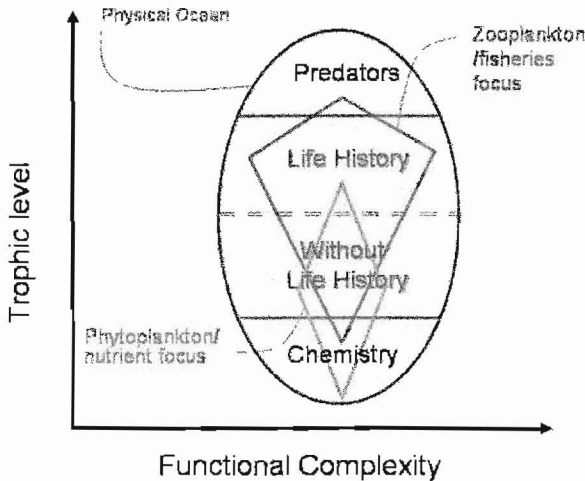


Figure 13.1 A diagrammatic representation of the *middle-out* approach, in which the dynamics of individual species at higher trophic levels are modelled at high resolution and forced by physical processes as well as higher and lower level biological processes modelled at coarser resolution (adapted from de Young et al. 2004).

In section 2, we discuss coupled physical nutrient-phytoplankton-zooplankton (NPZ) models, in the context of describing primary production cycles for linking with models of higher trophic levels. In many NPZ oceanographic models, zooplankton is treated as a closure term without much attention paid to individual species or to the dynamics of higher trophic levels (i.e., fish) as sources of mortality (Edwards and Yool, 2000). The Z compartment in NPZ models represents an ensemble of species each with potentially very different physiological and ecological functional relationships. Therefore, while NPZ models are useful for analysis of spatial and temporal patterns of primary production, they are not sufficient for

resolving the population dynamics in the detail necessary to understand variability in secondary production and recruitment. In Section 3, we discuss more realistic secondary production models in the form of coupled physical-zooplankton life history models. These models focus on the mesozooplankton (approx. 0.2–20mm in size: see Lenz, 2000), particularly planktonic copepods, which serve as a major link between hydrodynamic effects of climatic variability on primary producers and higher trophic levels (Cushing, 1982, 1996; Runge, 1988; Hansen *et al.*, 1994; Skreslet, 1997). Coupled physical-zooplankton life history models characterize the essential dynamics of the target species with decreasing resolution of predator and prey state variables. In section 4, we examine spatially-explicit models that focus on the growth, survival and spatial movement of the planktonic, early life stages of fish and harvested invertebrates such as shrimp, crab and lobster. Because the survival of these early life stages is a crucial (although not exclusive) factor determining recruitment (e.g. Rothschild, 1986), considerable effort has been made to accurately describe the feeding and movement of these early life stages in simulated flow and temperature fields.

Section 5 reviews examples of the present status of development of coupled biological-physical models in three coastal areas: the southern Benguela upwelling system, the western Gulf of Alaska and the northwest Atlantic. These case studies illustrate programmatic approaches to the multidisciplinary collaboration needed to develop the coupled models and acquire knowledge and data for their implementation in a given coastal region. In the concluding Section 6, we discuss the possibility that coupled model simulations of interactions with physical processes and dynamics at different levels of the pelagic ecosystem may be linked together to provide a comprehensive tool for analysis of coastal observing system data, habitat quality for early life stages of exploited species, recruitment and other coastal zone environmental issues.

2. NPZ Models

2.1 Overview

Nutrient-Phytoplankton-Zooplankton (NPZ) models have been widely used in biological oceanography for over 4 decades. While the basic three-compartment NPZ model has changed little over this time (Franks, 2002), modifications to this simple structure by increasing the number of functional groups (e.g., NNPPZZD) have made the ecosystem model a central tool in investigations of processes as diverse as global biogeochemical cycles and red tides in lagoons.

NPZ models are usually formulated using nitrogen as the models' currency. Nitrogen was chosen because (at that time) it was considered to be the main nutrient limiting oceanic primary production. Most field sampling programs do not measure biological properties in terms of nitrogen content, but rather in units such as chlorophyll *a* concentration, cell numbers and zooplankton displacement volume. This necessitates conversion from these measured properties to nitrogen for the model, potentially adding an additional level of inaccuracy and uncertainty to the calculations and model-data comparisons.

Nevertheless, the close coupling of nitrate and phytoplankton to physical forcings makes it possible for (simple) NPZ models to reproduce seasonal or annual cycles of chlorophyll and nitrate, and the spatial details of their distributions in

coastal areas (Figure 13.2). Assimilation of data into relatively simple ecosystem models in open ocean conditions has shown that they can also capture the seasonal dynamics of total chlorophyll at oceanic stations quite well (Spitz et al., 2001, Hurtt and Armstrong, 1999; Figure 13.3).

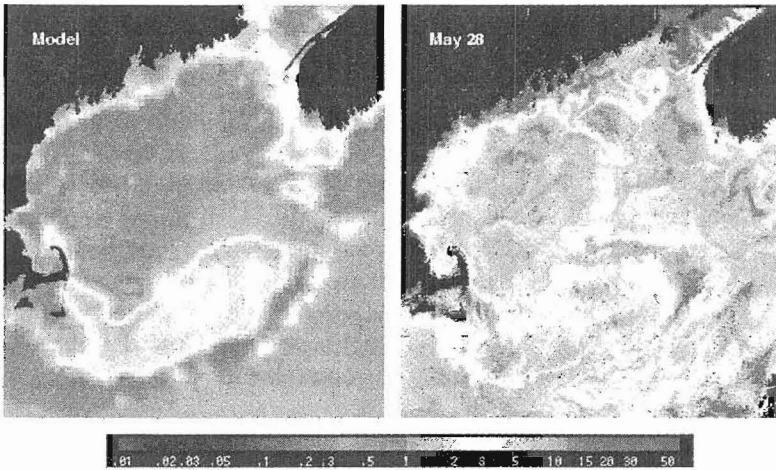


Figure 13.2 Surface chlorophyll *a* in the Gulf of Maine and on Georges Bank from a physical-NPZ model (Franks and Chen, 2001), and from satellite remote sensing. Note that this particular model did not include the nearshore dynamics, such as rivers and nutrient inputs, that lead to high phytoplankton biomass in these areas.

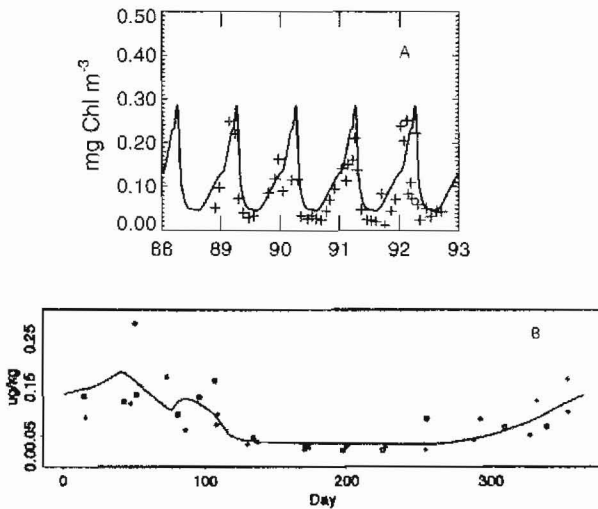


Figure 13.3 Simulation (lines) and data (points) of mixed-layer chlorophyll *a* at the BATS site using data assimilation. A) From Spitz et al. (2001). B) From Hurtt and Armstrong (1999).

The diversity of zooplankton assemblages and their size structure renders more difficult the task of reproducing zooplankton densities in space and time. Models are often parameterized for crustacean zooplankton. However, the dominant grazers in the ocean are the heterotrophic protists – single celled organisms that have substantially different growth and grazing rates than the crustaceans. More highly resolved models may include separate compartments for protist and crustacean zooplankton, allowing comparison of the model results to these two (or greater) broad categories (Doney, 1999; Denman, 2003).

When modeling the growth and population processes of zooplankton or larval fish, the basic role of an NPZ model is to supply a sufficiently accurate prey field: when is the food available, where is it, and how much of it is there? This information can be passed to more complex models of zooplankton and prescribed as its feeding component. Food is often represented in terms of the phytoplankton concentration, or chlorophyll *a*, which NPZ-type models can successfully reproduce because, as stated above, the spatial and temporal patterns of the phytoplankton are strongly coupled to the ambient physical forcings: an accurate physical model is essential to re-creating phytoplankton patchiness and structure particularly in regions of strong physical forcing such as the coastal waters.

2.2 Approaches to coupling NPZ models with physical models and higher trophic levels

An NPZ model is usually coupled to a physical model as though it were a set of tracers being moved by the advection-diffusion equation. Each state variable of the NPZ model will have a separate equation describing its motion in space and time, of the form

$$\frac{\partial C}{\partial t} + u \frac{\partial C}{\partial x} + v \frac{\partial C}{\partial y} + (w + w_s) \frac{\partial C}{\partial z} = \kappa_h \left(\frac{\partial^2 C}{\partial x^2} + \frac{\partial^2 C}{\partial y^2} \right) + \kappa_v \frac{\partial^2 C}{\partial z^2} + \text{biological dynamics} \quad (13.1)$$

where *C* is the concentration of the state variable (*N*, *P*, or *Z*), *u*, *v* and *w* are the horizontal and vertical water velocities determined by the physical model, *w_s* is the vertical swimming or sinking speed of the state variable, and *κ_h* and *κ_v* are the horizontal and vertical eddy diffusivities. The *biological dynamics* of equation (13.1) are the equations of the NPZ model. Typically *u*, *v* and *w* are obtained from a physical model run simultaneously with the biological dynamics. These models range from simple one-dimensional (1D) models with biological dynamics averaged horizontally over the mixed layer, to full 3D models with high-order turbulence-closure submodels (Franks, 2002; Denman, 2003).

Models of the dynamics of the higher trophic levels (large zooplankton and fish) are generally run separately from the coupled physical-NPZ model. The coupling between the physical-NPZ model and the higher trophic level model is through advection and diffusion of the higher trophic levels, the prey available to them, and the temperature field that affects the vital rates (e.g., ingestion, assimilation) of the higher trophic levels. In this case the “Z” term comprises total zooplankton, and

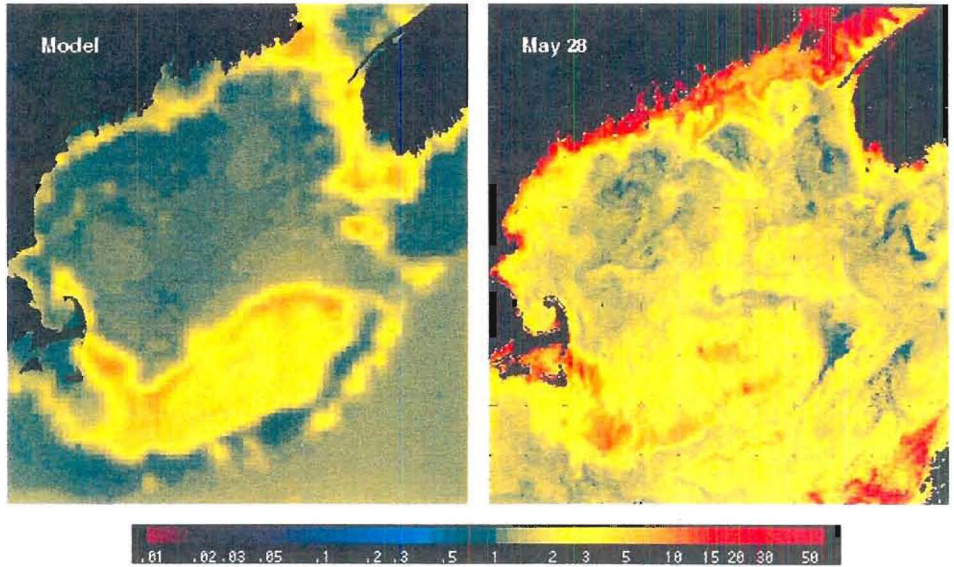


Figure 13.2. Surface chlorophyll *a* in the Gulf of Maine and on Georges Bank from a physical-NPZ model (Franks and Chen, 2001), and from satellite remote sensing. Note that this particular model did not include the nearshore dynamics, such as rivers and nutrient inputs, that lead to high phytoplankton biomass in these areas.

the spatially-explicit abundances or biomass of species in the higher trophic levels are depicted in a separate coupled dynamical model.

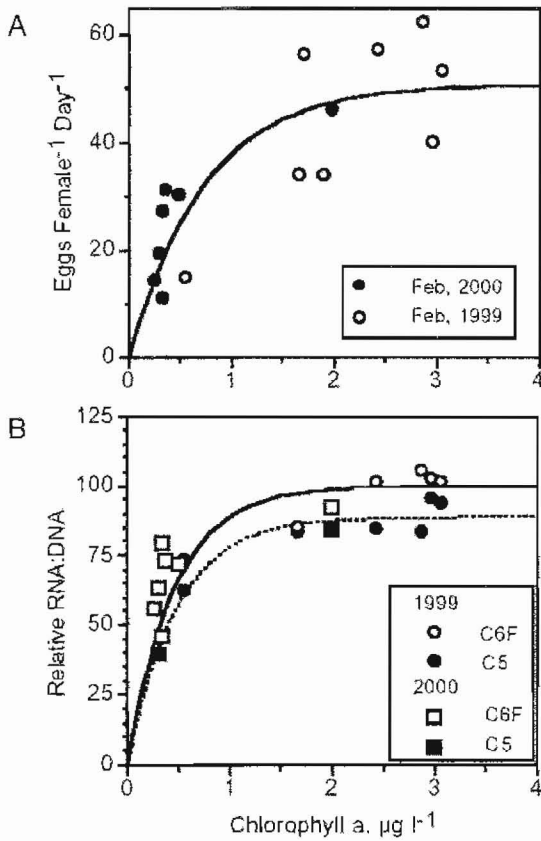


Figure 13.4 Observed egg production rate (A: eggs female⁻¹ d⁻¹) and relative RNA:DNA ratios (B: adult females and stage C5) of *C. finmarchicus* in the Gulf of Maine as a function of mean chlorophyll *a* concentration (adapted from Durbin et al., 2003).

In the field, bulk measures of food availability (such as chlorophyll *a*) may be sufficient to adequately represent food conditions in higher trophic level models in certain situations. For example, for copepods with a life cycle tied to the spring phytoplankton bloom (see Heinrich, 1962; Plourde and Runge, 1993; Melle and Skjoldal, 1998; Head et al., 2000), an NPZ model could be applied to generate the timing of the bloom. In turn, the phytoplankton bloom would drive the initiation of spawning in the copepod population whose life history and distribution may be described with a spatially explicit population dynamics model (Section 3). Moreover, linear or asymptotic relationships of egg production rate with chlorophyll *a* concentration, have been observed in the sea for a number of copepod species and coastal seas (e.g. Checkley, 1980; Runge, 1985; Peterson and Bellantoni, 1987; Armstrong et al. 1991; Dam et al., 1994; Harris et al., 2000; Calbet et al., 2002;

Durbin et al., 2003). In the Gulf of Maine and on Georges Bank, where high levels of phytoplankton production may occur even in winter, the relationship of weight-specific egg production rate to integrated chlorophyll *a* concentrations is well represented by an Ivlev function, even if chlorophyll *a* may only be a proxy for feeding on phytoplankton and microheterotrophs (e.g. Fig. 13.4). Observations from Georges Bank, the Gulf of Maine, the Scotian Shelf and Labrador Sea indicate that chlorophyll *a* concentrations $> 80 \text{ mg m}^{-2}$ are generally sufficient to sustain maximum, or near-maximum egg production rates of *C. finmarchicus* (Campbell and Head, 2000; Head et al., 2000; Durbin et al., 2003).

