

Coupled Biological and Physical Models

Present Capabilities and Necessary Developments for Future Studies of Population Connectivity

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The combination of wide-ranging spatial and temporal scales associated with the oceanic environment, together with processes intrinsic to the biology of marine organisms, makes the quantitative study of population connectivity a formidable challenge. Sampling over all scales, except for targeted field efforts that focus on selected processes of life stages in limited domains, is presently not possible (Gawarkiewicz et al., this issue). As such, modeling approaches that simultaneously include key physical dynamics and biological traits provide a way forward to investigate general ecological questions as well as provide qualitative assessments regarding connectivity of specific regions and populations (Cowen et al., 2000, 2006; Werner et al., 2001a). In some instances, model results have provided information of relevance to decision-makers in determining marine protected areas and other management strategies (Fogarty and Botsford, this issue). At a minimum, models can be used to generate hypotheses for empirical studies. Overall, coupled biological-physical models are critical tools for addressing the complex processes driving population connectivity in marine systems.



Marine population connectivity via larval dispersal is inherently a coupled bio-physical problem. Among the relevant physical processes on continental shelves and nearshore regions are wind- and buoyancy-driven currents, fronts and associated jets, tides (including residual currents, internal tides and bores), and surface and bottom boundary layers (Werner et al., 1997; Scotti and Pineda, 2007); additional wave dynamics, including Stokes drift and radiation stress, become important within shallow and nearshore reef structures (Monismith, 2007). In turn, these processes are affected via onshore/offshore forcing by eddies, large-scale current meanders, island wakes, and lateral intrusions (Caldeira et al., 2005). In the open ocean and at basin scales, western and eastern boundary currents, together with large-scale gyre circulation, provide oceanographic connectivity between locations separated over hundreds to thousands of kilometers (e.g., Cowen, 1985; Hare and Cowen, 1996; Tang et al., 2006; Kettle and Haines, 2006). However, physical processes alone do not determine the scales of population connectivity. Time scales of larval development and behavioral characteristics, including vertical migration and spatially explicit environmental differences, play important roles (Boehlert and Mundy, 1988; Tremblay et al., 1994; Hare et al., 1999; Bode et al., 2006; North et al., in press a).

Modeling must work hand in hand with field and laboratory studies to test model predictions and assumptions, better parameterize and initialize the models, and iteratively strengthen the model capabilities. Yet, the value of coupled biophysical models is unique as they

provide a mechanistic understanding of linkages. In this paper, we review some of the present capabilities in models used to study population connectivity, identify key challenges for the next-generation models, and consider areas of application in light of new technologies and management needs.

WHAT DO WE KNOW AND WHAT ARE OUR CAPABILITIES?

Modeling physical and biological systems has rapidly progressed in terms of the spatial and temporal resolution achieved and the complexity of processes involved (Werner et al., 2001b; Hofmann and Friedrichs, 2002; Kinlan et al., 2005). Computational capabilities and the development of novel algorithms have enabled the implementation of sophisticated ocean circulation models (Chassignet et al., 2006) and inclusion of detailed biological and geochemical processes within them (Rothstein et al., 2006a). Methods developed for nesting models and their extensions into various shallow-water environments provide opportunities for resolving more realistic larval transport pathways (Hermann et al., 2002). Additionally, developments in spatially explicit Individual Based Modeling (IBM) approaches allow for the inclusion of detailed parameterizations of biological variables required for quantitative estimates of larval dispersal (Werner et al., 2001a; Siegel et al., 2003). General points can be extracted from the large number of physical and biological processes that relate to the dispersal and recruitment of marine organisms, to help define the connectivity problem. First, the temporal and spatial correlation scales over continental shelves

may be relatively short (on the order of days and kilometers). Second, the relative contributions of key processes will likely be site specific and depend on coastal geometry, proximity to estuaries or deep-ocean boundary currents, seasonal stratification, and wind forcing (e.g., Sponaugle et al., 2002). Third, individual physical processes contain variable length and time scales. Thus, hydrodynamic transport, and dispersion modulated further by biological properties, is fundamentally a multi-scale process. It is recognized that highly resolved flow fields are needed in order to embed behavioral models within hydrodynamic models to examine processes involving biophysical interactions (North et al., in press b). While presently it is difficult to simultaneously resolve mesoscale and small-to-intermediate scale flow fields, particularly for simulations over long time periods, promising results have been obtained through the use of nested and unstructured grids (e.g., Fringer et al., 2006).

Using the spatial scales of populations' dispersal and connectivity as a framework for our discussion, we consider modeling capabilities at basin scales (of order 1,000 km), shelf scales (of order 100 km), and reef scales (of order 10 km). In each case, we present current capabilities for capturing the relevant processes and illustrate with specific examples.

Basin Scales

Representation of large-scale oceanic response to atmospheric forcing is at a point where relatively successful hindcasts of basin-scale El Niño-Southern Oscillation/North Atlantic

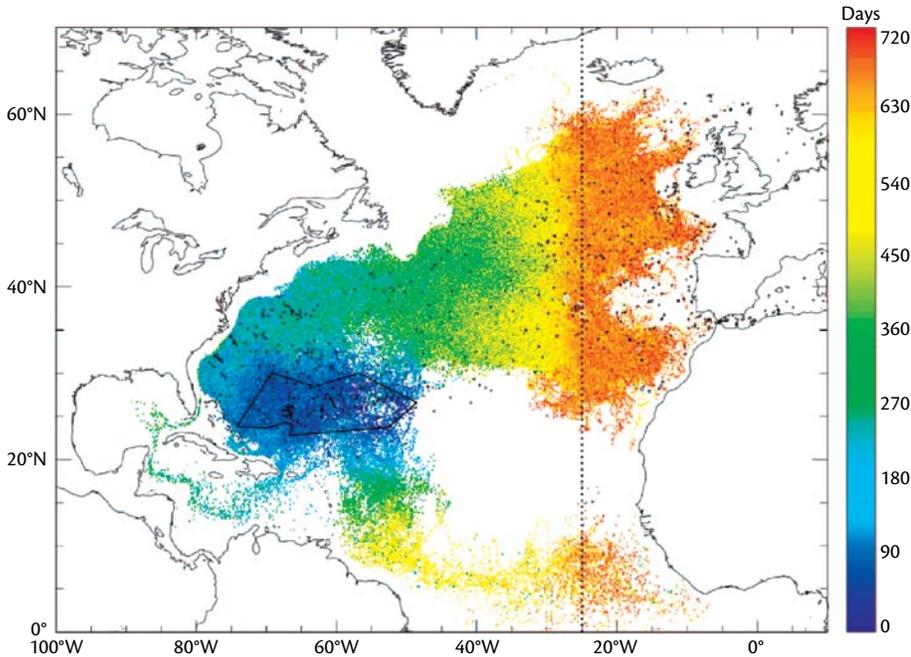


Figure 1. Trajectories of eel larvae successfully crossing 25°W within two years of release within the spawning polygon. Black "+" symbols show locations of larval captures. Trajectory colors indicate age after release in the Sargasso Sea polygon. From Kettle and Haines (2006) reproduced with permission from the Canadian National Research Council Press

