

Spatially-Explicit Individual Based Modeling of Marine Populations: A Review of the Advances in the 1990's

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Abstract

The utility of individual based models (IBMs) is that properties of ecological systems can be derived by considering the properties of individuals constituting them. Individual differences may be physiological, behavioral or may arise from interactions among individuals. The differences result in unique life histories, which when considered as a whole give rise to growth and size distributions that provide a measure of the state of the population. Early IBMs generally did not consider the effect of a spatially variable physical environment. Recent advances in ocean circulation models that include realistic temporal and spatial variation of currents, turbulence, light, prey, etc., have enabled IBMs to be embedded in model flow fields and for unique, sometimes behaviorally modified, Lagrangian trajectories to be computed. The explicit consideration of realistic spatial heterogeneity provides an additional factor that contributes to the differentiation among individuals, to variances in population structure, and ultimately to our understanding of the recruitment process. This is particularly important in marine environments where fronts, boundary layers, pycnoclines, gyres and other smaller spatial features have been hypothesized to play a significant role in determining vital rates and population structure. In this paper we will review the status of research on spatially-explicit IBMs, their successes, limitations and future developments. Examples will be drawn from approaches used in the past decade in GLOBEC, FOCI, SABRE and other programs.

Introduction

The utility of individual based models (IBMs) is that properties of ecological systems can be derived by considering the properties of individuals constituting them. One of the advantages of IBMs is the ability to account for rare individuals, or rare circumstances effecting a few individuals, which contribute strongly to determining population strength, or variance (*e.g.*, of growth rates) within populations. A review of the state of IBMs during the early 1990's can be found in DeAngelis and Gross (1992). There, it was suggested that "IBMs will be generally more useful for sedentary organisms rather than free ranging ones, due to how the plasticity of form is often coupled to local interactions and environmental conditions in the sedentary situation" (Gross *et al.* 1992).

In oceanic environments, where most marine organisms undergo planktonic life stages, *i.e.*, non-sedentary stages where the organism has little ability to swim against the current and is largely at the mercy of circulation (Werner *et al.* 1997), IBMs have, by necessity, focused on *explicitly* coupling the biological and ecological formulations to hydrodynamic models of varying degrees of three-dimensional and temporal complexity. It is the recent advent of quite sophisticated and realistic circulation models (*e.g.*, Blumberg and Mellor, 1987; Backhaus, 1989; Haidvogel *et al.* 1991; Lynch *et al.* 1996) that have enabled spatially explicit IBMs to become a *de facto* tool in large-scale efforts studying the interactions of marine organisms with their environment. The effects of variability in the physical environment (flow, temperature, salinity, turbulence, light, *etc.*) is explicitly considered in the study of dispersal, growth and mortality of the target

marine populations.

In a recent review of individual based models in ecology, Grimm (1999) proposes that studies using IBMs do so mainly for two reasons: a) for *pragmatic* reasons, i.e., "to study problems that cannot be addressed with state variables", or b) for *paradigmatic* reasons when the study is "driven by the suspicion that much of what we have learned from state variable models about theoretical issues... *e.g.*, regulation, *etc.*, would have to be revised if the discreteness, uniqueness, life cycles and variability of the individuals were to be taken into account". Most of the studies we review in this paper fall into Grimm's *pragmatic* category, for the simple reason that marine organisms experience unique trajectories during both their planktonic "drift" stages and after they have developed full swimming capabilities. Studying the end result of these unique trajectories cannot be as easily achieved using a state-variable approach. This does not mean that the use of spatially explicit IBMs is limited only to serving as a convenient tool. IBMs have contributed to revisiting fundamental theories on the structure of marine populations such as the migration triangle (Harden-Jones, 1968), match-mismatch (Cushing, 1974), and member-vagrant (Sinclair, 1988) and have provided information for fisheries management (*e.g.* see Heath and Gallego, 1997). Similarly, it should not be forgotten that IBMs are in fact ecological tools. As such they are often often used, and may be the only logical tool to use, for understanding complex interactions, synthesizing large data sets and/or stating hypotheses (Rice and Cochran, 1984; Crowder *et al.* 1992).

