Spatial Ecology of Atlantic Cod in the Gulf of Maine

Discussion paper

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Introduction

The New England groundfish fishery faces a socio-economic, political and, potentially, environmental crisis in response to the most recent Gulf of Maine (GOM) cod stock assessment (NEFSC 2011). The previous assessment in 2008 concluded that overfishing was not taking place, and the stock was on a trajectory to be fully rebuilt by 2014 (NEFSC 2008). The most recent assessment concludes that the stock is severely overfished (approx. 20% of B_{MSY}), experiencing overfishing (approx. 5 times F_{MSY}; NEFSC 2011), and cannot rebuild by 2014 even if F=0. Fishermen, on the other hand, report abundant cod, many large cod, and high catch rates, none of which seems to be consistent with a severely depleted stock.

In order to ensure that the outcomes are accurately predictable before catch limits are substantially reduced, many questions have been raised about decisions made during the assessment process. By most accounts, the assessment process was thorough and the review panel approved the approaches taken. However, given the gravity of the situation, a closer look at each decision and their cumulative effects is warranted. The investment of time, expertise and other resources into our scientific basis for management should be commensurate with the status of the stock, its value (socio-economic and ecological), and therefore the implications of either overfishing or drastic cuts in quotas. Compared to many, the 2011 benchmark assessment for GOM cod was data-rich, but the investment of time and other resources was typical for the SAW/SARC process. In light of the outcomes, not to mention their stark contrast from the previous assessment, stepping back for a deeper examination of the assessment process, as well as other key issues seems warranted.

Perhaps chief among the scientific issues not addressed during the assessment process are a series of questions about the spatial structure and dynamics of cod, questions which warrant a sharper focus as soon as possible. The benefits of sharper scientific focus will not always outweigh the costs, depending upon the attributes of both the stock and fishery. However, the value of GOM cod and the imminent crisis justifies further investigation. Therefore, this paper considers data and theory on the spatial ecology of GOM cod, and implications of alternative hypotheses to our status quo assumptions. This paper is not intended to be a comprehensive review, nor does it aim to reach conclusions on the issues addressed. Rather, the goal is to highlight key issues worthy of greater consideration and to help chart a path forward. The discussion herein is restricted primarily to the realms of population biology and population ecology. Aspects of behavioral ecology and ecosystem ecology (e.g., habitat, oceanographic and trophic effects) are alluded to briefly, but these and other disciplines also represent areas for deeper examination and understanding of cod stock dynamics.

Spatial assumptions underlying assessment models

Pertinent spatial questions fall within one of two overarching categories. The first are those related to our working definitions of cod stocks and spatial management units. A fundamental assumption of most assessment models is that the model describes a ‘closed’ population, with negligible immigration into and emigration from the stock area, either by movement of post-settlement individuals or dispersal of larvae (i.e., the “unit stock” assumption; Hilborn and Walters 1992). Several lines of evidence suggest that cod stock boundaries need to be reconsidered.

Even if the stock boundaries are defined appropriately, it is also important to understand the internal spatial structure of the stock. Methot and Punt (2004) highlight the following key assumptions regarding spatial pattern and process that underlie most stock assessment models:

> "Most fisheries stock assessments are based on the assumption that the fishery or the fish population is distributed homogeneously or freely mixes across the region being assessed. Any local patterns in density, age structure, or mortality are assumed to be ephemeral and to diffuse quickly throughout the population."

The authors raise this important point in the context of violations of the assumptions introduced by implementation of marine protected areas (MPAs) within the stock area, and use simulation modeling to illustrate the biases in assessment outcomes that can result. Possible effects of MPAs on assessment outcomes are relevant to GOM cod as well, given the presence of the Western Gulf of Maine (WGOM) and Cache's Ledge closed areas within the stock area, and quantifying those effects might change our perception of the stock. Or, perhaps more significantly, accounting for natural spatial variation and structure might result in a very different picture.

Concerns about stock structure assumptions that underlying New England fisheries are not new. In April 2009, a workshop brought together researchers and stakeholders to review the most recent findings and chart a path forward in terms of both science and management (Mendelson 2009), and a follow-up workshop in June 2011 built on the goals, themes and conclusions of the first (Feeney and La Valley 2011). At both workshops, Atlantic cod was the focus of more research and discussion than any other species, and is the species for which we probably have the richest understanding of spatial structure in the Northwest Atlantic. In fact, the New England Fishery Management Council's Scientific and Statistical Committee (SSC) recommended investigation of cod stock structure in two recent reports.

In November 2010, the SSC identified a research priority that included, "Improve knowledge on stock definition, stock movements, mixing, and migration through tagging studies, DNA markers, morphological characteristics and other means, focusing on: (a) short- and long-term movements, and (b) habitat use in relation to broad scale movements, with priority for monkfish, cod, pollock, silver hake and herring."

When asked for its advice on terms of reference for the GOM cod assessment (SSC 2011), the SSC recommended:

1. If time permits, SAW53 on Gulf of Maine cod should consider information on the small scale distribution of cod in the Gulf of Maine and advise on its management implications,
2. The Plan Development Team should take account of information on the small scale distribution of cod for both the Gulf of Maine and Georges Bank Management Units for future implementation or amendments of the Multispecies Fishery Management Plan,
3. There should be a comprehensive evaluation of scientific information on cod population structure and its management implications, including the possibility of revising management units. This evaluation should occur in time to be taken into account in the next management cycle, beginning with the 2014 fishing year.

Only the first recommendation was directed at the SAW 53 process itself, and it was proposed to be optional in light of the enormity of a benchmark assessment, and the limited time and competing demands of the assessment team. Consequently, and perhaps not surprisingly, the issue received little consideration. Indeed, very few assessments reconsider stock boundaries once they are drawn, incorporate sub-structure, or consider the implications of either omission or both. The implicit assumption is that the assessment is robust to violations of those assumptions, or that the uncertainty introduced is absorbed into the ABC buffer.

Some degree of spatial structure is the norm rather than the exception for most marine fish populations, but simplifications are perhaps warranted in many cases due to the complications that revising boundaries or incorporating sub-structure introduces for data collection, modeling and management. However, when the socio-economic or ecological significance of a given stock, and therefore the consequences of overfishing or drastic reductions in quotas, is sufficiently high, a more thorough examination and a greater investment of resources are warranted. Specifically, a more detailed scientific evaluation is in order to achieve the highest level of accuracy possible and guard against severe socio-economic and ecological impacts.