trajectories of particles/model organisms given hydrodynamics and behaviors) for the transport and migration of the leptocephali (larvae) of the European eel (*Anguilla anguilla*) across the North Atlantic Ocean from the spawning area in the Sargasso Sea to the adult range off Europe and North Africa. The success of larvae in reaching particular locations on the eastern side of the North Atlantic was found to depend on starting location in the Sargasso Sea, time of year of the spawning, and the depth in the water column at which the larvae were transported. Model results found the fastest cross-basin larval migration to take about two years, with the route from the Sargasso Sea to Europe taking many of the larvae past the North American East Coast during the first year (Figure 1). The model results are consistent with the hypothesis that the European eel and the American eel (*Anguilla rostrata*) could separate themselves on different sides of the North Atlantic basin on the basis of the different durations of their larval stages.

Increasing the biological information included in models can further the resolution of the drivers of population connectivity. For example, the additional effects of mortality and settlement substrate on possible dispersal outcomes show that physical dispersal alone can yield overestimates of population distribution (e.g., see Cowen et al., 2000, 2006; Paris et al., 2005, for case studies in the Gulf of Mexico and the Caribbean Basin). A clear illustration of this effect is provided in Figure 2, showing that while current trajectories might indicate the potential outcome of larval transport (Figure 2A), they fail to account for

Oscillation/Pacific Decadal Oscillation and related climate phenomena have been achieved, attesting to the quality of the data collected and the models' ability to capture relevant internal dynam-

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ics. Similarly, useful data-assimilation and nowcast/forecast systems are presently being developed, and applications from various communities worldwide are resulting in successful pilot efforts (e.g., GODAE, HYCOM, Mercator) that now routinely provide hindcasts, forecasts, and nowcasts of global ocean state estimates (see Lermusiaux et al., 2006). The realism achieved by the physical models has resulted in several successful biological/ecological studies, such as those on the distribution of the copepod *Calanus finmarchicus* in the subpolar North Atlantic by Speirs et al. (2006) and on the dispersal of American and European eels in the North Atlantic by Kettle and Haines (2006).

The latter study presents a Lagrangian model (i.e., a model that computes the

the true probability of successful downstream transport because larval concentrations are reduced by several orders of magnitude by along-trajectory diffusion and mortality of larvae (Figure 2B). Within 30 days, model larvae released from a 1-km² location near Barbados spread over 10⁶ km², representing a reduction of the original concentration of larvae by six orders of magnitude (Figure 2A). If mortality is included, there are not enough larvae occurring within any coastal region to sustain downstream populations from a source population, even when all larvae produced at the source leave the source area.

Shelf Scales

Over the last two decades, the advent and establishment of sophisticated and realistic coastal circulation models (e.g., Haidvogel and Beckmann, 1999), including unstructured and nested grids (Lynch et al., 1996; Greenberg et al., 2007), nonhydrostatic models (Fringer et al., 2006; Scotti and Pineda, 2007), and large-eddy simulations (LES; Lewis, 2005), have enabled the quantitative study of key physical processes in varying degrees of approximation. Similar to the developments in basin-scale modeling, public-domain “community” models, such as the Regional Ocean Model System (ROMS) and the Princeton Ocean Model (POM), render well-established approaches/protocols to be considered and tailored (with relative ease) to site-specific applications with known attributes and limitations. Useful data-assimilation and nowcast/forecast systems are presently being developed and applied with some having reached quasi-operational status, allowing for

sustained analyses of certain processes in limited area domains (see Robinson and Lermusiaux, 2002).

Taking advantage of the wide range of robust and advanced circulation models, spatially explicit IBMs have been used to determine trajectories, or Lagrangian pathways, of planktonic stages of marine organisms in realistic (i.e., spatially heterogeneous and time-dependent) flow

fields. IBMs keep track of individuals within a population, and have become a de facto modeling approach in efforts to study the interactions of marine organisms with their environments and to understand factors impacting dispersal and population connectivity (Werner et al., 2001a). The simplest of these studies ignores biotic factors such as feeding and predation, but includes imposed

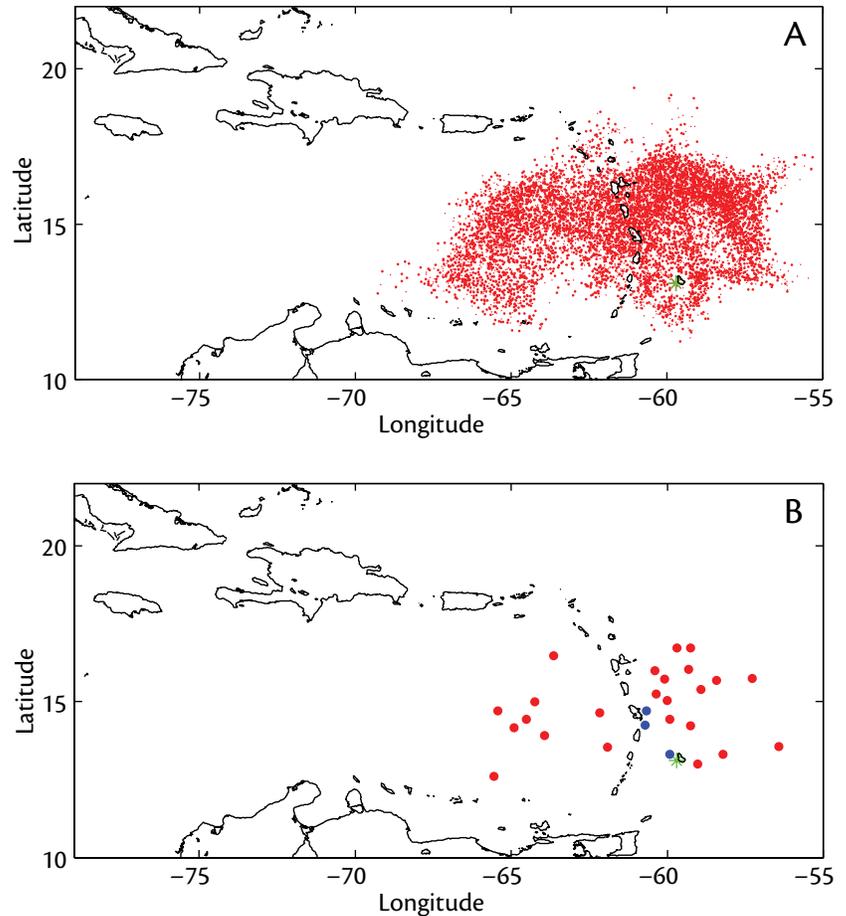


Figure 2. Simulation of the role of dispersal and natural larval mortality on the probability of successful recruitment. (A) Model results of a 30-day dispersal period initiated at the island of Barbados (*). Larvae are spread over a 10⁶ km² area resulting in a six-order-of-magnitude dilution of the initial concentration of larvae (i.e., 10,000 larvae km²). (B) Same simulation with the added effect of natural mortality during the 30-day larval phase (18% d⁻¹). Mortality further reduces the concentration of larvae by another three orders of magnitude. About 10% of these larvae (blue dots) find suitable habitat. Modified from Cowen et al. (2000) with permission from the American Association for the Advancement of Science.