Empirical determination of functional relationships (as illustrated in Fig. 13.4) that include critical food concentrations at which growth and reproductive rates are maximal are useful in linking species-specific zooplankton life-history models to NPZ models. Integrated chlorophyll fields generated by NPZ models could be used to show where and when food is limiting the vital rates of key species. Simple linear or non-linear models relating growth or reproduction to food below the critical concentration may be sufficient for many applications. Given the growing evidence that the critical concentration itself is function of grazer body size (the smaller the grazer, the lower the critical concentration, e.g., Richardson and Verheye, 1999; McKinnon and Duggan, 2001 and references therein), NPZ models may aid in predicting or diagnosing crustacean zooplankton size structure based on food availability.

2.3 Present challenges to linking coupled NPZ models with higher trophic level models

It is tempting to conclude that NPZ models are sufficiently advanced to the point of providing spatial and temporal distributions of food supply for application in higher trophic-level models. However, while relationships of growth and reproduction to bulk estimates of food concentration seem to work for some species in some regions, there are also many examples where such relationships do not hold. There is need for more work determining the relationships between phytoplankton and zooplankton growth and reproduction in key zooplankton taxa. For species and regions where relatively simple functional relationships do not work or are insufficient to capture variability in growth and reproduction, investigation of the relationship between food and zooplankton vital rates is a continuing need. In some cases phytoplankton is not a proxy for food for key zooplankton species—for example, the carnivorous euphausiid, *Meganctiphanes norvegica*—in which case a relationship is not expected. In other cases, food type, chemical composition (food quality) and size distribution, and the spatial/temporal distribution of food are important sources of variability in functional relationships with food concentration.

Prey composition and size structure

While it has been known for some time that prey type and quality are important to grazers, it has not yet been fully incorporated in modeling studies. Simple NPZ models cannot possibly capture the variety of prey available to higher trophic levels. With increasing understanding of the dynamics of the microbial loop, and recognition that many if not most copepods are omnivorous (e.g. Paffenhofer and Knowles, 1980; Harris, 1996), it has become evident that in certain situations it

may be necessary to include the dynamics of heterotrophic protists and microzooplankton in models of zooplankton prey. A heterotrophic protist may already be several trophic levels removed from the primary producers, which would have important implications for modeling of the transfer of primary production to higher trophic levels. Several models exist that incorporate microheterotrophs (e.g. Frost, 1987; Moloney and Field, 1991); unfortunately the complex versions can have undesirable numerical properties (oscillations). These oscillations are explored in detail in Armstrong (1999), and arise through the opposing effects of phytoplankton nutrient uptake (stabilizing), predator limitation (e.g., Steele and Henderson, 1981, 1992; stabilizing), and predator functional response (stabilizing or destabilizing, depending on the form of the functional response). Simplified versions of these size-structured models have been included in physical models (e.g. Carr, 1998), but such models still require significant development before being widely applicable. Furthermore, gathering field data on rates and biomasses of microheterotrophs is difficult, and is often not done in field programs. Thus there are few good data sets available to formulate and test such models.

Because of the implications for global biogeochemical cycles, variation in the chemical composition of phytoplankton is a core modeling activity in several research programs (Doney, 1999; Doney et al. 2002). Recent attempts to simulate the annual cycles at the Bermuda Atlantic Time Series (BATS) station using a range of NPZ-type models has shown that inclusion of a variable C:chlorophyll ratio of the phytoplankton is necessary to accurately reproduce the cycles of chlorophyll and nitrate (Hurtt and Armstrong, 1999; Spitz et al. 2001). Similarly, interest in iron limitation of phytoplankton growth has led to several models of phytoplankton that include the dynamics of the nitrogen, carbon, iron and silica content of the cells (Moore et al., 2002; Fennel et al., 2002). These models can sometimes reproduce the increased silicification of diatoms under iron stress (Hutchins and Bruland, 1998), and the varying N:C ratios of phytoplankton in different stages of bloom. Such variations are an important beginning in reproducing the prey fields actually encountered by foraging zooplankton. Amino and fatty acids and protein concentration are also known to influence growth and reproduction (e.g. Kleppel et al., 1998; Jonasdottir et al., 2002; Hazzard and Kleppel, 2003), though these are seldom included explicitly in ecosystem models. We still require a great deal of work in elucidating the chemical factors determining prey choice among zooplankton, and how to include these factors in models.

The size structure of the prey field is also an important determinant of zooplankton feeding (e.g. Steele and Frost, 1977; Berggreen et al., 1988). Discovery of the fundamental importance of photosynthetic cyanobacteria to primary production in the ocean and elucidation of the dynamics of the microbial loop have led to a new understanding of the dynamics structuring the planktonic ecosystem. One important empirical finding has been that, as the concentration of phytoplankton (measured as chlorophyll) increases in the ocean, phytoplankton are added in increasingly larger size classes—the abundance of phytoplankton in the smaller size classes first increases and then saturates. This appears to be a consequence of competition for nutrients (small phytoplankton are less limited by diffusion of nutrients to their cell surface), and grazing (grazers of small phytoplankton are small, fast growing, and efficient grazers). Modeling efforts have attempted to reproduce such size spectra in a variety of ways. Some models explicitly include

many state variables, one for each size of phytoplankton (e.g., Moloney and Field, 1991). However, this approach can greatly prolong the numerical calculation and, as mentioned above, usually results in unrealistic oscillations of the model's state variables. Armstrong (1999) found that a multi-phytoplankton model could be stable if the grazing pressure was modeled as a single grazer eating all size classes, rather than separate grazers for each size class. Another approach to including multiple size classes of phytoplankton is semi-empirical. An empirical relationship relating total phytoplankton biomass to the size spectrum of the autotrophs is used (e.g., Hurtt and Armstrong, 1999; Denman and Peña, 2002) to give an approximate spectrum while modeling only a single phytoplankton variable (total biomass). This temporally and spatially varying size spectrum can then be used to generate a locally varying average autotrophic growth rate, and a size-based grazing rate. This method is quick and simple to implement numerically, tends to be stable (there is only one phytoplankton state variable), and can give a more realistic representation of the food available to zooplankton.

Spatial and temporal scaling issues

All models of plankton dynamics produce results that are averaged both spatially and temporally. The degree of averaging usually depends on the questions being asked and the computer power available. Typically, models average temporally over a day, and/or spatially over the mixed layer. Vertical spatial averaging reduces out-of-phase oscillations in vertically adjacent layers that could generate unrealistically strong (and evanescent) gradients of properties in the euphotic zone. However, such averaging removes any ability of the model to reproduce vertical variations of food for higher trophic levels, including the deep chlorophyll maximum. Given the growing recognition of the stable microscale (< 1 m) vertical structuring of the euphotic ecosystem (Rines et al., 2002), and the plasticity of behavioral responses of zooplankton and ichthyoplankton to their food and physical environment (Tiselius, 1992, 1998; Davis, 1996, 2001; Franks, 2001; Incze et al., 2001), there is a growing need to assess the effects of this vertical structure on the growth and reproduction of zooplankton.

The addition of vertical resolution to simple models will add little except integration time. However, models with advanced turbulence-closure schemes and multi-compartment biological models have the potential to benefit from higher vertical resolution simulations. The trade off is always between the insights gained vs. the extra computational costs. While copepods may migrate hundreds of meters vertically each day, the scales over which they actually feed are still poorly known. Laboratory experiments have shown that zooplankton respond to microscale gradients of phytoplankton concentration (Price, 1989; Paffenhofers and Lewis, 1990) and it is possible that the important trophic interactions take place at this scale. However, as discussed earlier, in many cases vertically integrated chlorophyll standing stock is a workable proxy of food available for growth and reproduction. Whether a spatially averaged prey field is an appropriate measure for food available to zooplankton must be carefully considered, particularly if IBM's (Section 3) of zooplankton and ichthyoplankton are being used.

Temporal averaging (usually over a diel cycle) may help stabilize a model, but also removes any ability of the model to reproduce short (<1 d) timescale fluctuations in prey fields or grazing pressure. While it is clear that phytoplankton only

photosynthesize during the day, and many zooplankton—particularly the crustaceans—graze at night to avoid predation, the importance of these dynamics has been largely unexplored in ecosystem models (but see McAllister, 1971). A recent exception is a study by Flynn and Fasham (2003), which examines the sensitivity of a simple plankton model to the inclusion of a diel light cycle. They found that models with only a single phytoplankton group could be simulated well without a light cycle. When the model included two phytoplankton groups with different abilities to assimilate nitrogen in the dark, the inclusion of a light-dark cycle led to increased variability of N:C ratios, changes in nutrient regeneration and f ratios, and changes in the relative abundances of the different phytoplankton groups. This could have immediate effects on the quality of food available to the higher trophic levels.

Predictions using NPZ models

Models of plankton dynamics are increasingly being used to attempt to predict the effects of short- and long-term environmental perturbations (Hofmann and Friedrichs, 2002). Underlying these predictions is the assumption that the models have captured the appropriate dynamics to respond to such changes. Obtaining good agreement of models with past or current data, particularly when we must use empirical relationships in place of detailed mechanistic modeling, does not guarantee that the model will accurately reproduce the ecosystem response to future changes. The model is inherently structurally limited by the variables, transfer functions, and parameters that are used to build it. An NPZ model could not, for example, be used to predict a change from a crustacean-dominated ecosystem to a gelatinous zooplankton-dominated ecosystem under environmental stress.

One aid to prediction is data assimilation (Robinson et al. 1998). A promising data source is satellite-derived products such as surface chlorophyll concentrations. A few models have successfully assimilated remotely sensed pigment data to enhance their simulations of observations (Ishizaka, 1990; Armstrong et al., 1995; Friedrichs, 2002). Data assimilation can help improve the accuracy of short-term predictions (in the ocean this is probably up to 1–2 months for mesoscale circulations), but may not help in predicting the ecosystem response to decadal changes. Probably the best “predictive” models will continue to rely on the conceptual understanding gained through dynamic analysis of existing long-term data sets, and the ability to mechanistically reproduce observed long-time scale changes such as decadal oscillations and regime shifts in the plankton.

3. Coupled Zooplankton Life History Models

3.1 Overview

In contrast to phytoplankton, bacteria and protozooplankton, which are unicellular organisms with short life-cycles (one to ten days), planktonic metazoans such as copepods or gelatinous zooplankton have longer (weeks to years), more complex life cycles and diverse, species-specific physiological rates (e.g. ingestion, respiration and excretion) and behaviors (e.g. ontogenetic and vertical migration, feeding). Fish larvae do not feed equally on all developmental stages or species, but rather select their prey according to size, among other variables, typically preferring copepod naupliar stages. On the other hand, planktivorous juvenile and adult

fish, marine mammals, such as right whales, and sea birds feed preferentially on later developmental stages. A nitrogen-equivalent mesozooplankton biomass calculated by an NPZ type model usually cannot adequately represent very different food conditions for different predators. Thus, a first-order task in quantitative description of metazoan zooplankton population dynamics is the description of stage or size structure at the species level, allowing more accurate portrayal of food availability to higher trophic levels.

Modeling the life-history for all zooplankton species of a given ecosystem, and coupling those models with climatically driven circulation models, is unrealistic. One approach to the study of mesozooplankton population dynamics involves as a first step, the identification of key species (e.g. Fogarty and Powell, 2002). In temperate, subarctic and polar pelagic environments, the major zooplankton contributors to the pelagic ecosystem and recruitment dynamics can be narrowed down to a relatively small list. A feature of a relatively small number of key species is that it is possible, through field and laboratory study, to acquire quantitative knowledge of the physiology and behavior of the targeted species. This understanding can be applied to the formulation of a biological model that is, in a sense, custom fit for that species in a given geographic region. The key species targeted in these systems belong mainly to the Copepoda and Euphausiacea, which are prominent in the zooplankton, both by their presence in plankton net tows and their ecological roles (e.g. Banse, 1994; Eckman, 1994). Gelatinous zooplankton have also received a greater attention recently (e.g., Haskell et al., 1999). To illustrate the approach, particular reference will be made to copepod modeling, in particular to the planktonic copepod, *Calanus finmarchicus*, which dominates zooplankton assemblages in the subarctic North Atlantic.

After hatching, the development of a typical planktonic copepod such as *C. finmarchicus* passes through six naupliar stages and six copepodid stages (Fig. 13.5). The physiological rates and feeding behaviors vary non-linearly with stage and with environmental conditions (c.g., Campbell et al., 2001a). For example, the first naupliar stages (NI-II) develop using internal reserves and generally do not feed. In later stages, growth and development may be partially uncoupled as growth is mainly food dependent while development is generally temperature dependent (e.g., Vidal 1980). Furthermore, copepods exhibit other stage-dependent behaviors such as ontogenetic vertical migration and diapause, which are typical in many species, particularly at high and moderate latitude (e.g., Conover, 1988). Mortality, which generally results from predation or starvation, also depends on environmental conditions and may vary with developmental stage (e.g., Ohman et al., 2002), and is likely correlated with changes to the zooplankton predator assemblage.

The challenge for modelling copepod life cycles is therefore to quantitatively describe the change of population size and structure while accounting for environmental variability and transport. The following sections discuss the different approaches to coupling copepod population dynamics to circulation models. In Part 2 we describe existing structures of coupled copepod models and how they address demography, physiological rates, vertical migration and diapause, respectively. In Part 3 we outline directions for future research.

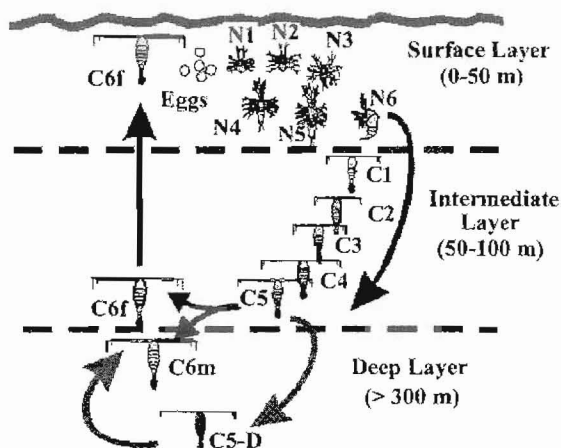


Figure 13.5 Schematic representation of *Calanus finmarchicus* life history. N1-N6: naupliar stages. C1-C6: copepodid stage 1 to copepodid stage 6 (adult, male or female). Stage C5-D: typical diapausing stage. Non-diapausing stage C1-C6, shown at approximate daytime depth, may undergo vertical migration to the surface layer at night.

3.2 Approaches to coupling copepod life history models to physical models

The representation of population demographics

Copepod life history models have traditionally considered the demographic structure of the population using variables to describe the biomass in different weight categories (i.e. weight-based or WBM) or the abundance in different life-stages (i.e. stage-based models, or SBM; see review in Carlotti et al., 2000). In WBMs, the transfer between the different weight classes depends on the growth rates, which are usually modeled as bioenergetic formulations of ingestion, respiration and egestion that can be complicated (Steele and Frost, 1977; Hofmann and Ambler, 1988, Slagstad and Tande, 1990, Bryant et al., 1997). Weights are usually related to stages through a prescribed classification based on observations. The variables in SBMs quantify stage abundances directly. The rate of change of the population size within a stage is typically based on empirical relations for development, using the reciprocal of stage durations for given temperature and food conditions. Such models can result in developmental diffusion (Lewis et al., 1994); to minimize this problem, some authors refined the demographic resolution to include age-within-stage (e.g. Davis, 1984, Lynch et al., 1998). Other models have also sub-divided the stages to describe weights within stage (e.g. Carlotti and Sciandra, 1989).

In contrast to modeling the population in terms of its abundance in a particular stage or class, there is an increasing trend towards modeling individual copepods as discrete entities, using a large number of individuals to represent the population. This approach is known as *i*-state configuration (e.g. Caswell and John, 1992) or more commonly in marine literature as individual-based modelling or IBM. IBMs keep track of a number of variables related to each individual (e.g. age, weight, stage, lipid content). Changes to these variables arise from the physiological responses to the environment (e.g. growth, development, reproduction), often de-

scribed by formulations that are analogous with the WBM and SBM (e.g., Voronina et al. 1979, Batchelder and Miller, 1989; Batchelder and Williams, 1995; Miller et al., 1998; Pedersen et al., 2001). However, since IBMs can keep track of an individual's history, these formulations can be adapted to account for individual variation in vital rates, such as that due to the length of time it has been starving (e.g. Crain and Miller, 2001, Batchelder et al., 2002). While IBMs provide for representation of individual variability, they can be computationally taxing and are not necessarily the approach of choice for representing linkage to higher trophic levels.