Spatial patterns in cod distribution and abundance

In some ways, science and industry are not reporting fundamentally different perceptions of GOM cod abundance. The vast majority of GOM cod harvest comes from the WGOM, and patterns of abundance in that area primarily shape fishermen's perceptions. There, cod consistently exhibit higher density than areas adjacent to the coast of Maine, the Scotian Shelf, or George's Bank (Fig. 1, 2). This pattern is consistent among periods of comparatively high (1970s), low (1990s) and intermediate (1980s, 2000s) abundance.

In periods of low to intermediate abundance in particular, the vast majority of the stock appears to be concentrated within the WGOM region. The assessment acknowledges this spatial pattern briefly, describing it as a "contraction" of the population (NEFSC 2011). Further explanation or a precise definition of contraction are absent, as are possible causal mechanisms. Contraction seems to imply movement of fish from peripheral areas to the WGOM center of mass, presumably in responses to changes in density or other environmental changes. Alternatively, areas outside the WGOM might represent separate stocks or sub-stocks that have been lost and not recovered, rather than areas abandoned by fish for more favorable habitat. These questions are critical because the causal mechanisms should shape our goals, expectations and management strategies, and also because such processes can represent violations of assumptions in the assessment model.

Stock boundaries

Although not evident from distribution and abundance data alone, other data call into question the assumption that our current stock boundaries do in fact capture unit stocks. This potential violation could have important implications for model outcomes and management responses.

Kovach et al. (2010) report genetic evidence for biological stocks of cod in U.S. waters that differ from the current management units (Fig. 3). The authors propose a northern spawning stock inhabiting coastal waters from Casco Bay to Massachusetts Bay, and overlapping with a southern spawning stock extending from Great Bay around Cape Cod into waters of the northern Mid-Atlantic Bight off southern New England. This southern stock includes areas of western George's Bank, and lies adjacent to a third stock covering the majority of George's Bank. Tallack (2009) studied growth of cod across the same area studied by Kovach et al. (2010) and found that parameter estimates were similar between the WGOM and Cape Cod/Southern New England regions, providing life history evidence in support of the proposed genetic stock units. Earlier, Begg et al. (1999) examined long-term growth data and found persistent evidence for a division between Eastern George's Bank and Western George's Bank.

The most recent Gulf of Maine cod stock assessment states that, "Recent reviews of historical and contemporary tagging studies (O'Brien et al. 2005; Tallack 2007; Loehrke and Cadrin 2007) suggest that while there is movement of fish between the Gulf of Maine and Georges Bank stocks, the degree of mixing is limited" (NEFSC 2011). However, estimates of movement rates reported in the 2008 Groundfish Assessment Review Meeting suggest extensive movement (Fig. 4; Miller and Tallack 2007). The review of tagging information in GARM III (Loehrke and Cadrin 2007) stated that,

> "Previous tagging literature documents similar pathways of movement between stock areas, but the frequency of residence and movement are different among studies. Most cod tagging was not designed to evaluate movement rates, and the proportional recaptures may not reflect changes in movement rates. Current stock boundaries for cod off New England are primarily based on an operational definition (e.g., demographic patterns) and practical limitations of monitoring fisheries (e.g., mixed-stock fishing trips). However, advancement of methods for exploring spatial population structure (genetics, otolith microstructure and chemistry, electronic tags, spatial analysis) as well as greater spatial resolution in fishery data suggest that investigation of stock structure should continue toward the objective of improving stock definitions for population modeling and stock assessment."

Similarly, in a review of recent tagging information, Tallack et al. (2009), recommend that,

> "Recent and historical cod tagging data (and genetic data) suggest substantial movements across current stock boundaries and considerable heterogeneity within current management units. Best available science indicates the need to re-visit, re-analyze and re-assess the stock management boundaries; this task will be best achieved by an interdisciplinary team."

If, rather than assessing and managing a GOM-wide stock we should be defining multiple stocks, including one that spans the WGOM, waters off Cape Cod and Western George's Bank, and Nantucket Shoals, then the area of higher cod density in the WGOM would no longer be a somewhat anomalous and geographically small portion within an otherwise depleted GOM stock area. Instead, this area would be a significant portion of a stock area with unknown status, but likely of lesser concern than the GOM at large.

The studies of both Kovach et al. (2010) and Tallack (2009) did not include Downeast Maine, the central Gulf of Maine, or the Scotian Shelf. Downeast Maine in particular has seen dramatic declines and almost no recovery of cod through time (Fig. 1, 2). The Downeast Initiative has recognized the fundamentally different state of cod in the region, and Ames (2010) has proposed an ecosystem recovery plan in response. An early examination of cod stock structure in U.S. waters based on rates of parasite infestation documented a sharp break at 44°N latitude, which is the approximate southern extent of the Downeast region (Sherman and Wise 1961; Fig. 5), perhaps supporting the hypothesis that the region represents a separate stock.

More recently, an analysis to identify major ecosystem planning areas also suggested that at least part of the Downeast region is ecologically distinct from rest of the Gulf of Maine and more closely aligned with the Scotian Shelf (SSC 2010; Fig. 6). However, this analysis did not identify the linkage between the WGOM and Nantucket Shoals/Southern New England suggested by the genetic and tagging data. Moreover, the Downeast/Scotian Shelf unit does not reach Casco Bay or even Penobscot Bay, areas within the coastal stretch of extremely low cod abundance (Fig. 1, 2). Therefore, the extent to which a broader ecosystem perspective provides insights into cod stock structure is unclear.

Stock sub-structure: metapopulation theory

Whether or not cod stock boundaries should be re-drawn, it is also possible that important sub-structure exists within stock units. Such sub-stocks or sub-populations would exhibit sufficient demographic independence to warrant distinct treatment in assessment models, but sufficient exchange to not warrant completely separate models. This balance between independence and exchange is the essence of metapopulation theory (Kritzer and Sale 2004).

Schlosser and Angermeier (1995), building on the work of Harrison (1991), present a useful framework of different types of metapopulations, and examine which best apply to several species of lotic fishes. Their framework can also serve as a useful guide for reconsidering spatial structure of cod stocks. Consideration of these issues represents drawing upon a richer body of ecological theory than is typical of fisheries science and management.

<u>Classical metapopulations and patchy populations</u>

Metapopulation theory envisions a network of smaller sub-populations linked through dispersal. Originally, the theory described sub-populations that were more or less equivalent in demographic traits, resulting in common extinction and recolonization probabilities across the system. An equilibrium proportion of habitat patches would be occupied by populations as a dynamic balance between extinction and recolonization. For marine species that generally produce more offspring and have greater dispersal potential than their terrestrial counterparts, the proportion will often be comparatively high in the absence of heavy exploitation (Kritzer and Sale 2004).