Classification of spatially explicit IBMs

Perhaps due to the pragmatic nature of most IBMs, as well a kind of communication gap

between scientists working in fresh and marine systems, IBMs have not evolved in a smooth manner. Models of striking different complexity appear simultaneously in the literature. For convenience, we will use the following classification scheme in this paper.

1. *Implicit-space*: Some of the first IBMs modeled "space" by calculating a volume searched by a particular larval fish. Hence, the spatial component is more of a device used to model feeding processes. Most contemporary IBMs still rely on this approach at some level, however, physical factors (turbulence, light) have all been used as modifiers in determining the volume searched.
2. *Static -space*: These models are spatially explicit, but generally lack a consideration of physical processes such as velocity or turbulence fields. Space is modeled as a series of regions or compartments, sometimes with region-specific prey or predator fields. Individual organisms are permitted to move about within or between the various compartments and hence may experience variable predator/prey abundances. Some of these models incorporate prey-dynamics devices, such as logistic equations with removal due to predation.
3. *Growth potential*: These models use fixed, non-mobile IBMs and a gridded spatial domain to develop maps of habitat quality, in a currency of growth rate potential, from measured attributes (prey abundance, temperature, *etc.*) of the system. Individuals are not permitted to move outside a homogenous volume of water (a grid cell), but conditions within the grid cell can be temporally dependent.
4. *Hydrodynamics and simple behaviors*: Space is modeled explicitly, and complex, realistic hydrodynamic models are used to compute particle trajectories and to provide a Lagrangian description of the flow. Particles may be passive in the

simplest approaches or behaviors may be prescribed (*e.g.*, as a function of particle "age" or "size").

5. *Hydrodynamics and static prey*: Lagrangian particles are given biological traits and the ability to sense their surrounding as they are advected by the flow. Particles “grow” depending on the unique feeding environments through which they are advected. Modifications to feeding by abiotic factors such as light and turbulence are explicitly included. However, prey fields are static.
6. *Full life cycle, multigeneration, multispecies models*: Several recent efforts have moved toward modeling the life cycles of suites of co-occurring species over many generations. These models generally do not incorporate hydrodynamic attributes of the system, but often have such features spatially and/or temporally dependent prey fields. The long time span of the simulation allows novel investigations of processes such as the evolutionary stability of particular behavioral strategies.

Clearly, the boundaries between these categories were chosen more to illustrate the development of the field than to provide a hierarchy for model classification. The boundaries are therefore somewhat arbitrary and any particular model may fit in more than one group. Furthermore, our focus is mainly on larval fish, though we do bring in examples of copepods, scallops and larger fish – all of which are tractable with this approach. Finally, our review is intended to provide a brief look at the development of the field over the past ten years and a snapshot of where it is now. We therefore provide more of an overview rather than a detailed analysis of each example presented.

Review of Existing Approaches

In this section, and based on the classification suggested above, we will discuss selected case-studies of spatially explicit IBMs in marine environments. We begin by considering the simplest approximation to spatial dependence and consider progressively more complex and realistic representations.

Implicit-space. Individual-based models, even models that are not spatially-explicit, generally require a consideration of space. In some of the first IBMs (Kitchell *et al.* 1977, Rice *et al.* 1983, Beyer and Laurence 1981; Laurence 1985) this was achieved by calculating a search volume for each larvae based on swim speed and reactive distance. This volume is multiplied by prey density and translated into an estimate of prey encountered per unit time. In some of models, larval position in the water column might be changed in some cartesian coordinate system. However, modeling space did not have the same priority as bioenergetic components and the key concern was to understand how the animal grew.

