

A FISHERIES PLAY IN AN ECOSYSTEM THEATER: CHALLENGES OF MANAGING ECOLOGICAL AND SOCIAL DRIVERS OF MARINE FISHERIES AT MULTIPLE SPATIAL SCALES

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ABSTRACT

Despite wide geographic distribution, many species function demographically as metapopulations composed of relatively small local stocks. Recent research on those and other species found larval retention is greater, dispersal distances shorter, and demographic connectivity therefore more localized than previously thought. We illustrate these patterns for two western North Atlantic fisheries species, Atlantic cod and American lobsters. Self-organizing spatial patterns also arise in the human social part of the system, but because of biological spatial complexity, geographic boundaries of social organization are unlikely to mirror those of ecological organization. Consequently, no set of management boundaries can perfectly delineate the distribution of organisms within an ecosystem or the social structure that has grown up around them. Reliance on any single scale of management creates perverse incentives—at large scales it encourages roving bandits, at small scales stationary banditry. Nevertheless, at smaller scales, social connectivity is high and feedback about ecological effects of human activity is less ambiguous, permitting rapid, but locally biased, learning. We argue that only strong governance functioning at multiple nested scales can negotiate the spatial restraints on fishing necessary to suppress these perverse incentives. We use an analogy with international trade to illustrate the incentive problems that arise when valuable resources cross ecologically arbitrary political boundaries. We conclude that the need for multiscale governance results from the spatial/temporal heterogeneity of biological systems. Implementing multiscale governance will be difficult so long as fishermen's rights and privileges are large-scale and species specific rather than smaller-scale and responsive to local ecosystem function.

G. Evelyn Hutchinson's 1965 book entitled *The Ecological Theater and the Evolutionary Play* explored how the evolution of organisms is nested within, and may be steered by, their ecological environment. In the same vein, we considered the ways fisheries management must nest within the social-ecological context of marine ecosystems. Our overarching goal was to provide insight into the complex spatial structure and dynamics of populations and ecosystems, which informs us of the kinds of management institutions and spatial boundaries most likely to facilitate human adaptation to those systems.

Virtually all species distributions are heterogeneous over their geographic ranges. The reasons differ at different scales, from very large (ocean basins) to very local (microhabitats). Isolation can result from the spatial distribution of species' suitable habitats or the presence of isolating barriers such as land masses, ocean currents, or simple distance and can create "local stocks" that maintain subpopulations demographically distinct from other subpopulations over the species' entire range. Subpopulations, if isolated long enough, may evolve into genetically distinct races, but even without such differentiation, subpopulations often function as relatively independent demographic units linked by "connectivity" to form "metapopulations."

Here, we review advances and prevailing concepts in the biology and ecology of metapopulations and connectivity and draw parallels with human systems, international trade in particular, in which multiscale governance has evolved in ways that encourage the flow of economically valuable goods and services across sometimes arbitrary administrative boundaries. We discuss the need to build strong multiscale governance that will generate the feedback and individual incentives consistent with sustainable ocean ecosystems. We illustrate these concepts with examples from the Gulf of Maine.

METAPOPULATIONS AND CONNECTIVITY: CAUSES AND IMPLICATIONS OF SMALL DISPERSAL KERNELS

Biological connectivity creates the genetic or demographic nexuses among and within metapopulations (Sale et al., 2005), especially for populations of marine animals that are not highly migratory, have larval dispersal stages, and recruit to habitats where they live relatively sedentary lives. Patterns of heterogeneity can result from at least three different connectivity relationships based on the spatial relationships between reproducing individuals and recruiting substocks (Fig. 1; Kritzer and Sale, 2004). This spectrum is defined by the proportion of young arriving to a local population or substock from local reproduction. Closed substocks (*sensu* Warner and Cowen, 2002) are those that result from local reproduction and persist by means of “self-recruitment” (Fig. 1A), wherein substantial larval dispersal occurs at relatively short distances (e.g., right side of Fig. 1A). Metapopulations are networks of substocks resulting from self-recruitment, together with occasional larvae arriving from adjacent subpopulations (Fig. 1B). Open populations are those that result from patchy recruitment of individuals from a common larval pool (Fig. 1C; Warner and Cowen, 2002). They result from regular long-distance connectivity between reproductive source populations and recruiting populations (right side of Fig. 1C).

As recently as the mid-1990s many (e.g., Caley et al., 1996; Warner and Cowen, 2002), perhaps most, researchers believed that recruitment and local dynamics were driven by open marine populations. In this view, marine populations would be maintained by long-distance dispersal via large-scale ocean currents, which transport larvae long distances depending upon the duration of their development (see, e.g., Roberts, 1997). Research over the past decade with larval tagging, genetic paternity analyses, and large-scale, high-resolution biophysical circulation models indicates, however, that larval retention and short-distance larval dispersal (i.e., more closed recruitment cells; Fig. 1A) are more common and more important demographically than previously thought (see, e.g., Warner and Cowen, 2002; Cowen et al., 2007; Steneck et al., 2009).

We understand larval dispersal (the physical and biological factors affecting larvae leaving a reproductive source) better than larval connectivity (the linkage between a reproductive source and the site of recruitment; Levin, 2006). Although most research focuses on larval dispersal and connectivity between natal and nonnatal areas (Jones et al., 2009), what matters most for management is demographic connectivity (*sensu* Kritzer and Sale, 2004; Fig. 2). Demographic connectivity is necessary to sustain or increase populations. It requires several sequential steps to create the necessary unbroken chain of events that links reproductive and recruiting populations (Fig. 2; Steneck et al., 2009).

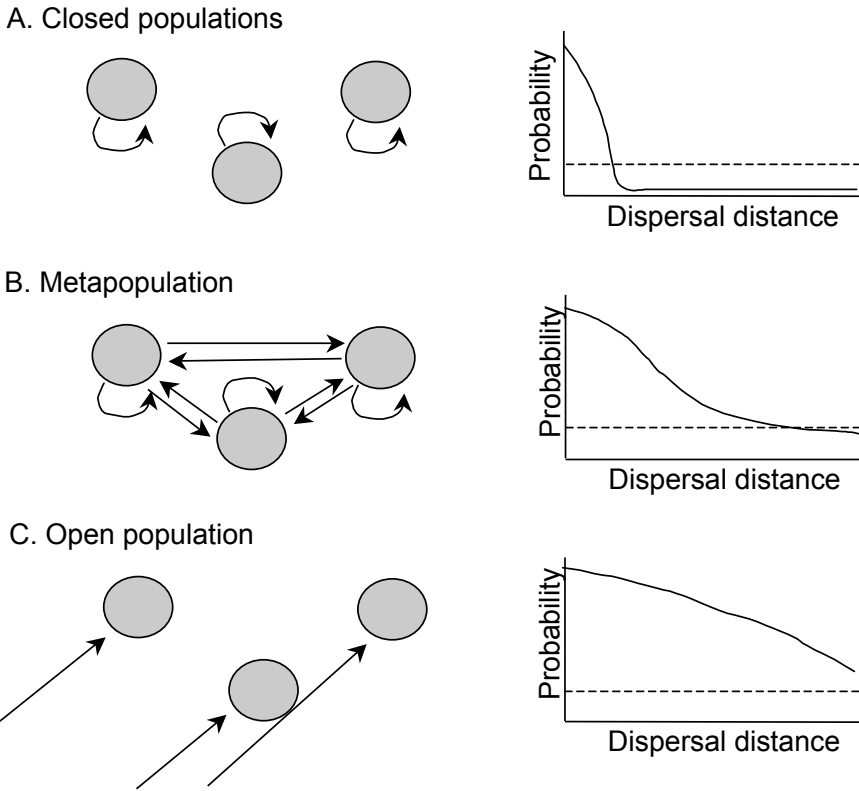


Figure 1. Heterogeneous population structure (left) and larval dispersal distances (right) resulting from (A) closed (i.e., isolated, self-recruiting) populations, (B) metapopulations (self-recruiting and larval exchange among subpopulations), and (C) open populations (single stock seeded from distant sources with patchy recruitment habitats; modified from Kritzer and Sale, 2004).