spawning times and locations, swimming behaviors, and larval-competency periods. Among the questions successfully investigated by such studies are the space-time pathways of larval fish from spawning grounds to nursery areas (Miller et al., 2006), larval retention on submarine banks and islands (Page et al., 1999; Paris and Cowen, 2004), effects of interannual variability of physical forcing on dispersal of larval fish populations (Rice et al., 1999), identification of spawning locations (Stegmann et al., 1999), dispersal barrier mechanisms (Baums et al., 2006), and long-term dispersal by tidal currents (Hill, 1994). Similar approaches focusing on invertebrates include the seeding of scallop beds on Georges Bank (Tremblay et al., 1994; Fogarty and Botsford, this issue), the behaviorally mediated connectivity of copepods between shelves and deep basins (Speirs et al., 2005) and their on-shelf retention (Batchelder et al., 2002), the impact of environmental quality and larval supply on recruitment of spiny lobsters in the Florida Keys (Butler, 2003), and the onshore transport of barnacles (Pineda et al., this issue).

The inclusion of the effect of feeding environment on successful dispersal and recruitment has been achieved by using temperature as a proxy for feeding environment or through more explicit, but still idealized, representations of spatially dependent (but temporally fixed) prey fields (see review in Werner et al., 2001a). Using these approaches, Lagrangian trajectories considered favorable for dispersal and retention or appropriate for transport into nursery areas are more narrowly defined to include only those trajectories where the

individuals encounter favorable feeding environments. Some of these studies have also been used to explore other spatially dependent interactions between predators and their prey. For example, the perception of prey by fish larvae can be effectively increased or reduced as a consequence of local variation in turbulence levels, which alters the volume searched (Dower et al., 1997). This requires models to capture not only the spatial distribution of biotic components but also their modulation by certain abiotic environmental factors.

Intersections of large- and small-scale physics affecting recruitment are discussed by Werner et al. (2001a), who consider modifications of the perceived feeding environment by turbulence at the smallest scales, including its effect on particle trajectories and on larval growth and survival. The authors found that regions of enhanced larval growth and survival—resulting from the enhancement of contact rates and effective prey concentrations by turbulence within the tidal bottom boundary layer—coincided with hydrodynamically retentive subsurface regions of Georges Bank defined in earlier studies (e.g., Werner et al., 1993). While the above studies have focused on higher-latitude environments, it is a greater challenge to model trophic interactions in subtropical and tropical regions that are typically characterized by high species diversity and oligotrophic waters. In effect, billfish, scombrids, and many coral reef fish larvae appear to have evolved high prey selectivity, perhaps to minimize competition (Llopiz and Cowen, in press, and recent work of author Cowen and Joel Llopiz, RSMAS). Such dietary niches require that models

of the organisms' feeding environments explicitly include specific prey types rather than general functional groups.

Is it clear from the discussion above that connectivity requires quantitative understanding of physical and biological processes integrated in space and time. One example of an area that illustrates the combined effects of variability in the hydrodynamic and feeding environments is the shelf region off South Africa in the Benguela Current system. Using model-based approaches, Mullon et al. (2003) consider evolutionary-based reproductive strategies and processes affecting survival and recruitment of pelagic fishes (sardines and anchovies) in the context of "Bakun's triad" (Bakun, 1996)—enrichment, enhancement, and retention (Lett et al., 2006). Of immediate relevance to population connectivity is the ability to use models to determine the selection of the source/spawning regions by the populations, and the subsequent spawning-to-nursery area transport of the fish larvae and the biotic processes that determine along-transit survival success (see Figure 3).

Reef Scales

For smaller scales encountered at reefs, from 1–10 km, the details of the interactions among topography, wind, tidally driven currents, and wave motions become increasingly important (Legrand et al., 2006; Monismith 2007; Tamura et al., 2007). The flow near shallow coral reefs is particularly complex and encompasses a multiplicity of scales: at the largest scales, flows include eddies produced by island wakes, while at the smallest scales of flow, we need to consider flows around single coral colonies. Circulation

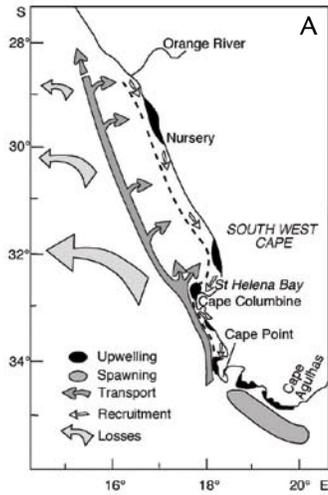
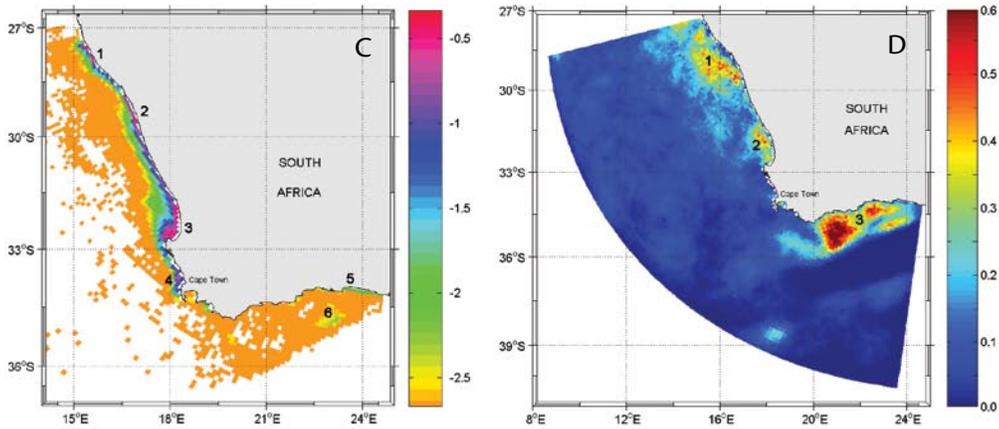
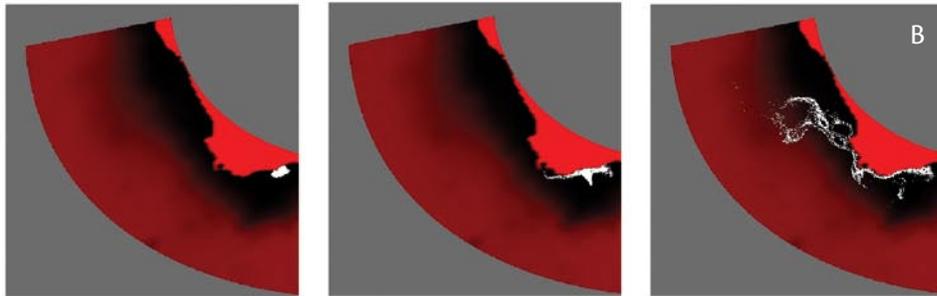