Introduced at this stage were models of foraging dynamics to investigate prey choice (Werner and Hall 1974; Pyke 1984; Crowder 1985) . These efforts eventually shed light on the ecological consequences of size-dependent predation under conditions of variable growth rate (Rice *et al.* 1993). As small scale physics associated with feeding became better understood fairly advanced treatments of feeding, enhanced by turbulent mixing, were developed (MacKenzie *et al.* 1994; Dower *et al.* 1997, Megrey and Hinckley 2001) and have become a mainstay in larval trophodynamic modeling (see Fig. 1).

Static-space. A logical advance was the development of models which explicitly defined space, usually in terms of spatial, but not temporal, variation in prey abundance. In these models, larval fish moved through regions, or patches (Letcher *et al.* 1996), with fixed levels of prey. Most of these models did not include physical factors such as turbulence. Instead, the focus was on how time should be allocated within patches, how predation factors into cohort survival, or how movement decision rules effected the outcome of the experiment (Tyler and Rose 1997).

Growth potential. 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 IBM 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 (see Fig. 2). In brief the water column was divided into a number of discrete cells. Biotic and abiotic variables in each cell were specified from field observations and input into fish foraging and growth models. 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. Understanding the details of the distribution may be as important as knowing the mean conditions. 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.

Hydrodynamics and simple behavior. Taking advantage of the advent of sophisticated and robust circulation models which capture realism on relevant spatial and temporal scales (see review by Haidvogel and Beckmann, 1998), perhaps the best established use of spatially explicit IBMs focuses on determining trajectories, or Lagrangian pathways, of planktonic stages of marine organisms in realistic flow fields. The main difference (and step-up) from the above "growth potential" category is that the flow field actively transports the modelled organisms through a spatially heterogeneous field (see Fig. 3). 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 pathways of larval fish from spawning grounds to nursery areas (Bartsch *et al.* 1989, Ådlansvik and Sundby 1994), retention on submarine banks (Foreman *et al.* 1992; Helbig *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) and migration of adult fish populations (Thomson *et al.* 1994; Rand *et al.* 1997; Walter *et al.* 1997), identification of spawning locations (Quinlan 1999; Hare *et al.* 1999; Stegmann *et al.* 1999) and the implied long-term dispersal by tidal currents (Hill 1994). A similar approach, focusing on the seeding of scallop beds on Georges Bank is discussed in Tremblay *et al.* (1994). The exchange of copepods between deep ocean basins and shelf regions is described by Slagstad and Tande (1996), Hannah *et al.* (1998), Miller *et al.* (1998), Bryant *et al.* (1998), Gallego *et al.* (1999), Heath *et al.* (1999) and Heath (1999).

Although lacking in key biological variables, the use of spatially explicit IBMs in this simplified form has been clearly established as a necessary first step in describing the environment sensed by marine organisms. Approaches that considered feeding environment implicitly through its relation to temperature are 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.

Hydrodynamics and static prey. After the determination of Lagrangian pathways, the

next level of complexity commonly introduced into spatially explicit IBMs is an imposed spatially-dependent (but temporally fixed) prey field based on field observations. Using these approaches, Lagrangian trajectories that are considered favorable for retention or appropriate for transport into nursery areas are more narrowly defined to include only those trajectories where the individuals encounter favorable feeding environments.

Studies of this type include Werner *et al.* (1996) and Hermann *et al.* (2001). Figures (4 and 5) show particle trajectories through spatially variable prey fields and the resulting distribution of larval sizes.

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.* 2001). 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.

Full life cycle, multigeneration, multispecies models: Rose *et al.* (1996) simulated a population over a time span of 200 years using a combined individual-based, Leslie matrix model approach in a spatially explicit context. The individual-based model was used to describe the first year of life, thereby providing year class information to the Leslie matrix, which then projected the population through time (one year) and generated abundance information for the next generation. The model was spatially explicit in that the IBMs were placed in a 150 x 150 x 1.5m compartment which had time variable physical conditions (temperature, light, turbidity) and time varying prey populations (both benthic and pelagic prey were used, dynamics modeled using a modified logistic curve). Density-dependence was investigated toggling the effect of predation on zooplankton population dynamics.