Ames (2004) has thoroughly examined spatial structure of cod populations along the coast of Maine (Fig. 7A). He describes a series of sub-populations, each composed of several finer scale spawning components that each utilize one or more still finer scale spawning grounds. Howell et al. (2008) and similar tagging studies in Massachusetts Bay also suggest fine-scale structure further west within the Gulf of Maine involving fidelity to spawning sites. Sherwood and Grabowski (2010) found local forms of cod within the Gulf of Maine as well. A synthesis of information on larval dispersal, life history, genetics and tagging provides evidence for the presence of fine-scale, sub-stock structure in the Gulf of Maine (Runge et al. 2010).

Within the frameworks of Harrison (1991) and Schlosser and Angermeier (1995), sub-populations comprised of local spawning groups constitute patchy populations with rates of exchange among internal spawning components that are higher than exchange rates outside of the sub-population. These (patchy) sub-populations might then collectively form a larger interdependent metapopulation. . At both the scale of spawning groups within sub-population and the scale of the overall metapopulation, redundancy and exchange among finer scale sub-units is critical for the integrity of the larger system.

Smedbol and Wroblewski (2002) illustrate this interdependency. They describe spatial structure of cod along the coasts of Newfoundland and Labrador in Canada similar to that reported by Ames (2004) along the Maine coast (Fig. 7B), and model the behavior of the system to better understand spatial responses to fishing pressure (Fig. 7C). The model shows high patch occupancy under a wide range of parameters in the absence of exploitation, but much lower occupancy (i.e., localized extinction) in the face of overfishing. Svedang et al. (2010) present similar insights attained by accounting for spatial structure of North Sea cod.

If cod off some or all of the coast of Maine represent a distinct stock, the system might be trapped in a state of low patch occupancy following high exploitation. The decline of cod in this region has led to drastically reduced fishing effort, which should re-balance the extinction-recolonization dynamics and result in recovery of more sub-populations. However, Smedbol and Wroblewski's (2002) model suggests that this can take many years if the colonization parameter is naturally low and the system is starting from a sufficiently low level of occupancy (Fig. 7C), which could explain the continued low abundance. If the GOM does represent a unit stock, recolonization along the coast of Maine would presumably originate in the WGOM, but recolonization potential of cod in the GOM generally is unclear, as discussed below.

Mainland-island, source-sink and basin theories

The preceding section described research on cod populations in coastal areas of the Gulf of Maine, where spatial structure has been described on the relatively fine scales. In the eastern part of this coastal region, depletion has been most severe (Fig. 1, 2). Determining the potential to recover cod further east in the Gulf of Maine, and subsequently developing and executing a strategy to do so, should be a priority. However, the most pressing concern is the potential for drastic quota reductions to adversely affect the large number of fishermen working in the WGOM, where fish are relatively abundant locally.

The stark contrast between the abundance of cod in the WGOM and elsewhere in the stock area during periods of both high and low overall abundance (Fig. 1, 2) suggests that, if the GOM truly does represent a single unit stock, it has clear internal structure at higher scale than local spawning groups, which might be relevant to understanding its productivity, dynamics and, ultimately, status. Specifically, unlike a classical metapopulation or patchy population, both of which assume sub-units that are more or less demographically equal, the WGOM might represent a stronger and more stable sub-stock or sub-population within a GOM-wide metapopulation.

Such spatial inequities within a system are described by the related concepts of mainland-island and source-sink metapopulations. The common features of these concepts are one or a few large, productive and essentially extinction-prone sub-populations (the mainland or source) that subsidize or recolonize one or more sub-optimal sub-populations (islands or sinks) through migration and dispersal processes. Boorman and Levitt (1973) first developed the mainland-island concept to explain the dynamics of gene frequencies in peripheral island populations in response to selection or drift in the "fixed" mainland population, but without delving into the mechanism behind its fixedness. Pulliam (1988) developed the demographic theory for such a spatial structure, defining a source population as one with a net reproductive surplus (i.e., finite rate of population growth, $\lambda>1$) and a sink as one with a net deficit ($\lambda<1$). Often, the mainland-island and source-sink concepts are considered synonymous (e.g., Schlosser and Angermeier 1995).

One important property of source-sink dynamics is that a greater proportion of the overall metapopulation is located within the source as its reproductive surplus decreases and/or the reproductive deficit of the sink increases (Fig. 8). Either change or both is consistent with increasing fishing pressure, and might explain the greater proportion of cod in the WGOM during periods of low to intermediate overall abundance (Fig. 1, 2).

MacCall (1990) developed a “basin” model of spatial dynamics that has properties similar to the source-sink and mainland-island concepts. In MacCall’s model, a population is always concentrated in habitat patches that yield the greatest reproductive success, measured in terms of population growth rate. Population growth declines with increasing density, eventually causing abundance to increase in habitats that are inherently inferior but can yield comparable reproductive success due to lower density. The distribution of population growth potential across the landscape traces one or more conceptual basins that fill from deepest to shallowest as abundance increases (Fig. 9). The deepest basin represents the best habitat, is analogous to a source or mainland population, and should always contain some fish that can serve to replenish other areas, unless the entire population goes extinct.

If cod in the GOM represent a unit stock, it seems to exhibit source-sink or basin structure with the WGOM being the source or deepest basin. Moreover, the temporal changes in the relative distribution of fish across the stock area as overall abundance rises and falls are consistent with predictions of each theory (Fig. 8, 9). An important question, then, is what spatial response would be expected to lowering quotas to further increase abundance?

MacCall’s theory addresses this question in terms of the property “viscosity”. Like liquids, a viscous population is one with greater spatial inertia and lower responsiveness to changes in density. Viscosity is determined by both random or undirected dispersal, and directional migration. In cod (and most marine organisms), the former will occur primarily at the planktonic larval stage, while the latter will primarily occur post-settlement.

Although larval dispersal generally has the potential to lower viscosity, wind and current patterns in the GOM generally work against transport out of the WGOM, and instead result in local advection (Churchill et al. 2011). On the other hand, adult cod exhibit a diversity of migratory behaviors, but movement patterns across the Northwest Atlantic generally show greater fluidity and lower viscosity than cod in the Northeast Atlantic (Robichaud and Rose 2004). However, less sedentary fish might be inherently more vulnerable to exploitation, and closed areas might have increased selection for more sedentary fish (Sherwood and Grabowski 2010), resulting in increased viscosity of cod in the GOM. That would result in slower expansion from the WGOM source/basin to outlying areas as abundance increases.

<u>Hybrid metapopulations</u>

Schlosser and Angermeier (1995) expand upon Harrison’s (1991) framework by adding a “hybrid” metapopulation, which is one that exhibits features of both classical metapopulations and source-sink/mainland-island structures. In other words, hybrid metapopulations contain small patch structure within larger sub-populations/sub-stocks that might be sources or sinks. In addition to the work of Ames (2004) describing fine-scale population structure of cod along the coast of Maine, finer scale structure has also been documented within the WGOM (e.g., Lindholm et al. 2007). Therefore, unless genetic or other distinctions between the WGOM and other parts of the GOM suggest truly independent stocks, the region most likely represents a hybrid metapopulation.