Figure 3. (A) Schematic of anchovy egg and larval dynamics in the southern Benguela Current. The eggs and larvae are transported from western Agulhas Bank spawning sites off the west coast of Africa. (B) Modeled particle tracks (white dots) in the Benguela Current system of transport over a six-week period (courtesy of Christian Mullon); the land mass is in red and the depth contours are the remaining shaded areas. (C) Enrichment intensity obtained through simulated particle upwelling; regions 1–4 are the most enriched off the west coast (compare to the schematic in 3a). (D) Map of simulated pattern of retention. Values correspond to the proportion of particles retained averaged over the period 1992–1999 and depth. Note that the retention areas are located near the enrichment areas. Recruitment for both anchovy and sardine is considered to occur predominantly off the west coast; the high retention predicted for Region 3 may not result in observed successful recruitment. Figures adapted from Mullon et al. (2002) with permission from the Canadian National Research Council Press and Lett et al. (2006) with permission from Blackwell Publishing



models have proven to be effective in describing hydrodynamic features and biological or material transport around atolls, barriers, and fringing coral reefs (Kraines et al., 2004). However, to properly and quantitatively capture these features, high-resolution and accurate

bathymetric mapping of both inner and outer reef areas is essential (Wolanski et al., 2004; Legrand et al., 2006).

Satellite-derived mapping and spatial analyses of the global coral reefs are particularly useful for generating the seascape layer (e.g., Coral Reef Millennium

Mapping; Andrefouët et al., 2005). The coupling of geographic information system (GIS) and Lagrangian models in highly fragmented habitats, such as coral reefs, permits analyses of metapopulation dynamics (i.e., patterns of individual movement between geographi-

cally separated populations) by tracing the size and arrangement of population patches in transition matrices. Cowen et al. (2006) used the transition matrix output to map larval flow (i.e., using graph theory, *sensu* Urban and Keitt, 2001) between 50-km segments of coral reefs in the Caribbean. At the regional scale, their results matched the realized dispersal derived from genetic and biogeographical studies (Taylor and Hellberg, 2003; Baums et al., 2006; Purcell et al., 2006). Similar modeling approaches have been utilized for the Great Barrier Reef

(e.g., Bode et al., 2006).

It is also important to integrate the topography and habitat attributes along Lagrangian pathways, as they have been shown to affect individual behaviors and movement through time (Paris et al., 2005). For example, at local reef scales, Gerlach et al. (2007) used a multidisciplinary approach (i.e., hydrographic modeling, population genetics, sensory/behavioral experiments) to demonstrate that larvae utilized olfaction to enhance return to their natal reef, greatly modifying passive dispersal between adjacent

reefs (3–23 km distant). Integration of both sensing and orientation abilities of individuals and attributes of the reef into coupled biophysical models should generate better quantitative assessment of the influence of behavior on connectivity at small scales.

Finally, a series of Great Barrier Reef (GBR) studies by Wolanski and Spagnol (2000), Wolanski et al. (2003b), and Legrand et al. (2006) illustrates present hydrodynamic modeling capabilities integrating across scales, from the shelf down to reefs (see Figures 4 and 5). Extending over 2500 km along Australia's northeastern continental shelf, the GBR comprises almost 3000 individual reefs ranging in area from 0.01–100 km². Processes resulting from the wind- and tidally driven flow range from meters to hundreds of kilometers, and from minutes to years (Wolanski et al., 2003a), requiring that models resolve processes as small as 10–100 m while at the same time including the larger-scale background dynamics. When such models are merged across a range of spatial and temporal scales (Wolanski et al., 2003a), two-way nesting may be needed to allow feedback of processes between each grid size through parameterization and establishment of boundary conditions (e.g., Sheng et al., 2005; Greenberg et al., 2007).

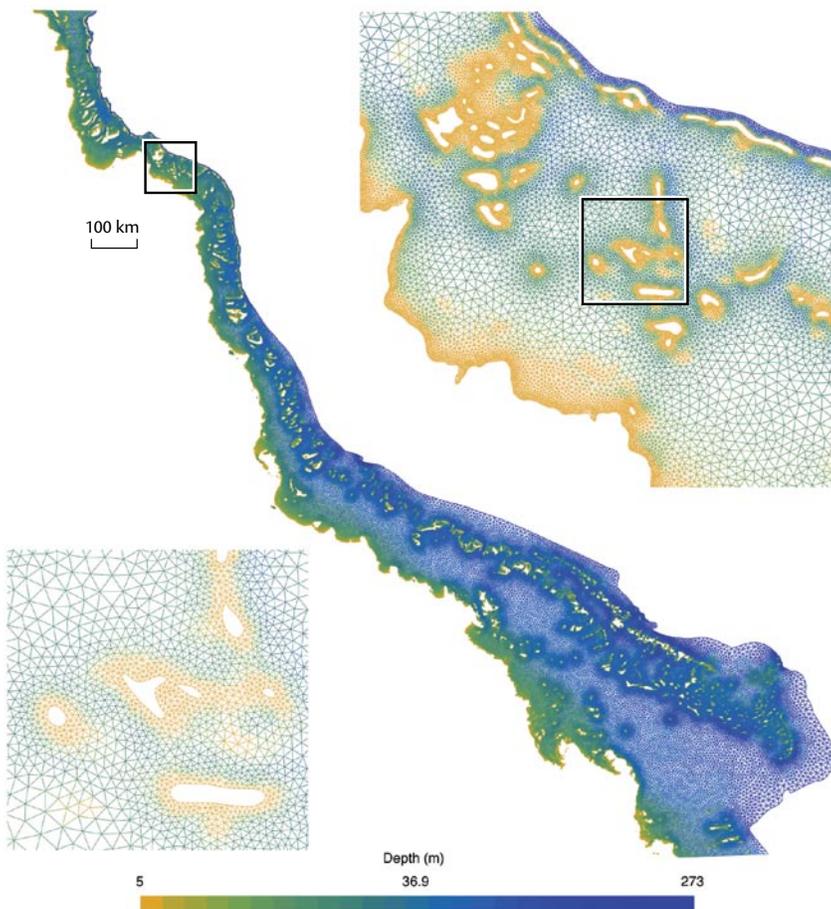


Figure 4. Computational finite element mesh of the Great Barrier Reef (NE coast of Australia) with zoomed in views illustrating the range of element sizes. Colors indicate local water-column depth. Redrawn from Legrand et al. (2006) courtesy of Eric Deleersnijder and Jonathan Lambrechts

WHAT MODELING ADVANCES ARE NEEDED TO CONTINUE TO IMPROVE OUR QUANTITATIVE DESCRIPTION OF CONNECTIVITY?