IBM vs Eulerian models

There are two basic approaches to coupling copepod life history models with circulation models. The first uses an Eulerian framework, akin to spatially-explicit NPZ models, which consider copepod population densities as concentrations. The biology and circulation are thus coupled using an advection-diffusion-reaction equation, which describes the local rate of change of population abundance affected by biological rates, currents and turbulence (e.g., Davis, 1984; Lynch et al., 1998; Zakardjian et al., 2003). Vital rates may be dependent on local food conditions and temperature derived from the circulation models, and behavioral movement can be included through a behavioral advection and/or diffusion term (Zakardian et al., 2003)

While the coupling with circulation models is straightforward, the advection-diffusion-reaction equation solves for copepod abundance is subject to the same kinds of numerical issues as can arise in circulation models (e.g. negative concentrations in advection-dominated flows). The transport/mixing routine in these models is presently costly computationally, so that the number of stage, age or weight classes may be a strong limitation. For example, while circulation models typically have 5–10 variables being transported, the number of variables in the higher resolution population models can be very high (e.g. 87 variables in the Lynch et al, 1998 study). Spatially structured population models (e.g., Gurney et al., 2001) are attempts to use an age-structured matrix model of population dynamics in an Eulerian framework. This approach permits the use of a complex weight or age structured matrix for the biological part of the model, which have been shown to clearly resolve the copepod demography and dynamics (see the review of Carlotti et al, 2000) but requires specific preprocessing of the physics, i.e., defining the mixing and transport matrix operator. In Gurney et al. (2001) the mixing or transport matrix operator is defined from multiple particle trackings with surface velocity fields from a 3D circulation model. A model by Bryant et al. (1997) simply used daily horizontal exchange coefficients between grid cells calculated from a 3D circulation model. Both models are however limited to 2D (horizontal) grids.

A second approach for coupling the copepod life history with the circulation uses a Lagrangian framework (i.e. particle tracking) wherein particular particles are followed as they move to different locations. Each particle can represent a cohort with the same history (e.g. ensemble approach as in Carlotti and Wolf, 1998; population sub-sampling as in Miller et al., 1998), or it can represent an individual copepod (Batchelder et al., 2002). Trajectories for a number of particles are simulated by considering the displacement due to local currents and turbulence, the physiological history of the individual or cohort is computed as the particle

moves through the environment. With an IBM, the particle can also be given behavior specific to its unique state.

The simulation of numerous trajectories, usually 10^3 – 10^5 particles, needed to gain insight into the population dynamics is computationally demanding. Hence, while the Lagrangian approach may perform well for qualitative study, its applicability to quantitative estimation of transport, exchange between sub-population and simulations over long time periods may be limited by the cost of analysis, although this situation continues to improve with advances in technology. Lagrangian water column models use an approach that follows the development of a cohort in a water mass that is assumed to be isolated (e.g., Heath et al., 1997). In these models, a time series of physical conditions (turbulent mixing, temperature) prevailing in the water column are extracted from a drift scenario and are used to drive the copepod life history model. This approach allows the use of complex physiological models of copepods life history (as an age or weight structured model) and trophic coupling with primary producers (e.g., Heath et al., 1997). However, the assumption of an isolated water column transported as a whole is only valid perhaps for the upper layer of the ocean (0–100 m). Vertically sheared circulation that prevails for example in the North Atlantic or on coastal shelves, in conjunction with the range of possible diel and ontogenetic vertical distributions of copepods like *C. finmarchicus*, restricts their applicability.

The above-mentioned models can incorporate demographic resolution with varying degrees of computer efficiency. The question is how realistic must the population demography be in order to achieve the research objectives. It is clear from Table 13.1 that few studies have ventured into extension of coupling the population models with circulation models in three dimensions. Increasing the spatial dimensions of Eulerian models has limited the use of population models to the simplest formulations, i.e., SBM (Lewis et al., 1994; Zakardjian et al., 2003). Models with higher demographic resolution (e.g., age-within-stage) have to-date been applied only in 1D or 2D (e.g., Davis, 1984; Carlotti and Radach, 1996; Lynch et al., 1998). A detailed application of a coupled IBM is the work of Batchelder et al. (2002) in a 2D physical framework.

Since each approach has its own advantages and disadvantages, it is better to consider them as complementary. Local process studies may need good resolution of individual growth and population demography, such as source regions of copepods to Georges Bank (e.g., Miller et al., 1998; Hannah et al., 1998), for which the IBM approach has been applied. For larger scale studies, seasonal evolution of stage abundance, described with a simpler stage-based model coupled with realistic circulation patterns, can capture within the right order of magnitude the effect of advection on regional population dynamics of a target species (e.g., Zakardjian et al., 2003).

3.3 Present challenges and issues facing coupled copepod life-history models

Food limitation of growth and reproduction

An important frontier in the development of coupled copepod life history models is the inclusion of the effects of food limitation on vital rates (growth, reproduction, mortality) i.e., how to link to the output of the NPZ models. The effect of food supply occurs more on growth and reproductive rates (e.g. Runge, 1985; Campbell

TABLE 13.1.
 Characteristics of coupled physical-copepod life history models (list not all-inclusive)

Authors	Species	Type of life-cycle model	Type of coupling	Dimensions	Lower trophic level coupling	Egg production	Development times or growth rate	Mortality	Diapause	Vertical migration behavior	Length of simulations
Voronina et al., 1979	<i>Calanoides acutus</i> (Antarctic)	IBM	Lagrangian probabilistic	x,z,t	Seasonally varying phytoplankton biomass	f(food)	f(age,depth)	f(food,age,depth)	Coupled with the migration behaviors	Seasonally and latitudinally varying stage-specific migration behavior	1 year
Miller et al., 1998	<i>Calanus finmarchicus</i> (Georges Bank)	IBM	Lagrangian	x,y,t	No	f(temp)	f(temp)	Imposed stage-specific mortality rates, increased for 2nd generation	Imposed probability of ascent and descent, increased for 2nd generations	No	250 days
Batchelder et al., 2002	<i>Metridia spp</i> (Oregon Coast)	IBM	Lagrangian	x,z,t	Driven by a NPZ model	f(food, temp)	f(food)	Imposed stage-specific mortality rates	No	Yes	120 days
Heath et al., 1997	<i>Calanus finmarchicus</i> (Northern Scotland)	ABM	Lagrangian water column drift	x(t), y(t), t	Coupled with a NPZD model	f(food)	f(food)	Imposed mortality rates on eggs and CV1 used as fitting parameters	No	No	50 days
Pedersen et al., 2001	<i>Calanus finmarchicus</i> (Norwegian coast)	ABM	Lagrangian	x,y,z,t	No	Limited to a imposed time-window	f(temp)	No	Imposed time of ascent and descent	yes	180-210 days
Wroblewski, 1982	<i>Calanus marshallae</i> (Oregon coast)	SBM	Eulerian	x,z,t	No	No	Constant and equivalent to development times at 10°C	Imposed stage-specific mortality rates	No	yes	1 month
Davis, 1984	<i>Pseudocalanus spp</i> (Georges Bank)	AwSBM	Eulerian	Θ^*,t (angular coordinates)	No	f(temp)	f(temp)	tuned stage specific mortality rates	No	No	60 days

Lewis et al., 1994	<i>Pseudocalanus spp</i> (Georges Bank)	SBM	Eulerian	x,y,z,t	No	Imposed and constant	Imposed stage-specific molting rates	Imposed stage-specific mortality rates	No	No	20 days (wind events)
Gupta et al., 1994	<i>Coullana canadensis</i> (Saco Estuary)	SBM	Eulerian	x,t	No	Imposed with seasonal variations	f(temp)	Imposed stage-specific mortality rates	No	No	1 year
Carlotti and Radach, 1996	<i>Calanus finmarchicus</i>	IBM and WwSBM	Eulerian	z,t	Coupled with a NPZD model	f(weight, temp, food/	f(food, temp)	Imposed stage-specific mortality rates	Imposed diapause at stage CV for imposed temperature and food conditions	No	1 year
Carlotti and Wolf, 1998	<i>Calanus finmarchicus</i>	IBM and WwSBM	Lagrangian	z,t	Coupled with a NPZD model	f(weight, temp, food/	f(food, temp)	Imposed stage-specific mortality rates	Descent of CIV and CV depending on stored lipids	DVM = f(light,food)	240 days (spring to autumn)
Lynch et al. 1998	<i>Calanus finmarchicus</i> (Gulf of Maine)	AwSBM	Eulerian	x,y,t in 3 layers	Monthly phytoplankton biomass fields from observations (MARMAP)	f(temp, food)	f(temp, food)	Imposed stage-specific mortality rates	Imposed rate of emergence from diapause	C5s move between layers	90 days (growing season)
Zakardjian et al. 2003	<i>Calanus finmarchicus</i> (Eastern Canadian waters)	SBM	Eulerian	x,y,z,t	No	Imposed seasonally varying eggs production rates	Temp-dependant	Stage-specific, seasonally-varying and temperature-dependent mortality rates	Imposed seasonally and latitudinally varying probability of ascent and descent	Stage-specific vertical swimming behaviors	1 year
Bryant et al., 1997	<i>Calanus finmarchicus</i> (North Sea)	WwSBM	Box-transport model	x,y,t	Seasonally varying phytoplankton biomass fields from CPR data	f(food)	f(food, temp)	f(foodtemp)	No	No	8 months (Apr to Dec)
Gurney et al., 2001	<i>Calanus finmarchicus</i> (NE Atlantic)	ASBM	Spatially structured model	x,y,t		No	Temp-dependant	No	No	No	Some weeks

et al., 2001b; Jonasdottir et al., 2002) rather than development times, on which the first order influence is temperature (e.g. McLaren, 1978; McLaren and Corkett, 1981; McLaren et al., 1989; Vidal, 1980). Nevertheless, experimental and field data show that starvation can also affect development (e.g. Campbell et al., 2001b) and starvation has been hypothesized to be a source of mortality, especially in naupliar stages. In some regions (e.g. the Gulf of St. Lawrence) there is empirical justification for use of a food-independent reproductive rate (Runge and Plourde, 1996) as a first order approximation (e.g., Zakardjian et al, 2003). Food limitation is nevertheless a fundamental issue for studies of inter-annual or inter-decadal variability in the context of coastal ecosystem change (e.g. Lynch et al. 1998).

Of the sixteen coupled models in Table 13.1, eight do not address food limitation. Three of the remaining models (Voronina et al., 1979; Bryant et al, 1997; Lynch et al., 1998) use as forcing functions averaged phytoplankton fields (as chlorophyll) derived from field observations in the region of study. Five models include detailed parameterization of food effects, with phytoplankton as the prey field in terms of carbon or nitrogen concentrations derived from coupled NPZ models run jointly with the coupled copepod life history model. These latter models have been applied to a one-dimensional water column (Carlotti and Radach, 1996; Carlotti and Wolf, 1998, Heath et al., 1997), and to a two-dimensional coastal upwelling area by Batchelder et al. (2002).

As discussed in Section 2, relationships between chlorophyll *a* (or estimates of microplankton nitrogen or carbon concentrations) and growth and reproduction of planktonic copepods (e.g. Fig. 13.4) are one way to address food limitation in population dynamics models. These relationships are obtained empirically by measurement at sea of growth and reproductive rates of the target species and ambient food concentration in the region of study. As such they need to be determined for each different key species and coastal region. As the empirically determined rates represent means for the population food concentrations typically presented as integrated water column standing stock (or a mean water column concentration), they would be particularly suitable in Eulerian approach. In cases where bulk measures of food do not yield significant relationships with growth or reproduction, or to address growth and reproduction as functions of size and chemical composition of prey as well as issues related to fine-scale spatial and temporal scaling, then the details of feeding behavior could be modeled, and growth and reproduction expressed as the difference between assimilated ingestion rates and metabolic rates, as reviewed by Carlotti et al. (2000). These approaches would be particularly suitable for the Lagrangian approach to coupled models, in which individual growth rates and responses to fine scale variability in prey concentration and composition could be tracked. Comparison at the same location and time period of an Eulerian approach using empirically determined relationships between food and growth and reproductive rates with a coupled IBM model that deduces growth and reproduction from functions expressing feeding, assimilation and metabolic rates would provide insight into the sensitivity of simulated abundance and spatial distribution to the way in which food limitation is addressed in the model.

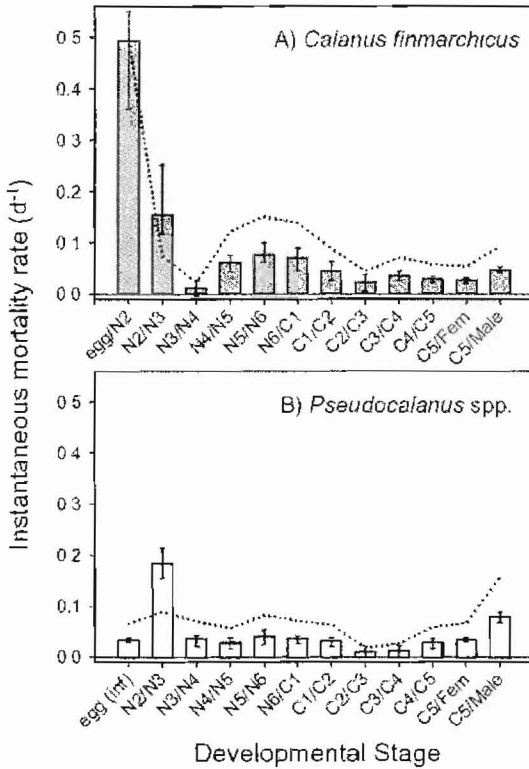


Figure 13.6 Calculated mortality rates for life stage pairs of *C. finmarchicus* and *Pseudocalanus* species based on over 2000 measurements of egg production rate and stage abundance at U.S. GLOBEC Georges Bank broadscale survey stations, 1995–1999. Dotted lines show median rates; histograms show calculated extremes (from Ohman et al., 2002).

Mortality, ecological closure of copepod life history models

Accurate depiction of mortality schedules is one of the greatest challenges in the modeling of marine population dynamics. Good demographic studies of mortality in the sea are rare and in many models, mortality rates are crudely imposed as values from limited observations. Tuning (i.e., an *a posteriori* adjustment) of these mortality rates is often needed in order to scale the overall development of the population (e.g., Davis, 1984; Heath et al., 1997; Miller et al., 1998). In copepod populations, mortality is observed to vary with developmental stage (Fig. 13.6), season and across regions (e.g., Ohman and Hirche, 2001; McLaren et al., 2001 Ohman et al., 2002). Predation is certainly a major cause of mortality; other sources include starvation, temperature (which may be especially important at the geographic limits of a species' range), viruses and parasites. A recent study of the *C. finmarchicus* population in the Norwegian Sea showed that high mortality rates of *C. finmarchicus* eggs and early naupliar stages were positively correlated with the depth-integrated abundance of *Calanus* stage C5 and C6f, suggesting cannibalism as an important factor in the density dependent control of zooplankton populations (Ohman and Hirche, 2001; Ohman et al., 2004). Various

invertebrate and vertebrate predators of copepods such as krill, fishes, birds and whales may locate and aggregate in dense patches of their prey (Wishner et al., 1988; Lavoie et al., 2000), from which we can infer that mortality rates may be locally higher than the mean schedules that are generally used in the models listed Table 13.1.

