What Happens in an Estuary Doesn't Stay There

Patterns of Biotic Connectivity Resulting from Long Term Ecological Research

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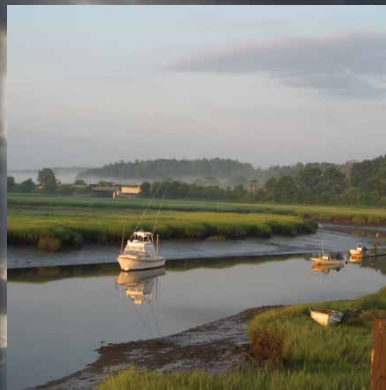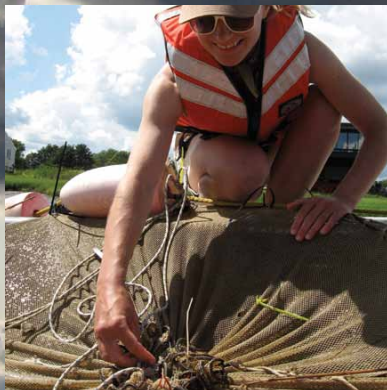
ABSTRACT. The paucity of data on migratory connections and an incomplete understanding of how mobile organisms use geographically separate areas have been obstacles to understanding coastal dynamics. Research on acoustically tagged striped bass (*Morone saxatilis*) at the Plum Island Ecosystems (PIE) Long Term Ecological Research site, Massachusetts, documents intriguing patterns of biotic connectivity (i.e., long-distance migration between geographically distinct areas). First, the striped bass tagged at PIE migrated southward along the coast using different routes. Second, these tagged fish exhibited strong fidelity and specificity to PIE. For example, across multiple years, tagged striped bass resided in PIE waters for an average of 1.5–2.5 months per year (means: 51–72 days; range 2–122 days), left this estuary in fall, then returned in subsequent years. Third, this specificity and fidelity connected PIE to other locations. The fish exported nutrients and energy to at least three other coastal locations through biomass added as growth. These results demonstrate that what happens in an individual estuary can affect other estuaries. Striped bass that use tightly connected routes to feed in specific estuaries should have greater across-system impacts than fish that are equally likely to go anywhere. Consequently, variations in when, where, and how fish migrate can alter across-estuary impacts.

INTRODUCTION

Migration is an essential component of the life history of marine fishes (e.g., Campana et al., 2011), anadromous fishes (e.g., Marschall et al., 2011), and freshwater fishes (e.g., Buzby and Deegan, 2000). By acting as vectors connecting spatially disjunct estuaries, migratory fish can translocate nutrients and transform energy. Long-distance migration between geographically distinct areas is an adaptive response that allows animals to take advantage of spatial variation in the seasonal fluctuation of resources (e.g., Baker, 1978). This form of connectivity has the potential to propagate events from one estuary to another estuary (Reiners and Driese, 2001). However, variations in when, where, and how fish migrate can dampen or intensify these across-system effects (Figure 1).

A framework does not currently exist to link migratory connectivity, geographic specificity, site and route fidelity, or individual variation within and across geographic areas. Migratory connectivity (how events at any single location can affect other locations) can be characterized depending on geographic specificity (the degree to which individuals or groups of individuals use the same places) and fidelity (the extent to which individual migrants use an area repeatedly within and across years). For example, if coastal migrants move everywhere (Figure 1a) or forage briefly in a series of different estuaries (Figure 1b), specificity and fidelity to a localized foraging area would not occur. The resulting weak or nonexistent connectivity can reduce across-system impacts. In contrast, the presence of strong connectivity,

specificity, and fidelity (Figure 1c–f) can create across-system heterogeneity in trophic transfer between migrant fish and their prey. As a result, some locations will be strongly connected and others will not. In addition, internal structure that results when not all fish behave the same (i.e., groups of individuals exhibit distinct behaviors) can further strengthen or weaken the impact of fish migrations (Figure 1d–f). Here, we use the example of the southward fall migration of striped bass (*Morone saxatilis*) to explore the complexity of these long-distance biotic connections.

Spawning fidelity has been documented for many fish (e.g., Scholz et al., 1976; Quinn, 2004; Starcevich et al., 2012), but limited evidence exists for fidelity to a specific location for foraging (Buzby and Deegan, 2000; Solmundsson et al., 2005). Research on routes used by migratory organisms has exploded with the advent of low-cost tracking technology, but, at present, there is no consensus on consistency of routes or migration timing within and across species (e.g., Melnychuk et al., 2010; Welch et al., 2011; Brodersen et al., 2012). Furthermore, although an increasing number of distinct behaviors by individuals is being documented within populations (e.g., Secor et al., 2001; Pautzke et al., 2010; Sih et al., 2012), a general framework for patterns, drivers, and consequences of individual variation in migratory fish is lacking. These gaps in existing knowledge are troubling because failing to account for this individual

variation in migration patterns can misrepresent population dynamics, community trends, and ecosystem impacts. For example, different fish behaviors within a population can have implications for a variety of fisheries management issues (e.g., Conrad et al., 2011).