At each of the scales considered in the previous sections, it is clear that quantitative modeling of population connectivity poses unique challenges in

terms of the physics and biology needed to capture the underlying dynamics. Physical and biological processes occur at multiple scales and they generally overlap and interact. For instance, many source regions are located in the near-shore environment, where there remain fundamental issues in resolving near-shore (e.g., wave-dominated) physics and its coupling to inner shelf dynamics. In turn, inner-shelf circulation can be affected by processes occurring along the outer edge of the continental shelf, where shelf and oceanic dynamics interact and are often influenced by strong boundary currents in the presence of increased levels of mixing and internal wave fields. At the same time, a critical aspect of the modeling necessary for understanding population connectivity is the incorporation of behavior and other biological processes into models. In the following sections, we briefly discuss elements of our modeling capabilities that need to be improved.

Physics and Hydrodynamics

Advances are needed to better represent models' *internal* physical dynamics, particularly at intermediate/submesoscale to small scales, such as frontal dynamics (Gawarkiewicz et al., this issue), wave-induced and boundary-layer processes (Monismith, 2007), and other nonhydrostatic flows (e.g., Scotti and Pineda, 2007). For example, aperiodic, submesoscale eddies that develop along the interface between the Florida Current and the steep Florida shelf edge have been shown to significantly influence (positively and negatively) the delivery of certain coral reef fish larvae to settlement habitat along the reef track (Sponaugle

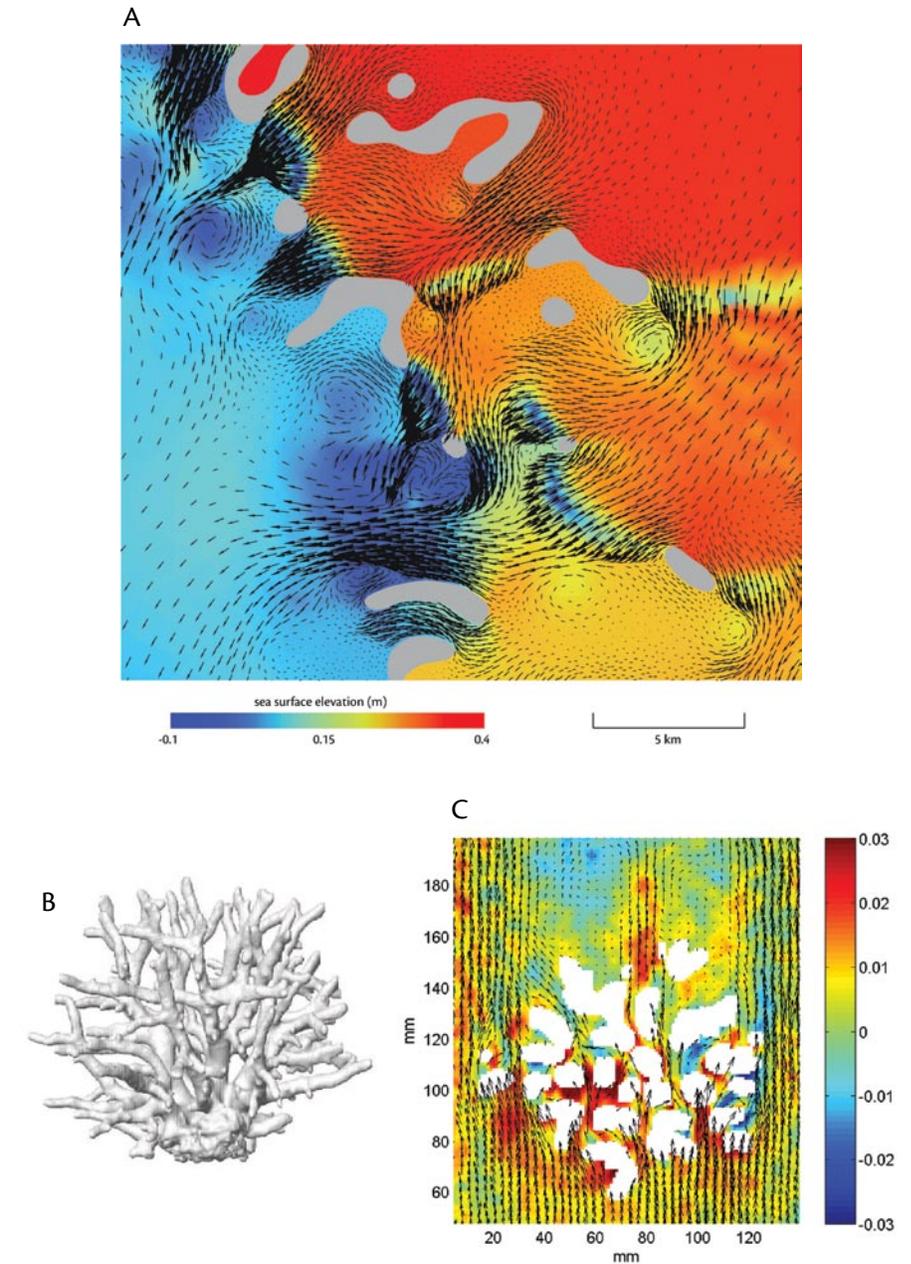


Figure 5. (A) Sample velocity fields in the vicinity of reefs and islands in the Great Barrier Reef (courtesy of Jonathan Lambrechts and Eric Deleersnijder). (B) Coral colony (from Monismith, 2007, reprinted with permission from the Annual Review of Fluid Mechanics, Volume 39 ©2007 by Annual Reviews, www.annualreviews.org) (C) Laboratory measurements of the streamwise (arrows) and vertical flow (color) within the colony measured by magnetic resonance imagery, yet to be modeled and merged within larger-scale domains (image from Chang, 2007; courtesy of Sandy Chang).

et al., 2005; D'Alessandro et al., 2007). Additional modeling efforts are to realistically capture these eddies' features (e.g., Fiechter and Mooers, 2003).

There is also a need for better specification of *external* forcing surface fluxes (which continues to challenge all circulation models), especially at event scales.

