Editorial

Connectivity in the life histories of fishes that use estuaries

Historically, coastal fisheries biology has focused on the theme of estuarine dependency with emphasis on microhabitat use. Ironically, however, few fishes that we associate with estuaries are in fact obligatory users. What then are the causes and consequences of estuarine habitat use? At the Estuarine Research Federation 2003 Seattle Meeting, we explored "connectivity" in the life cycles of fishes and invertebrates that use estuaries. Connectivity here refers to the dependence of fish production and population dynamics on dispersal and migration among multiple habitats. Further, we propose that spatial dynamics of estuarine and coastal fishes, by dint of their diversity, represent key resiliency mechanisms in fisheries and habitat management.

At first blush, connectivity seems an unfortunate term in describing the spatial dynamics of estuarine-associated fishes. In many disciplines it has become jargon and trite. The term emerged with telecommunications and simply means the ability to connect or interconnect: a fairly trivial attribute of fish life cycles. On the other hand, the second more technical definition in the Oxford Dictionary describes a more interesting element to connectivity: "… capacity for the interconnection of platforms, systems, and applications." Capacity implies the potential storage and use of information that is differentially transmitted across platforms, systems, and applications. Important synergism occurs in the diversity of sources, routes, and destinations of information in systems of connectivity; so too in the complex life cycles of fishes. Here, we suggest that connectivity implies the enhanced storage of genetic and energetic pools due to variable migration and dispersal patterns across habitats and ecosystems. The so-called storage effect, i.e., increased population resiliency due to life history variations, has emphasized variations in demographic schedules (Chesson, 1994; Secor, 2000; Fromentin and Fonteneau, 2001; Francis, 2003). We propose that variance associated with spatial dynamics (i.e., connectivity) as a key component of the storage effect.

Before we move on to complex life cycles, there are other definitions of connectivity in aquatic ecosystems, which have relevance to estuary-associated fishes. In landscape ecology, connectivity refers to the spatial arrangement of habitat. An example is the seasonal patchiness of suitable habitats in the Chesapeake Bay for sturgeons. Based upon an ecophysiological model, Niklitschek and Secor (2005-this issue) show that both the volume and arrangement of sturgeon habitats are highly dependent upon climate, suggesting that population growth may be dependent upon favorable nursery volumes that occur only once in a decade. The interplay of climate and connectivity among habitats may be a particularly important attribute of estuarine ecosystems, which due to their restricted sizes and hydrology, are strongly influenced by climate (see also Able and Ray papers, 2005-this issue). Climate-driven inter-annual and inter-seasonal changes in estuaries will dictate how habitats within estuaries are structured, ordered, and connected. Another example of habitat connectivity is for oysters in the Chesapeake Bay. Apart from some popularly held views, oysters did not historically carpet the Chesapeake Bay. Rather as McCormick (2005-this issue) reviews, their historical distribution was likely governed by complex hydrology and bathymetry that favored settlement and varying degrees of self-recruitment. Still, historical oyster beds provided important structuring at local and regional scales, providing important habitat connectivity now long absent in the Chesapeake Bay ecosystem.

In "habitat triage for exploited fishes," Levin and Stunz (2005-this issue) apply a life table modeling approach to rank essential fish habitats within the life cycles of an estuarine-associated fish: red drum. Life stage schedules of vital rates are analyzed to determine which life stage offers the greatest potential for population increase. Then, habitats associated with critical life history stages are prioritized and evaluated for their potential effects on population growth rate. A similar approach was recently used to examine the influence of regionally varying vital rates in the Chesapeake Bay on population growth rates of blue crabs (Miller, 2003).

The role of complex life cycles in fisheries and habitat management is well exemplified by the fact that many coastal and estuarine fisheries depend upon production of larvae and juveniles that have occurred elsewhere. An enduring question in fisheries oceanography is whether fish are "self-recruiting." Given the opportunities for larval dispersal in open-ocean, coastal, and estuarine systems, how do populations persist? The issue of whether recruits originate from local or distant sources has long been emphasized in coral reef systems, but more recently estuaries and coastal fishes have become focal experimental systems. Gillanders (2005-this issue) and Herzka, (2005-this issue) respectively, review the use of otolith elemental chemistry and stable isotope ratios in soft tissues as very promising approaches in studying connectivity between estuarine and coastal habitats. In particular, chemical composition of otoliths or soft tissue can identify larval or juvenile habitats of origin. Herzka and Gillanders provide critical reviews of the theoretical underpinnings of these approaches, past applications, and appropriate design and statistical analysis in related connectivity studies.

A common pattern in life cycles of estuarine-associated species is coastal spawning followed by larval ingress into estuaries and settlement by juveniles in nursery habitats. Ingress is a critical and complex component of connectivity that controls the rate of exchange of individuals between coastal and estuarine habitats. Estuarine ingress by larval fishes, crustaceans, and other invertebrates has been a key question in fisheries oceanography, well exemplified by the numerical circulation model developed by Brown et al. (2005-this issue) on larval red drum ingress into Galveston Bay, Texas.