Implications of revising spatial foundation

This paper has considered pronounced spatial patterns in the distribution of Atlantic cod in the Gulf of Maine as a source of potentially significant inaccuracies in our stock assessments, and drawn upon other data and theory to examine possible alternative realities than those upon which current assessments are based. Resolving these issues is critical because, on the one hand, drastic management action in response to an overly inaccurate assessment would cause severe and undue socio-economic harm. But, on the other hand, downplaying assessment outcomes in response to these concerns if the assessment is reasonably accurate could lead to severe ecological impacts, delayed rebuilding or stock collapse, and eventually severe socio-economic harm.

There are two fundamental questions related to spatial structure of cod stocks: whether or not current stock boundaries are appropriate, and whether or not greater spatial resolution is needed within stock units. Following a thorough review and synthetic analysis aimed at resolving these uncertainties, the answer to either or both of these questions could be yes or no, resulting in four general outcomes that might result:

1. No change to current stock units and within-stock spatial resolution.
2. Revised stock boundaries without inclusion of internal structure.
3. No change to stock boundaries, but inclusion of internal structure.
4. Revised stock boundaries and inclusion of internal structure.

These outcomes are depicted, and some of the implications of each are summarized, in Figure 10. Generally, if the answer to either question or both is yes, the accuracy of our assessments should improve, but potentially at the cost of new uncertainties. One type of uncertainty common to outcomes 2, 3 and 4 is the assignment of historical catches monitored under current stock areas to new stock areas and/or sub-stocks. If defining more than two stock areas and/or the inclusion of internal structure is warranted, another source of uncertainty would be the lower sample sizes resulting from partitioning of survey and other data to more spatial units. Also, if internal structure is warranted, whether or not new stock areas need to be defined, model complexity might increase considerably (e.g., estimation of catchability coefficients for multiple sub-stocks, as well as new dispersal/migration parameters).

Defining sub-stock units would not necessarily require new allocation of quotas at that finer level, but not doing so could necessitate management measures (e.g., uncertainty buffers or other mechanisms) that are robust to the uncertainty in location of catch. In other words, the implications of a given level of catch from a spatially structured stock will vary depending upon how it is distributed among sub-stocks, especially when those sub-stocks exhibit source-sink or basin dynamics. Optimal harvest strategies for spatially structured populations are generally defined not only by how much is caught, but also where it comes from.

Finally, regardless of whether any changes are made to the spatial foundation for assessment and management of cod, scientific and management discussions about spatial issues are needed. We should define in detail our understanding and assumptions about how cod populations are structured and how their dynamics unfold in space. And, we should define explicit expectations and goals for how the population will respond to management across stock areas. Does rebuilding mean continued accumulation of fish in the WGOM region? Or are we expecting fish to redistribute more widely across the GOM? Or are we expecting some combination of those outcomes? And how quickly do we expect change to become evident in different areas?

Each of these scenarios has very different implications. For example, continued accumulation in the WGOM but not elsewhere (i.e., if viscosity is high) will likely cause increasing tensions as fishermen concentrated in the WGOM see even greater numbers of fish, but face continued restrictions. Doubling biomass in the WGOM would double encounter rates of fishermen, but would also still result in an overfished stock by the current assessment model (i.e., approx. 40% B_{MSY}). On the other hand, if distribution of cod more widely across the GOM is expected, achieving that goal could have important ecological and conservation benefits, but could come at a socio-economic cost. Furthermore, growing biomass outside the WGOM might not significantly increase sustainability of the overall stock if the areas being replenished are sinks, and therefore contribute little production. Ultimately, the GOM cod crisis presents serious challenges, but also a unique opportunity to re-think the scientific ideas and data we bring to bear on management challenges, and how we define our management goals and understand trade-offs.

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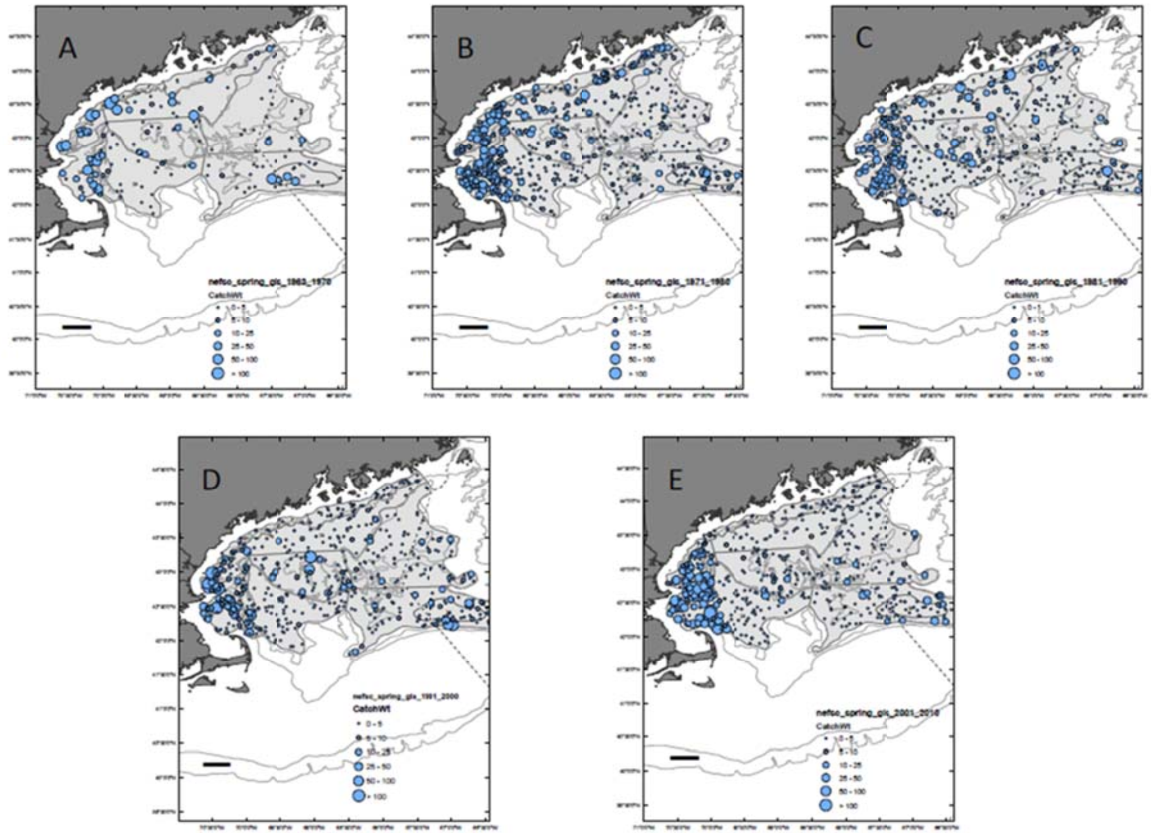