Striped bass is a model species for examining connectivity, specificity, fidelity, and internal structure of long-distance migrants. US Atlantic coast striped bass spawn primarily in three locations (Hudson River, Delaware River, Chesapeake Bay; Collette et al., 2002), migrate north along the Atlantic coast in late spring, feed in the waters off New England and southern Canada in summer, and return south in the fall (Mather et al., 2009). After recovering from population declines in the early 1980s, striped bass have been abundant in estuaries and coastal waters since 1995

(Richards and Rago, 1999). This highly visible example of conservation was the result of a successful collaboration among coastal researchers and state and federal fisheries managers (Field, 1997). Because striped bass move widely along the Atlantic coast, have broad physiological tolerance, and consume a wide variety of prey (Ferry and Mather, 2012), the conventional (but untested) wisdom has been that any particular migratory striped bass could and does feed anywhere along the coast within their general migration range.

The type and degree of impact that fish migrations can have on estuary structure and function, predator population dynamics, and prey community interactions depends on how fish move from place to place, including how long they stay and what they do in any given place. Here, we ask three specific

questions about biotic connectivity. We illustrate the potential outcomes of these questions using the fall coastal migration of striped bass during which these fish are returning south toward their natal estuaries after a summer of foraging (Figure 1). The fall migration represents the most immediate coastal connection between striped bass that were acoustically tagged in summer in the Rowley River and in Plum Island Sound within the Plum Island Ecosystems (PIE) Long Term Ecological Research (LTER) site and other coastal locations. The first question is: do strong connectivity, geographic specificity, and site fidelity exist between the starting estuary (estuary e1 in Figure 1, PIE) and other coastal locations during the southward striped bass migration in the fall (estuary e2-5 in Figure 1), and, if so, what locations do striped bass connect?

OVERARCHING QUESTION:

Do coastal fish migrations exhibit connectivity, specificity, fidelity, and internal structure that could transfer nutrients and transform energy across estuaries?

	a.	b.	c.	d.	e.	f.
	H₀	H₁	H₂	H₃	H₄	H₅
Description:	All Fish Go Everywhere	Stair-Step Along the Coast	Simple Migration	Feeding -> Overwinter -> Spawning	Functional Concentration	Structured Migration
Connectivity:	No	No	Yes	Yes	Yes	Yes
-Specificity	No	No	Yes	Yes	Yes	Yes
-Fidelity	No	No	Yes	Yes	Yes	Yes
Internal Structure:	No	No	No	Simple	Simple	Complex
Across-Estuary Heterogeneity	No	No	Yes	Yes	Yes	Yes

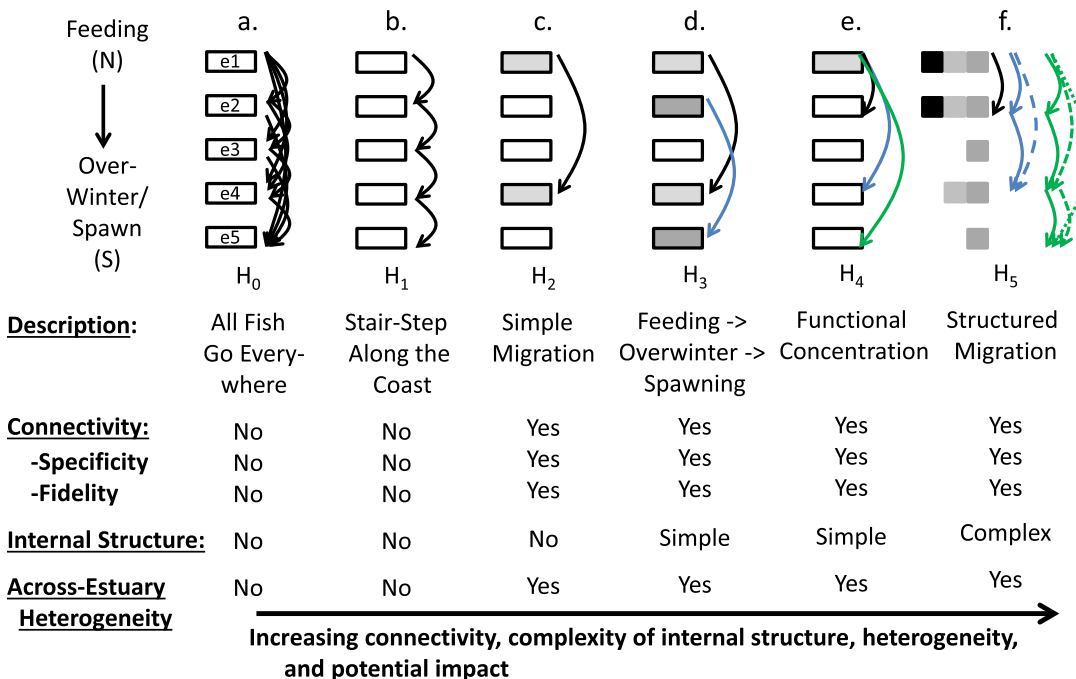**Increasing connectivity, complexity of internal structure, heterogeneity, and potential impact**

Figure 1. (a–f) Conceptual framework showing six possible outcomes for our research on biotic connectivity. These alternative outcomes reflect different combinations of connectivity, specificity, fidelity, internal structure, and heterogeneity. The scenarios are based on a southward migration of striped bass from foraging estuaries (north) to overwintering and spawning estuaries (south). Each box represents an estuary. e1 = Plum Island Ecosystems (PIE).