Demographic analyses of copepod mortality can be realized. Methods to estimate mortality rates, including Wood's Population Surface method and the Vertical Life Table method (Wood, 1994; Ohman and Wood, 1996; Aksnes and Ohman, 1996; Ohman et al., 2002; Ohman et al., 2004) and have been applied to study mortality of *C. finmarchicus* across its range. In addition to quantitative estimates of abundance of life stages, accurate knowledge of temperature dependent development rates and, for mortality of planktonic eggs of broadcast spawners, determination of egg production rate is also required. Alternate methods of estimating mortality of zooplankton size fractions from automated particle counters such as the Optical Plankton Counter (Edvardsen et al., 2002; Zhou, 1998) may also prove useful. Until we are capable of dynamically modeling mortality rates from predator abundance and their feeding behavior and from other sources, we will have to rely on empirical determination of seasonal and spatial variation in mortality based on field studies of the populations of the key species of interest.

Vertical distribution and migration: copepods are not just drifters

In response to vertical gradients in time and space, copepods may vertically migrate. Copepod diel vertical migration allows escape from vertebrate or invertebrate predators (e.g., Ohman et al., 1983; Frost, 1988; Bollens and Frost, 1989; Dodson, 1988) or unfavorable warm temperature (e.g., Wishner and Allison, 1986). Seasonal vertical movements play an important role in the life cycles of many species. Typically, older pre-adult stages inhabit deep water in winter then migrate to surface waters to spawn in spring (Conover, 1988). Both ontogenetic and diurnal migrations may be stage-specific and can range from several meters to several hundred meters (e.g., Wishner and Allison, 1986; Heath et al., 2000). This implies the capacity to swim at several body lengths per second. *C. finmarchicus*, for example, may swim at velocities of more than 50–100 m h⁻¹ (e.g., Heywood, 1996). Such vertical movements are one order of magnitude higher than typical vertical velocity fluctuations in the ocean but one order of magnitude less than typical horizontal velocities. Hence, copepods may be free of vertical advection or turbulent mixing but are always subject to transport by horizontal currents prevailing at their resident depth.

The ability to vertically migrate has great implications for population dynamics in areas of strongly sheared circulation, such as coastal seas, where its interaction with the swimming ability of marine planktonic copepods can yield stage-specific patterns of transport (e.g., Gupta et al., 1994; Hannah et al., 1998; Zakardjian et al., 1999). Results from 2D and 3D coupled models that include vertical migration behavior show first order effects of vertical migration on local copepod population dynamics (e.g., Wroblewski, 1982; Hill, 1991; Lynch et al., 1998; Batchelder et al., 2002; Zakardjian et al., 2003), as previously suggested by studies of Lagrangian trajectories of passive particle both in the coastal sea (Hannah et al., 1998) and the open ocean (Bryant et al., 1998; Harms et al., 2000). In special cases, such as shal-

low vertically homogeneous water of the littoral zone, the interactions between swimming behavior and circulation can be neglected (e.g., Lewis et al., 1994).

The challenge is to build both the observational data base and the fundamental biological understanding of control of stage-specific diel vertical migration and seasonal migrations of target species in each region of study in order to adequately represent vertical distribution in spatially explicit models. There is considerable knowledge of copepod vertical migration behavior (e.g. Frost, 1988; Frost and Bollens, 1992; Bollens et al. 1993, 1994; Kaartvedt, 1996; Falkenhaug et al., 1997). However, vertical migration behavior and consequently vertical distribution may be both stage- and site specific, depending for example on the type of predator (e.g., Tande, 1988), suggesting that a site-independent deterministic formulation may not be possible at this time. We must rely on acquiring extensive observations of vertical distribution at sea, even for a well known species like *C. finmarchicus*. Coupled 3D modeling can be used to identify areas in which the interaction between circulation and vertical distribution are especially critical, for example Cabot Strait and the continental slope of Nova Scotia to *C. finmarchicus* population dynamics in the coastal NW Atlantic (Zakardjian et al., 2003), which can contribute to the design of field studies.

Diapause: a biologically induced seasonality

In temperate and polar regions, the life-cycle of planktonic copepods often includes a diapause phase: a quiescent period, generally in winter, during which the animals wait (at depth) for favorable conditions for reproduction and growth, which usually follow the development of the spring phytoplankton bloom. *C. finmarchicus* undergoes diapause mainly in stage C5 (Fig. 13.5), but diapause may occur in stages C3-C4 (Conover, 1988) in other species of the genus and even in the egg stage other calanoid copepod species, such as *Labidocera aestiva* (Marcus, 1982). The interruption in individual development can even lead to multi-year life cycles, as for *Calanus hyperboreus* (Conover, 1998). The match between the timing of arousal from diapause and the seasonal variation of environmental conditions, mainly temperature and food abundance, may crucially influence interannual variation in population dynamics (e.g., Hirche, 1996; Head et al., 2000). The coupling of the diapause response with seasonal variations in circulation can be another important factor controlling interannual variability of population abundance over large areas (de Young et al. 2004). For example, *C. finmarchicus* overwinters in the deep North Atlantic Ocean at depths between 500 to 1000 m (Miller et al., 1991). Colonization of the Norwegian, Faroe and North Sea coastal shelves depends on the timing and speed of ascent in relation interannual variations in the northeast Atlantic circulation (Aksnes and Blindheim, 1996; Slagstad and Tande, 1996; Bryant et al., 1998; Heath et al., 1999; Gaard, 1999, 2000; Pedersen et al., 2001).

While the physiological responses to diapause are reasonably well known (e.g., Hirche, 1996), there is much less understanding of the environmental or physiological cues that induce entry into diapause or the processes that control emergence from diapause. In present models (Table 13.1) diapause is generally ignored or parameterized simply. Diapause can be neglected in seasonal models that address processes during the active period (e.g. Davis, 1984; Lewis et al., 1994; Batchelder et al., 2002). In other cases, diapause is generally prescribed through

imposed probabilities of ascent and descent based on empirical observations of life cycle timing (e.g., Miller et al., 1998; Lynch et al., 1998; Zakardjian et al., 2003). Carlotti and Radach (1996) used prescribed temperature and food conditions and Carlotti and Wolf (1998) used lipid allocation criteria but without any experimental rationale. Recently, more sophisticated, empirically based models or genetic algorithms for timing of entry into and exit from diapause are promising (e.g. Hind et al., 2000; Fiksen, 2000) for application in the coupled models. Nevertheless, both field observations of the timing of entry and emergence from diapause and new experimental studies are warranted in order to deterministically formulate diapause in models of population dynamics.

4. Trophodynamic models of the early life history of fish

4.1 Overview

Recognition of the critical role played by the fine scale dynamics of the physics and lower trophic levels to understanding larval fish growth and survival (e.g. Heath, 1992) has led to increasing effort devoted to developing coupled physical-biological models (see reviews in Heath and Gallego, 1997; Werner et al. 1997; Lynch, 1999; Werner and Quinlan, 2002). Larval fish dynamics are highly dependent on the physical and biological conditions experienced by the individual (e.g., Rice et al., 1987; Cowan et al., 1997). These conditions in turn vary in time and space (Heath, 1992). Slight differences in the trajectories of individual larvae can mean the difference between success and death (e.g., Bartsch et al., 1989; Hare et al., 1999). Subtle differences in the encounter rates of larvae with their zooplankton prey or with their predators can lead to small changes in growth and mortality rates, which in turn can have order of magnitude effects on larval fish cohort survival (Houde, 1987).

Because the spatial distributions of temperature, zooplankton, and other factors important to larval fish growth and survival are greatly influenced by the physics of water movement (i.e., hydrodynamic transport), coupling individual-based fish larvae to spatially-explicit NPZ and zooplankton life history models is a logical approach for simulating larval fish growth and survival. Fisheries scientists have often developed models of larval fish growth and survival that go into great detail on larval feeding behavior, while the zooplankton prey are treated as a forcing variable (e.g., Vlymen, 1977; Beyer and Laurence, 1980) or by side-stepping the issues of fine-scale spatial variability by using implicit approaches such as statistical distributions that mimic encounter rates in patchy environments (e.g., Rose et al., 1999; Winemiller and Rose, 1993).

While not a necessity, the larval fish component of many coupled physical-biological models uses a Lagrangian approach, which tracks individual larvae through space and time. Individual-based modeling has gained enormous popularity in the past ten years (Judson 1994; DeAngelis et al., 1994; Grimm, 1999; Werner et al., 2001a). A Lagrangian individual-based approach is useful in coupled bio-physical models because few larvae survive (Winemiller and Rose, 1992; Sale, 1990), and it is the history of experiences of the larvae and local interactions (between larvae and its prey and larvae and its predators) that can be important to determining the rare survivors. Accurately simulating individual experiences that vary among individuals and representing the effects of local interactions is difficult

with other, more aggregated modeling approaches (e.g., matrix projection modeling—Caswell, 2001) but is, at least conceptually, relatively straightforward to implement with an individual-based approach.

Here we first review the various ways fish larvae are coupled to hydrodynamic and lower trophic level models. These range from using the hydrodynamics only to transport fish larvae to individual fish larvae being imbedded into the physical models and fully participating in the ecological dynamics (i.e., zooplankton and fish affecting each other). We then discuss three general issues that arise when fish larvae are coupled to physical and lower trophic level models: reconciling temporal and spatial scales between fish larvae and the physical models, how to include the effects of the fish on the lower trophic levels (i.e., feedbacks), and how to represent behavior-related movement of the larvae in a spatially explicit setting.

4.2 Approaches to coupling fish larvae to physical models and lower trophic levels

We begin with Lagrangian (particle tracking) approaches, and then present progressively more complex models that include larval growth via either abiotic effects such as temperature or via bioenergetic formulations of larval feeding and growth.

“Simple” Lagrangian models.

In its simplest form, the coupling is achieved through the advection of passive and/or behaviorally active larvae to determine retention, transport pathways to nursery grounds, etc., through the use of spatially-explicit IBMs (Individual Based Models). Taking advantage of the advent of sophisticated and robust circulation models that capture realism on relevant spatial and temporal scales (e.g., Blumberg and Mellor, 1987; Backhaus, 1989; Lynch et al., 1996; Haidvogel and Beckmann, 1998), perhaps the best established use of IBMs focuses on determining Lagrangian trajectories of planktonic stages of marine organisms in realistic flow fields. The simplest of these studies ignore biotic factors such as feeding and predation; but include imposed swimming behaviors, spawning locations, etc. Among the topics successfully investigated by these studies are the space-time trajectories of larval fish from spawning grounds to nursery areas (Bartsch et al., 1989; Ådlandsvik and Sundby, 1994; Quinlan et al., 1999; Epifanio and Garvine, 2001), retention on submarine banks (Foreman et al., 1992; Werner et al., 1993; Page et al., 1999), effects of interannual variability of physical forcing on dispersal of larval fish populations (Lough et al., 1994; Hermann et al., 1996; Rice et al., 1999), identification of spawning locations (Hare et al., 1999; Stegmann et al., 1999) and the implied long-term dispersal by tidal currents (Hill, 1994). Several of these studies included an imposed behavior on the particles (e.g., Werner et al., 1993; Hill, 1994; Hare et al., 1999) and/or considered the effect of turbulent *kicks* on the larvae's location in the water column (e.g., Werner et al., 2001b) and found that the vertical position of the fish larvae in the water column can affect the results obtained through simple passive advection.

Although lacking in key biological variables, the use of these simple Lagrangian models has been clearly established as a necessary first step in describing the environment sensed by larval fish, their dispersal/retention, the identification of source or spawning regions (Quinlan et al., 1999; Stegmann et al., 1999) and potentially

their recruitment at a population level (Page et al. 1999). The Georges Bank study of Page et al. (1999) compares empirical (field) observations on season and location of cod and haddock spawning with (model-derived) seasonal and geographic patterns of residence times. They conclude that fish populations may select areas and times of the year for spawning that enhance the probability of retention on Georges Bank, thus finding support for the member-vagrant hypothesis (Sinclair, 1988) of the regulation of geographic pattern in populations for marine species. While this particular example was simplified by not including aspects of the organisms' feeding environment and growth characteristics, it is clear that we are on the verge of using Lagrangian models to answer biologically complicated population dynamics questions.

Environmental effects on growth.

Approaches that consider feeding environment implicitly through its relation to temperature include those of Hinckley et al., (1996) and Heath and Gallego (1998). Hinckley et al. (1996) showed the sensitivity of the population's size distribution as a function of trajectories through variable temperature fields (where growth was based on a Q_{10} relationship), as well as the differences that arise in horizontal dispersal due to differences in rates of growth and vertical behavior. In Heath and Gallego (1998), temperature (resulting from a circulation model) was used as a proxy for feeding environment: prescription of the 3-D temperature field was used to determine individual growth rates of larval haddock. It was found that the *model-derived* spawning locations resulting in the highest larval growth rates (as the larvae are advected in the model domain) coincided with the *observed* preferred spawning locations.

Bioenergetic models: including prey fields explicitly.

The next level of complexity commonly introduced into spatially-explicit physical-biological models of larval fish is an imposed spatially-dependent (but temporally fixed) prey distribution based on field observations.

The typical bioenergetics model is based on an equation that relates the new weight (W) of a larva to its previous weight plus gains and minus losses (e.g., Beyer and Laurence, 1980; Rudstam, 1988):

$$\frac{dW}{dt} = [C - (R + S + F + E)] \cdot W \quad 13.2$$

where C is consumption, E is excretion or losses of nitrogenous excretory wastes, F is egestion or losses due to feces, R is respiration or losses through metabolism, S is specific dynamic action (or losses due to energy costs of digesting food), and t is time. The units of C , E , F , and S are weight prey · weight fish⁻¹ · time⁻¹. Consumption and respiration are weight- and temperature-dependent. Water temperature experienced by a larva affects maximum consumption and respiration. The number of prey encountered depends on prey type, the swimming speeds of the prey and the fish larva and turbulence.

These studies are a first step to introducing realistic representations of the spatial distribution of key variables such as temperature, oxygen, light levels, prey

availability, etc. In Brandt et al. (1992) a bioenergetic model was embedded in a spatially heterogeneous representation of its physical (estuarine) habitat, as determined by field measurements, to obtain the spatial distribution of growth rates of the target fish. From the spatial distribution of fish growth potential, Brandt et al. (1992) were able to define the portion of the habitat volume that will support various levels of fish growth. Furthermore the resultant *growth volumes* can provide a mechanism for assessing the suitability of a particular habitat to support a species introduction and can aid in the definition and monitoring of ecosystem health.

Similar approaches, based on model-derived spatial structure of prey and habitat (circulation, turbulence and temperature) are discussed in Fiksen et al. (1998) and Lynch et al. (2001) who produced Eulerian maps of potential larval fish growth rates. Fiksen et al. (1998) examined the interactions between vertical profiles of wind-induced turbulence and light to define regions in the water column where highest ingestion rates can occur for certain fish larvae. Lynch et al. (2001) found that, during early spring on Georges Bank, the distribution of certain prey (*Calanus finmarchicus*) is better matched spatially with the spawning location and subsequent drift of cod and haddock larvae than other potential prey (*Pseudocalanus* spp.). Additionally, it was found that spawning in regions of high turbulence is detrimental to young larvae, suggesting that for survival of the earliest larval life stages spawning should occur away from these regions.

A natural extension to these diagnostic approaches is the computation of individual Lagrangian trajectories within the prey field. In this manner, trajectories that are considered favorable for retention or appropriate for transport into nursery areas are more narrowly identified to include only those trajectories where the individuals encounter favorable feeding environments. Studies of this type include Hermann et al. (2001) and Werner et al. (1996 and 2001b). These studies have also been used to explore other spatially-dependent interactions between predators and their prey. For example, the perceived prey field by fish larvae can be effectively increased or reduced as a consequence of local variation in turbulence levels, which alter volume searched (MacKenzie et al., 1994; Dower et al., 1997; Werner et al., 2001b). This requires models to capture not just the spatial distribution of biotic components, but also their modulation by certain abiotic environmental factors. An example of the intersection of large and small scale physics affecting recruitment is given in Werner et al. (1996) in which the effect of the feeding environment, modified by turbulence at the smallest scales, on larval growth and survival was examined. They found that regions of larval survival (with growth rates comparable to field values) coincided with the hydrodynamically retentive subsurface regions of Georges Bank. However, these retentive regions were a subset of those defined by Werner et al. (1993) and Lough et al. (1994). The increase in larval survival in these smaller areas was due to an enhancement of contact rates and effective prey concentrations by turbulence within the tidal bottom boundary layer.