Figure 1. Spatial and temporal patterns in the distribution and abundance of Atlantic cod in the Gulf of Maine estimated by the NEFSC spring bottom trawl survey. Data are mapped for the 1960s (A), 1970s (B), 1980s (C), 1990s (D), and 2000s (E). Abundance peaked in the 1970s, declined through the 1980s and especially 1990s, and has begun to recover through the 2000s. However, abundance in all time periods and the rate of recent recovery have not been consistent across the stock area, with greater abundance and stronger recovery evident in the Western Gulf of Maine, west of approximately 70°W longitude. (from NEFSC 2011)

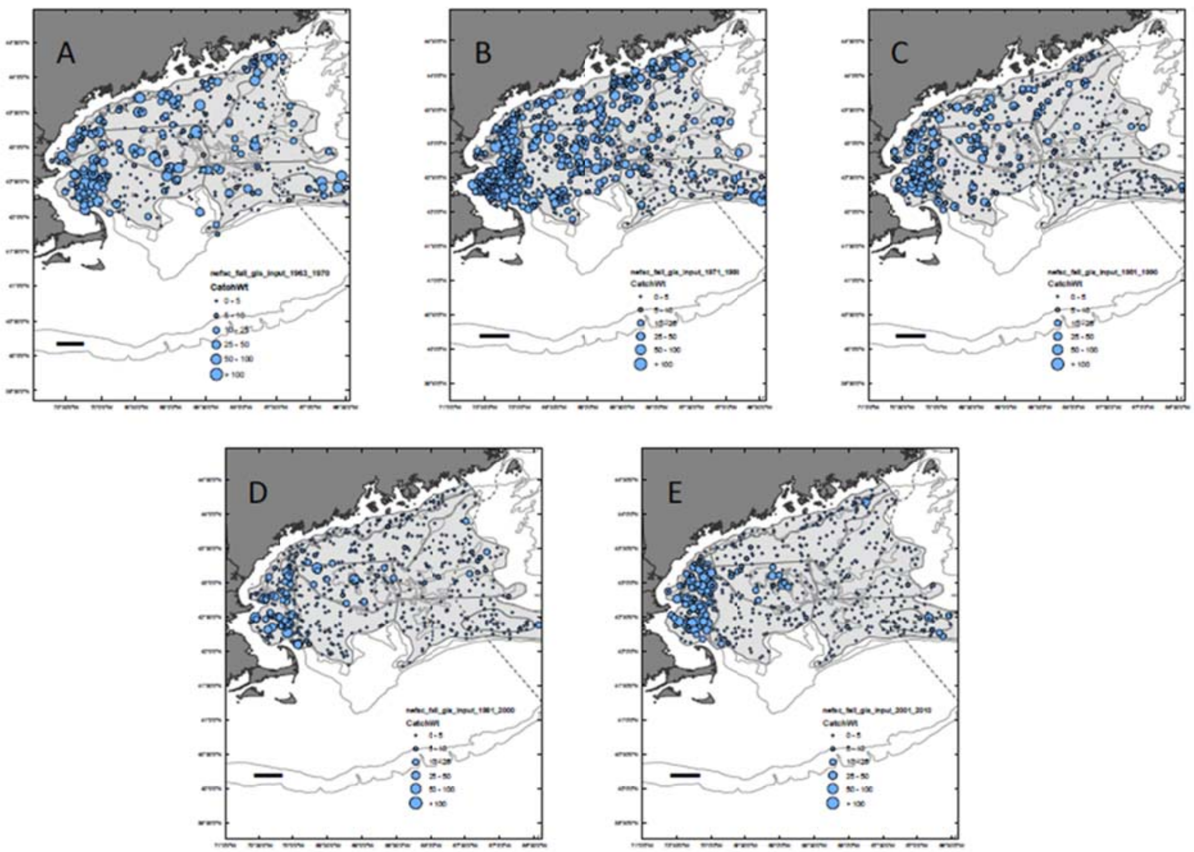

Figure 2. Spatial and temporal patterns in the distribution and abundance of Atlantic cod in the Gulf of Maine estimated by the NEFSC spring bottom trawl survey. Data are mapped for the 1960s (A), 1970s (B), 1980s (C), 1990s (D), and 2000s (E). Spatial and temporal patterns of distribution, abundance, depletion and recovery are similar to those observed in the spring trawl survey described in Figure 1. (from NEFSC 2011)