We predict that all striped bass do not go everywhere equally (H_0, Figure 1a), but instead individuals connect specific estuaries (H_{2-5}, Figure 1c–f). The second question is: are individual estuaries equally important during the summer migration (H_{1-3}, Figure 1b–d) or do specific estuaries aggregate summer residents that subsequently return to a variety of southern coastal locations in fall (H_{4-5}, Figure 1e–f)? And the third question is: do distinct groups of striped bass exist within the southward coastal migration (i.e., internal structure; H_{3-5}, Figure 1d–f), and, if so, do these within-population groups vary across years? We close by assessing what future data are needed to better understand patterns and ecological consequences of connectivity related to mobile predators.

METHODS
Study Site
PIE is a coupled watershed and estuary within the Acadian zoogeographic province (Ayvazian et al., 1992) that is located on the north shore of Massachusetts, USA. PIE is north of the Hudson River (523 km as the fish swims), Delaware River (708 km), and Chesapeake Bay (934 km), the three most important natal estuaries for migratory striped bass. The PIE estuary is a shallow, vertically well-mixed system dominated by salt marsh habitat with a mean tidal range of 2.9 m, which creates highly variable bathymetric structure and a mosaic of channels, islands, and sand bars (Deegan and Garritt, 1997). The surface area of water in the estuary ranges from 12.8 km^2 (average low tide) to 20.0 km^2 (average high tide) (Vallino et al., 2005) and includes major river inputs, numerous tidal creeks, and a large open bay.

Acoustic Tagging
Migratory striped bass, caught in PIE in spring-summer, were implanted with VEMCO V13 coded acoustic transmitters in 2005 ($n = 14$), 2006 ($n = 46$; Pautzke, 2008), 2009 ($n = 50$), and 2010 ($n = 35$; Kennedy, 2013). These tags had a frequency of 69 kHz, a ping rate of 20–180 s, and an estimated tag life of 100–365 d. We used acoustic tags because this type of tag allows for multiple detections of individual fish over long time periods and large spatial scales. Tagged two- to six-year-old striped bass were 335–634 mm in total length (TL), and their mean sizes were 419 mm in 2005, 433 mm in 2006, and 510 mm in 2009–2010 (age and length relationships; Gary Nelson, Energy and Environmental Affairs, Massachusetts government, *pers. comm*., 2013). These fish represented a mixture of migrating mature and immature fish, and were the most common sizes observed in PIE. Striped bass, caught by hook and line, were held in a large, continually aerated holding tank, anesthetized in clove oil (Pautzke et al., 2010), and surgically implanted with acoustic tags (less than 2% of the weight of the tagged striped bass). The incision was closed with dissolvable sterile sutures, fish were injected with oxytetracycline

(0.1 mg kg^{-1} of fish), placed in a recovery tank filled with ambient estuary water until the fish swam upright, and then were released at the capture location. The entire tagging process took less than 12 min (mean: 2005–2006, 11 min; 2009–2010, 5.4 min). In caged control experiments, tagged and untagged fish survived similarly (Pautzke et al., 2010; Kennedy, 2013).

Arrays
Tagged striped bass were tracked using stationary VEMCO VR20, VR1, and VR2W receivers at PIE and five other general areas along the Atlantic coast. Receiver arrays, mostly deployed for other research, were distributed from PIE to Delaware Bay during fall to spring of 2005–2011 (Table 1). These receivers detected acoustic signals emitted as tagged fish swam within range (a radius of about 300 m in PIE; Pautzke et al., 2010; Kennedy, 2013). Numbers of receivers in each array area varied annually (e.g., 4–182). Not all arrays were deployed every year. For example, the Long Island Coast array was only functional in 2010–2011. No tagged striped bass were detected in the Chesapeake Bay, which had only a few, smaller arrays throughout and no gating coverage of the estuary mouth.

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Data Processing and Analysis

Data from receivers within PIE were downloaded biweekly, and the raw detection data were sorted and filtered. Detection data from VEMCO stationary receiver arrays outside of PIE were shared via personal communication with individual researchers within the Atlantic Cooperative Telemetry Network (ACT; http://www.theactnetwork.com). To examine specificity and fidelity, we quantified the number of days tagged fish spent in PIE in summer, when they left in the fall, and whether they returned the following spring. To examine connectivity, we plotted trajectories, identified general groupings based on final winter destinations, and then compared frequency of pathways across years.