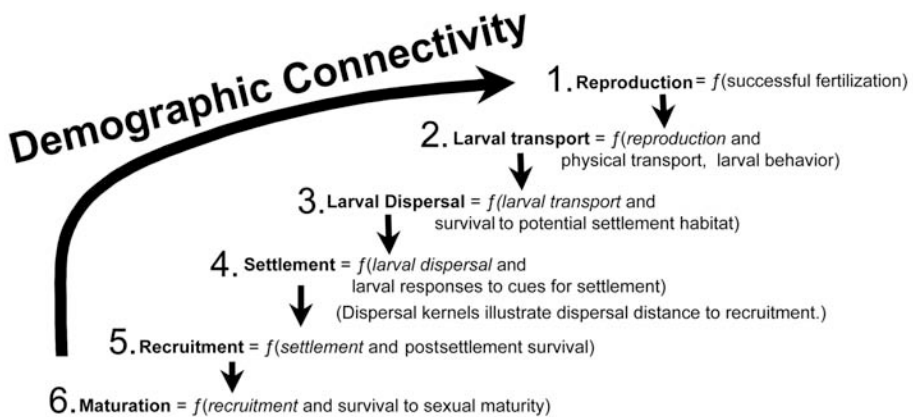


Figure 2. Six sequential steps leading to “demographic connectivity.” Each step (boldface) is a function of several other processes (in parentheses). Explicit linkage among steps is illustrated with arrows (modified from Steneck et al., 2009).

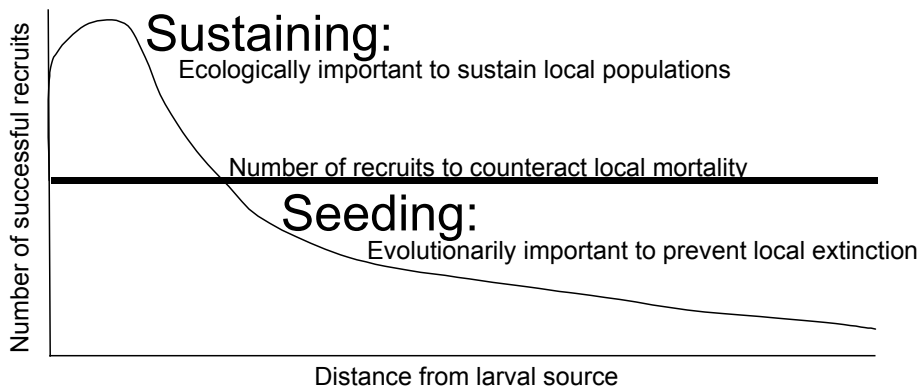


Figure 3. Sustaining and seeding portions of dispersal kernels determine potential nearby demographic connectivity and distant genetic connectivity. The horizontal line identifies the rate of recruitment necessary to counteract local rates of mortality (after Steneck, 2006).

The distance between a reproductive source and sufficient recruits to sustain or increase the population (steps 1–5 in Fig. 2) is usually illustrated as a probability-density function or a curve called the dispersal kernel (Fig. 3). The shapes of dispersal kernels vary (e.g., right side of Fig. 1), but for all, the distance from a reproductive source at which recruitment matches or exceeds the rate of local mortality defines the sustaining or ecologically important portion of the dispersal kernel (above the horizontal dashed lines in Figs. 1, 3). Beyond the sustaining distance, larval dispersal tends to reseed locally extirpated parts of the metapopulation and plays an evolutionarily important role, promoting gene flow. Although most managers are interested in the sustaining portion of dispersal kernels, most studies have used molecular genetics (i.e., gene flow) to report on the spatial range of seeding portions of kernels (reviewed by Jones et al., 2009).

We now have several reasons to realize that the sustaining portion of dispersal kernels is smaller and more local than previously suspected. Early studies assumed that larvae passively diffused by advection as they developed into competent late-stage larvae or postlarvae able to recruit to juvenile or adult habitats (Cowen et al., 2007). Most empirical studies show, however, that passive diffusion rarely describes patterns of dispersal, because larvae can actively swim and/or control their buoyancy; in addition, larval mortality reduces the realized range of dispersal significantly from that predicted from passive diffusion and larval duration (Cowen et al., 2000, 2006). These factors, combined with small-scale turbulence (i.e., eddies), effectively shrink dispersal ranges by half or more (Steneck et al., 2009). Many recruitment cells are therefore naturally more closed than open (Cowen et al., 2000, 2006; Warner and Cowen, 2002; Cowen and Sponaugle, 2009).

Elevated rates of mortality (from fishing, for example) that reduce broodstock abundance or declines in the receptivity of recruitment habitats (also caused by fishing, for example) will further shrink the range of the sustaining portions of dispersal kernels (Fig. 4; Steneck, 2006; Steneck et al., 2009). Connectivity will probably decline even further with loss of habitats or substocks, as dispersal stepping-stones disappear, and produce dysfunctional metapopulation networks (Figs. 5, 6; Hughes et al., 2005; Steneck, 2006).

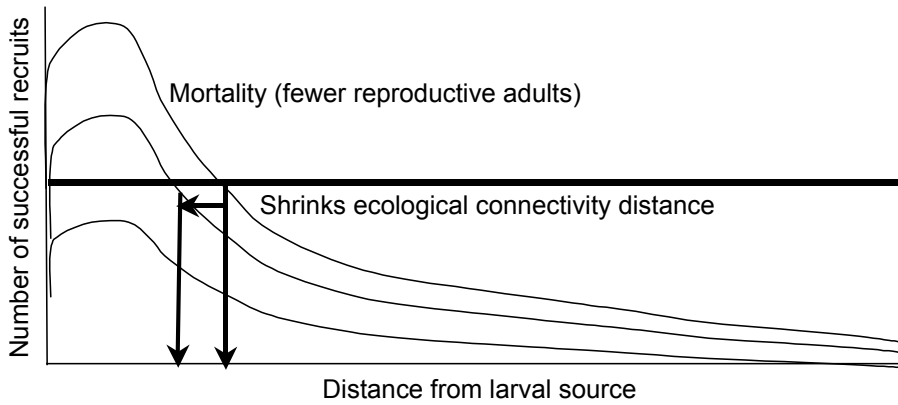


Figure 4. How elevated rates of mortality can reduce the number of reproductive adults and thus shrink the range of demographically relevant recruitment (after Steneck, 2006).

Several recent field studies support the hypothesis of short larval dispersal and significant self-seeding (right side of Fig. 1A) of a closed population. Coral-reef fish studies using isotope-tagged larval fish found that about 60% of two fish species self-recruited to the same reef despite having larval durations ranging from less than 2 wks to greater than 1 mo (Almany et al., 2007). Importantly, 40% of the fish recruited to adjacent reefs 10s of kilometers away, clearly demonstrating small-scale metapopulation structure with very strong nodes of self-recruitment (Jones et al., 2009).

The emerging picture is that, although larval duration, passive dispersion, and large-scale oceanographic mass flow may suggest a maximum dispersal potential for a cohort of larvae, the realized dispersal and especially recruitment at demographically relevant rates take place much closer to reproductive sources than previously imagined. Therefore, genetically connected metapopulation networks may be composed of demographically closed, self-recruiting cells. Of course, the mobility of adults ranges considerably from organisms that are sessile to those that are highly migratory. For ecosystem-based management, patterns of multiple species distributions and their mobility must be considered together.

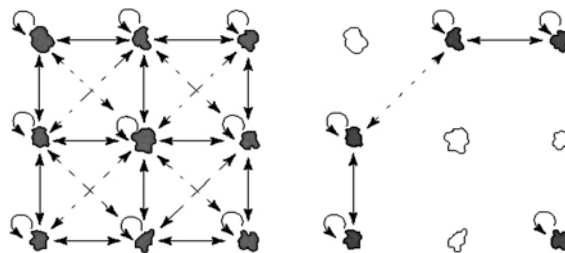


Figure 5. Functional (left) and dysfunctional (right) metapopulation networks. Solid and dashed arrows represent either demographic or genetic connectivity (strong and limited or sporadic, respectively). Disappearance of stepping-stones reduces the ability of larvae to disperse to adjacent reefs (modified from Steneck, 2006).

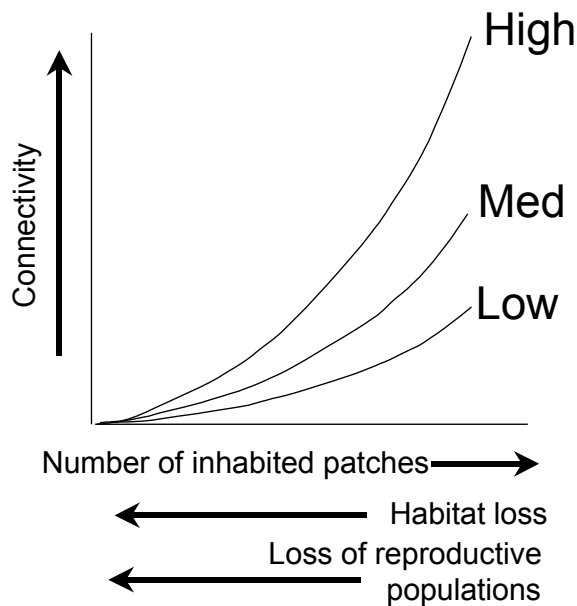


Figure 6. The regulation of connectivity based on the number of inhabited patches, habitat loss, and loss of reproductive populations (e.g., Fig. 4) (modified from Hughes et al., 2005).