For instance, strong winds and the passage of hurricanes have been correlated with large recruitment pulses for some species of fish and lobster (Shenker et al., 1993; Eggleston et al., 1998). More generally, extreme meteorological events are common for the Caribbean region, and properly capturing such events is important because their spatial environmental autocorrelation can have important implications for the source-sink dynamics of metapopulations (Schiegg, 2003). As a corollary, a potential increase in storm frequency during the warming of the tropical oceans (Trenbreth, 2005) could affect the patterns of population connectivity.

Because trajectory accuracy is important for connectivity models, capturing the effects of sub-grid-scale representations without the introduction of artifacts is essential. Yet, sub-grid-scale parameterizations (i.e., physical mixing processes) are not well understood and thus not well modeled. Mixing, sub- and super-diffusive features, and critical shear stress are examples of sub-grid-scale processes in need of quantitative revisiting. Recent Lagrangian work by Veneziani et al. (2005) reveals that the eddy field is characterized by two distinct regimes, a background flow associated with nonlooping trajectories, and coherent vortices generating looping trajectories. The latter flow regime is prominent at the shelf break and around oceanic islands and atolls and should be parameterized using a Lagrangian stochastic model (LSM) with a relative vorticity factor that correctly simulates the trapping effect of particles (e.g., Paris et al., in press). In contrast, the background flow regime can be parameterized by

simple diffusivity. It is well known, however, that where the hydrodynamics are especially complex, such as in the vicinity of reefs and within coastal boundary layers in general, particle-tracking algorithms need to be adapted to anisotropic vertical and horizontal diffusivities to avoid spurious accumulation of particles (Werner et al., 2001b; Spagnol et al., 2002). Properly accounting for effects such as “form drag” near the bottom of or around reefs (e.g., Wolanski, 1987; Monismith, 2007) and the effect of wind-driven shear stress (or Stokes drift) and gravity waves near the free surface can have a significant effect on estimating fluxes across these boundaries. Future key observations afforded by observing systems and observatories will significantly assist in the improvement of model treatments of the processes at sub-grid scales.

The interaction of stratified flows with topography remains unresolved, particularly where topographic variations are abrupt (e.g., at the shelf break, promontories, oceanic islands), leading to flow regimes with attached or shed eddies and large-amplitude internal waves, and where consequent mixing may co-occur (Boyer and Tao, 1987; Pineda, 1994). Similarly, uncertainties remain concerning the actual topographic data for a variety of reasons, including inadequate sampling and changes of bottom features over time, particularly in shallow nearshore, estuarine, and reef regions. High-resolution hydrodynamic observations are necessary for the development of models capable of operating in areas of steep topography, as organisms may exploit topographic eddies and associated secondary circulation features for

retention, fronts for accumulation, and internal bores for two-way transport.

The coupling to far-field models and the two-way coupling across scales continue to be a focus of research for several groups (Hermann et al., 2002; Sheng et al., 2005; Chassignet et al., 2006). As individuals from a population leave a local domain, their trajectories need to be determined within a larger domain that encompasses downstream local populations and the metapopulation network. Ideally, a series of two-way nesting grids from basin scale, to shelf scale, and further to local scale should be employed, with higher resolution both for spawning and recruitment areas. This will be particularly important as we consider longer time scales (e.g., climate scenarios) where biogeographic shifts in the distributions of populations and their connectivity are likely to be affected (Vikebø et al., 2007).

Biology and Behavior

A fundamental difference between recruitment and connectivity models is the focus on temporal and spatial scales. In recruitment studies, emphasis is on the temporal patterns (i.e., when) and the quantitative aspects (i.e., how much) of successful dispersal. It is therefore important to identify the physical-biological interactions that drive high recruitment versus low recruitment; behaviors related to feeding and growth are key. On the other hand, in connectivity studies, the emphasis is on spatial patterns related to population linkages. Such models need to be spatially explicit and resolve the scales of source and sink populations. Therefore, initial conditions and accuracy of the trajec-

tory become important issues in which larval behavior (i.e., swimming and orientation) plays a large role. The survival consequences of individual movements also emerge as a key component in population connectivity (Cowen et al., 2000). While there is no general agreement at the present time on the best way forward, the use of agent-based (or individual-based) modeling is central to successful modeling. A general issue is the disparate range of time and length scales for physical processes (e.g., internal waves, fronts, eddies, gravity currents) that interact with the biological time and length scales, such as the organisms' vertical position in the water column, larval duration, and length, timing, and location of spawning.

Larval connectivity pathways conducive to self-recruitment are essential for population persistence (Hastings and Botsford, 2006; Gaines et al., this issue). Life-history traits, driven by selective pressure of the species' natural habitat, may have evolved to exploit hydrographic regimes that improve the odds of larvae returning close to the parent population (Strathman et al., 2002). Physical processes can also influence biological processes, such as the timing of reproduction, larval transport and behavior, and the timing of settlement (Cowen, 2002). Induced behavior (e.g., diel vertical migration, foraging, predator avoidance, directional horizontal swimming in response to environmental cues) and emerging properties (i.e., larval stage duration, age/stage-dependent vertical migration, mortality) have been shown to influence population connectivity as much as currents do (Paris et al., in press) and can reduce dispersal (Gerlach

et al., 2007). All behavioral traits are variable in essence, and thus modeling of behavior has to be probabilistic to account for these variations. Offline stochastic modeling systems using archived fields from oceanographic models with proper subsampling (e.g., Hermann et al., 2001) are now efficiently used to generate likelihoods of larval exchange from high-frequency releases of active particles from numerous source locations (Cowen et al., 2006).

Marine organisms are generally not passive. Among various behaviors, organisms swim actively, migrate vertically, and change their buoyancy (e.g., Cowen, 2002; Fuchs et al., 2007). Behavior can arise in response to environmental cues, or it can be ontogenetically triggered (i.e., during the process of larval development), with eventual schooling behavior emerging as the organisms reach juvenile or adult stages, which, in most cases, signal increasing sensory abilities and survival (e.g., Codling et al., 2007). Many studies have established the importance of vertical behaviors in population dispersal, retention, settlement, and connectivity; larvae located at different depths will be subjected to different currents and thus their Lagrangian trajectories will be different (e.g., Werner et al., 1993; Batchelder et al., 2002; Paris and Cowen, 2004); their trajectories are also influenced by their pelagic phase duration (Tremblay et al., 1994). Similarly, directed horizontal swimming rates have been shown to significantly affect distributions of individual organisms (e.g., Werner et al., 1993). It is safe to say that behaviors can be complex and their explicit consideration is essential in many cases. At the same time, the effect

of the hydrodynamics may be dominant during spatially and/or temporally restricted phases of the pelagic duration of organisms (e.g., Koehl and Powell, 1994) but should not preclude the influence of behavior in general. The question from the modeling standpoint is not whether behaviors should be included, but rather how they should be included. North et al., (in press a) provide guidelines on how behavioral experiments in the field and in the laboratory can provide information to modeling studies, and in turn how these behaviors may be imposed in models in response to, for example, external cues, foraging, avoidance of predators. The study of small-scale interactions of water, larvae, and their prey on scales of a few kilometers to meters is without doubt an important research need.