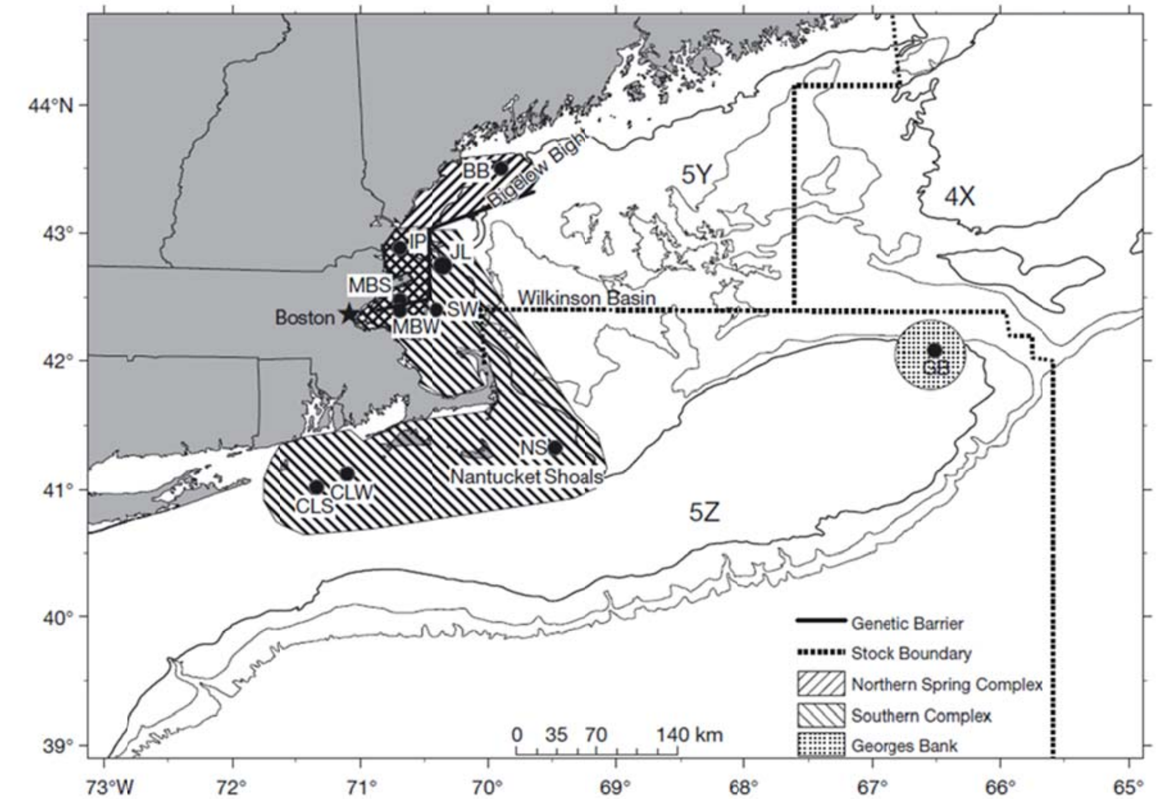

Figure 3. Current boundaries of Atlantic cod stocks in U.S. waters, and proposed biological stock units based on population genetic structure. Sampling locations for the genetic analysis are marked and labeled. (from Kovach et al. 2010)

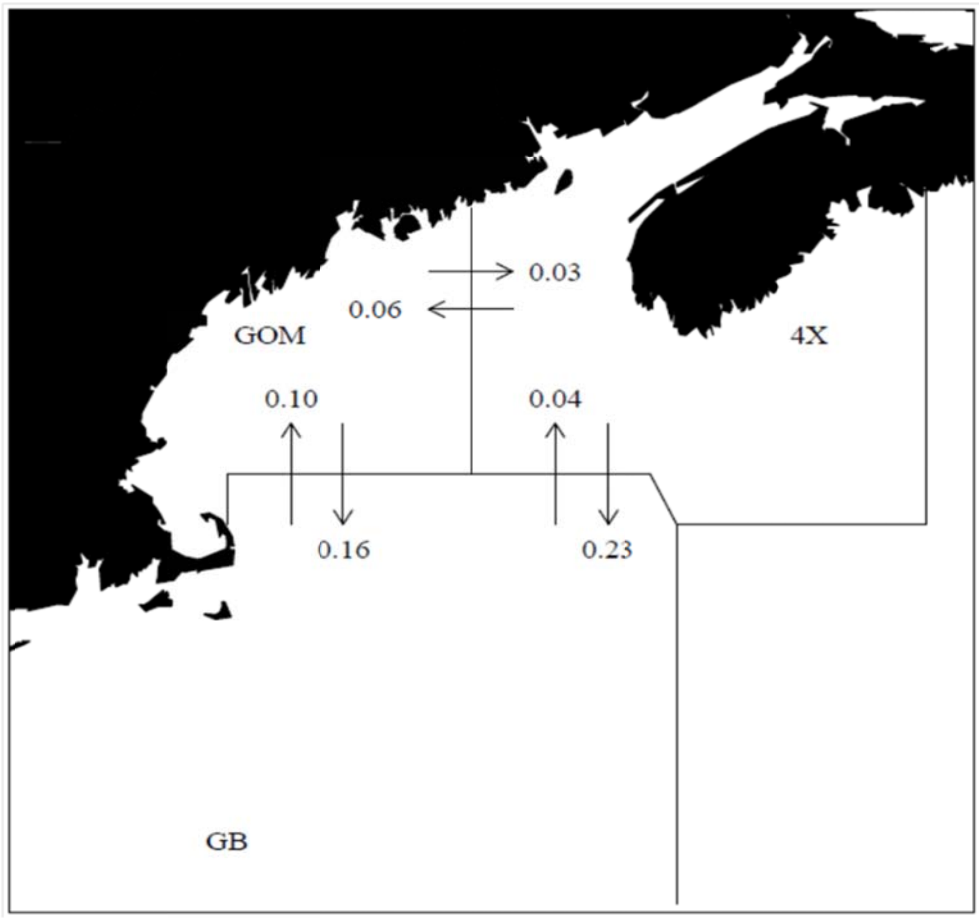

Figure 4. Regional estimates of instantaneous migration rates of Atlantic cod among management units. (from Miller and Tallack 2007)

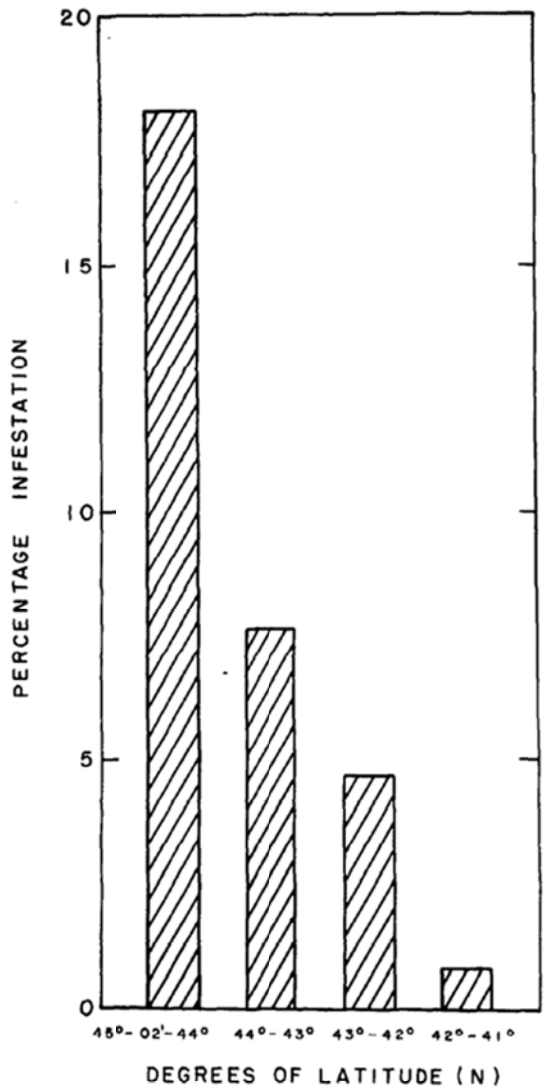

Figure 5. Rate of infestation of the cod parasite *Lernaeocera branchialis* in waters off New England, suggesting a sharp break at 44°N latitude, the approximate location of Penobscot Bay and the beginning of the Downeast Maine region. (from Sherman and Wise 1961)