SPATIAL STRUCTURE OF ECOSYSTEMS: EXAMPLES FROM THE GULF OF MAINE

An ecosystem is a natural community and its environment; together they are treated “as a functional system of complementary relationships, and transfer and circulation of energy and matter” (Whittaker, 1972: 1). Assembly rules governing membership in any given natural community and the factors governing the transfer of energy are nested over multiple spatial scales but are strongest locally. In the marine realm, thermogeography corresponds with, and probably drives, much of marine biogeography (Adey and Steneck, 2001). Ocean currents drive thermogeographic patterns as well as the distribution of nutrients, which drives plankton communities trophically important for planktivorous larvae of fisheries species (Townsend, 1992). Those factors, along with depth and substrate, account for most of the variance in the distribution of most marine organisms, and as a result, numerous species have similar distribution patterns (Methratta and Link, 2006).

In the Gulf of Maine, the drivers of species distributions also drive ecosystem structure. For example, water depths define distributions of many marine organisms, including groundfishes (fishes that live on or near the seafloor), which, historically in the western North Atlantic, have included Atlantic cod (*Gadus morhua* Linnaeus, 1758), haddock (*Melanogrammus aeglefinus* Linnaeus, 1758), winter flounder (*Pleuronectes americanus* Walbaum, 1792), Atlantic pollock (*Pollachius virens* Linnaeus, 1758), white hake [*Urophycis tenuis* (Mitchill, 1814)], silver hake (*Merluccius bilinearis*, Mitchill, 1814), American plaice (*Hippoglossoides platessoides*, Fabricius, 1780), monkfish (*Lophius* spp.), and others. Patterns of distribution and abundance of all of these and other groundfishes are heterogeneous (Collette and Klein-MacPhee, 2002), but groups of groundfishes show coherent mesoscale patterns. For example, Atlantic cod, haddock, and winter flounder are most abundant in shallow portions of

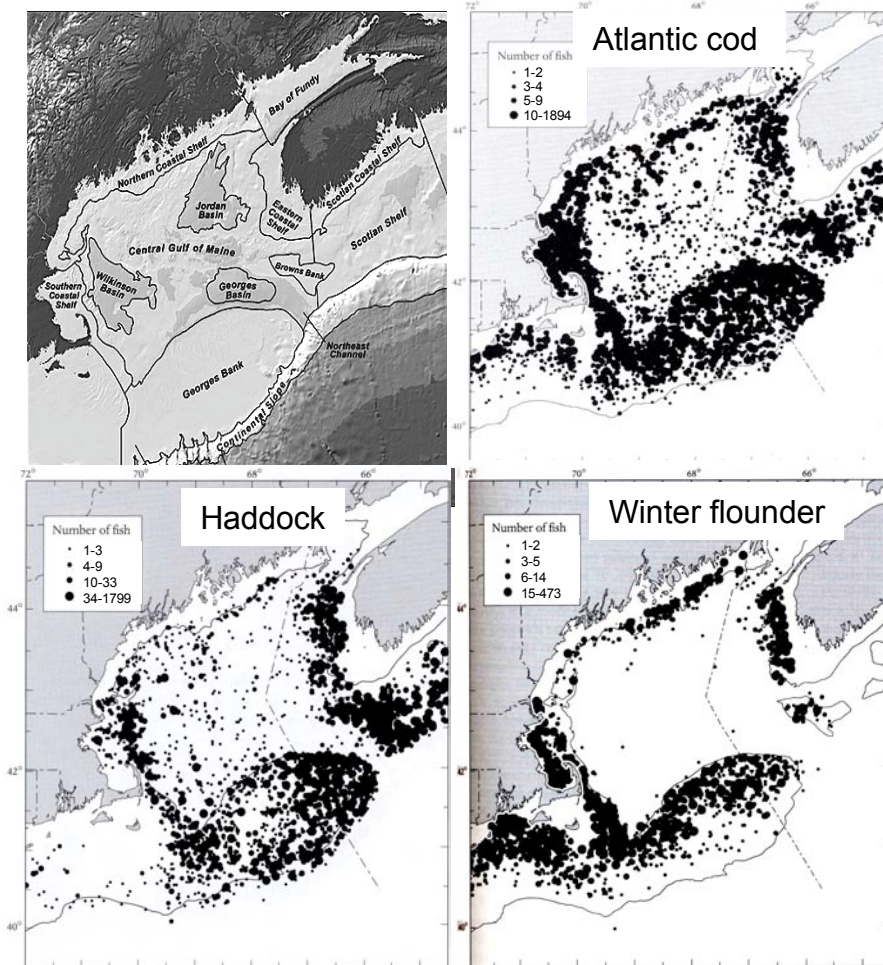


Figure 7. The Gulf of Maine's habitats or "physioregions" (from Gulf of Maine Census of Marine Life) (upper left) and spatial patterns of groundfish species distributions resulting from NEFSC bottom-trawl surveys from 1968 through 1996 (from Collette and Klein-MacPhee, 2002). Atlantic cod (spring trawls), haddock (spring trawls), winter flounder (fall trawls).

offshore banks (e.g., Georges and Brown's banks) and coastal zones but are rare in the central Gulf (Fig. 7). This ring around the Gulf of Maine pattern is observed for other species, including the American lobster (*Homarus americanus* Milne Edwards, 1837; Steneck, 2006), so it is clearly not only applicable to fishes. Nevertheless, other species have a different pattern of distribution and abundance, occupying the central, deep portion of Gulf of Maine and found only rarely on offshore Georges Bank. Examples include groundfish species such as silver hake, Acadian redfish (*Sebastes fasciatus* Storer, 1854), American plaice, and witch flounder (*Glyptocephalus cynoglossus* Linnaeus, 1758; Fig. 8). Nested within these patterns are relatively stable but smaller-scale patterns driven by smaller-scale processes. For example, the biota in coastal Maine north and east of Penobscot Bay differs from that in regions south and west of the bay because of two different coastal currents affecting the physical and

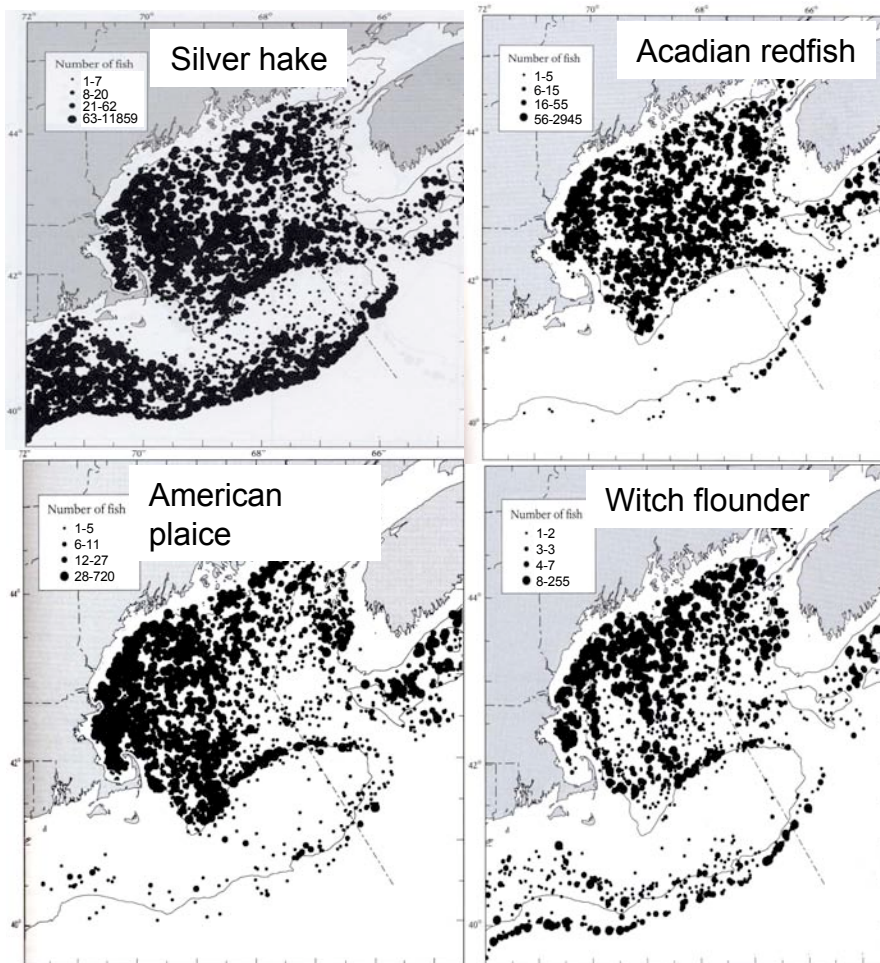


Figure 8. Spatial patterns in groundfish species distributions resulting from NEFSC bottom trawl surveys from 1968 through 1996 (from Collette and Klein-MacPhee, 2002). Silver hake (spring trawls), Acadian redfish (fall trawls), American plaice (spring trawls), and witch flounder (fall trawls).