4.3 Present challenges and issues facing coupled models of fish early life history

Coupling fish larvae to physical models raises important issues about scaling of physical and life history processes, trophic feedbacks, and movement and behavior.

Scaling

The time step and spatial resolution of the physical model are dictated (or limited) by numerical considerations, which may not coincide with the ideal time step and spatial resolution for simulating growth and survival of fish larvae. Simulating purely advective and dispersive transport of passive particles is in a relatively advanced state of development. Scaling issues arise when the particles have behaviors, and especially when simulated growth and mortality are dependent on dynamic prey and predators. The generally fine-scale of the physical models would involve simulating fish larval behavior on the scale of minutes at the spatial resolution of the hydrodynamics. Larval fish ecologists are often more comfortable simulating larval dynamics on scale of hours to daily, and therefore also at a coarser spatial resolution that matches the longer time step. Output from the hydrodynamics and lower trophic models are often aggregated to some extent to permit coarser simulation of the larval dynamics. How to aggregate the output without losing dynamically-relevant variability is an important consideration. An illustration of the complexity of this scaling is the walleye pollock coupled biophysical model (Hermann et al., 2001), which meshed together a 257 x 97 x 9 nonuniform grid, (with approximately 4 km resolution in the horizontal, variable resolution in the vertical) and 135 sec time step for hydrodynamics), a 20 x 20 x 100 grid (with 20 km resolution in the horizontal, 1 m resolution in the vertical, and a 0.1 day time step) for the NPZ component and a continuous spatial domain for the larval fish IBM (with a combination 24hour/1hour time step) for the larval fish dynamics.

Trophic feedbacks

Including the effects of the larval fish on the lower trophic levels (consumption of zooplankton and addition of nutrients via excretion and egestion) can additionally complicate the modeling. Most coupled biophysical models use the hydrodynamics and lower trophic level predictions as input to the larval fish component. This enables the lower trophic level models to be solved independently of the larval fish dynamics. However, separate solution of the lower trophic and larval fish models prevents any density-dependent effects from operating. Perhaps under most average conditions, the effects of larval fish, on their prey and on nutrients, is small enough to be ignored. But it may very well be that the rare set of conditions when such feedback effects are important is of most use to those interested in fish recruitment. Density-dependent effects may be elusive as they may operate only under certain conditions (e.g., years of high egg production and low food production), but such effects are not possible to predict (or dismiss) if the coupled biophysical model do not include the capability to include these feedbacks. Yet, including these feedbacks would require that the lower trophic level component and the larval fish component models be solved simultaneously. For some situations, this can create computational limitations on the analyses and heartache for the programmer. Linking larval fish models where full hydrodynamics and fully evolving population dynamics co-occur will likely be attempted in the next five years (see Ault et al. 1999 for an example of such a linkage using McKendrick-von Forester equations and a 2D hydrodynamic model). We are now beginning to see the first attempts at fully-evolving models (e.g., Hermann et al., 2001; Hinckley et al., 2001).

Movement and swimming behavior

Like other zooplankton, fish larvae exhibit active movement not related to advection. Active movement can be critical because such movement can greatly affect the transport, environmental conditions and prey experienced by the individual larvae (Tyler and Rose, 1994). Modeling active movement by fish remains a difficult area. We do not really know why larval fish move, especially on the scale of minutes to hours and over relatively short distances (e.g., meters). Externally imposed (and/or passive) behaviors (e.g., Werner et al., 1993; Hare et al., 1999) may not make sense as the coupled biophysical model move more and more towards simulating the growth and survival of the larvae. Such static approaches to movement will be likely replaced by model-derived behaviors that include components maximizing some biological characteristic, such as reproductive value (Giske et al., 1994; Fiksen and Giske, 1995; Fiksen et al., 1995), survival to maturity (Railsback and Harvey, 2002), or short-term tradeoffs between growth and mortality (Tyler and Rose, 1997). Dynamic programming methods allow organisms to "find" optimal habitats by balancing risks of predation, growth, and advective loss. The issue of how to represent active movement on fine scales is important but remains unresolved at this time. The realism of predicted growth and mortality from coupled models may very well rely on how well we can model fish movement.

5. Case Studies: The application of coupled physical-biological models in coastal environments

Within the past decade, considerable progress has been made in the application of coupled physical-biological models of secondary production and recruitment processes to a number of coastal regions around the world, including the Baltic Sea (e.g. Hinrichson et al., 2002), the northeast and northwest Atlantic Ocean (e.g. Bryant et al., 1997; Heath and Gallego, 1998; references below), the northeast and northwest Pacific Ocean (e.g. Batchelder et al., 2002; Kishi et al., 2001), the Gulf of Alaska (references below), and the Benguela upwelling system (references below). Common features to all the regional applications are developments of region-specific 3-D circulation models and the involvement of large, multidisciplinary programs to facilitate cross-disciplinary collaboration and data collection. Differences in approach and emphasis and focus of the research questions are also evident, depending on the particularities of the regional system and the objectives and structure of the multidisciplinary programs, including how the large programs are funded. Here we provide brief summaries of coupled physical-biological modeling in three regions, the southern Benguela upwelling system, the coastal northwest Atlantic Ocean, and the western Gulf of Alaska, to illustrate the present status of application of models to coastal systems.

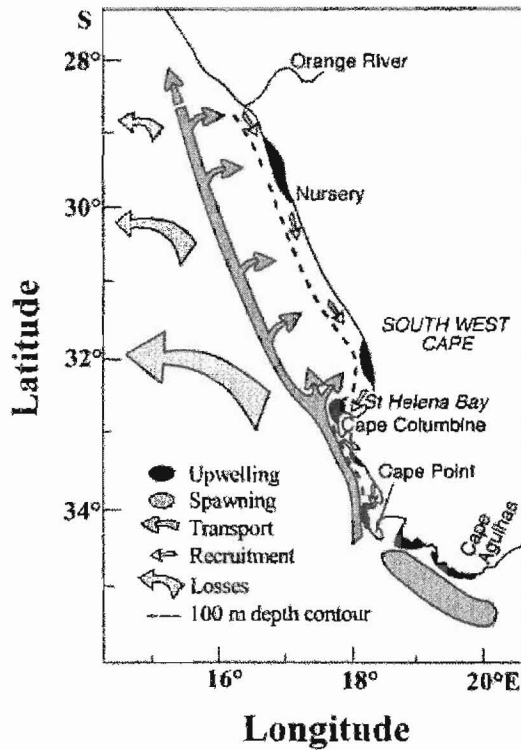


Figure 13.7 Conceptual model of the advective influence of the Benguela Current System on the life history of anchovy (from Pillar et al., 1998 and Parada et al., 2003). Anchovy eggs and larvae spawned on Agulhas Bank are transported north, some to the inshore nursery area.

5.1 The southern Benguela upwelling system

The Benguela Current and its associated upwelling system is one of the most productive ocean environments in the world (Shannon and O'Toole, 2003; Field and Shillington, in press). Conceptual understanding and data acquisition within the region advanced considerably during the late 1980's and 1990's during the Benguela Ecology Program (e.g. Pillar et al., 1998). The dominant, harvested fish in the Benguela upwelling system are species of anchovy (*Engraulis encrasicolus*) and sardine (*Sardinops sagax*), both of which are adapted to the dynamics of upwelling environments. The emergent paradigm of the anchovy life cycle in the southern Benguela is that adults spawn on the Agulhas Bank during austral spring and summer. The eggs and larvae are transported by a coastal jet to a nursery area located approximately 500 km to the north along the west coast of S. Africa and Namibia (Fig. 13.7). Successful recruits are believed to be larvae that find themselves in the inshore nursery area, where they grow into juveniles and mature, then move southward back to Agulhas Bank to spawn at age 1, completing the life cycle. Variability in transport of eggs and larvae from spawning to nursery grounds is considered to be a first order determinant of anchovy recruitment success (Huggett et al., 2003; Parada et al., 2003 and references therein). The coupled physical-

biological models reported here were developed as part of the multi-disciplinary IDYLE program, a bilateral research program funded jointly by agencies and institutions within the Republic of South Africa and France.

The regional circulation model to which biological processes are coupled is a high-resolution, 3D, eddy resolving hydrodynamic model (Penven et al., 2001) based on the Regional Ocean Modeling System (ROMS: Haidvogel et al., 2000). The model uses stretched, terrain-following coordinates in the vertical and orthogonal, curvilinear coordinates in the horizontal, yielding a resolution of 9 km at the coast and 16 km offshore, with 20 variable levels in the vertical. The model is forced with averaged winds, heat and salinity fluxes determined from the COADS ocean surface monthly climatology. It is forced at the offshore boundaries by seasonal, time-averaged outputs of a larger, basin-scale model. In studies published to date, the hydrodynamic model was run for 10 years and forced by a repeated climatology. While there was no interannual variability in the winds and other forcing processes, there were differences in simulation outputs between years, attributed to intrinsic mesoscale activity resulting from oceanic instability processes within the model structure (Penven et al., 2001).

The biological applications of the hydrodynamic model focus on the interaction between advection and characteristics of spawning and distribution of eggs and larvae of anchovy in the southern Benguela Current System (e.g., Mullon et al., 2002; Huggett et al., 2003; Parada et al., 2003). The approach and results are summarized in Mullon et al. (2003). Individual-based models of eggs and larvae of anchovy were coupled to the output from individual years of the hydrodynamic model. In a series of trial runs, parameters were varied sequentially in order to assess the relative importance of factors that may influence successful transport to the inshore nursery area. Variables included timing, location and frequency of spawning activity on Agulhas Bank (Huggett et al., 2003), release depth and buoyancy of eggs (and early larval stages, assumed to be the same as egg buoyancy) (Parada et al., 2003), growth and mortality as a function of temperature (Mullon et al., 2003) and active vertical migration behavior of larvae (Mullon et al., 2003). Success was measured by the number of larvae older than 14 d (the age at which larvae are considered capable of maintaining their location) arriving in the inner nursery area within the duration of the trial (typically 90 d). A typical model run was initiated with 5000–10,000 individual eggs; in all, over 20,000 trials were conducted. Success percentages from the trials were analyzed statistically using multi-factor analyses of variance. Among the results of these simulation experiments are that eggs spawned on western Agulhas Bank and having a density of 1.025 g cm^{-3} are most successfully transported to the nursery area (Fig. 13.8) and that transport success is greatest among actively swimming larvae keeping a target depth of 40–60 m (Mullon et al., 2003). In general, the impacts of variability in spawning location, egg buoyancy, the direction and intensity of the jet current, the effects of temperature on growth and mortality, and vertical migration behavior on transport success were quantified, although it is not possible to quantify precisely the relative importance of each factor.

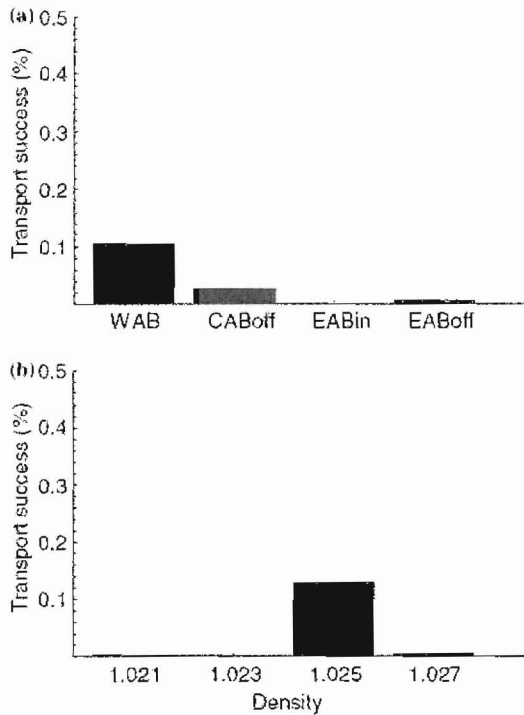


Figure 13.8 Transport success (%) of anchovy larvae in the southern Benguela Current System in relation to (a) location of spawning area (WAB=Western Agulhas Bank, CAB = Central Agulhas Bank, EAG = Eastern Agulhas Bank and (b) changes in specific density (g cm^{-3}) of anchovy eggs. From Mullon et al. (2003).

While the focus has been on impacts of advection on retention of larvae in nursery areas, research in the Benguela Current System has laid the groundwork for development of coupled physical-biological modeling simulating dynamics of phytoplankton and zooplankton production. For example, Plaganyi et al. (1999) describe a population dynamics model of a dominant planktonic copepod, *Calanoides carinatus*, that uses satellite derived estimates and chlorophyll a concentration and sea surface temperature as primary inputs. Plaganyi et al. (2000) develop a model of growth rates of juvenile anchovy as a function of abundance of *C. carinatus*, a major component of their diet.

Improvements to the hydrodynamic model of the Benguela Current System, including incorporation of finer scale variation in winds (e.g., Blanke et al., 2002), will allow greater power for addressing interannual and interdecadal variation in factors identified as having first-order impact on larval survival. An analysis of measurements of extreme oceanographic events in the southern Benguela during 1999–2000 (Roy et al., 2001) indicates that record high recruitment of anchovy in 2000 resulted from a synergistic temporal sequence of upwelling events leading to favorable transport and production of phytoplankton and zooplankton prey. There is the potential for future development of the Benguela Current System coupled

models to address impacts of the climate-forced variation in upwelling events and transport processes on secondary production and anchovy recruitment.

5.2 *The northwest Atlantic coastal ocean*

The northwest Atlantic (NWA) coastal ecosystem extends southward from the Labrador Sea, along the Scotian Shelf, including outflow from the Gulf of St Lawrence, and through the Gulf of Maine and around Georges Bank (Townsend et al., in press). It is a mid-latitude, subarctic region with marked north-south variation in the seasonal cycle of ocean temperature. Important freshwater river inputs influence seasonal stratification and mixing and drive an extended estuarine circulation that advectively couples the region's shelf systems. The banks and inshore areas of the northwest coastal shelves serve as retention and nursery areas for early life stages of fish. Because it is a flow-through system, interannual and decadal scale variations in climate influencing the Labrador Sea and Gulf of St. Lawrence have impacts for the Scotian Shelf and Gulf of Maine (e.g. Loder et al., 1988; Greene and Pershing, 2003).

Here we focus on developments in coupled physical-biological modeling of Georges Bank and the Gulf of Maine. Annual fish production on Georges Bank has been among the highest of the world's shelf ecosystems (Cohen and Grosslein, 1987). The Georges Bank GLOBEC program (e.g. Wiebe et al., 2002), initiated in the mid-1990's, targeted study of physical-biological processes controlling population dynamics of several dominant species: the planktonic copepods *Calanus finmarchicus* and *Pseudocalanus* spp. and the early life stages of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*). The conceptual model (Colton and Temple, 1961) for the early life history of cod and haddock on Georges Bank is that spawning takes place in late winter-early spring (February-April) in the northeast peak of the Bank. A semi-closed gyre transports the eggs and larvae in a clockwise direction around the Bank, particularly along the southern flank (Fig. 13.9). At some point, the larvae are either retained or presumably lost as vagrants (as defined in Sinclair, 1988) in a drift exiting the Bank at its southwest corner (e.g., Werner et al., 1993; Page et al., 1999, and references therein). The planktonic copepods, *Pseudocalanus* spp., *Oithona* spp and *Calanus finmarchicus* are observed to be dominant prey during the cod and haddock larval phase (e.g. Kane, 1984; Lough and Mountain, 1996).