Behavior can be implemented in IBMs by simple rules (e.g., seeking to maximize growth or to minimize mortality risk). However, these simplifications are probably not realistic as other trade-offs need to be considered that may vary with stage and age, and over generations when longer time scales are considered. Additionally, variability in the environment can be large enough that it may override these life-history-based assumptions. Alternatives to imposing "simple" and likely unrealistic behaviors are to consider modifications of behavior through adaptation (e.g., Giske et al., 2003). Dynamic programming methods allow organisms to "find" optimal habitats by balancing risks of predation, growth, and advective loss. Examples include the adapted random walk (Huse, 2001), optimization of self-recruitment in isolated islands (Irison et al., 2004),



Models should guide in the design of field experiments, and in turn observations should improve the model parameters.

and individual-based neural network genetic algorithm (ING) (Giske et al., 1998) that allow adaptive behaviors to emerge in populations in complex environments. The ING method provides a way to implement behavior in individual-based models. One example is provided by Strand et al. (2002) wherein an individual-based model that uses artificial evolution is used to predict behavior and life-history traits on the basis of environmental data and organism physiology. In their approach, evolutionary adaptation is based on a genetic algorithm that searches for improved solutions to the traits of habitat choice, energy allocation, and spawning strategy. Behaviors emerging from model studies can complement results from field and laboratory efforts and allow predictions to be attempted.

Another developing area of research involves linking population genetic models with bio-oceanographic models. Modeling the flow of genetic material presents a significant challenge, both in terms of simulation and analysis because of its ability to persist through time. This persistence can lead to complex dispersal patterns; dynamics are further compli-

cated by recombination, selection, and behavioral interactions. Many aspects of classic population genetic theory involve assumptions that are incompatible with contemporary studies (e.g., the assumption of equal and even migration), are too simplified for practical application, or else are inscrutable to nonspecialists. Novel and flexible approaches, such as object-oriented frameworks (Johnathan Kool, RSMAS, *pers. comm.*, 2007), are required. It is also important that these systems be accessible in order to ensure that they can be put to use by the people who need them. Despite the difficulties involved, the potential rewards are worth the effort, as it would provide researchers with a means of exploring community and ecosystem-scale evolutionary questions and validating them with empirical evidence (e.g., validating connectivity patterns using genetic marker data).

Model Validation and Skill Assessment

Modeling has to work hand in hand with empirical studies to test model predictions and assumptions, better parameterize the models, and iteratively

strengthen model capabilities. However, model solutions themselves need to be validated, which is not straightforward, given the complexities of the processes contributing to the computed realizations. Formal procedures for skill assessment of physical models have been discussed (e.g., Lynch and Davies, 1995), but quantitative skill assessment of biological models is still relatively undeveloped (Arhonditsis and Brett, 2004). Validation of trajectory paths can be accomplished using a combination of acoustic and hydrographic (e.g., ADCP, CTD), Lagrangian (e.g., satellite-tracked floats, fluorescent wax particles), tagging or mass marking (e.g., otoliths), and plankton sampling tools (e.g., trawls, optical sampling). It may be possible to validate population-connectivity results by use of geochemical signatures (Becker et al., 2007; Thorrold et al., this issue) or genetic tools (review by Planes, 2002; Hedgecock et al., this issue). Measurements of postlarval supply at multiple sites can also produce a very consistent validation of the connectivity results without providing explicit knowledge of the source locations.

FUTURE DIRECTIONS AND APPLICATIONS

As we look forward, models can be expected to provide test beds for developing field-testable hypotheses, means for refining existing ecological and evolutionary theories, guidance for better experimental designs, and possible future scenarios in light of expected climate/global change; ultimately, they should be useful to resource managers. We consider these points briefly in our concluding remarks.

Models Assisting the Design of Field Sampling

As physical and biological models progressively mature, they should be expected to provide hypothesis testing and help guide sampling protocols and observatory/observing system design. For example, numerical simulations based on high-frequency, quasisynoptic, in situ measurements of physics and larval distributions have proven effective in testing larval transport hypotheses (e.g., Helbig and Pepin, 1998; Paris and Cowen, 2004). While observational capabilities for high-resolution and rapid measurements of physical properties are relatively advanced, observing systems for determining larval distributions are less so. Real-time, in situ observing systems will be useful in defining the oceanographic environment, including variability of the hydrographic and velocity fields, and in determining the Lagrangian pathways of identifiable larvae from source areas. Additionally, relevant technologies continue to emerge (e.g., imaging systems—see Benfield et al., 2007), and remote observing systems will identify episodic events (e.g., by triggering inten-

sive sampling) and temporal variability over long time scales. However, the proper deployment and design of such field deployments is not trivial as attested by the wide range of processes discussed above. In turn, the effectiveness of the sampling strategies is determined by the accuracy with which the observations can be used to reconstruct the state of the natural system being measured. Given the limited opportunities for evaluation of sampling strategies against objective criteria with purely observational means, numerical models offer a framework for investigation of these issues (Walstad and McGillicuddy, 2000), and observation system simulation experiments (OSSEs) become of central importance in experimental design of questions addressing population connectivity.

The aim of OSSEs is to model observation systems with the intent to quantify their sampling properties and optimize their design (i.e., OSSEs attempt to simulate unknown ocean properties to better measure and discover them). OSSEs can be utilized for multiple purposes including to: (1) guide the design of an observation system and its components; (2) optimize the use of observational resources; (3) assess the impact of existing or future data streams (e.g., for nowcasting and forecasting of requisite accuracies); (4) understand the interactions of system components and improve system performance; (5) evaluate and validate system performance using quantitative error estimates; and (6) compare data-assimilation methods (GLOBEC.INT, 1994). OSSEs continue to be used to assess, for example, physical oceanographic array designs in the tropical and coastal oceans. Based

on the present status of modeling and data-assimilation systems, the development of adequate capabilities for implementation of useful OSSEs in observing systems for use in studies of population connectivity may be achievable on the time scale of a few (two to five) years (Rothstein et al., 2006b).