biological oceanography of these regions (Townsend, 1992). Specifically, the Eastern Maine Coastal Current is well mixed and provides relatively nutrient-rich and cooler than average water during the summer; whereas the Western Maine Coastal Current is more stratified, maintains lower nutrient levels, and is warmer at the surface during the summer. These oceanographic differences can drive demographically important ecological processes such as larval dispersal and recruitment. Some species within Maine's coastal zone have distinctly different regional rates of settlement, recruitment, and growth. For example, higher rates of settlement have been reported for lobsters (Palma et al., 1999; Steneck and Wilson, 2001), crabs (species of *Cancer* and the Asian shore crab, *Hemigrapsus sanguineus* (De Haan, 1853); Stephenson et al., 2009), and sea urchins (*Strongylocentrotus droebachiensis* Müller, 1776; Vavrinec, 2003) in areas south and west of Penobscot Bay.

CASE STUDIES OF SPATIALLY COMPLEX SPECIES: ATLANTIC COD AND AMERICAN LOBSTER

As examples, we focus on two managed species, Atlantic cod and American lobster, considering first large-scale patterns of distribution, abundance, and connectivity in both space and time; then prevailing thoughts on the genetic structure of selected stocks; then the relatively stable fine-scale spatial heterogeneity observed within populations in the Gulf of Maine. We review recent research on both species indicating that they may be demographically self-recruiting metapopulations. The strong implication is that the fine-scale population structure of these species must somehow be nested within the larger, traditional spatial domains currently used for their management.

Atlantic Cod: Local Stocks Nested Throughout the North Atlantic.—Atlantic cod inhabit most regions of the North Atlantic. Numerous discrete stocks have been identified by a variety of approaches, such as molecular genetics, tagging, meristics, and timing of spawning and recruiting populations (see ICES, 2005, for a massive review). Microsatellite studies show that the North Sea and eastern English Channel populations are genetically distinct. Not surprisingly, they are also significantly divergent from Canadian Scotian Shelf and Barents Sea populations (Hutchinson et al., 2001). Within the western North Atlantic's Gulf of St. Lawrence, otolith trace-element composition revealed four distinct subpopulations in a region around the mouth of the Gulf, separated by less than 20 km. Cod subpopulations displayed distinct migratory behaviors and "no evidence of large-scale mixing" across the region (Campana et al., 1999: 1873). Multidisciplinary studies combining microsatellite polymorphic DNA ecology and oceanography found remarkably localized cod stocks down to individual embayments (Ruzzante et al., 1999).

A review of 174 Atlantic cod tagging studies (Robichaud and Rose, 2004) showed that most individuals were sedentary (41%) or homed to exactly the same area (18%) or nearly the same area (20%) annually. Only about 20% dispersed over large areas without recognizable return migrations. Studies in Maine and Labrador found site fidelity in both spawning and feeding sites (Perkins et al., 1997; Green and Wroblewski, 2000). These distinct local stocks can be maintained by oceanographic features and/or by biological differences in spawning times that act effectively as "barriers to gene flow between and among neighboring and often contiguous cod populations in the NW Atlantic" (Ruzzante et al., 1999: 79). In fact, five local spawning populations were identified along contiguous inshore areas on the outer coast of Newfoundland and Labrador (Wroblewski et al., 2005). Such distinct spawning sites may be occupied for relatively short periods followed by significant mixing of stocks while the fish are feeding. Like that of salmon, this mixing does not erase fishes' fidelity to their natal spawning sites and, consequently, does not eliminate the need to recognize the spatial heterogeneity of the metapopulation. Asynchronies in local stock abundance also inform us about demographic independence among substocks of Atlantic cod metapopulations, evident of course over large distances and long periods of time, such as the codfish declines off the coast of England in the 1400s. These were the impetus for English exploitation of healthy stocks near Iceland and led to the Cod War of 1532 (Kurlansky, 1997). More recently, collapses in the Barents Sea were clearly not related to events on the Grand Banks, on Georges Bank, or in the North or Baltic seas. Collapses in one area did not trigger collapses elsewhere as might be expected if a single North Atlantic stock relied on a single larval pool (e.g., Fig. 1C). These unsur-

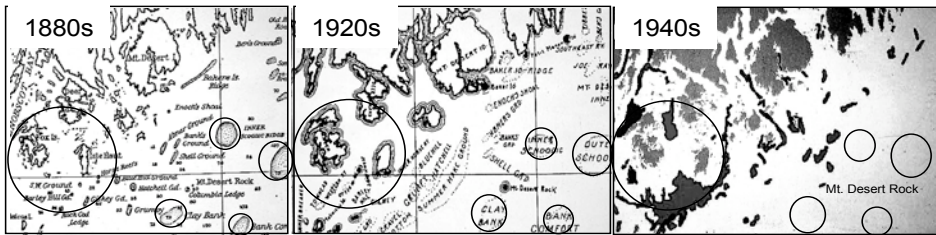


Figure 9. Historic charts of fishing grounds and spawning ground for Atlantic cod from the mouth of Penobscot Bay to beyond the Schoodic Peninsula, Maine. Each of the three panels spans 100 km. From left to right, charts are from Collins and Rathbun (1887), Rich (1929), and Ames (1997). The large circle illustrates the location of spawning aggregations that were fished after the 1930s but not before. The four small circles represent the locations of discrete fishing grounds fished during the 1800s through the 1920s but not after that period.

prising broad-scale asynchronies are simply evidence of the demographic separation of stocks at that scale, but smaller-scale asynchronies have also resulted from serial extirpations.

Western North Atlantic cod stocks have undergone serial depletions at relatively fine scales. Archeological and early historical data show that abundant and large (i.e., meter-long) cod were present and harvested in coastal Maine for millennia (Steneck, 1997; Jackson et al., 2001; Lotze and Milewski, 2004). Early fisheries studies along the coast of Maine mapped fishing hot spots that remained stationary for over a century (Fig. 9; Collins and Rathbun, 1887; Rich, 1929). In the 1930s, technological advances allowed fishers to concentrate on spawning aggregations and thereby to deplete coastal cod stocks within about two decades (Steneck, 1997; Ames, 2004). By the 1940s, populations in small areas that had been described as fishing hot spots for more than a century had been extirpated. Distinct areas known to have fish in the 1880s (Fig. 9, left) still maintained them in the 1920s (Fig. 9, middle) but not in the 1940s (Fig. 9, right). During this time, offshore cod stocks in Canada and the United States were still relatively abundant. Much later, those offshore populations declined significantly, from the mid-1980s to the early 1990s (Steneck, 1997; Hutchings and Ferguson, 2000), but the remaining stocks still maintained clear spatial structure. Significantly, the spatial decline of stocks in Atlantic Canada followed a trajectory similar to that in the United States. In Canada, offshore cod stocks collapsed in the late 1980s and early 1990 (Myers et al., 1997), but some inshore stocks remained viable (Wroblewski et al., 2005). In recent years in the southern Gulf of Maine, coastal cod maintained at least the abundance levels of the inshore Canadian stocks while eastern coastal stocks remain depleted (Maine DMR, <http://www.maine.gov/dmr/rm/trawl/index.htm>). Fine-scale hot spots and cold spots appear to be persistent over time. Early cod distribution charts were developed from oral histories from fishermen (e.g., Fig. 9). The accuracy of those spatially detailed charts was supported by subsequent fisheries-independent trawl surveys (Fig. 10). For example, abundance patterns of cod during the 1940s showed distinct fishing and spawning grounds around Penobscot Bay and Mt. Desert (Fig. 10, left panel). The same aggregations of abundance (e.g., numbers 1, 3, and 4 in Fig. 10, middle panel) were found with fisheries-independent trawl surveys. Persistent regions of low densities were also evident (e.g., number 2 in the left and middle panels). Continuing declines in cod stocks in the last decade have left all four of these areas devoid of cod (trawl-survey data, Fig.