Numerical modeling of the regional circulation began well before GLOBEC (e.g. Greenberg, 1983; Isaji and Spaulding, 1984), but quantitative description improved with larger and more readily available hydrographic datasets and increasing computational power. A number of 3D models have been developed for the area, including QUODDY (Lynch and Naimie, 1993; Naimie et al., 1994, Naimie, 1996; Lynch et al., 1996; Loder et al., 1997, Loder et al., 2001), ECOM and FVCOM (Chen et al., 2001; Lewis et al., 2001) and CANDIE (Sheng et al., 1998). These models all solve primitive equations for heat, fluid, mass and momentum transport, incorporating advanced turbulence closure schemes (e.g. Mellor-Yamada level 2.5), and solve the equation of state relating temperature and salinity to density. Their main differences lie in the numerical methods employed to integrate the governing equations (i.e. finite difference, finite element, finite volume), their spatial and temporal resolution, and their domain of application. By

prescribing realistic topography and forcing with historical data for tides, temperature, salinity, and winds, the various models generated representations of the regional currents, turbulence and temperature fields.

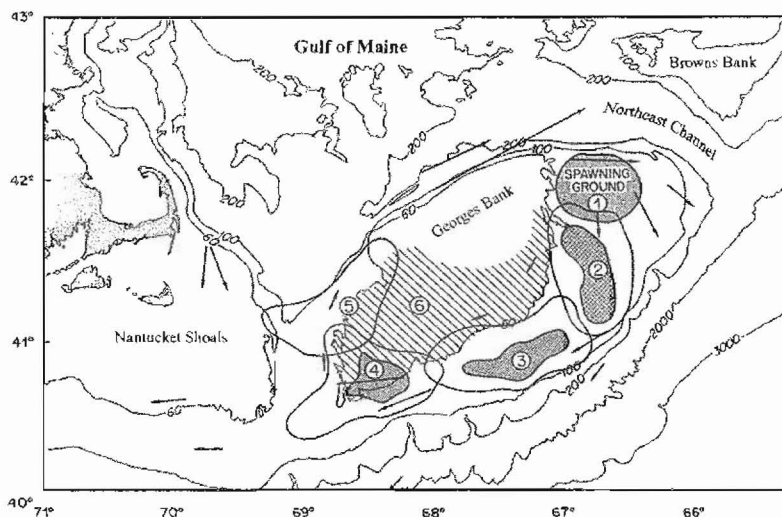


Figure 13.9 Conceptual model of advective influences on the early life history of cod on Georges Bank (from Colton and Temple, 1961). Cod eggs and larvae spawned on the northeast peak are transported to the southwest along the southern flank and are either retained on the crest or advected off the Bank. For main circulation features in the coastal northwest Atlantic Ocean, refer to Townsend et al. (in press).

Coupled physical-biological modeling in the northwest Atlantic includes NPZ, copepod life history and larval fish trophodynamic approaches. Circulation and mixing effects on planktonic production have been studied by coupling NPZ-type ecosystem models with the regional circulation fields. Winds typical of winter storms were shown to result in large exchanges of bank waters and large losses of plankton production on the bank (Lewis et al., 1994). Simulations for early summer yielded phytoplankton distributions consistent with satellite chlorophyll images. Predicted phytoplankton fields were relatively insensitive to removal of modeled advection, indicating the primary importance of vertical mixing in structuring the plankton around the Bank (Franks and Chen, 2001).

A number of models have investigated the transport of copepod populations onto and around Georges Bank. Early simulations used idealized flows (e.g. Davis, 1984; Lewis et al., 1994), whereas later more realistic circulation fields were used. The advective supply of *Calanus finmarchicus* to the Bank and the relative importance of transport vs. *in situ* biological processes was explored with Lagrangian particle tracking (Hannah et al., 1998) and with Eulerian-based models (Lynch et al., 1998; McGillicuddy et al., 1998). Biological components of these models quantified processes such as reproduction, development and mortality at a particular demographic resolution, including stage-based (Lewis et al., 1994), age-within-

stage (Lynch et al., 1998), and individual-based (Miller et al., 1998). Because chlorophyll levels on the Bank were generally high, the initial hypothesis was that copepods were food-satiated. Hence, most models assumed vital rates were maximal, and based them on temperature-dependent empirical relationships developed in the lab (e.g. Miller et al., 1998; Lynch et al., 1998). These studies indicate that seasonal variation in the flow and processes influencing timing and emergence from diapause and vertical distribution of the copepods strongly affects rates of supply from the Gulf of Maine and retention on the Bank. Simulations showed that spatial and temporal patterns of *Calanus* recruitment of the first generation were consistent with data only when the model considered food-limitation of populations in the low-chlorophyll Gulf of Maine (Lynch et al., 1998), a prediction that could be tested with the appropriate field study. Evidence for food limitation of *Calanus* has since been found on Georges Bank (Campbell et al., 2001b).

Zakardjian et al. (2003) developed a 3D physical-biological model depicting the population dynamics of *Calanus finmarchicus* in the Gulf of St. Lawrence and Scotian Shelf and Gulf of Maine (Fig. 13.10). One of the objectives of the study was to examine how the local *Calanus* populations are maintained in this interconnected, advective regime (see Townsend et al., in press). A stage-based life history model consisting of the 13 distinct life stages as well as diapausing CV and immature female stages was coupled to the nonlinear z-level ocean circulation model (CANDIE: Sheng et al., 1998). CANDIE was run in diagnostic mode over a full one-year cycle and the stored output was called up at each time step for the calculation of fluxes through grid boundaries, abundance, total spawning production and mortality. The model results indicate that the GSL population is self-sustaining, but that the fluxes of *Calanus*, notably an export to the Gulf of Maine and potentially important input from offshore slope waters, play an important role in controlling abundance on the shelf.

One way of testing the accuracy of the coupled models is to initialize the model with one set of observations, say the abundance of a copepod species on a spatial grid, run the model forward in time to the date of the next set of observations, and then compare the simulated results with the observed data. Small differences between the predictions and observations would impart confidence that the coupled model is capturing the essential biological and physical processes controlling the population dynamics. McGillicuddy et al. (1998) introduced an alternative technique, called adjoint data assimilation, for cases when the discrepancies are large, or when limitations in the model or data do not allow proper investigation of the forward problem. The adjoint data assimilation technique essentially iterates backward in time from the second set of observations in order to find the biological reaction term, R (in two dimensions, $R(x,y)$), that minimizes the misfit between the observations and predictions. Assuming that the advective fields are correctly characterized, the sign of $R(x,y)$ indicates, for that point in the grid, whether population growth or mortality was dominant. In combination with ancillary data on, for example egg production rates and predator abundance, this method provides insight into the population control processes across the spatial grid.

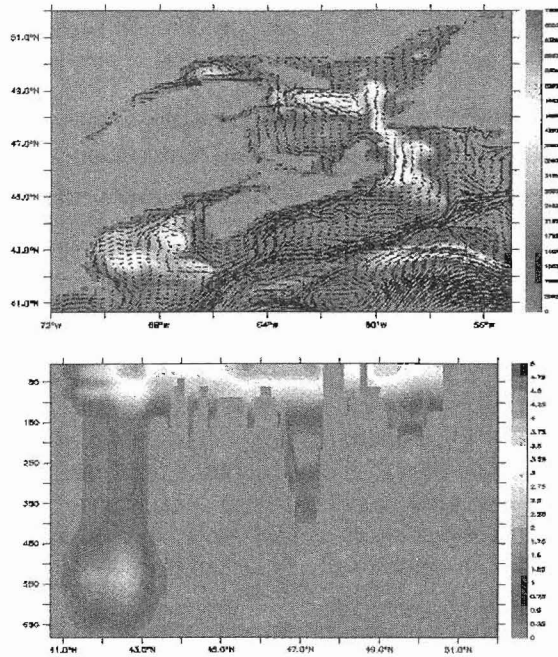


Figure 13.10 A) Surface currents and simulated, depth-integrated abundance (no. m^{-2}) of *C. finmarchicus* (all stages) in early June in the Gulf of St. Lawrence, Scotian Shelf and Gulf of Maine system based on a *Calanus* life history model coupled to the 3-D mean climatological circulation calculated from the CANDIE finite difference model (redrawn from Zakardjian et al., 2003). B) Vertical section at 59°30' W of *Calanus* total abundance ($\log[\text{no. m}^{-3}]$) from (A) showing the stage-specific vertical distribution in the simulated model results. The deepest abundance mode (300 m in the Gulf and 550 in the slope water) represents diapausing CV and males.

The newly developed circulation models have been used to investigate the role of advection for the retention, dispersal and growth rates of larval fish. The fate of larvae spawned on the northeast peak of the Bank was explored through the use of Lagrangian particle tracking (Werner et al., 1993), wherein particles represented early life stages of fish and exhibited various swimming behaviors (passive, fixed-depth, age-dependent migrations, and lateral swimming). Simulations demonstrated large advective losses, such that most larvae were carried out of the region. Particle tracking was also used to estimate the seasonal variation in residence times for water parcels (Page et al., 1999). Particles, initially distributed Bank-wide, were advected with seasonal mean flows for 60 days, revealing large geographic and seasonal differences in residence times. The relative role of advection vs. food limitation was explored by coupling a particle-tracking mode with a trophodynamic model (Werner et al., 1996; Werner et al., 2001b). Larval growth rates are related to encounter, ingestion and assimilation of prey, and incorporated effects of turbulence on contact rates (Fig. 13.11). Prey density was estimated from data, and turbulence levels were derived from the circulation model. Advective losses were found to be on the order of 20% of the larvae spawned, and the region of highest retention coincided with the region of highest growth. Near-bed turbulence played a big role in increasing contact rates, but high values close to the

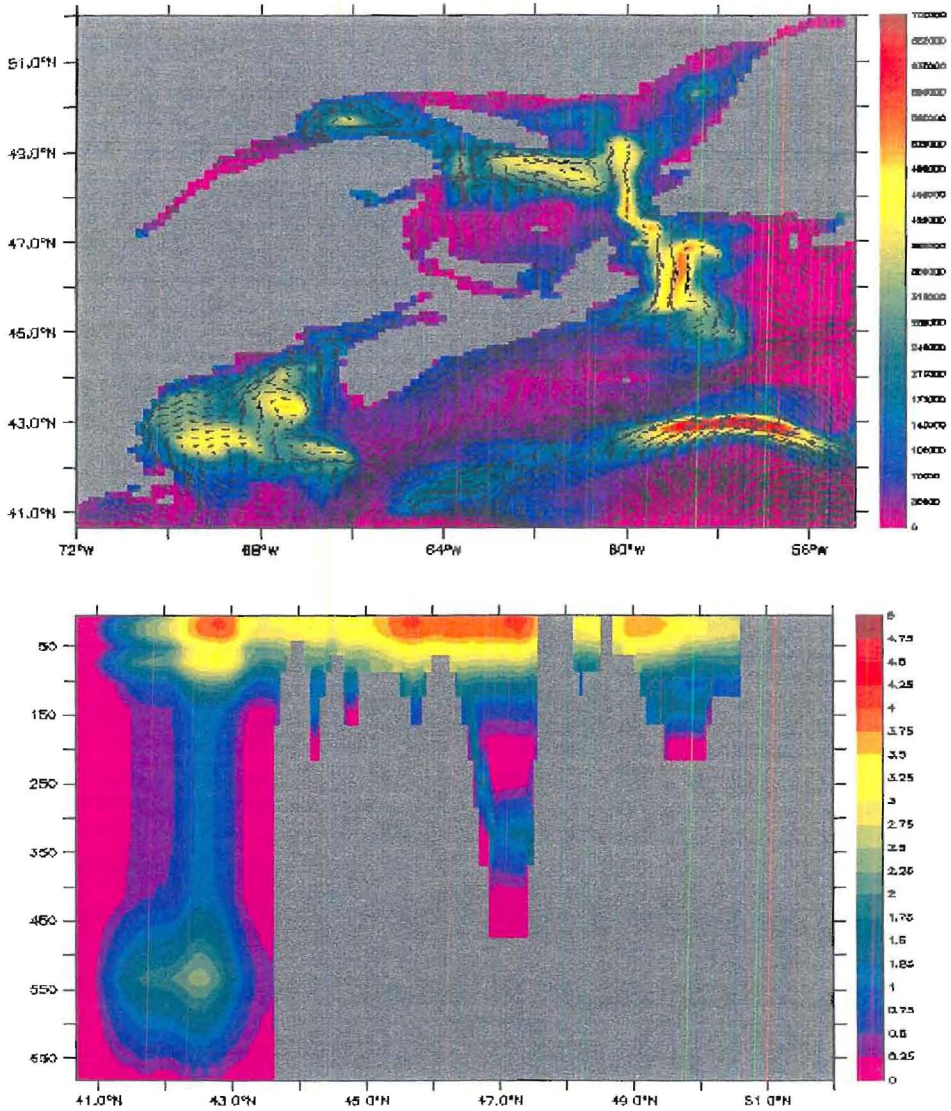


Figure 13.10. A) Surface currents and simulated, depth-integrated abundance (no. m²) of *C. finmarchicus* (all stages) in early June in the Gulf of St. Lawrence, Scotian Shelf and Gulf of Maine system based on a *Calanus* life history model coupled to the 3-D mean climatological circulation calculated from the CANDIE finite difference model (redrawn from Zakardjian et al., 2003). B) Vertical section at 59°30' W of *Calanus* total abundance (log[no. m⁻³]) from (A) showing the stage-specific vertical distribution in the simulated model results. The deepest abundance mode (300 m in the Gulf and 550 m in the slope water) represents diapausing CV and males.

bottom decreased the larvae's capture success and thus the smaller number of survivors close to the bottom.

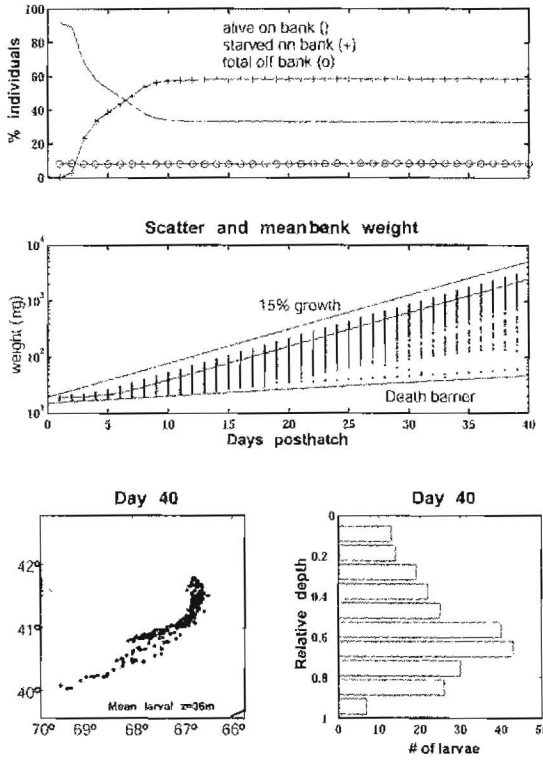


Figure 13.11 Post-hatch history of modeled cod larvae on Georges Bank (from Werner et al. 2001b) including advection, feeding, and effects of turbulence on encounter rates and capture success. Top panel, the percentage of larvae alive (solid line), starved on-Bank (solid line with crosses), and advected off the Bank (solid line with open circles); second panel, the daily size distribution (micrograms) for the live larvae on the Bank, the 15% per day growth curve, the death barrier and the mean daily weight of those live larvae still on the Bank. Bottom left and right panels show, respectively, the horizontal distribution of the live larvae 40 days post-hatch and their vertical distribution relative to the local bottom-depth.

Historical data indicated a large degree of spatial variation in the seasonal prey fields (Meise and O'Reilly, 1996; McGillicuddy et al., 1998). Seasonal and geographic variation in food limitation of larval fish growth rates was investigated from an Eulerian perspective (Lynch et al., 2001). Prey fields were estimated using spatially-explicit zooplankton data and a zooplankton population dynamics model to generate maps of egg and naupliar abundance. Turbulence fields were derived from the circulation model. These spatially-varying fields were then used as input for a simplified model of fish growth to produce maps of the instantaneous fish growth rates as derived from different prey types. Model simulations indicate that

small cod larvae could not survive on a diet of *Calanus finmarchicus* alone, whereas large larvae could. It showed that *Pseudocalanus* abundance was sufficient in certain areas to sustain high growth rates, but these could be mismatched with areas of where cod spawning and advection occurred.