The individual based section of this technique was extended to simulate a community of fish in Lake Mendota by McDermont *et al.* (2000) for a time span of 100 years. In this work, individuals representing a set of six species were tracked in three spatial boxes representing littoral, epilimnic and hypolimnic zones. Shifts between the three differing habitats were ontogenetically based. This model was used to investigate various scenarios such as stocking a particular predatory species or examining the effects of a die off. Complex phenomena associated with predation and competition, such as density-dependent growth, compensatory and depensatory mortality and food-web responses, were captured in this simulation and point to the importance of developing advanced multispecies simulations.

Discussion and Future Directions

During the past decade, the use of spatially-explicit IBMs in the study of marine systems has proven quite useful on a number of fronts. Coupled with spatially and temporally realistic descriptions of the physical environment, IBMs provide a tool to explore factors contributing to the individuals' unique time-histories and thus provide the ability to extract information about the population based on the variance among the individuals.

Returning to Grimm's (1999) discussion on pragmatic versus paradigmatic reasons for using IBMs, we find most applications in marine systems fall into the pragmatic category. Namely, IBMs have been largely used because they are the best (or most logical) tool to use to study these systems. However, the study of Page *et al.* (1999) is a good example of the use of an IBM approach to address a fundamental population level question. They compare empirical (field) observations on season and location of cod and haddock spawning with (IBM-derived) seasonal and geographic patterns of residence times and find 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 IBMs to answer biologically complicated population dynamics questions.

Linking spatially-explicit IBMs where full hydrodynamics and full (non-static) population dynamics co-occur will likely be attempted in the next two to five years (see Ault *et al.* 1999 for an example of such a linkage using McKendrick-von Forester

equations and a 2D hydrodynamic model). This will allow further exploration of ideas such as Cushing's match-mismatch hypothesis where spawning strategies are related to timing of food availability and consequently the observed variability of certain marine populations. One reason that these studies have not yet taken place is that to date the population dynamics of prey (*e.g.*, copepods) have been studied separately from those of the predators (*e.g.*, fish larvae). These are now at a point where we are beginning to see the first attempts at integrating of these approaches (*e.g.*, Ault *et al.* 1999, Hermann *et al.* 2001, Hinckley *et al.* 2001).

The added complexity of more realistic prey distribution will invite advances in approaches to determine behavior. Externally imposed (and/or passive) behaviors may not make sense in view of the added detail of the feeding environment and 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; and Fiksen *et al.* 1995). Dynamic programming methods allow organisms to "find" optimal habitats by balancing risks of predation, growth and advective loss.

In parallel to the application of IBMs to specific (or site-specific) systems, theoretical studies are also underway addressing the issue of how to translate, or scale, the system from IBMs into models for aggregated quantities such as densities. Pascual and Levin (1999) address questions of when variability at the individual level is essential to the dynamics of aggregations and at which spatial scales should densities be defined? In their study they identify spatial scales where certain predator-prey systems and other oscillatory ecological systems may display a dynamic regime at an intermediate scale of aggregation, one in which local interactions are still important. As advances in spatially-

explicit IBMs continue, integration of such theoretical developments into modeling of specific (or pragmatic) studies will need to be considered.

Potential Links to Management Questions

IBMs have been used to address management concerns in several different areas. For instance, IBMs were used to investigate the optimal stocking time and size for fingerling walleye (*Stizostedion vitreum vitreum*) (Madenjian *et al.* 1991) and the accumulation of polychlorinated biphenyls in lake trout (*Salvelinus namaycush*) (Madenjian *et al.* 1993). However, one of the most compelling roles for spatially-explicit IBMs is in the arena of fisheries management. IBM studies are currently generating testable hypotheses relevant to fisheries recruitment and should have an impact on how populations are managed. IBMs offer a platform to study recruitment problems at the appropriate scales (see for example SABRE, GLOBEC, FOCI) and can also help us unravel the complex foodweb interactions (McDermot *et al.* 2000). This suggests an increasing role for spatially explicit IBMs not only in research, but perhaps also in practical management applications.