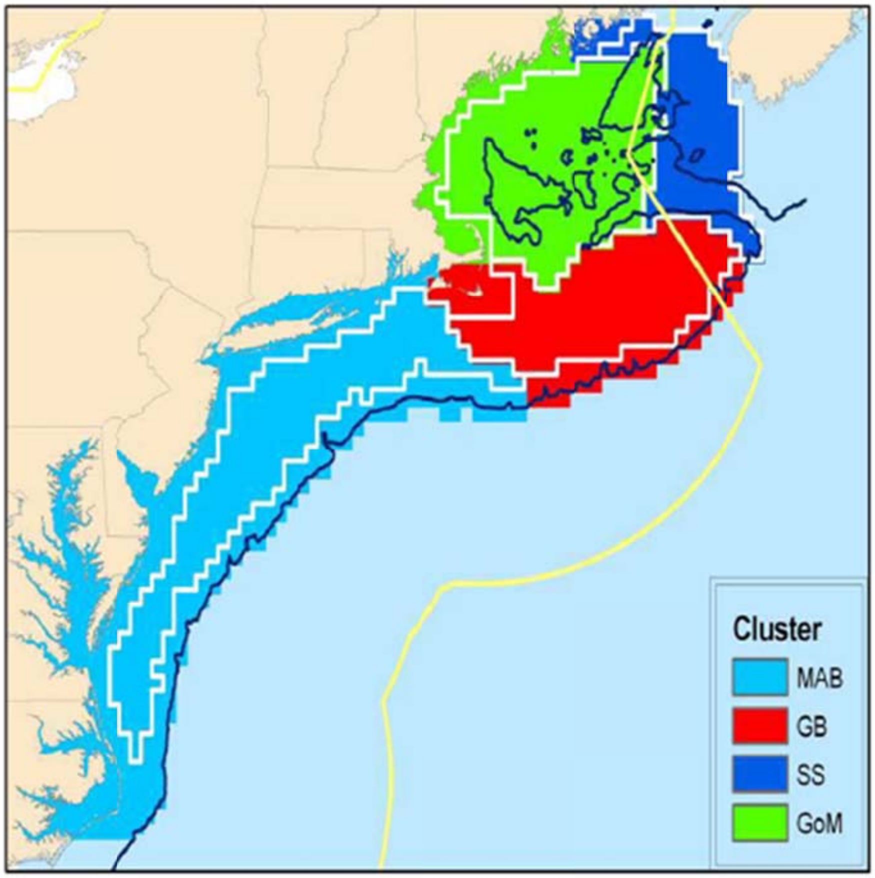

Figure 6. Proposed marine ecosystem planning units along the Northeastern United States based on a multivariate analysis of diverse biological and physical data. Three major areas differentiate (Mid-Atlantic Bight, George's Bank, Gulf of Maine), along with a smaller area in Downeast Maine more closely linked to the Scotian Shelf. (from SSC 2010)

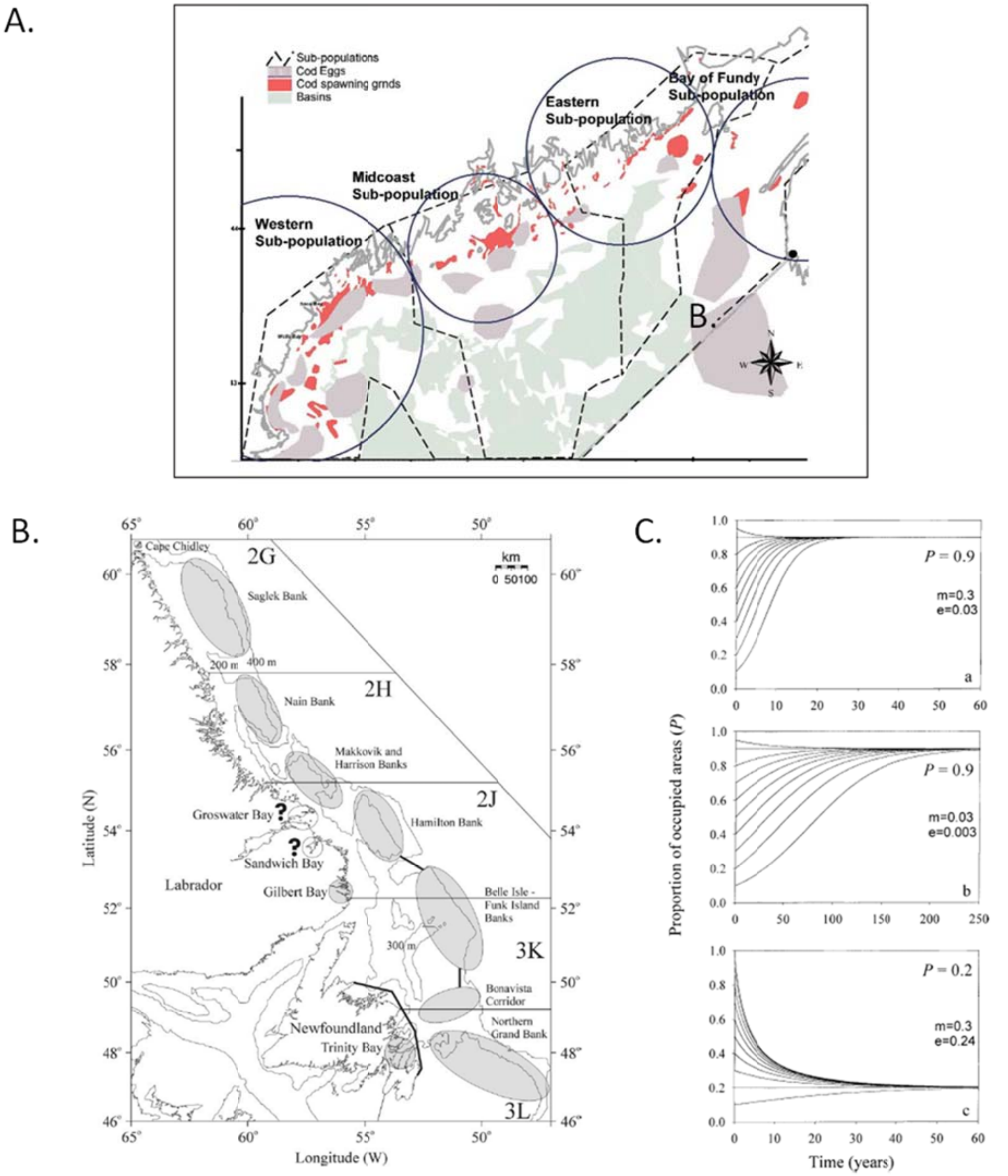

Figure 7. Metapopulation structure and dynamics of Atlantic cod.

A. Fine-scale population structure of Atlantic cod along the coast of Maine as revealed by historical records and local ecological knowledge.