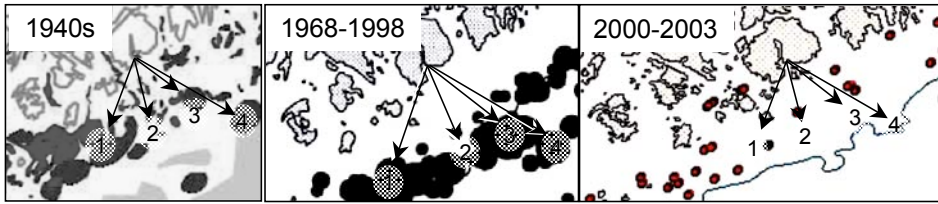


Figure 10. Discrete local stocks determined from oral histories from fishermen (left panel, from Ames, 2004), from U.S. federal (National Marine Fisheries Service; Collette and Klein-MacPhee, 2002), and from combined U.S. federal and Maine state trawl surveys (right panel). Each chart covers about the same area. Four features of presence (identified as numbers 1, 3, and 4) and one of relative absence (number 2) show good spatial correspondence between the two methods (compare left and middle panels). More recently, local stocks in those areas have been sufficiently depleted that no cod have been recorded from those sites (right panel in Figure 9).

10, right panel). Since the mid-1990s, the fishery in these areas and eastward to the Canadian border has been economically extinct (Maine DMR trawl surveys and personal communications with local fishers). Finally, very small but persistent substocks of cod and other groundfish [e.g., pollock; Atlantic wolf-fish, *Anarhichas lupus* Linnaeus, 1758; and cusk, *Brosme brosme* (Ascanius, 1772)] documented by Rich (1929) remain on Cashes Ledge in the middle of the Gulf of Maine. Groundfishes there are significantly larger and more abundant than fish of the same species found in coastal zones (Witman and Sebens, 1992; Steneck, 1997; Steneck and Carlton, 2001). An average population density of about 20 cod per cubic meter per hour was recorded in multiple stationary videos from this site (Steneck, 1997). Importantly, size classes ranged from young of the year to individuals exceeding 20 kg in weight (Steneck, 1997, pers. obs.) suggesting this was a stable, closed, self-recruiting population surrounded by depleted stocks in the Gulf of Maine.

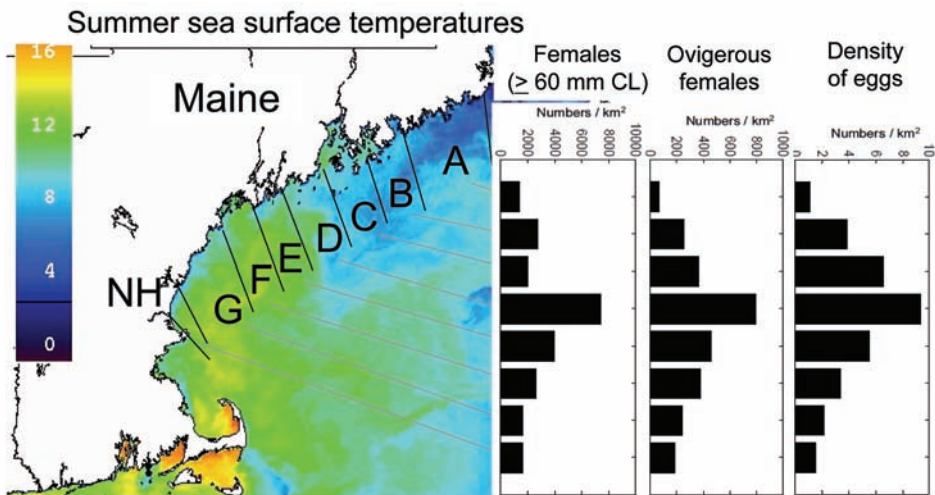


Figure 11. Patterns of distribution and abundance of juvenile and reproductive female lobsters along coastal Maine and New Hampshire relative to the seven lobster zones in Maine and one in New Hampshire (NH). Representative summer sea-surface temperatures are shown for the Gulf of Maine coast (courtesy of Univ. Maine School of Marine Sciences). Note that two long-shore currents flowing from northeast to southwest dominate this stretch of coast. The Eastern Maine Coastal Current is cool in the summer and flows from zone A to zone D; the Western Maine Coastal Current flows from D past New Hampshire.

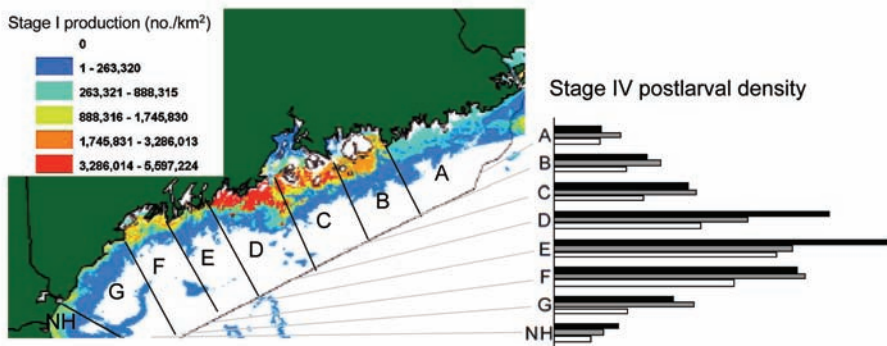


Figure 12. Patterns of distribution and abundance of newly hatched stage I lobster larvae (representing location of ovigerous lobsters at the time their eggs hatch) and, to the right, the distribution and abundance of stage IV postlarvae (i.e., the settling stage for this species) for years 2000–2003 (represented in three bars per zone). Letters A–G designate the seven lobster zones of Maine; NH, New Hampshire (from Incze et al., 2010).

The asynchronous patterns of depletion and persistence we just described contradict the conclusions of Rothschild (2007), who found large-scale regional coherence in the decline of Atlantic cod. Rothschild used the very broad-scale fisheries statistical zones defined by the North Atlantic Fisheries Organization. Analysis at this scale obscures fine-scale, asynchronous stock structure. In addition, when fishermen are free to roam across stock boundaries and respond to the same (global) price signals, they tend to allocate fishing effort preferentially to the more abundant stocks. This allocation effect tends to equalize CPUE, giving the appearance of broad-scale biological coherence, but in the presence of strong annual variability, local stocks can be pushed past a critical threshold and suffer serial extirpation (Wilson et al., 1999).

In sum, genetic distance, tagging, meristics, timing of spawning, and recruitment studies over the last decade have revealed considerably more fine-scale stock structure than was previously apparent or assumed. This structure does not appear to be a nice neat assemblage of stocks in which each subpopulation is spatially discrete. The range of adjacent stocks may (or may not) overlap while, at the same time, spawning groups appear to maintain separation through fidelity to site-specific spawning areas. Generally, local cod stocks in the western North Atlantic behave as though they are demographically independent, distinct, and separate components of a large metapopulation.

American Lobster: Growing Evidence for Local Stocks, Hot Spots, and Cold Spots.—Detailed large-scale spatially and ontogenetically explicit data are unusually abundant for the American lobster in the Gulf of Maine (see, e.g., Steneck and Wilson, 2001; Wahle et al., 2004; Butler et al., 2006; Incze et al., 2010). Lobster postlarvae settle in relatively shallow waters (i.e., upper 20 m, within SCUBA sampling depths) to specific cobblestone or small shelter-providing substrates (Wahle and Steneck, 1991, 1992), where they are easily sampled and quantified. Because postsettlement mortality is low, rates of settlement are good indicators of juvenile and adult population densities and local landings (Palma et al., 1999; Steneck and Wilson, 2001; Wahle et al., 2004).