A case in point is the development of workable management plans for species such as scallops with benthic adult and pelagic larval stages. Spatially explicit IBMs are particularly valuable in these circumstances because they can more closely model the actual process of recruitment. In these kinds of applications, realistic descriptions of habitat, hydrodynamics, larval transport pathways and adult growth and survival can provide a mechanistic understanding of how recruitment variability arises from various modeled forces and how local populations may be interconnected.

Spatially explicit IBMs may also be useful in designing and assessing marine protected areas (MPAs). These models capture important aspects of population dynamics as well as drift and transport processes. This allows one to quantify the degree of connectance and exchange between adjacent and distant areas (either protected or not) in a realistic and meaningful way. This can provide a method of configuring MPAs to address a great many different objectives (biomass protection, generation of fishable biomass, maintenance of source/sink populations in a network of MPAs). This is extremely relevant information for managers.

Because spatially explicit IBMs can offer mechanistic suggestions as to how and why populations exist in certain systems (Huse and Giske 1998, Quinlan *et al.* 1999), we have an inroad into understanding variability in marine population as well as a testbed for developing field testable hypotheses and refining ecological theory.

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Figure 5. Size distribution of modeled individual cod larvae during 40 days post-hatch (from Werner *et al.* 1996).

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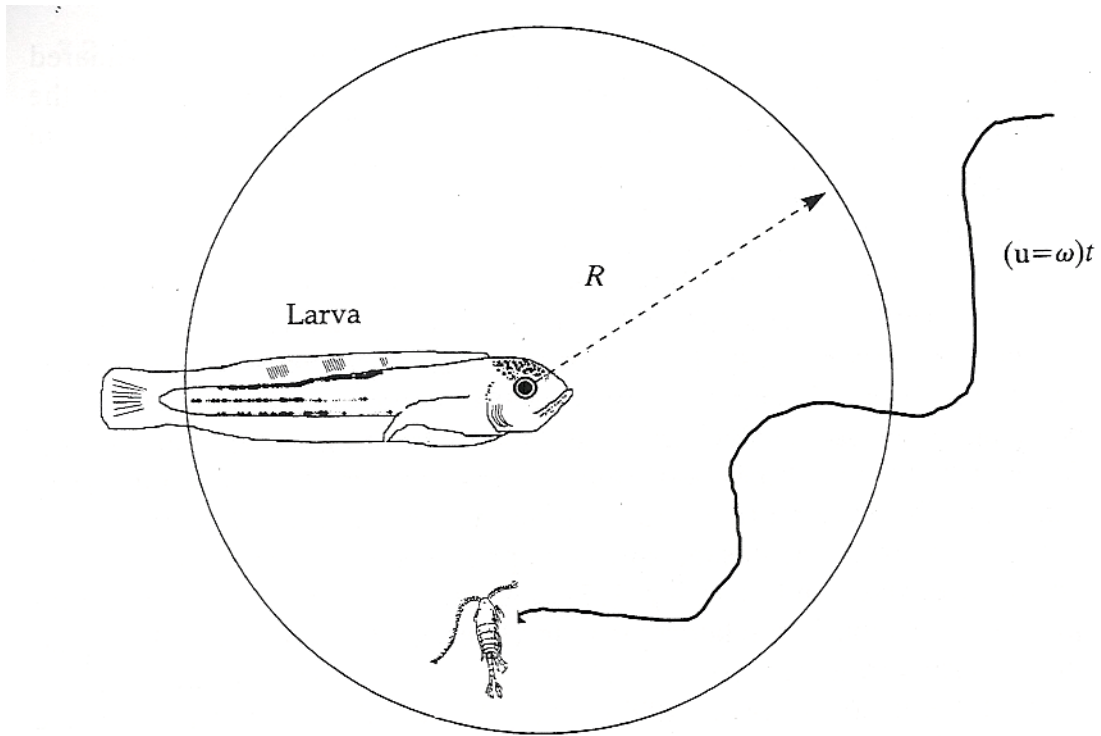


Figure 1. Schematic of encounter between a fish larva and its prey. The larval reactive distance is R (from Dower *et al.* 1997).