To identify discrete groups of fish that had similar southward migration patterns, we used network community detection analysis and nonhierarchical cluster analysis. Network analysis is a useful approach for quantifying complex connections among objects (Dale and Fortin, 2010). Network community detection analysis (Newman, 2006; Pons and Latapy, 2006) was used to group fish based on shared migratory destinations. For this analysis, we used the "leading.eigenvector.community" function in the "igraph" package in R (Csardi and Nepusz, 2006; R Core Team, 2013). For the nonhierarchical cluster analysis, we used a Euclidean distance matrix on the date of arrival and departure at each migration stop for each fish, combined with the partitioning around medoids (pam) function in the "cluster" package. The "clusterboot" function in the "fpc" package was used to calculate Jaccard bootstrap mean values for each cluster (values > 0.60 confirmed cluster patterns and values > 0.75 indicated stable clusters) (Hennig, 2010). Clusters were displayed in Principal Components Analysis (PCA) ordination space for each year.

RESULTS

Striped Bass Connectivity, Specificity, and Fidelity to PIE

Tagged striped bass in PIE exhibited strong specificity and fidelity to PIE. Our tagged striped bass exhibited a strong site attachment to PIE in all years. Across four years, tagged striped bass resided in PIE an average of 1.5–2.5 months (51–72 days) per year (Figure 2a). Energy and nutrients gained in PIE were exported to other locations along the coast as 100% of fish in all years were detected exiting PIE in the fall. During fall-winter,

Table 1. Location of acoustic arrays along the East Coast of the United States, showing array number, general location, latitude, and longitude. Not all arrays were functional in all years. Multiple arrays could be present within a general area. Only the general areas are shown on Figure 2.

Array	General Location	Year	Latitude	Longitude
1	Plum Island Estuary (PIE)	2005	42.720°N	−70.808°W
		2006		
		2009		
		2010		
		2011		
2	Massachusetts Coast (MA)	2009	41.768°N	−69.899°W
		2010		
		2011		
3	Long Island Sound (LIS)	2006	41.226°N	−72.316°W
		2007		
		2009		
		2010		
		2011		
4	Hudson River (HUD)	2006	40.706°N	−74.027°W
		2009		
		2010		
		2011		
5	S. Long Island Coast (LIC)	2010	40.542°N	−73.478°W
		2011		
6	Delaware River and Bay (DE)	2006	39.107°N	−75.266°W
		2007		
		2009		
		2010		
		2011		

36–98% of striped bass were detected elsewhere along the coast (Figure 2a). Furthermore, about two-thirds of our fish (64–74%) returned to PIE the following spring (Figure 2a).

Connections Among PIE and Other Estuaries

Striped bass that were seasonal residents of PIE connected PIE to other coastal areas. In the fall/winter, tagged striped bass were detected in three general locations outside of PIE. Group 1 (23–24%) was last detected within the Hudson River, a known natal estuary (Figure 2b); group 2 (11–37%) was last detected in or near Delaware Bay, another known natal estuary (Figure 2c); and groups 3a and 3b (16–40%) were briefly detected at one or more arrays outside of PIE (although not in any terminal natal estuary; Figure 2d–e). Variation existed in the routes striped bass used to get to their overwintering locations but these connections between PIE and other estuaries were similar across years (Figure 2b–e). Although many fish passed through one or more of the arrays near Long Island, no fish that ended up in the Hudson River visited the Delaware River and no Delaware River fish visited the Hudson River (Figure 2b–c).

Internal Structure

Individual migration pathways existed within the general coastal migration of striped bass. When the final destination and stopovers were examined (Figure 3), four destinations (gray, red, blue, green) and six types of routes (solid and dotted lines) were observed in 2009 (Figure 3a–d), and there were five destinations (gray, red, blue, green, aqua) and nine routes (solid and dotted lines)

in 2010 (Figure 3e–h). In both years, all tagged striped bass were connected through PIE and coastal Massachusetts (Figure 3a,e, gray). When the PIE connection was removed, other connections

among destinations and routes were easier to identify (Figure 3b,f). The green group went to the Hudson River (HUD) either directly (solid line) or indirectly (dotted line) via Long Island

Connectivity, Specificity, and Fidelity in Southward Striped Bass Migration

a.