Because lobsters have no hard parts that persist through molts, present microgeochemical tools cannot be used to track larval source-sink dynamics, but recent re-

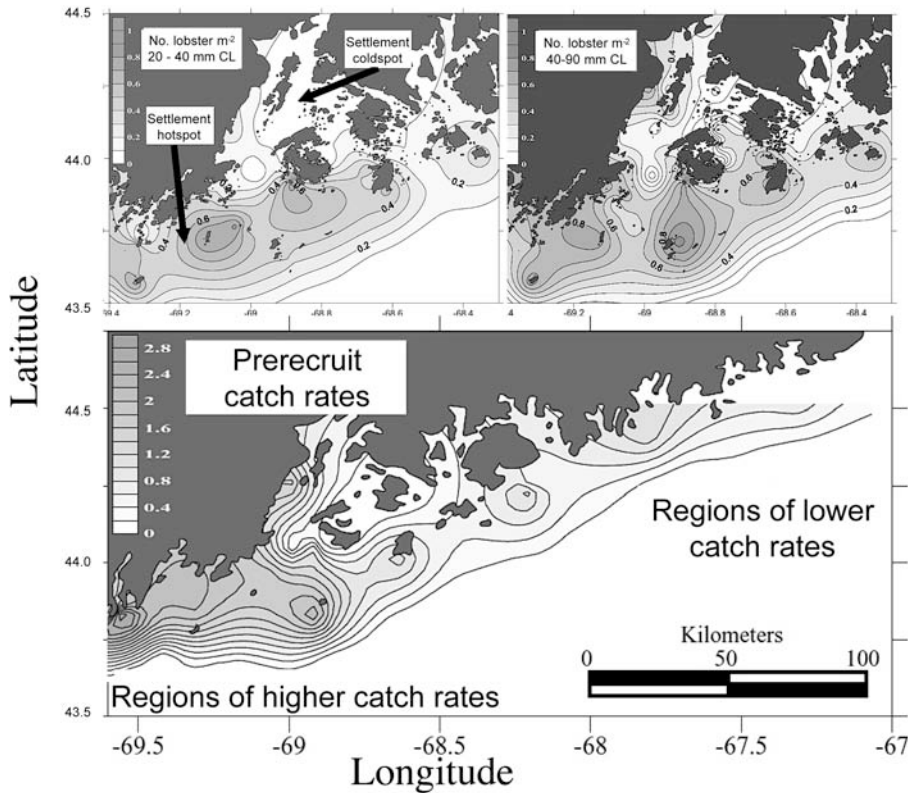


Figure 13. Small-scale patterns of settlement and juvenile lobster abundance (top two maps) and prerecruit (< 83 mm CL) catch per trap haul of lobsters in Penobscot Bay, Maine (Zone C in Fig. 12; lower map) (from Steneck and Wilson, 2001).

search using detailed demography, biophysical oceanographic models, and improved estimates of pelagic larval development and duration allow models to predict connectivity between egg production (source) locations and competent postlarval (sink) locations (Incze et al., 2010). Using this approach for 17 locations in the coastal Gulf of Maine (New Brunswick and Nova Scotia, Canada; Maine, New Hampshire, and Massachusetts, USA), Incze et al. (2010) determined 15 of the locations to be self-recruiting. To illustrate the scale of local stocks for American lobsters, the geographic patterns of abundance for distinct ontogenetic phases were plotted in the seven lobster-management zones in Maine (established in 1997 by the state of Maine, working with the lobster-fishing industry) and for New Hampshire (Figs. 11, 12; Incze et al., 2010). The abundance of juvenile and ovigerous females peaked in lobster management zone D. The abundance of eggs corresponds spatially with the abundance of newly hatched stage I larvae (Figs. 11, 12). Larval lobsters require between 30 and 90 d to develop, depending on water temperature and food availability (Annis et al., 2007). All stages peak around zone D except for lobster postlarvae (stage IV), which peak in zone E. Region-wide patterns of settlement and landings corresponded with the patterns of larval and postlarval abundances (Figs. 12, 13). Specifically, settlement was greatest around the western mouth of Penobscot Bay and extended to the southwest. Within the broad region of generally high settlement and juvenile abun-

dance are regions up the estuary (Palma et al., 1999) and in localized areas of Penobscot Bay where larval delivery and settlement are low. These “cold spots” (Fig. 13) led to cold spots for adult lobster population densities (Fig. 13A,B) and for catch rates of lobsters in traps (Fig. 13C). Subsequent research suggested the low-population-density “settlement cold spots” are persistent at least approximately for decades (Incze et al., 2010). The evidence therefore suggests that local populations of reproductive lobsters are primarily responsible for local patterns of settlement, population densities, and landings (Figs. 11–13). These patterns drive the densities of fishers and lobster traps (Steneck and Wilson, 2001), and importantly, they generate for local fishers evidence of a reasonably clear connection between their fishing activity and the local population of lobsters. In fact, fishermen working at a scale that closely approximates the relevant demographic scale of recruitment cells probably get stronger feedback about the impact of their fishing than do scientists using sophisticated statistical approaches who sample and analyze at a broader and demographically less appropriate scale. Each of the lobster-fishing zones established in Maine has an elected council that is empowered to manage those aspects of the fishery whose impact is principally local (Figs. 11, 12; Acheson, 2003). These lobster zones are now nested within a broader scale of management by the state of Maine and the Atlantic States Marine Fisheries Commission. Neither the local zones in Maine nor the area fished by a typical lobster fisher corresponds precisely to the scale of recruitment cells. Consequently, and significantly, fishermen do not believe that the results of their actions are fully contained within specific localities. They do not believe, for example, that each zone should have the ability to change the minimum or the maximum size of landed lobster, because they feel the relevant scale of reproduction is broader than any zone. Nevertheless, they do believe that localization is sufficient for individual and collective restraint within their zones to pay off in the long run (personal communications with the authors). This belief, correlated as it is with reasonable feedback from the resource, is the basis for a conservation ethic strong enough to elicit effective informal enforcement (Acheson, 2003). At the same time, that ethic is reinforced by self-interested action that creates the preconditions for effective local-scale collective action (Wilson et al., 2007). In short, because the lobster population and its management in Maine operates at a variety of scales, feedback about human activity also occurs in varying strengths at a variety of scales; the multiscale—local, state, and federal—governance of this species in Maine reflects considerable logic. This social and ecological structure stands in stark contrast to that of the cod fishery. In that fishery, a single broad management boundary (for fishing, not stock assessment) has led to a spatial scale of fishing that appears to bear little relationship to the scale of substocks described above.

MANAGEMENT IMPLICATIONS OF SPATIAL COMPLEXITY IN THE BIOLOGICAL REALM

Scale(s) and Feedback.—Recognition of spatial complexity in the biological realm reveals a number of difficult management problems. Accepted biological knowledge of open populations in the 1970s and dating back to the 1930s (Halliday and Pinhorn, 1990) led managers to design management institutions whose boundaries were appropriate to the broad, nonlocal scale thought to characterize marine populations. Those same assumptions about biological scale led economists to conceptualize the management problem as if the feedback captured within the typical management boundary reflected the relevant events affecting a single discrete stock. “Feedback”

as we use it here is information received by management about the consequences of a particular act or sequence of acts, such as the effect of a closed area or biological changes that affect the harvest rate. Thus, feedback is both the formal articulation of data from public scientific and administrative processes and the informal, but articulated, private observations of fishers and other users of the resource that also enter the public realm. The feasible temporal and spatial scale of public feedback is essentially an economic question. As the costs of observational technology and of communications and analysis decline, smaller-scale, more detailed, and more frequent feedback becomes increasingly feasible.

Not actively considered at the time management boundaries were created was the nature of the feedback that might arise if fish stocks were composed of discrete metapopulations within those broad-scale boundaries or if the spatial distributions of several population components overlapped in significant ways. In either of these instances, unless the factors affecting the abundance of all these localized stocks all operated in the same way, to the same extent, and at the same time on each stock, the feedback received by management operating at a broad scale would be extraordinarily noisy. Attempts to manage by adjustment of fishing effort to the presumed conditions of stocks defined at a broad scale, by means of limited entry, fleet quotas, individual transferable quotas or any other form of restraint set to the same scale, would probably be haphazard at best. Importantly, the resulting private feedback—the connection fishermen make between their actions and the status of stocks—would be without any systematic signal (Wilson, 2006). Matching fishing controls to the scale of the managed stock is not a new idea; it is a basic principle of single-species fisheries management. What is new is the realization that no single scale is relevant for all, or even many, fisheries stocks.

The implications of metapopulation structure for ecosystem-based management are profound. Localized stocks are not isolated from the ecosystem in which they reside; the nested metapopulation structure observed in fish populations reflects the nested modules in the ecosystem as a whole. Consequently, we can reasonably presume that ecosystem dynamics create stronger intra- and interspecific interactions within local modules of these nested systems than over the much larger footprint of the entire ecosystem. When this structure is ignored, when management monitors and manages on a species basis at a broad scale, feedback relevant to each species is noisy and haphazard, and almost by design, feedback about the system is effectively obscured. In addition, because fishers are licensed by species (or species group), private feedback that might inform management about smaller-scale, cross-species events in the system—events that are essentially irrelevant to the license holder—is almost completely lost.