Anadromous species represent a special class of life cycles that are dependent upon coastal, estuarine, and freshwater habitats. Duffy et al. (2005-this issue) examine the role of Puget Sound as important juvenile habitat for five Pacific salmon species by comparing their seasonal patterns in abundance in delta areas, nearshore exposed sites, and northern and southern regions that diverge in bathymetry, temperature, and salinity. Chinook salmon populations can show considerable diversity in estuarine dependency. In this issue, Bottom et al. examine alternate estuarine habitat use patterns by juvenile Chinook salmon in the Salmon River Estuary, and evaluate whether the frequency of patterns (e.g., duration of freshwater and estuarine residency, size and time of estuarine entry) is affected by habitat restoration programs and hatchery influences. Indeed Pacific salmon may represent a "guild" of estuarine dependent species; another estuarine associated guild are the US Atlantic clupeids (shads, river herrings, and menhaden) (Ray, 2005-this issue). Ray argues that both these guilds have developed an estuarine dependent adaptive complex within larger meta-estuarine (clupeids)

or meta-fluvial (salmonids) coastal ecosystems. Opportunistic life histories within species, and redundancies across species are viewed as principal determinants in guild dynamics and stability. Finally, Kraus and Secor (2005-this issue) contrast two primary juvenile habitats (freshwater versus brackish) for white perch among estuaries in the Chesapeake Bay. While white perch juvenile populations show inter-annual synchrony in abundance, the relative ranking of these two nursery habitats varies among estuaries within the Chesapeake Bay.

Connectivity of fishes that use estuaries is essentially a different version of the issue of estuarine dependency, which has in recent times moved from qualitative evaluations based upon occurrence data to a more sophisticated view that estuarine dependence among species is dynamic, varies across species ranges, and varies with the type of estuary (Able, 2005-this issue). Based upon a literature review, Able erects a new system of classifying facultative estuarine dependence. Then, drawing from an intensive long-term series of distribution patterns across a New Jersey coastal ecosystem, Able promotes the view that issues of estuarine dependency can be most productively resolved through comparative studies utilizing similar sampling along the estuarine-coastal ecotone.

Contributions in this series have thus provided valuable direction in the nascent field of connectivity of estuarine fishes. Our goal here was to represent and define connectivity in estuarine fishes broadly rather than concentrate on a single system, approach, or process. As a result of the special symposium on fish connectivity, we have identified a set of research themes that should lead to new scientific insights, and utility in fisheries and habitat management:

(1) *Spatially explicit models of estuarine fish/invertebrate production and life cycles*. Spatial management and essential fish habitat designations are increasingly primary considerations in management. Models of fish production across estuarine-coastal gradients will require spatially explicit inputs on vital rates, yet show promise in improved identification and ranking of habitat value.

(2) *Physical processes favoring estuarine use by fishes and resource invertebrates*. This is not a new issue, but new empirical and modeling approaches have emerged that may lead to better understanding of the role of climate on larval/juvenile ingress into estuarine and coastal nurseries. Also, the growing discipline of fisheries oceanography is providing improved understanding of relevant scales of physical processes that are likely to regulate ingress.

(3) *Complex life cycles: connectivity between coastal and estuarine essential fish habitats*. An emerging

theme is that most estuarine associated species can show a diversity of estuarine habitat use patterns defined by phenotypic plasticity, the availability of habitat, and other environmental and biotic controls. Understanding the dependency of estuarine or coastal fisheries on young produced elsewhere will require new approaches (e.g., otolith microchemistry and soft tissue stable isotope analysis) and more synoptic sampling across the estuarine-coastal ecotone.

(4) *Metapopulation dynamics within and among estuaries*. Over broader spatial and temporal scales, we should consider complex life cycles in the context of metapopulation source-sink dynamics. In some instances, differential exchange among estuaries or between coastal and estuarine regions may have primarily ecological (within-generation) consequences. Such populations can be considered patchy populations or structured by contingent membership (Secor, 1999). Over generations, differential exchange will entail colonization opportunities and extirpation risk and should be considered more formally as a metapopulation system. Further, adaptive complexes or guilds of estuarine-associated species may be mutually dependent as suggested by Ray in this issue.

(5) *Fishes and invertebrates as nutrient delivery systems*. Many anadromous and estuarine associated species were once more dominant members of the estuarine-coastal biota than they are now and could have played a role in structuring ecosystem nutrient flows. While this has been suggested for salmonids and menhaden, little evidence exits for this elsewhere. Such evidence, historical or otherwise, would lead to increased priority for ecological allocations of certain species (e.g., menhaden) but also place priority on understanding and managing around complex life cycles exhibited by estuarine associated fishes.

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