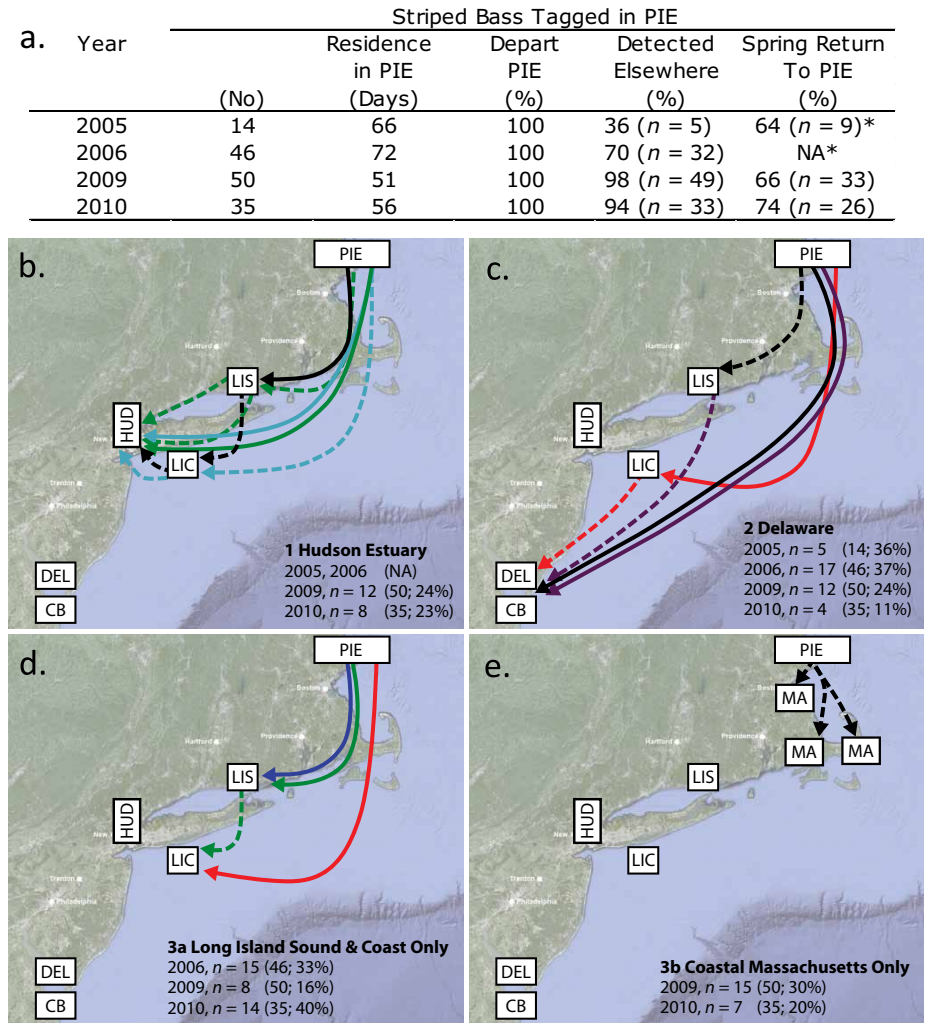| Year		Striped Bass Tagged in PIE			
		Residence in PIE	Depart PIE	Detected Elsewhere	Spring Return To PIE
	(No)	(Days)	(%)	(%)	(%)
2005	14	66	100	36 ($n = 5$)	64 ($n = 9$)*
2006	46	72	100	70 ($n = 32$)	NA*
2009	50	51	100	98 ($n = 49$)	66 ($n = 33$)
2010	35	56	100	94 ($n = 33$)	74 ($n = 26$)

Figure 2. Connectivity, specificity, and fidelity in striped bass migrations for four years. (a) The number of tagged striped bass, PIE mean residence time (days), the percent of fish that departed PIE in the fall, percent of tagged fish that were detected elsewhere along the coast, and percent of tagged fish that returned to PIE the following spring. (*Data from 2005 and 2006 are taken from Pautzke, 2008; Mather et al., 2010; Pautzke et al., 2010). Fall/winter destinations for striped bass feeding in PIE are shown, including (b) Hudson River (group 1), (c) Delaware River (group 2), or last location the tagged fish were detected in fall, including (d) Long Island and (e) Coastal Massachusetts (groups 3a–b). PIE = Plum Island Ecosystems. MA = Coastal Massachusetts. LIS = Long Island Sound. LIC = Long Island Coast. HUD = Hudson River. DEL = Delaware Bay. Data at the bottom of each frame are numbers of fish that used each route in a specific year. In parenthesis are the numbers of fish tagged that year and percent of fish that used each route relative to the numbers of fish tagged that year. For reference, Chesapeake Bay (CB) is shown. Trajectories include multiple years: 2005, 2006, 2009, and 2010. *Background maps from Google Maps*

Sound (LIS) or the southern Long Island Coast (LIC) (2009: Figure 3b–d; 2010: Figure 3f–h). The red group went to Delaware Bay (DEL) either directly (solid line) or indirectly (dotted line, Figure 3b–d,f–h). The blue and aqua groups were strongly associated with LIS or LIC (solid lines, Figure 3b–d,f–h) but could also be weakly connected to other locations (dotted line, Figure 3f–h). Cluster analysis identified the same six (2009, Figure 3c) and nine groups (2010, Figure 3g) as the network route analysis.

DISCUSSION

Factors Influencing the Degree of Impact

The degree of impact that biotic connectivity has on source and recipient ecosystems depends on characteristics of fish movements. At least four conditions may influence how much fish migration affects distant estuaries: (1) the fidelity of migrants to spawning, overwintering, and feeding grounds; (2) whether specific connections exist among feeding, overwintering, and spawning locations; (3) the degree of within-population specialization in movement patterns; and (4) the reason that fish visit distant locations. If migrating fish visit many locations, stay in any specific estuary for only a short period, exhibit no consistent links across locations, are equally likely to go anywhere, and are not actively feeding, then little across-system impact would be expected.