B. Comparable structure of cod populations along the coasts of Newfoundland and Labrador.

C. Estimated equilibrium proportion of occupied patches under different values of the extinction, *e*, and colonization, *m*, parameters. Changing the scale of these parameters affects the rate at which equilibrium is attained, but not the final value (top and middle panels). In contrast, drastically increasing extinction risk by overfishing substantially lowers the equilibrium occupancy.

(A from Ames 2004; B and C from Smedbol and Wroblewski 2002)

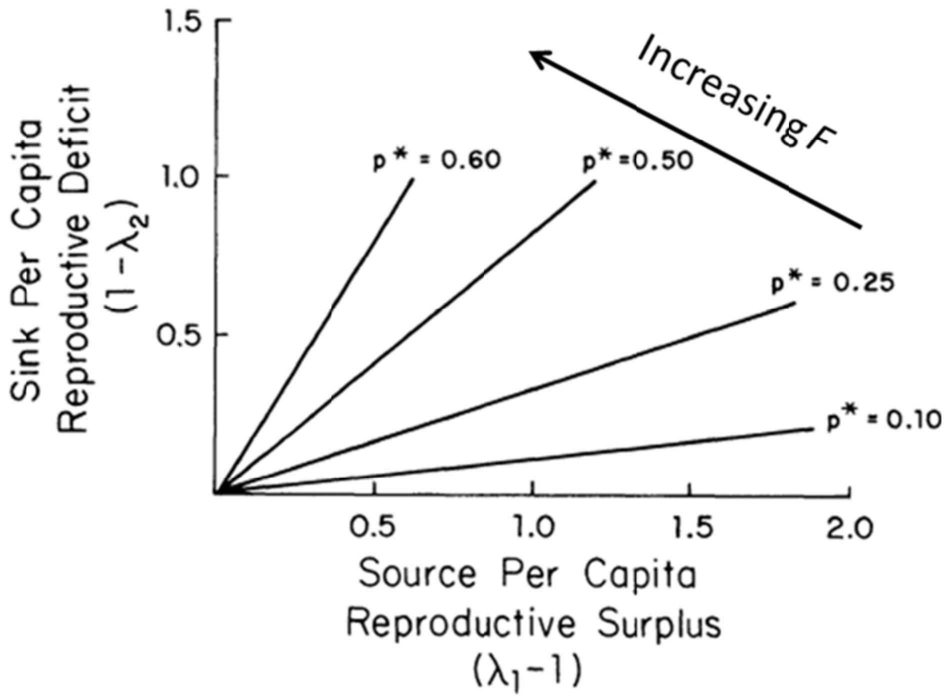

Figure 8. Proportion of a generalized metapopulation within the source population as a function of the reproductive surplus in the source and the reproductive deficit in the sink. Higher fishing pressure would reduce the source surplus and increase the sink deficit, thereby resulting in greater concentration of the population in the source. (modified from Pulliam 1988)

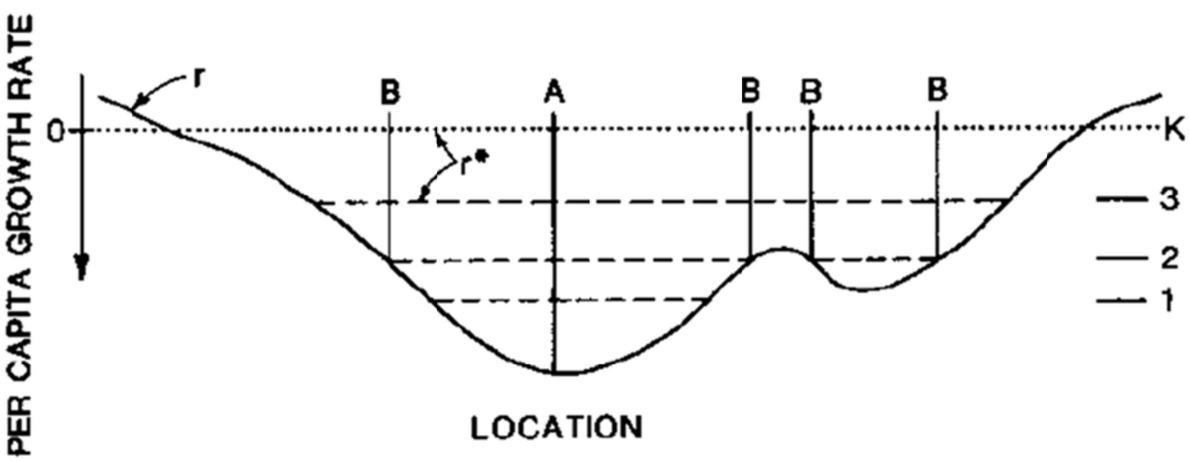

Figure 9. The Basin Model describing geographic distribution of marine fish populations. The curved line tracks per capita population growth rate (increasing in value moving downward) across a heterogeneous landscape. "A" represent the optimal habitat in this landscape with the highest population growth rate, in which the population is always concentrated. As abundance increases from level 1 to levels 2, 3 and eventually the carry capacity, K, additional habitats are occupied due to density dependent limitations on the local abundance in preferred habitats. (from MacCall 1990)

Inclusion of internal structure?	Revised stock boundaries? No	Revised stock boundaries? Yes
No	1 • Changes to status quo quotas (i.e., those determined by current ABC control rule) only possible through other changes to modeling approach (model choice, data inputs, etc.) or policy changes.	2 • Survey and other fishery-independent data are simply divided among assessment models differently. • Uncertainty could increase if sample sizes decrease significantly within any new stock area, esp. if more than two new stocks result. • Potentially significant difficulties partitioning historical catch among new stock units. • Benefits of assessment history for current stock units is lost. • Some potential new stocks (e.g., Downeast Maine) would potentially be not only overfished, but collapsed and economically and ecologically extinct.
Yes	3 • Need to specify assumed mechanisms underlying stock dynamics and define spatially-explicit expectations. • Important challenges with model selection/development, finer scale data inputs, partitioning historical catches, and new parameters (esp. exchange rates). • Uncertainty reduced by improved accuracy, but potentially increased by sample size and model complexity issues. • Some potential new sub-stocks (e.g., Downeast Maine) would potentially be not only overfished, but collapsed and economically and ecologically extinct. • Greater need for science and management beyond quota-setting (e.g., targeted spawning closures, habitat protection, rebuilding forage fish stocks) to address localized depletion.	4 • Combined implications of both outcomes 2 and 3.

Figure 10. Potential outcomes of a re-evaluation of spatial structure of Atlantic cod in U.S. waters, and scientific implications of each outcome. Each quadrant's number refers to numbered outcomes discussed in the text.