Regions of the NWA have a good foundation of physical models. Considerable progress has been made toward the development of region-specific, coupled physical-biological NPZ, copepod life history and larval fish trophodynamic models. Extensive physical and biological data collected over the multi-year field studies in the NWA coastal regions is available for investigation of interannual variability. Field and process studies of vital rates, including reproduction and mortality, reveal empirical patterns relationships and patterns that offer simplifications of complex ecological interactions. The development of alternate modeling approaches such as adjoint data assimilation offer the prospect of new insights into processes controlling population dynamics. The challenge is to advance and link models of the three trophic levels into a comprehensive depiction of ecosystem dynamics and influences of climate variability.

5.3 The western Gulf of Alaska

Walleye pollock, *Theragra chalcogramma*, a widely distributed and dominant groundfish species in ecosystems across the North Pacific Ocean, supports one of the world's largest fisheries (Bailey et al., 1999). Spawning in this species is constrained to a relatively small number of locations during certain, predictable times of year. In the Gulf of Alaska, most of the walleye pollock constitute one stock that migrates to a limited area (40 km by 80 km) in Shelikof Strait to spawn during the first week in April. Larvae hatching from the free-floating eggs released at depths of 150–250 m drift downstream in the Alaska Coastal Current, a very strong (25–100 cm s⁻¹) current that transports larvae either to an inshore juvenile nursery or into the offshore Alaskan Stream (Fig. 13.12), where they are presumably lost to the stock (Kendall et al., 1996a). Larvae are frequently found in large patches associated with eddies. There is considerable potential for interannual and interdecadal forcing functions (e.g. storms, freshwater input, wind-generated turbulence) to influence the successful survival of the walleye pollock from egg to juvenile stages.

Understanding of walleye pollock dynamics in the western Gulf of Alaska has advanced considerably since establishment in 1984 of The Fisheries Oceanography Coordinated Investigations (FOCI) program by the U.S. National Oceanic and Atmospheric Administration. At the outset, knowledge on the life history of pollock and the dynamics of the physical environment in this region were very limited. Initial field and process studies focused on understanding the life history of pollock, identifying important biological processes, and examining the nature of the regional circulation (see, for example, references in Kendall et al., 1996b). As these aspects became better understood, field operations switched to maintenance of time series of selected biological and physical characteristics, studies of biophysical processes, and development of methods for analysis of factors influencing interannual changes in rates of survival. Since 1992, FOCI has analyzed biological and physical time series relative to a working conceptual model of the recruitment process (Megrey et al., 1995) and used these data and models to forecast future

recruitment on a qualitative basis (i.e. weak, average, strong). This prediction significantly simplifies the stock projection analysis and facilitates interpretation by fisheries managers by limiting the number of viable recruitment scenarios. While present forecasts of year-class strength (Megrey et al., 1996) do not use coupled physical-biological models directly, they are used to identify gaps in knowledge, synthesize information, organize conceptual ideas, expand the spatial and temporal characteristics of field observations, generate hypotheses of linkages and interactions among sets of biological and physical factors, and provide information into the fisheries management stream.

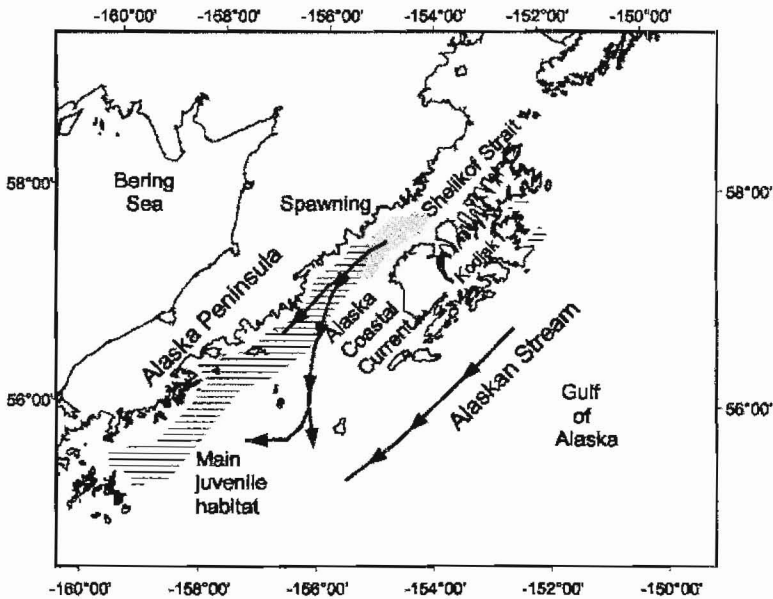


Figure 13.12 Conceptual model of the early life history and advective influences of walleye pollock in Shelikoff Strait, Gulf of Alaska. Eggs and larvae spawned in Shelikof Strait are transported to the southwest to either the inshore nursery area or the offshore Alaska Stream. (from Kendall et al., 1996b)

The circulation model used in the western Gulf of Alaska system is a primitive equation rigid-lid hydrodynamic model based on the Semispectral Primitive Equation Model (SPEM) of Haidvogel et al. (1991) and modified for this region (Stabeno et al., 1995a; Hermann and Stabeno, 1996). The spatial domain of the model comprises the northern Gulf of Alaska from east of Shelikof Strait to west of the juvenile habitat area (vicinity of Shumigan Islands) and contains a total of ~250,000 grid points with approx. 4 km spacing and nine vertical levels in the finely resolved area between Kodiak and the Shumigan Islands. The model is forced by twice-daily winds and monthly fresh-water runoff. Physical factors that pose challenges to proper representation of the area included complex bathymetry with many islands, mesoscale (~20 km) meanders and eddies, strong vertical shear (estuarine-like flow), and strong forcing by winds and freshwater runoff. SPEM has reproduced the observed general spatial features of circulation (Stabeno et al.,

1995b). The physical model has been validated with Eulerian (moored current meters) and Lagrangian (drogued drifters) data from field experiments (Hermann and Stabeno, 1996). The model is capable of generating eddies similar to those observed in terms of spatial scales and frequency of occurrence.

The biological model consists of a stochastic individual-based model (IBM) of egg and larval development (Hinckley et al., 1996). The IBM follows the unique life history of each fish from spawning to September of their 0-age year and therefore provides specific information about survivors. Velocity fields from the hydrodynamic model provide the physical spatially-explicit context to move individuals through space. The model also employs a spatial tracking algorithm for each individual that includes vertical migration according to life stage. Horizontal transport, egg development time, growth, and behavior are governed by velocity, salinity and temperature fields generated by SPEM. Low-pass filtered velocity and scalar fields from SPEM are stored once per model day, then used as input for multiple runs of the biological model. More recent advancements include the addition of an NPZ model to provide food for feeding pollock larvae (Hermann et al., 2001: Fig. 13.13). The zooplankton term in this model comprises the large planktonic copepods, *Neocalanus spp.*, the mesozooplankton species that graze much of the primary production and the smaller *Pseudocalanus spp.*, the dominant prey for larval pollock in this region. The submodel for *Pseudocalanus* is stage structured, with egg, nauplius, copepodid and adult compartments.

The hydrodynamic, NPZ and IBM larval fish models have been linked into a coupled physical-biological model system. For each simulated year, the SPEM model is run to obtain velocity, temperature and salinity fields that are subsequently stored. The NPZ model is run through the spring period covering the plankton phase of the walleye pollock life history, using the SPEM-generated physical forcing and storing the 3-D output of stage-specific abundances of *Pseudocalanus* prey. The IBM larval fish model is then run using the SPEM and NPZ stored output to force advection and growth of individuals. Hence, in this coupled system, there is no dynamic linkage between the larval fish predators and their copepod prey.

This coupled model system has been used to explore the relationship between physical oceanographic processes and their effect on biological variability, hindcast the early life history of walleye pollock, and to assess the possible physical causes of interannual variability in recruitment. Modeled spatial distributions qualitatively compare favorably with observed distributions of larvae and juveniles (Hermann et al., 1996: Fig. 13.14). Interannual differences in wind and freshwater runoff lead to differences in the modeled spatial paths of individuals, and in the distributions of population attributes such as growth rates and size distributions. Results from SPEM show that during 1978 (the strongest year class) larvae were more likely transported into coastal waters along the Alaska Peninsula, while in 1990 (a below average year class) they remained in the sea valley where currents then result in transport offshore (Stabeno et al., 1995b). This latter scenario supports FOCI's original transport hypothesis as it implies a loss of recruits.

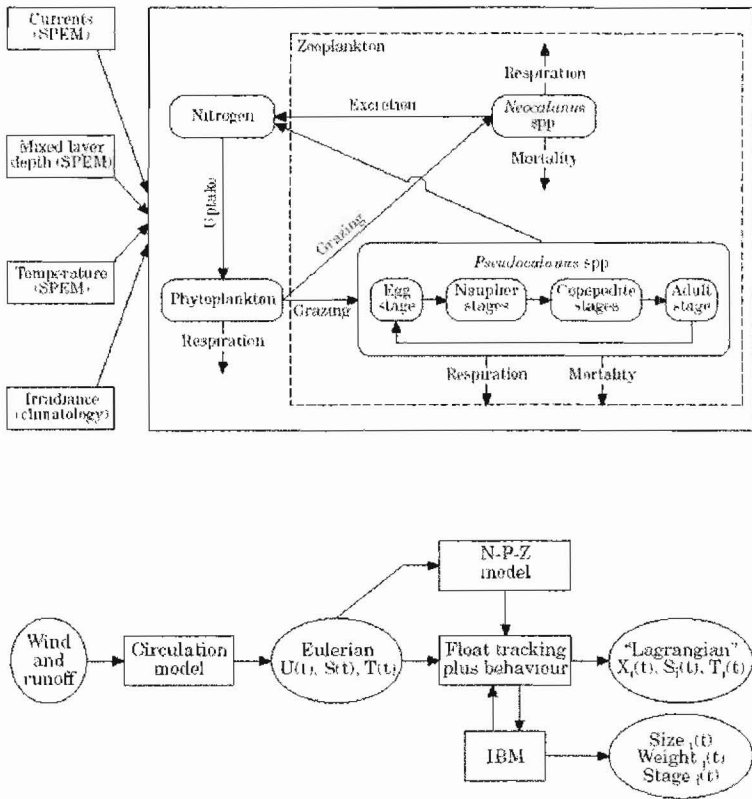


Figure 13.13 Summary of the coupling between the hydrodynamic model, the individual-based model and the NPA model (lower panel) and the flowchart of the nutrient-phytoplankton-zooplankton (NPZ) model (upper panel) (from Hermann et al., 2001).

The coupled model has also been effective in conducting “model experiments” to test the viability of competing hypotheses. For example, Hinckley et al. (2001: Fig. 13.15) used the coupled model system with winds and runoff forcing representative of two years of good recruitment, 1978 and 1994 to examine hypotheses about the timing and location of pollock spawning. In an approach similar to the Benguela upwelling system studies, five regions (1–5) and four spawning times (Early, Middle, Late, Very Late) were considered, where “1-Middle” represents typical observed spawning. Results show that fish spawned to the south of Kodiak Island (3-Middle) or much earlier or later than the observed spawning period (e.g. 1-Very Late) do not reach the Shumagin Island nursery area as juveniles by early September. However, the region and time of spawning which did allow successful transport to the nursery area (e.g. 4-Late) was much broader than the observed region and time. Hence simulation experiment results indicate that factors other than physical transport alone must be considered to explain the spawning location and timing of this stock.

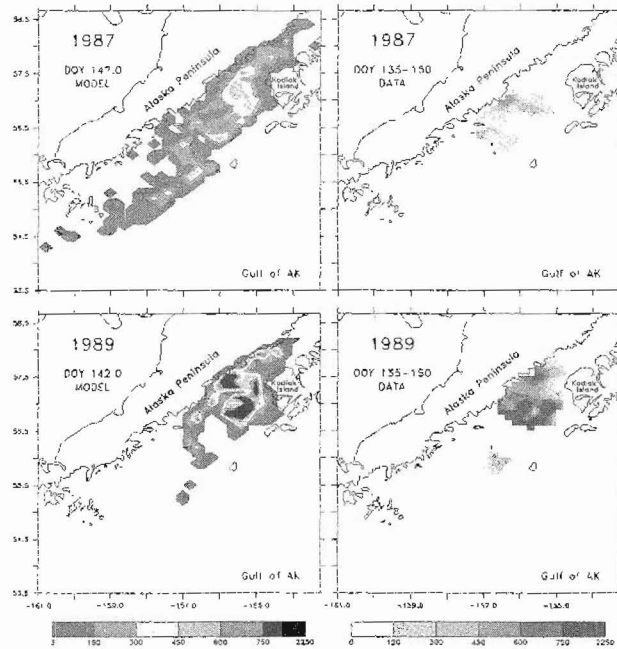


Figure 13.14 Comparison of model output to field observations, Shelikof Strait. Plotted is depth-integrated abundance of larvae ($\#/10\text{m}^2$) in mid-May of 1987 and 1989 (from Hermann et al., 1996)

In a newer initiative, a suite of nested physical and biological models is under development as part of the West Coast U.S. GLOBEC program. Components of this suite include: 1) multiply nested circulation models spanning basin to regional to local scales; 2) a lower trophic level (NPZ) model including salmon prey items, driven by those circulation fields; 3) an individual-based salmon model which receives circulation and NPZ model output. A preliminary implementation of this approach (Hermann et al., 2002) consisted of two physical models. The Spectral Element Ocean Model (SEOM) (Haidvogel and Beckmann, 1999) was implemented for a global domain, and provided both tidal and subtidal boundary conditions for the S-Coordinate Rutgers University Model (SCRUM) (Song and Haidvogel, 1994), used as the regional model of the Coastal Gulf of Alaska. Recently, the nested GLOBEC circulation models have been based on the Regional Ocean Modeling System (ROMS) (Haidvogel et al., 2000). Output from the regional circulation models are used to drive the NPZ model (presently for salmon prey) for the near-coastal area encompassing the shelf and shelf break. Resulting circulation and prey fields are used as input to a spatially-explicit IBM fish model (of juvenile salmon). The goal behind this new work is to create a tool to investigate interannual and decadal changes in the physical environment of the central Gulf of Alaska, while exploring linkages between physical forcing and biological production.

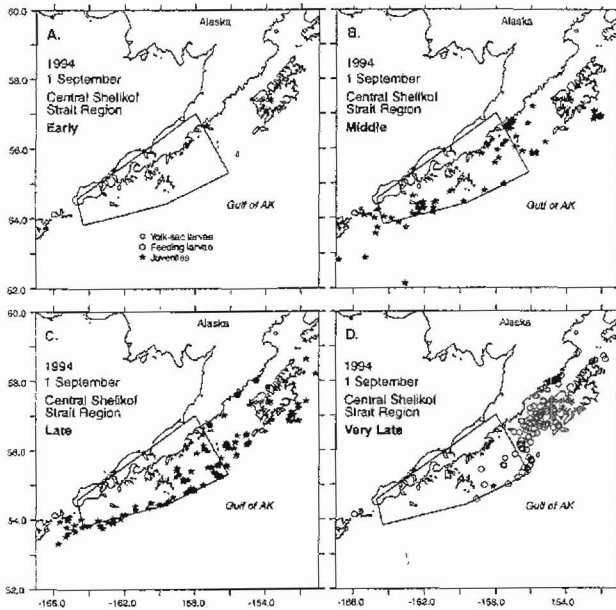


Figure 13.15 Results of model experiments looking at the effect of spawning location, time of spawning, depth of spawning, on the success of spawning products reaching the nursery area. (from Hinckley et al., 2001).

6. Applications and the future of coupled physical-biological modeling in coastal marine ecosystems

Sustainable use of marine resources and the management of coastal marine ecosystems are contemporary, real-world problems placing demands on the research community for greater understanding of marine ecosystem functioning (e.g. Barange, 2003). The complexity of the issues, already daunting, is exacerbated by predictions of global change, manifestations of which may include biologically significant increases in ocean temperature and changes in circulation at the regional and basin scale. The scientific contribution to marine resource management will continue to require advances in understanding of the coastal ocean that cut across disciplines, notably but not exclusively physics, biology and geochemistry. Understanding must be distilled into quantitative language for incorporation into models that link variation and change in the physical environment with the dynamics of species and species groups from the level of individuals to communities.