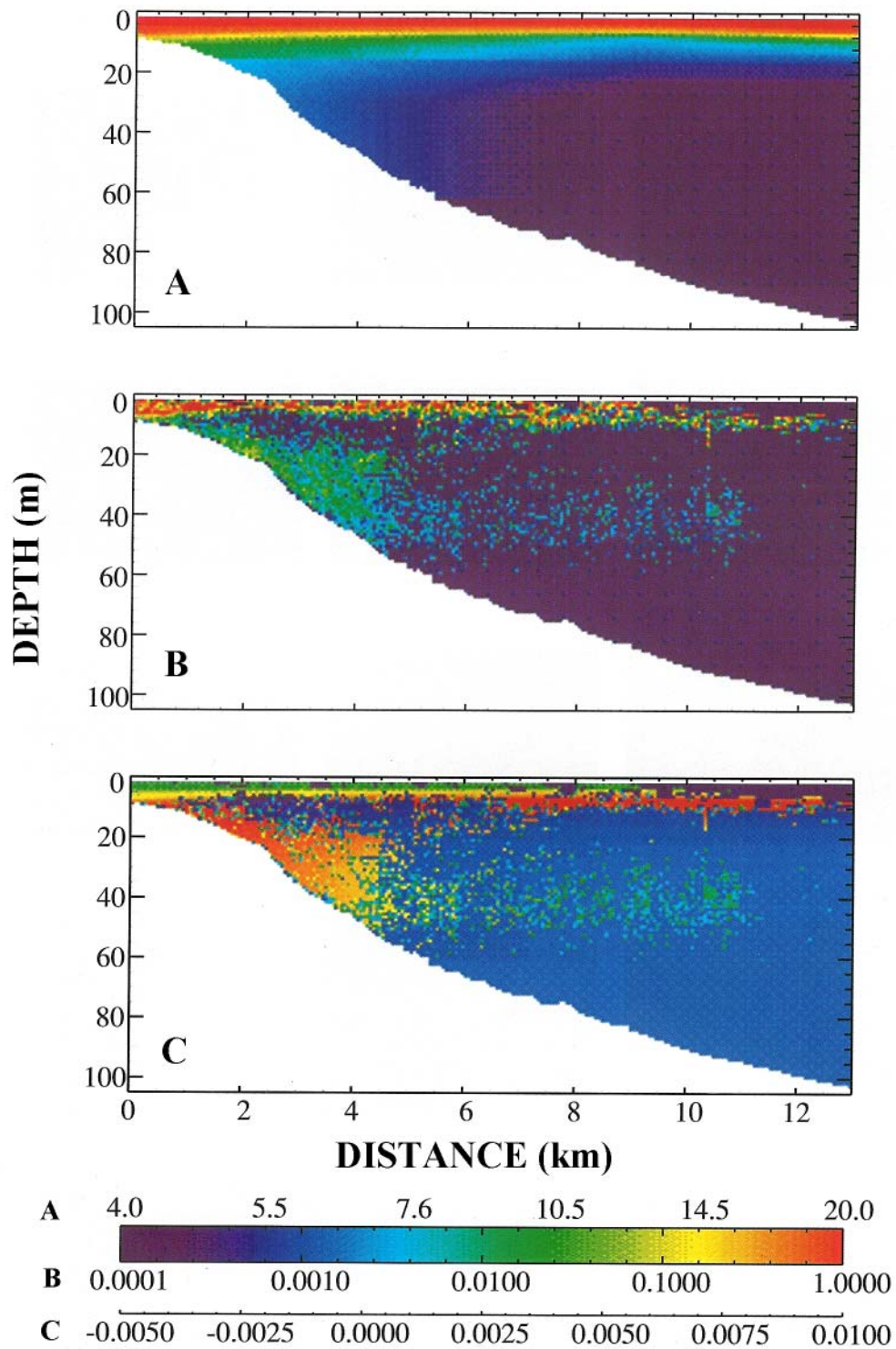


Figure 2. Cross sectional map of Lake Ontario transect showing (A) measured water temperature, (B) measured prey fish biomass density and (D) modeled growth potential (from Mason and Brandt 1996)