Predictions and Future Scenarios

Over the past several decades we have learned about longer-term fluctuations that occur within the bounds of “natural” variability (e.g., El Niño, Pacific Decadal and North Atlantic Oscillations). The ecological impacts of a changing climate are already evident in terrestrial and marine ecosystems, with clear responses of both the flora and fauna, from the species to the community levels (e.g., Harley et al., 2006). The continued influence of humans on climate will result in further changes in abundance and distribution of marine species; thus, there is a need to estimate the nature and severity of the possible ecological consequences in order to develop strategies to manage marine resources. The physical forcing of a changing (e.g., warmer) climate is hypothesized to have important consequences that can impact marine populations, for example, changes in wind patterns and intensities that in turn can impact the strength of ocean currents, and increased stratification in the surface layers caused by the warming of surface ocean waters or increased freshwater fluxes. The dispersal of populations (particularly during the early life stages) will be directly affected by changes in currents and temperature (e.g., O’Connor et al., 2007). One example is that described by Vikebø et al. (2007), who explore the

effects that a reduction of the thermohaline circulation (THC) may have on larval drift and development of Arcto-Norwegian cod. Using a regional model forced by a global climate model, they find a reduction in the THC relative to present-day circulation. The impact of the change in circulation and ocean temperature on the cod results in a southward and westward shift in the distribution of cod from the Barents Sea onto shelf regions, a reduction in the predicted individual growth of the pelagic juveniles, and an increase in the number of larvae and pelagic juveniles that advect towards regions where they are unable to survive (see Figure 6). Our ability to link exist-

ing coupled biological-physical models to climate models capable of examining climate-change scenarios will be critical in assessing potential direct and indirect impacts of climate change on population connectivity and the ultimate usefulness of the model to resource managers.

Models as Management Tools

The management of living marine resources is inherently spatially dependent. Understanding how marine populations are connected in space and time will provide an essential component to management of marine resources that is presently not available. For instance, the design of marine protected areas

(MPAs) or the exploration of future scenarios requires a quantitative description of population connectivity. An understanding of spatial linkages over populations will also contribute to the explanation of variability in fisheries (see Fogarty and Botsford, this issue; Jones et al., this issue). In these applications, realistic descriptions of habitat, hydrodynamics, larval transport pathways, and adult growth and survival will provide a mechanistic understanding of how local populations may be interconnected. Validated, spatially explicit models will also be useful for designing and assessing MPAs in that they will provide the degree to which populations are connected and

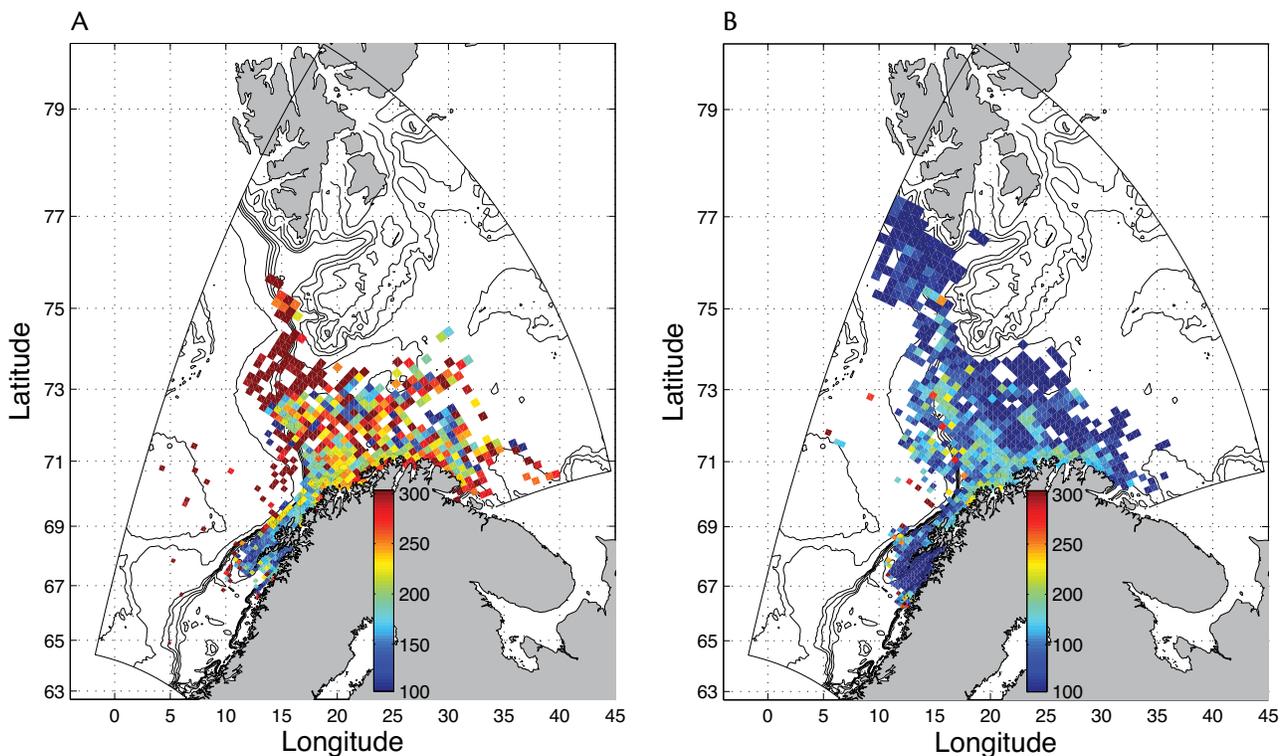


Figure 6. Simulated distribution of pelagic juvenile cod with (A) the ocean and atmospheric forcing for the present day, and (B) for changed climate (today + 50 years) scenario run. The color scale indicates wet weight in milligrams. These results indicate that in the +50 year run pelagic juveniles will have lower weights. The distributions also indicate that a higher number of larvae and pelagic juveniles are advected to the west of Spitsbergen (to the northwest) in the +50 year run. From Vikebø et al. (2007) with permission from Blackwell Publishing

estimates of the exchange between adjacent and distant areas. Models will offer insights into the mechanisms of how and why populations exist in certain systems and bring increased understanding of the variability in marine populations.

CONCLUDING REMARKS

We reviewed present-day capabilities of modeling population connectivity in marine systems, showing that simultaneous inclusion of physical and biological processes is essential to properly describe and quantify organisms' dispersal, settlement, and ultimate distribution. We also discussed some of the remaining challenges. Model formulations need to better represent physical dynamics, particularly at intermediate and small scales (i.e., at scales of kilometers or less); rapid advances in the use of unstructured meshes and the development of novel algorithms that allow for multiscale problems are both promising and necessary. Another element of paramount importance is the better representation of larval behavior and environmental gradients and cues in coupled models. And, certainly, more quantitative and sustained measurements are required of key physical and biological properties. We suggest that modeling and observational improvements should not occur independently of each other. Models should guide in the design of field experiments, and in turn observations should improve the model parameters. Finally, encouraged by the advances achieved in the past few decades, models addressing population connectivity will be used to pose and address ecologically relevant questions, will have forecasting capabilities, and will be useful to resource managers.

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