Connectivity, Fidelity, Specificity

The vector of coastal striped bass migration connected a northern estuary (PIE) to two distant spawning locations:

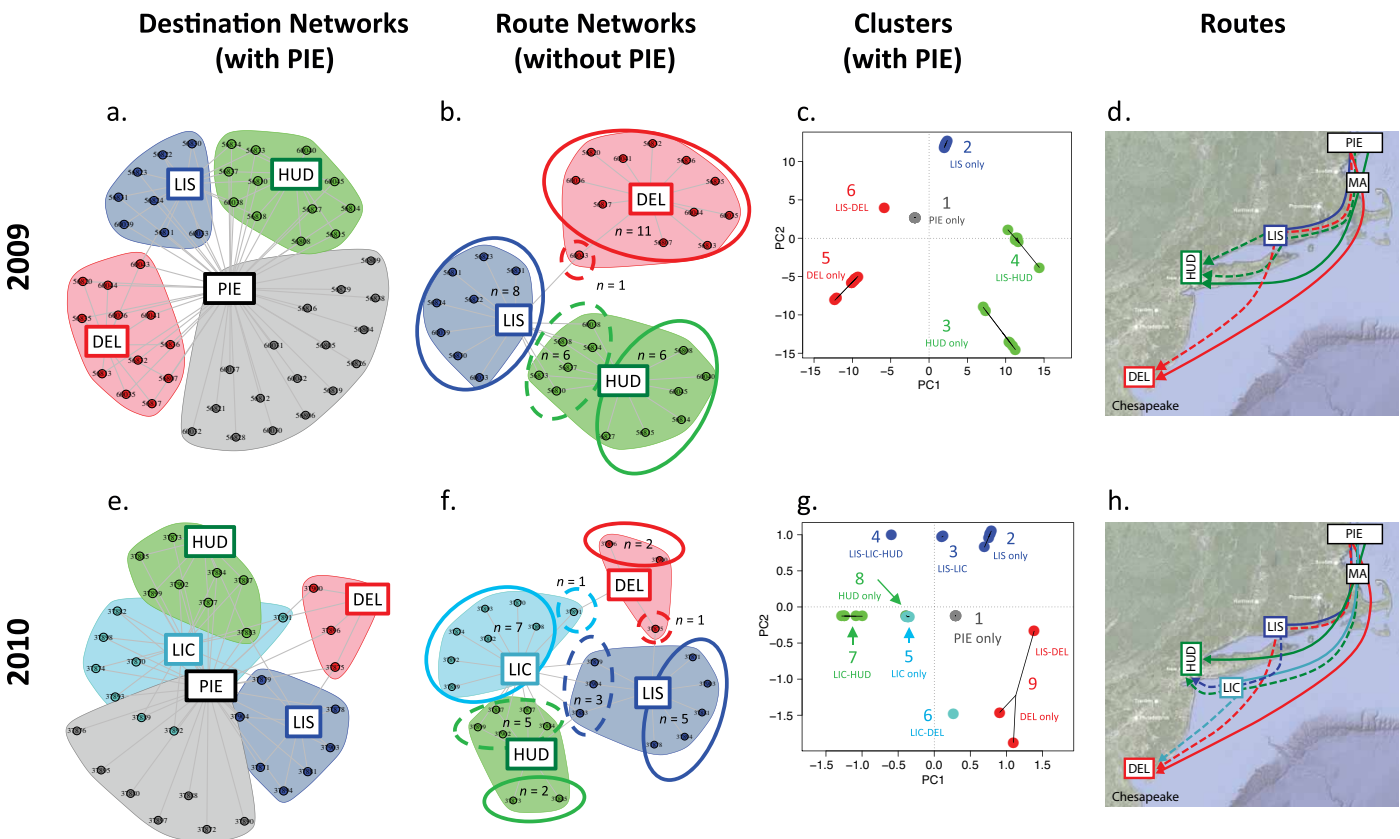## Internal Structure in the Southward Striped Bass Migration

Figure 3. For 2009 and 2010, the (a, e) destination networks including PIE, (b, f) route networks without PIE, (c, g) cluster analysis groups displayed in Principal Components Analysis (PCA) ordination space, and (d, h) the observed southward migration routes of striped bass. Colors in all panels correspond to groupings from community detection analysis. For 2009 (a–d), the four destinations are shown in gray, red, green, and blue, and the six types of routes are indicated as solid and dotted line circles. For 2010 (e–f), five destinations are shown in gray, red, blue, green, and aqua, and nine routes are indicated by solid and dotted line circles. Jaccard bootstrap mean values indicated stable clusters for groups that contained more than one individual striped bass (range = 0.74 to 1.00). (c, g) Colors used in the cluster analysis and (d, h) for the trajectories correspond to route networks.