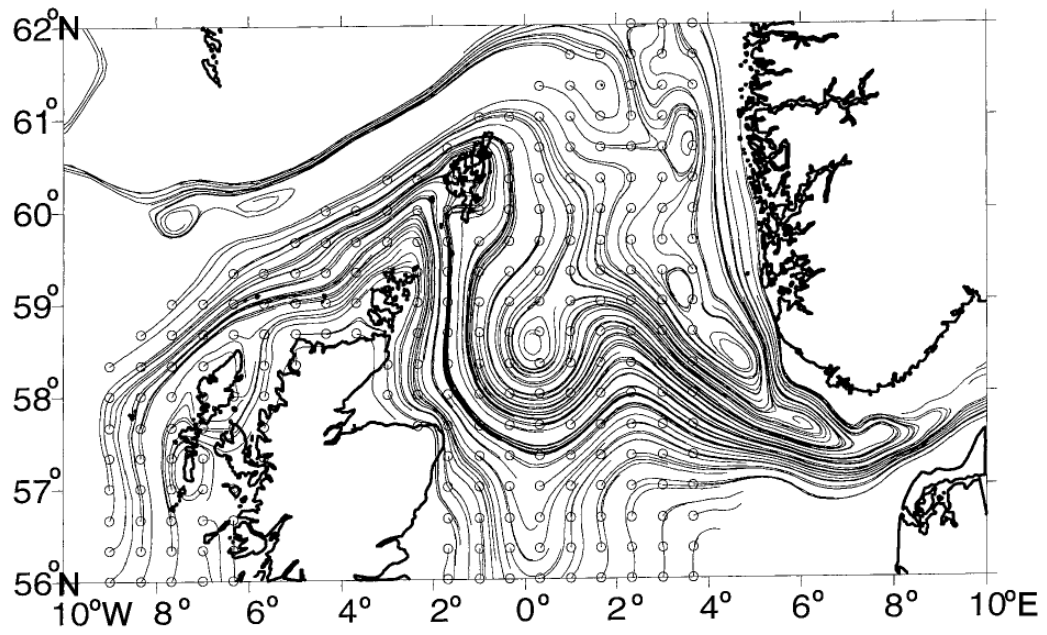


Figure 3. Trajectories of particles from release location on the North Sea continental shelf (from Heath and Gallego, 1997).