In Sections 2–4 we reviewed the approaches and status of three classes of physical-biological models. NPZ models, in the context of the problem here, address the simulation of primary production as a food resource for higher trophic levels. The Z in these models represents total zooplankton biomass and serves as a closure term for the model. Needs for finer spatial and temporal scale predictions of prey for exploited fish and invertebrate resources place challenging demands on the NPZ models to address the biochemical composition and size structure of the P term and to resolve the heterotrophic and microzooplankton. The second class of models, which we have called coupled zooplankton life history models, resolves

the spatially explicit population dynamics of key zooplankton (typically copepod) species or species groups. Two general approaches, Eulerian (advective-diffusive models) or Lagrangian (Individual Based Models) may be used; issues facing development of these models include characterization of food limitation, vertical migration behavior and diapause. The models of fish larvae focus on the processes controlling growth and survival of larvae in the simulated temperature and flow fields. Individual Based Models are generally used in this context, and understanding of the complexities of feeding behavior of fish larvae and their vertical movements are two of the issues facing their development. Common challenges to the development of models in all three classes include temporal/spatial scaling and characterization of mortality. The former is relevant to the linkage of hydrodynamics link to phytoplankton/microplankton (as food), food availability to zooplankton and zooplankton to fish. Improper scaling can distort models results by inaccurately depicting interactions and creating artificial model responses. The mortality issue is critical for realistic simulation of zooplankton and larval fish dynamics. For the time being, we will have to rely heavily on empirical relationships derived for the region, time period and species of interest, not only for mortality but also for functional linkage relationships such as the dependency of zooplankton growth and reproduction on indices of food availability.

In Section 5, we examined the application of coupled models in coastal waters of southwest Africa, the northwest Atlantic and the Gulf of Alaska. Notable is the need for multidisciplinary effort and considerable resources (both manpower and time) in order to develop sophisticated coupled models for site-specific application. Questions were addressed with a diverse tool box of models capable of evolving with increasing data and knowledge of the system of interest. In the northwest Atlantic, 3-D coupled models depicting secondary production and growth and survival of fish larvae are in an active research phase but are not yet applied in a management context. In the Benguela Current System and Gulf of Alaska, coupled models have been developed and applied to synthesize, guide and interpret research and understanding of recruitment processes, and to supply information in a limited sense to fisheries management. Coupled models of the type described here have also been developed for application in other coastal ecosystems, but in general have not yet entered operationally into the activity of marine resource management.

There is, nevertheless, an emerging synthesis of data and knowledge that will continue to move coupled modeling toward the mainstream of marine resource management. Systems of independent models in the three broad classes discussed above, each of which is coupled to a hydrodynamic model describing current and temperature fields for a particular coastal ocean or shelf sea, can be developed. Each of these coupled biophysical models represents a quantitative integration of processes and interactions in one part of the pelagic ecosystem. Examples of how the various coupled models could be linked in a hierarchical structure, which could be called linked coupled models (LCMs), are shown in Fig. 13.16. In Fig. 13.16a, a coupled physical-NPZ model simulates spatially explicit food resources for key zooplankton species that produce prey for target species of fish larvae; the distribution of both fish and zooplankton are also by the flow and temperature generated by the regional circulation model. Fig. 13.16b illustrates linked coupled

models for simulation of regional trophic structure with greater resolution of predator sources of mortality on target species (in this case *Calanus* species).

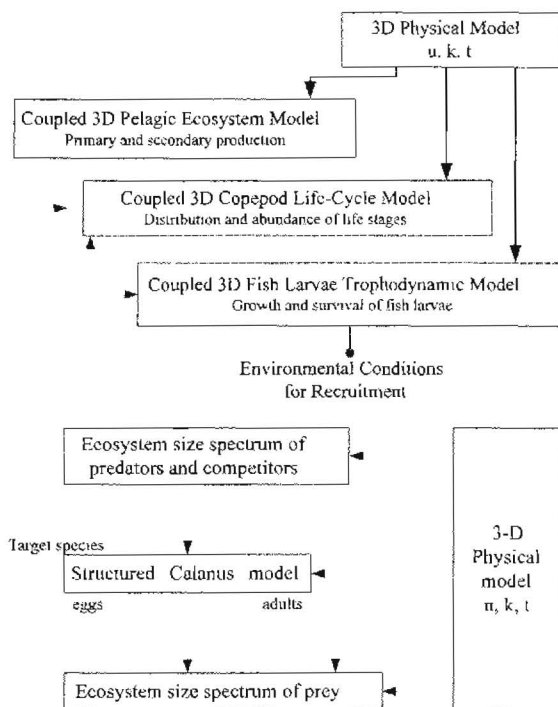


Figure 13.16 Examples of possible interrelationships among various components of linked coupled models (LCMs) for coastal shelves. A): Trophic structure system in which population dynamics of target species are parameterised in detail, linked to lower resolution models of describing prey and predator abundance. B): LCM for use in describing environmental conditions for survival of fish or invertebrate larvae in a coastal system

Given these possibilities, the following subsections examine the potential, data needs and limitations of coupled simulation model systems in the application to resource management issues.

Coastal Ocean Observing Systems and model-data interactions

There is world-wide movement toward establishment of a global ocean observing system (e.g. Holland and Nowlin, 2001). In the United States, for example, development of an Integrated Ocean Observing System (IOOS) for U.S. coastal regions has been initiated, with plans to become operational within the next decades. Among the seven major goals of IOOS are to improve predictions of climate change and its effects on coastal populations, protect and restore healthy coastal marine ecosystems and sustain living marine resources.

A vital role for LCMs is in the organization, analysis and interpretation of coastal ocean observing data. Functions of the coupled biophysical models include contributions to identification of measurement variables, design of sampling frequency and location, and interpretation of data with respect to the goals of observing systems, such as the evaluation of habitat quality and environmental conditions for recruitment success (as discussed below).

The interaction between coastal ocean observing systems and LCMs also address data needs of the coupled biophysical models. The model-data interactions can be categorized as follows:

1. Data are needed to define boundary conditions and external forcing, to specify initial conditions and to meld (Robinson et al. 1998) with dynamic components of the LCMs in order to run site and time specific simulations. For example, wind and boundary hydrographic data for a given year would be used to run simulations of surface circulation to track, say, the distribution of fish and invertebrate larvae in the Gulf of Maine for that year. Section 2 mentions satellite-derived surface chlorophyll data that can be assimilated into NPZ models for diagnostic and predictive simulation of prey fields.
2. Data are needed for verification of the model simulations. In addition to high frequency hydrographic and current data (independent of observations used for data assimilation) for validation of circulation models, coastal observing system measured variables may include chlorophyll and high frequency zooplankton abundance data from moored sensors, target copepod life history data from fixed stations for comparison with simulated life cycles and surveys of larval fish abundance for validation of simulated distribution in, say, marine protected areas.
3. Data are needed for adjustment of empirical relationships supporting the biological dynamics. As discussed in sections, many biological relationships must be determined empirically, following the early modeling approaches described by Riley (1963 and references therein). For example, the relationship between egg production rate and chlorophyll a standing stock in the Gulf of Maine (Fig. 13.4) was determined from measurements at sea during process cruises. The mean vertical distributions of *Calanus* life stages used in the coupled copepod life cycle-physical model of Zakardjian et al. (2003) were derived from data collected over a decade starting in the early 1990's. Given the potential for genotypic and consequently phenotypic change of target species in response to global climate change, these relationships may need to be periodically verified, as there is presently no suitable theory to allow dynamic adjustments of physiological or behavioral depictions in the biological models. The need to update these relationships for accurate simulation by LCMs of observational data should be considered in the development of coastal ocean observing systems.

The role of secondary production in biogeochemical cycles in the coastal ocean

Continued and planned (e.g., Doney et al., 2004) investigation of biogeochemical cycling and elemental fluxes in the coastal ocean requires greater resolution of the role of secondary production. The *middle-out* coupled physical-biological modeling

approach for key zooplankton species or species groups can contribute information on life cycle and spatial distribution needed to resolve temporal and spatial variability in grazing and elemental vertical fluxes in the coastal ocean, for example the flux of carbon to the sediment in areas of coastal upwelling. Additionally, development of coupled models for prediction of shifts in composition and distribution of key zooplankton species or species groups is a direction identified for further development of the coupled biological-physical zooplankton models.

Habitat and environmental conditions for recruitment success

Better understanding of how spatial and temporal variation in environmental factors affects larval fish growth and survival is not only of general research interest but also has application to ecosystem-based resource management. Coupled physical-biological models provide a formal method to quantify how environmental conditions affect larval growth, retention and mortality. For example, coupled simulation systems outlined in Fig. 13.16a can be used to diagnose whether environmental conditions in a given year were poor, average or exceptional for growth and survival of larvae. As mechanistic understanding and prediction of climate-induced physical and secondary production variation improves, LCMs can also be used to predict whether environmental conditions for larvae will improve or deteriorate in a multi-year time frame. This information can be fed into the decision-making process for determining appropriate quotas for sustainable fisheries. Coupled models are ideal for identifying the environmental conditions that result in the rare individuals surviving the larval period (e.g., Werner et al., 1996), and may be used in a sensitivity analysis mode to examine the effects of different processes on larval growth (e.g., turbulence: Megrey and Hinckley, 2001; Werner et al., 2001b).

Coupled physical- biological models can make an important contribution to understanding fish habitat quality. Quantifying habitat quality is of vital importance to effective long-term fisheries sustainability, and consideration of essential fish habitat is required by law (Sustainable Fisheries Act, Public Law 104–297) to be included in fisheries management plans. Most previous analyses of habitat quality have generally relied on a correlation approach; if organisms are found in locations then the environmental conditions in those locations must be good habitat (e.g., Minello, 1999). Whereas this approach is clearly unsatisfactory for determining habitat quality of fish larvae, linked physical-biological models, as discussed above, provide a tool for both quantifying and predicting future retention and growth characteristics of a given location. A limitation may be that habitat quality must be quantified on a grand scale (many species in many locations), whereas the development of coupled biophysical models proceeds on a site-specific basis, and each application involves a significant effort. Other issues related to habitat, such as determining the effectiveness of Marine Protected Areas, may also be addressed by coupled model analyses.

Recruitment prediction

For most of the past century, a branch of fisheries science has focused on the general problem of predicting the number of young at birth that will survive to some size or age, termed recruitment (Bradford, 1992; Cushing, 1996; Needle, 2002). The relationship between spawners and the subsequent survival of their progeny to

recruitment is fundamental to fisheries management (Rose and Cowan, 2003). Understanding the causes of variation in growth and survival of larval fish, as discussed earlier, is an important component of recruitment prediction because much of the eventual interannual variation observed in recruitment in marine fish can be attributed to variation in growth and mortality during early life stages (Shepard et al., 1984; Houde, 1987; Rose and Summers, 1992).

By enabling better understanding of the causes of variation in larval growth and mortality, coupled physical-biological models can play a major role in helping to understand the relationship between spawners and recruitment. One of the major problems with spawner-recruit data is that the high degree of variability can confound interpretation of the relationship between the two (Walters and Ludwig, 1981). Very noisy data can be incorrectly interpreted as no relationship between spawners and recruits, which would imply almost infinite density-dependence (constant recruitment regardless of the number of spawners) and therefore lead to over harvesting (Hilborn and Walters, 1992). Coupled physical-biological models can play a role in the recruitment question by providing a tool for deciphering the variation in the larval stage contribution to recruitment variability.

However, because of the complexity of recruitment prediction, it remains to be seen whether coupled physical-biological models can be of general value beyond the assessment of environmental conditions and habitat quality for larval stages. Major progress on the recruitment question will require that the models include potential density-dependent effects on larval growth and mortality. There are very few examples of coupled physical-biological models that allow for density-dependent mortality via numerical or functional responses of the predators of the larvae. Predation mortality of larvae is critical to the recruitment question (Bailey and Houde, 1989; Leggett and DeBlois, 1994). Furthermore, the larval life stage is but one component of process recruitment, and only one part of the life cycle. Fish exhibit complex life histories that involve life stages that use different habitats (Rose, 2000).

Sissenwine (1984) and others consider that the juvenile stage is critical to understanding density-dependence and recruitment variability. Cowan et al. (2000) concluded that density-dependent growth in marine fish was most likely to occur in the late larval and juvenile life stages. Recent analyses document density-dependent mortality in the juvenile stage (Myers and Cadigan, 1993), and suggest density-dependent adult growth may be more widespread than previously thought (Lorenzen and Enberg, 2002). Population dynamics and population regulation are likely the result of the complex mix of different processes occurring in different life stages. Improving our knowledge of larval stage growth and mortality (even with density-dependence) may not help in predicting overall recruitment if significant density-dependent effects occur after the larval stage.

Extending the coupled physical-biological approach to post-larval life stages is likely not appropriate for many situations, as the rationale for coupling larvae to physical models diminishes for post-larval life stages. Movement of juvenile and adult fish depends more on biological factors and individual decisions and less related to the physics (Tyler and Rose, 1994). In addition, juvenile and adult fish generally spend less time feeding than larvae, and tend to eat larger prey that are themselves less controlled by physical transport. Indeed, many harvested fish species eventually become piscivorous, where the prey becomes larval and juvenile

fish. Thus, the important role played by the physical-biological models for larval fish of generating transport, temperature, and prey fields will be much more difficult to achieve for simulating juvenile fish and likely impossible for simulating adult fish.

In the long run, then, recruitment prediction may require models (necessarily not one model) that together encompass the full life cycle. These models should be capable of predicting, at least in qualitative terms, trends in growth and mortality rates and possible density-dependent effects. Coupled physical-biological models can likely be extended to include invertebrate predators of larvae (i.e., mortality) and density-dependent growth, but not much beyond the early larval life stage. We know enough about the ctenophores and medusae (e.g., Brietburg et al., 1999) to at least attempt to include them in coupled models. We envision that coupled physical-biological models including density-dependence and invertebrate predators will be used for the larval life stage. A series of linked models, each temporally and spatially scaled to their particular life stages, would enable full life simulations over multiple generations; the physical-biological modeling being one component in this chain. Individual-based models (albeit spatially simple) of early life stages of fish have been coupled to age-structured matrix projection models for adults (Rose et al., 1996; Rose et al., 2003).

Concluding remarks

The rapid increases in our ability to make detailed measurements, coincident with advances in numerical modeling, data assimilation approaches, etc., portend great advances in coupled physical-biological modeling over the next decades. Coupled physical-biological models are ready now to provide information on habitat quality for larval fish. In situations when recruitment is set in or just after the portion of the larval stage, then insights into recruitment variability and forecasts of potential recruitment may be possible. Coupled physical-biological models should also play a role in understanding the dynamics of many fish species in which recruitment is not fully determined until after the larval stage, although non-trivial improvements in the current state of the models will be required. Allowing for density-dependent feedbacks and including predators to permit prediction of mortality are significant challenges for the next generation of coupled models. Effort is needed on creative ways to mesh models that operate on different biological, spatial, and temporal scales.

Continued developments of coupled physical-biological models that include fish, requires close collaboration between oceanographers (bottom-up view of the food chain) and fisheries researchers (top-down view of the food chain). The marriages of spatially-explicit physical, plankton production models, the biologically-complex but spatially simple models of larval fish growth and survival and perhaps eventually including full life cycle models of resource species require a multidisciplinary effort. The computer becomes the medium through which the quantitative synthesis of distilled understanding of different disciplinary perspectives is expressed. Simulation with validated dynamics present hypotheses and predictions that can be tested against data, and therefore become an element of scientific methodology (Robinson et al., 1998; Robinson and Lermusiaux, 2002). Computer-

generated graphics and animations become the means of communication to both experts and non-experts of the complex, integrated synthesis of system knowledge.

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