Hudson and Delaware Rivers. Our tagged striped bass may also have traveled to the third major spawning location, Chesapeake Bay, but no gate was present in this system to detect coastal migrants. The migratory striped bass that we tagged in summer in Plum Island exhibited strong, within-year site specificity and fidelity to PIE (i.e., many fish stayed in this single estuary for a prolonged period). Tagged fish also returned to PIE the following spring, demonstrating across-year site fidelity. Although the striped bass we tagged went to multiple locations, they did not go everywhere. In fall, these migrants moved south to two different overwintering locations, adjacent to known natal estuaries, as well as to other general coastal locations, after which they were undetected. In a related study, 85% of the striped bass (mean = 426 mm TL, SE = 2, n = 97) caught in Massachusetts estuaries from spring through fall ate a seasonally dependent mix of fish and invertebrates (Ferry and Mather, 2012). This result demonstrates that active feeding occurs during the summer migration. The occurrence of migratory striped bass in multiple estuaries through spring-summer-fall (Mather et al., 2009), the seasonal residence of individual striped bass in specific estuaries (Able and Grouthues, 2007; Pautzke et al., 2010), and active foraging during the migration (Nelson et al., 2003) have been reported previously. However, individual striped bass have not been previously observed to stay a long time in a few foraging estuaries, leave those foraging estuaries in the fall, travel to specific, but different, overwintering areas, then return to the same northern estuaries the following year, as we observed here.

Because of their strong fidelity and specificity, striped bass have the potential to alter dynamics within and across estuaries. Striped bass can act as transport vehicles and export nutrients and energy to other estuaries hundreds of kilometers away. For example, the biomass striped bass gain in a single estuary like PIE could increase spawning stock biomass of coastal striped bass in the Hudson and Delaware estuaries. This increased striped bass biomass may intensify predation pressure on prey in connected natal estuaries, and eventually feed back to PIE across years. Migrating striped bass can potentially move substantial amounts of energy across estuaries. Thus, what happens in one estuary may impact distant locations. The magnitude of export of nutrients and energy by migrating fish from one coastal location to another location depends on many variables (e.g., cumulative time at each location, location-specific temperatures, location-specific amount-type of food consumed, fish size). In runs of a bioenergetics model parameterized for striped bass (Hartman and Brandt, 1995) and incorporating system- and season-specific temperatures and diets (Ferry and Mather, 2012), subadult and young adult striped bass (650–1,000 g) that stay in PIE from spring through fall (72 d) could consume 0.05 (spring), 0.01 (summer), and 0.05 (fall) grams of prey per gram of body weight per day. As a result, these fish could remove more than their initial body weight in prey from the source estuary and translocate the resultant biomass to another estuary. At present, the magnitude of this trophic transfer across systems is unknown.

Empirical tests are needed of how much energy is translocated across estuaries as well as how this export changes across system, years, seasons, and fish sizes. Consequently, variations in how fish migrate (e.g., estuary-specific trajectories, fidelity, migration timing, type of connectivity, and foraging behavior) will determine the degree of across-system impact that migrants have in PIE and other estuaries.

Internal Structure

Not all tagged migratory striped bass behaved the same, confirming the existence of internal structure in the coastal migration. Internal structure is any behavior(s) that results in consistent within-population differences among groups of fish. Striped bass tagged in PIE in summer went to at least three overwintering destinations (excluding PIE) via six (2009) and nine (2010) different routes. This diversity in movement groups, for the same-sized striped bass, was observed across multiple years although the composition of each group varied temporally. Behavioral groups are recognized with increasing frequency in ecology and fisheries (e.g., Conrad et al., 2011). For example, contingents related to spawning behavior and movements have been documented for Hudson River striped bass (Wingate and Secor, 2007), and different behavioral groups of striped bass have been observed within feeding estuaries (Able and Grothues, 2007; Pautzke et al., 2010). As a result, this within-population diversification can have ecological and evolutionary consequences (e.g., Chapman et al., 2011; Dall et al., 2012; Sih et al., 2012).

Fish Migrations

Few generalizations exist about specificity and fidelity of fish-related biotic connections even though reports of fish movements among distant spawning, foraging, and overwintering areas (the migration triangle of Harden Jones, 1968) are increasingly common. The return of fish to natal systems for spawning is the classic example of strong geographic specificity (e.g., Scholz et al., 1976; Quinn, 2004). In addition, many anadromous fish are assumed to return to the freshwater locations where they were spawned (untested spawning site fidelity; e.g., Frank et al. 2011). Prolonged fidelity to a specific locality for foraging, however, is less common (Buzby and Deegan, 2000; Solmundsson et al., 2005). Interestingly, migratory bull trout (*Salvelinus confluentus*), like migratory striped bass, remain in localized marine habitats during their migration (Hayes et al., 2011). Generalities about routes that fish use to transit among feeding, foraging, and overwintering locations are also limited at present. Diverse fish migration strategies exist across species and populations with potential survival consequences (Melnychuk et al., 2010; Dempson et al., 2011; Welch et al., 2011). Individual fish can be consistent in fidelity and migration timing but this consistency can vary across individuals within a population (Brodersen et al., 2012). Furthermore, environmental conditions may alter patterns of fish distribution and movements (Bottom et al., 2005). Geographic connectivity (i.e., specific links among feeding, spawning, and overwintering; Webster et al., 2002) is of increasing scientific interest in migratory fish research, but, again, general patterns of

connectivity have yet to be established. Thus, although an increasing number of puzzle pieces exist, a framework that unifies spatial and temporal patterns of fish movement (Nathan et al., 2008) and integrates disciplines (Giuggioli and Bartumeus, 2010) is still in its infancy. Here, we contribute to the maturation of this conceptual framework by proposing conditions that may explain variation in the impact of biotic connectivity across spatially segregated estuaries.