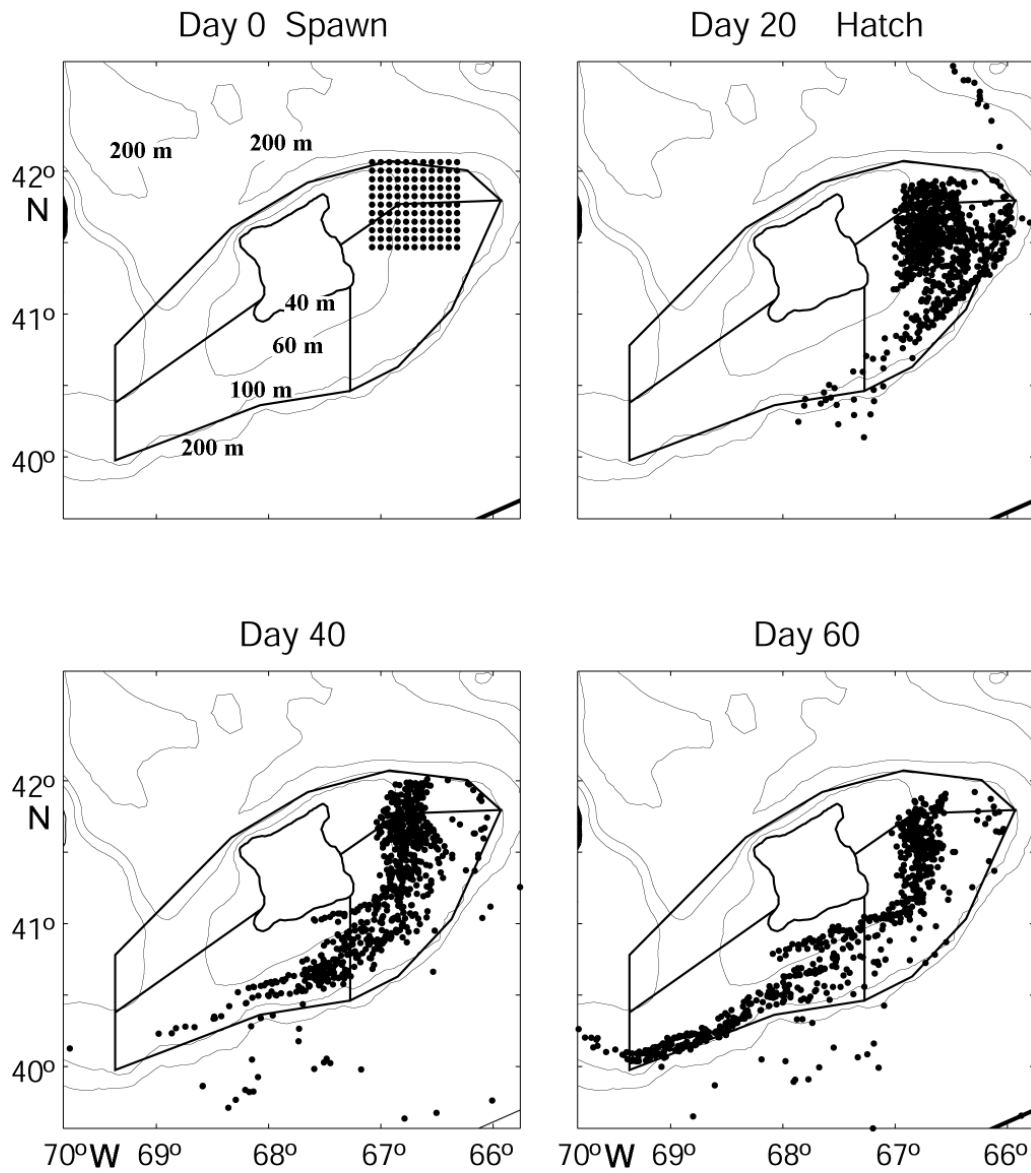


Figure 4. Particle locations advected passively on Georges Bank. Spawning location and positions 20, 40 and 60 days post-spawn (from Werner *et al.* 1996).

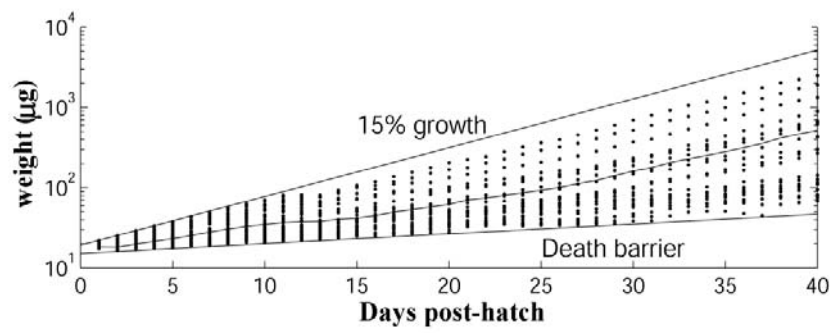


Figure 5. Size distribution of modeled individual cod larvae during 40 days post-hatch (from Werner *et al.* 1996).