Consequently, our new knowledge about the spatial complexity of stocks points to a fundamental management problem. When we design our management institutions to operate at a single large scale and on a species rather than a system basis, we incorrectly characterize the demographically relevant scale of ocean resources and, of course, minimize our observation of localized interspecific interactions. As a result, we introduce considerable noise into system feedback and seriously diminish our ability to learn, adapt, and manage effectively. A simple, but powerful, principle that should guide our attempts to manage these complex systems is to organize our governing institutions so that we detect localized signals and facilitate both public and private feedback. Getting good feedback is not the only component of manage-

ment, obviously, but it is a necessary condition for learning. Without good feedback, all management is a wild guess, and obviously, in those circumstances our ability to sustain these complex systems is substantially impaired.

Scale(s) and Incentives.—A second, closely related but less obvious aspect of spatial complexity in the biological realm concerns the private incentives that are generated by inappropriate, especially single-scale, management boundaries. If we choose to manage at any single scale, no matter which, we tend to create perverse private incentives that confound our attempts at stewardship and conservation. For example, if we manage only at a local level and have no institutions of governance that restrain fishing at broader scales, we create very strong incentives for locally beneficial actions that have globally detrimental effects, i.e., intercept fisheries, or in economists' jargon, stationary banditry (Olson, 2000). Consider a stock, such as mackerel, that migrates along the coast. Under local management only, fishermen in each locality have a strong incentive to intercept the fish before they leave their area. Both public and private actors see the benefit of feedback relevant to human activity at the local level (when do the fish arrive, how many are there, when will they leave) but acting on feedback about the broader-scale impact of local, intercept-fishery actions is not favored by any private incentives, institutional means to incorporate, or collective ability to act. The fishermen of every locality wind up engaged in a collective race to catch the fish before their neighbors. Even if each local area were under the control of a single sole owner with near-perfect property rights at that scale, the inability of the governance system to restrain behavior leading to broad-scale externalities would lead inevitably to the depletion of any stock that was so incautious as to wander across local boundaries.

At the other pole, if we manage only at a broad scale, without local governance, we set up strong incentives for fishers to adopt mobile technology that permits ready access to all local stocks and raises the risk of serial depletion (Wilson et al., 1999; Wilson, 2006). Even immobile local fishermen operating within broad-scale boundaries have no incentive to conserve a local stock if fishers from elsewhere can reap the benefits of that restraint (Berkes et al., 2006). If local fishermen detect a local stock of, say, cod beginning to rebuild, they face a difficult decision in the absence of local governance: if they wait, the fish and the stock might grow, but if they wait too long, fishermen "from away" will learn about and harvest the stock. Consequently, everybody—local and mobile fishermen—has a strong incentive to harvest "economically ripe" populations before someone else does. As a result, without local governance, feedback at a broad scale helps us to understand the cumulative long-term impact of fishing, but at the same time, this single-scale institution sets up strong incentives that raise the risk of repeated depletions or, as we appear to have witnessed in New England, extirpation of local stocks (Figs. 9, 10).

In the real world, the circumstances of management scale are often not as cut and dried as in the examples above. Usually, because of spatial complexity in the biological realm, management boundaries will be imperfect, creating more or less noisy and incomplete feedback as well as perverse incentives. We might therefore reasonably ask whether management institutions might be designed (or redesigned) in ways that improve feedback and learning at ecologically relevant scales and, at the same time, reduce the perverse incentives that arise from inappropriately scaled management.

ECONOMIC EXCHANGE ACROSS BORDERS

A practical answer to this question is not easy, but realizing that humans have a long history addressing very similar issues is helpful. The management of international trade and the management of ocean ecosystems may seem to have little in common, but both are concerned with the rules that govern human behavior regarding the movement of valuable resources across sometimes arbitrary boundaries. Many positive and negative lessons can be learned from the trade experience. Below we discuss trade as an analogy that helps us understand and provides us with some object lessons about the human side of the management of mobile resources.

Cross-Boundary Trade: Feedback and Incentives.—Political-economic boundaries, like administrative fishing boundaries, are imperfect and, from some perspectives, often make little sense. From the standpoint of economics alone, drawing a boundary down the center of New York harbor (one side is in New York, the other is in New Jersey) would appear very arbitrary and likely to impede trade, but the practical impediments are much less than one might at first imagine. Carefully crafted institutions permit the movement of valuable goods and services across that boundary without significant restriction. For most people these institutions are almost completely transparent. A New York merchant need not worry if she sends a truck with valuable goods to New Jersey; it will not be hijacked, the driver will not be held hostage, and the government of New Jersey will not impose special fees or taxes that protect New Jersey residents from her competitive activity. Effectively, the institutions that assure the free flow of trade across this boundary lead to very strong economic connectivity manifest in the large volume of valuable resources that cross the boundary. The effectiveness of these institutions might be best illustrated by comparison with another urban area. The political and economic boundaries that divided Berlin until 1990 were as arbitrary as those in New York harbor, but because no cross-boundary institutions allowed trade, economic connectivity was almost nil. In one case institutional structure increased system connectivity; in the other, it suppressed connectivity. Both were the result of deliberate collective action.

As in fisheries, the feedback and private incentives generated by trading institutions can be illustrated from two opposite perspectives. Consider, first, trading activity in a world in which no rules govern behavior at a scale broader than the local level. In these circumstances, because local governments are not constrained to act nicely toward strangers, they have a strong temptation to become stationary bandits (Olson, 2000), that is, to hold nonlocal traders and goods hostage, to rob them, and/or to apply onerous levies on their movement. These incentives are very similar to the intercept-fishery incentives that arise with only local management of marine resources, but an interesting and important aspect of cross-boundary trading is that, so long as traders are able to decide whether to trade or not, local, stationary bandits realize they cannot act too badly. If they do, the flow of valuable goods and services across their borders will cease entirely. Killing the golden goose makes no sense. Consequently, both traders and local government have strong incentives to work out agreements that facilitate the flow of at least some goods and services across boundaries. Put differently, they have an incentive to invent broader-scale governance. A “trading tragedy” arises when neighbors, both of whom know all about the golden goose, are not able to negotiate mutual restraints that set the terms under which they might profitably trade. Without such agreements, i.e., without institutions governing activity at a broader than local scale, cross-border trade grinds to a halt. Any goods

that try to move across borders are hijacked or held hostage, and consequently, trade, production, consumption, and wealth decline in each locality.

At the other end of the scale, in a world in which local governance is weak or absent, strong incentives for plundering rather than trading arise—what economists call roving banditry (Olson, 2000; and in fisheries, Wilson, 2006; Berkes et al., 2006). Why bother to cultivate, conserve, and produce if one can steal with impunity from one's neighbors? Like stationary bandits, however, even the most powerful roving bandit must restrain its behavior if it is interested in the long-run sustainability of its activities; if the bandit does not, all its victims will disappear or refuse to produce anything of value. Consequently, over the long run, the typical roving bandit's solution to sustainability is to steal only enough that its victims have some slight incentive to continue producing. To do so, the roving bandit must invent a form of local governance, one that allows it to skim some value from the local economy. These solutions are called colonialism, imperialism, empire, occupation, and the like. As history attests, these top-down replacements for effective local governance are another human tragedy that arises from incomplete, usually single-scale, governance.

Both instances of single-scale governance create individual incentives that effectively curtail any private to public feedback about the circumstances arising at the nongoverned scale. For an individual agent engaged in activities at a nongoverned scale, any feedback it provides might reveal the disadvantages of its actions and might raise the possibility that new governance at that scale might restrain the agent's activities (and profit). As a result, few or no private incentives favor providing accurate feedback to public managers. Instead strong, management-induced, incentives arise to produce biased, incomplete, or false public feedback that is consistent with self-interest.

System Organization and Feedback.—The solution to the impairment of these incentives and feedback is effective multiscale governance, that is, strong governance at both local and broader scales (Ostrom and Janssen, 2004; Ostrom, 2009). Most complex systems tend to be organized in what Simon (1996, 2002) refers to as a nearly decomposable system architecture, what Levin (1999) calls ecological modularity, and what Vincent Ostrom (1991) terms polycentric organization of governance. Common to all these conceptions is the idea of a loosely nested system in which local system components generate tight feedback loops. In human systems, those loops inform government about the particular circumstances that drive the self-interest of its various constituencies and, consequently, bring their expectations and fears to the trade negotiation table. The frequent presumption that a negotiation about trading rules that is well informed about the particulars of the parties' comparative advantage is more likely to reach an agreement that diminishes both roving and stationary bandit incentives cannot be relied on. The nonfungible investments in skills and capital made by the parties who have relied on the (preagreement) protections of tariffs or other measures that determine the terms under which trade takes place, e.g., the beneficiaries of stationary-bandit policies, make those agreements much more difficult to achieve.