Animal Migrations

Beyond fish, there is a large volume of basic and applied research on animal migration that focuses on a variety of taxa, ecosystems, and conceptual frameworks (e.g., Webster et al., 2002, Wilcove and Wikelski, 2008). This substantial and rapidly growing literature on biotic connectivity is diverse. For example, many studies examine how migratory mammals connect terrestrial landscapes (e.g., Boone et al., 2006; Morrison and Bolger, 2012). Long-distance migration research has been dominated by avian studies (e.g., Catry et al., 2011; Vardanis et al., 2011; Stanley et al., 2012). However, the rapidly increasing body of literature on fish movements can add significant new dimensions to general migration theory (e.g., Radinger and Wolte, 2013). Migration represents an extreme case of motility. In ecology, movement is important to a diverse array of concepts such as population regulation (e.g., Hixon et al., 2002), across-system subsidies (Polis et al., 1997), and metapopulations and meta-communities (Kritzer and Sale, 2004; Holyoak et al., 2005; Logue et al., 2011). Concepts related to spatial segregation of mobile organisms (e.g., trophic relay

[Kneib, 1997]; shifting interaction zones [Kneib, 2000]) have also played key roles in estuarine ecological dynamics. A critical synthesis of this voluminous and expanding literature is needed that connects and integrates results of movement studies across taxa, ecosystems, and disciplines to identify information gaps and guide future research needs.

Future Directions

Although new tracking technologies provide the ability to answer a host of research questions about patterns, causes, and consequences of movement, an integrated research strategy for migration is needed that combines multiple perspectives, disciplines, and approaches (Bowlin et al., 2010). First, coastal researchers and managers need to tag fish of similar species and sizes at similar times using similar methods in order to better understand general patterns of connectivity, specificity, and fidelity. Standardized tagging and monitoring should be undertaken in an array of estuaries along the coast across seasons and years. Without this expansion of standardized tagging and consistency in monitoring, we will never know if tagged fish visit other estuaries, if the movement patterns we observed in PIE are unique or a general rule, nor will we understand how variation in connectivity affects distant ecosystems. Second, researchers need to better understand across-year variability. We found both similarities and differences in routes and destinations used by striped bass across years (Mather et al., 2010; this study 2009 vs. 2010). This result likely reflects both natural variations in patterns and methodological differences. Third, researchers need to provide complete

trajectories for individuals across the range of migration (i.e., how locations of migratory fish change through time). For the data presented here, we need to link the southward and northward migrations. These complete trajectories are difficult data to obtain but are essential to understanding migratory connectivity. Fourth, researchers need to quantify fitness consequences of migration strategies (e.g., the effect of time or behavior at specific feeding or over-wintering locations on survival, growth, and reproductive success). In addition, a better understanding is needed of the mechanisms underlying migration. For example, fish spawned in Delaware Bay that repeatedly migrate north to PIE may forage more effectively in PIE by learning how to feed under specific conditions. They may return to the same foraging location with which they have had success for several years. As a result, they may become more efficient predators, maximizing their growth, intensifying their top-down impact on prey, and consequently exercising a stronger effect on estuarine productivity. As discussed above, better estimates are also needed of energy and nutrients exported by migrating animals. Finally, our understanding of biological connectivity would benefit tremendously from coupling ecological studies of coastal fish movements with concurrent oceanographic studies of physical processes, such as currents, that might influence fish migration (e.g., energy landscapes; Wilson et al., 2012).

Applications

Estuaries are spatially and temporally complex ecosystems used by important commercial fishes and shellfishes,

including many migratory fish. Many of the most spectacular migrations are severely threatened by human activities (Wilcove and Wikelski, 2008). Harvest and fishing pressure, as well as other anthropogenic effects such as hypoxia and coastal river dams, can adversely affect biotic connectivity. Our results suggest that a more holistic approach is needed to coastal management rather than the site-specific management of estuarine and coastal resources that is often undertaken at present. Agencies at both state and federal levels seek to develop approaches to fisheries management that ensure long-term sustainability. A better understanding of patterns, consequences, and causes of biotic connectivity at a range of scales would support the development of these cohesive, coast-wide conservation strategies.

CONCLUSION

In summary, our research has advanced what is known about patterns of biotic connectivity, especially the complexity and heterogeneity of fish migration. The long-term focus of LTER research at PIE permits the development of increasingly complex questions that could not be anticipated a priori (Dodds et al., 2012). Our research started with simple striped bass distribution-feeding relationships, progressed to local movements, evolved to coastal movements, and finally advanced to making connections across estuaries. This type of sequential, focused, in-depth research on variations in when, where, and how fish migrate is essential for a much-needed understanding of how biotic connectivity affects coastal ecosystems.

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