Domestic trade within the United States is an interesting instance in which an agreement to regulate the external trade of each state was worked out in 1787 under circumstances in which few or no local interests depended on the protection of pre-existing barriers to trade. The interstate commerce clause of the U.S. Constitution (Article 1, Section 8, Clause 3), which incorporates this agreement, is a rather clear

example of broad-scale governance that addresses the flow of valuable resources across political-economic boundaries. The clause is one of the clearly stated, or enumerated, powers of the federal government. It gives the federal government the right to regulate commerce between the states but not trade that takes place entirely within the boundaries of any state. We can assume the drafters of the constitution were motivated by a sense that trade among the states would be beneficial to the inhabitants of the states. Concern was undoubtedly felt that each state might be tempted to act like a stationary bandit and tax trade in order to raise revenues and/or to pursue other measures benefiting local producers at the expense of competitors in neighboring states. By itself, the interstate commerce clause might have simply generated unintended, broad-scale roving-bandit incentives, but the Constitution is careful to maintain the strength and relative independence of local (i.e., state) governance. Consequently, the balance created by strong local and strong national governance brings into the public dialog, principally into the courts, feedback about both local and broader, national-scale interests. This balance makes free trade across the relatively arbitrary boundaries of the states possible and (imperfectly) minimizes both stationary and roving-bandit incentives.

At the international scale many similar multiparty agreements are intended to restrain the level of tariffs or other barriers that hinder trade. These are well known today by their acronyms, such as NAFTA, CAFTA, EU, and WTO. The point of these agreements is to create rules that alter the terms under which individuals (and governments) interact with one another. By doing so, these rules open the door to extensive economic opportunities and result in greatly expanded economic connectivity. These benefits can only be achieved through effective multiscale governance—international, national, within nation states, and even down to the very local level. To the extent that governance at any one of these levels fails or is weak, either stationary- or roving-bandit incentives arise, leading to behavior that discourages economic connectivity.

In short, although the particular circumstances of cross-boundary movements in ocean ecosystems are very different from those of commercial trading, the general problem is similar. In economics the practical problem of connectivity is building rules that encourage the flow of valuable goods and services across already existing and imperfect administrative boundaries; in ocean ecosystems, the problem involves building both rules and imperfect administrative boundaries in order to maintain an existing cross-boundary flow of valuable biological activity. In both instances, a failure to create rules at any particular scale tends to generate either roving- or stationary-bandit incentives that reduce system connectivity.

Within-Boundary Feedback and Incentives.—The other side of the trade analogy concerns the incentives and the feedback that arise within the boundaries of a local area. The path to the current globalized economy was not easy and straightforward. Each step of the way was marked by arduous negotiations made necessary by the alterations to economic connectivity within each local economy introduced by each new cross-boundary trade agreement. An economy is like an ecosystem in that the health of each element within it depends upon its other elements. A change in the rules governing trade, consequently, means each new (or proposed) trade agreement imposes disadvantages on those parties in each country whose skills, capital investment, and career and business plans are adapted to (or are protected by) the current (preagreement) regime. The fixity of these investments gives these parties strong

incentives to resist new trading arrangements. Tight local feedback brings their interests to the table and often scuttles the chances of agreement. The problem, of course, is that even though new trading rules often create very promising economic opportunities for the economy as a whole, many people within that economy who depend on the protections afforded by the preagreement set of trading rules lack the flexibility needed for easy acquisition of new skills, capital investments, and business and career plans. Consequently, they tend to bear the costs of new trade agreements, while the potential benefits accrue to others. Their opposition to increased economic connectivity is entirely understandable.

Viewed from a slightly different perspective, the time and cost of adaptation to a new set of trading rules generates a pattern of short-term costs and long-term benefits very similar to the problem that confronts any new conservation rule in fisheries. The sources of the problem are also very similar. Individuals adapt their skills, boats, business plans, and careers to the rules in place before any new rules. Today, those adaptations generally reflect the broad-scale boundaries and single-species rules that science thought appropriate in the 1970s. In the Gulf of Maine, scallopers are heavily invested in the boats and gear that are appropriate for fishing for scallops at the scale of current management boundaries; the same holds for groundfishermen, herring fishermen, sea-urchin divers, lobstermen, and so on. Each works at a scale and with a technology and sells to markets that reflect the rules that define the scale and species of the management regime in which they work, and of course, each group of fishermen brings to the public dialog feedback that reflects their interests. The problem is not that fishermen are self-interested; it is that, by and large, their interests and the existing institutions of the social-ecological system reflect scientific ideas about scale and system that are rapidly becoming outmoded. The result is great political difficulties in developing new rules that might improve demographic connectivity and suppress incentives to roving and stationary banditry. Put differently, we have built into our current management system a set of private incentives that are driven by scientific conceptions of the ocean that are large scale and single species rather than multiple scale and ecosystem based.

DISCUSSION

As concerns over the fate and management of the biosphere and its ecosystems escalate, so too do the calls for their more effective management. Addressing these calls, Christensen et al. (1996: 665) listed the criticality of “spatial and temporal scale” as the first of four fundamental precepts for ecosystem management. For oceans, ecosystem-based management is defined as “...an integrated approach to management that considers the entire ecosystem, including humans” (McLeod and Leslie, 2009: 4). In fact, a consensus is growing that the next generation of management should be “a place-based approach, and coupled [social-ecological] systems...across a range of spatial scales from a local...to an entire large marine ecosystem....” As such it must be “implemented over a range of scales, acknowledging the connections and leaky boundaries among scales” (McLeod and Leslie, 2009: 4).

Accordingly, we now know that the spatial structures of many marine species within ecosystems interact at smaller scales and in more spatially complex and dynamic ways than previously suspected. Their hierarchical organization is nested in space and in time as a result of evolutionary and ecological processes resulting in

foodwebs, assemblages, species, and races or local substocks (Hutchinson, 1965; Post and Palkovacs, 2009). Similarly, social connectivity and governance can be, and should be, nested in space. In both the biological and human social contexts, most interaction strengths are strongest at the smallest spatial scales. Further, smaller-scale components of the system tend to operate at higher rates than those at larger scales. Because each species differs considerably from others in the extent of its range, the structure of its populations and subpopulations, the timing of its life cycle, and almost every other aspect of its existence, “perfect” ecological or social boundaries that fully contain the effects of events within a population or an ecosystem will never exist.

Human adaptations to this complexity depend on the public and private feedback received about the effect of human actions on these populations and systems. The interactions within and across the boundaries that contain human activity (i.e., administrative boundaries) and the imperfect ecological boundaries that delineate the nested components of populations and the ecosystem define the nature and the scale of human feedback between populations and the ecosystem. Smaller-scale management of marine fisheries is a logical next step resulting from the paradigm shift over the past several decades. Until relatively recently, ecological (e.g., Caley et al., 1996) and fisheries science assumed the most appropriate boundaries were those that encompassed the broadest spatial scales of the “open” (i.e., “panmictic”) single-species populations. Few managers in the recent past considered the idea that the populations, their drivers, and the structure of the ecosystems are nested. The convention has been to manage single species at relatively large scales, but doing so impairs feedback and creates perverse incentives leading to serial depletion of spatially complex populations (Berkes et al., 2006; Wilson, 2006). Eventually, the result is erosion of the structure and function of the entire ecosystem, as has happened in the Gulf of Maine (Steneck, 1997). We argue that these fisheries “plays” must be considered within the broader ecosystem “theater” in which they reside.

Management boundaries and the institutions that accompany them, including fishing rights, must be reorganized around multiple nested boundaries that reflect as closely as possible the biological complexity of the ocean. Nevertheless, all management boundaries will be imperfect because of that spatial complexity, but strong multiscale governance tends to compensate for these imperfect boundaries by creating strong incentives for cross- and within-boundary rules that suppress the spatial manifestation of the race to fish, incentives to so-called roving and stationary banditry. This scenario contrasts with single-scale management in which no one has an incentive to stop the spatial race to fish. Given the current relatively broad-scale nature of fisheries management, the practical implication of multiscale management requires the creation of strong local governance. New smaller-scale governance will allow better capture of the tight, fast-paced feedback at local scales and, consequently, better understanding of the way local actions scale up to broad-scale patterns.

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