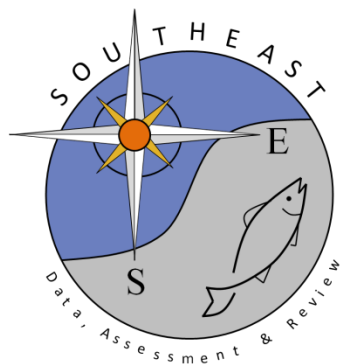


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ARTICLE

Managing a Marine Stock Portfolio: Stock Identification, Structure, and Management of 25 Fishery Species along the Atlantic Coast of the United States

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Abstract

In this review, stock identification methods used, resulting stock numbers and boundaries, and assessment and management context were explored for all 25 species managed by the Atlantic States Marine Fisheries Commission (ASMFC). This included invertebrates and vertebrates distributed between Maine and Florida, with a few species ranging across all these states and some ranging into the Gulf of Mexico and the Canadian Maritimes. The effects of larval dispersal or mixing of adults in the marine environment were evident. Marine and catadromous spawners were recognized and treated as a unit stock (e.g., northern shrimp *Pandalus borealis*, American Eel *Anguilla rostrata*, Atlantic menhaden *Brevoortia tyrannus*, Bluefish *Pomatomus saltatrix*, Tautog *Tautoga onitis*), a metapopulation (American lobster *Homarus americanus*, Atlantic Herring *Clupea harengus*), or two stocks, north and south of Cape Hatteras, a major biogeographic boundary, (Black Sea Bass *Centropristis striata*, Scup *Stenotomus chrysops*, Red Drum *Sciaenops ocellatus*, Summer Flounder *Paralichthys dentatus*). Estuarine and anadromous spawners were structured and managed at a finer spatial scale (horseshoe crab *Limulus polyphemus*, Atlantic Sturgeon *Acipenser oxyrinchus*, American Shad *Alosa sapidissima* and the river herrings Blueback Herring *A. aestivalis* and Alewife *A. pseudoharengus*, and Spotted Seatrout *Cynoscion nebulosus*). A broad suite of stock identification methods have been applied to ASMFC species and reviewed here in five categories: life history traits, other phenotypic traits, genetic traits, natural marks, and applied marks. An interdisciplinary mix of methods has been achieved for a few species (Striped Bass *Morone saxatilis*, Winter Flounder *Pseudopleuronectes americanus*), but only a few or no stock identification methods have been applied to others (Spiny Dogfish *Squalus acanthias*, Hickory Shad *A. mediocris*, Spot *Leiostomus xanthurus*, Spanish Mackerel *Scomberomorus maculatus*). Clinal phenotypic variation has contributed to several long-standing debates about stock structure; some of these have been recently reevaluated as a unit stock (Atlantic Croaker *Micropogonias undulatus*, Weakfish *Cynoscion regalis*), and others are still debated. For some ASMFC species, other priorities (e.g., bycatch) dominate the uncertainty of the assessment or management process. Otherwise, stock identification remains a research priority for most of these species. Continued research of this subject should consider (1) research priorities tabulated by ASMFC review panels, (2) strategic use of interdisciplinary stock identification methods, (3) use of experiments or reaction norms to separate phenotypes from genotypes, (4) genetic surveys at a seascape scale, (5) demonstration of contingent (nongenetic) structure and its implications for management, and (6) simulation modeling. Obstacles to adopting finer-scale structure into assessments or management of ASMFC fisheries include: (1) multiple stock units are apparent but boundaries are not clear, (2) monitoring requirements for smaller areas or for mixed-stock catches are not cost effective, or (3) mixing rates within a metapopulation or across biogeographic boundaries are poorly described.

Fisheries exploit stocks of fish, and historically, fishery stock units were defined by patterns in fishing activity alone. This created, and in many cases continues to create, mismatches of bio-

logical processes and management action (Halliday and Pinhorn 1990; Lear 1998; Waldman 2005a). Recognition of a “harvest stock,” or similar terms, where the effects of exploitation on

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one stock is independent of another stock, is an improvement in terminology but does little to clarify the biological basis of a stock (Hammer and Zimmermann 2005). A stock should comprise all age-classes, be self-reproducing, and express at least one distinguishing biological feature (Lebedev 1967). Phenotypic information has a long history of use in defining stocks, particularly the use of vital rates to measure and manage independent population units, but additional work is often required to distinguish a genetic versus ecophenotypic basis for such variation (Secor 2005; McBride 2014). The genetic basis for defining stocks has broad utility for fisheries management, but strictly genetic definitions are confounded by low levels of gene flow (i.e., straying), recent colonization events, poor sampling coverage, low resolution of pioneering genetic methods, and difficulty of incorporating purely genetic data into the management process (Grunwald et al. 2008; Waples et al. 2008; Reiss et al. 2009). One existing definition that captures a modern synthesis of both phenotype and genotype is “a group of organisms whose demographic/genetic trajectory is largely independent of other such groups” (Waples 1998). Herein, I use the term stock in this modern context to recognize it as a biological population that is subject to the effects of fishing.

Defining a stock's spatial boundaries is the first step of the assessment process (NRC Committee on Fish Stock Assessment Methods 1998). Misspecification of the number of stocks can obscure the stock–recruitment relationship (Frank and Brickman 2000). Incorrect stock boundaries or poorly known mixing rates confound estimates of immigration and emigration (Hammer and Zimmermann 2005). When multiple stocks are fished as a simple aggregate, not only is the measurement of stock dynamics confounded, smaller stocks are at risk of overexploitation or extirpation (Ricker 1958; Hilborn 1985; Smedbol and Stephenson 2001; Reich and DeAlteris 2009). Loss of genetic diversity is a concern, particularly with regard to small stocks for which there is typically insufficient data to assess their status (Slaney et al. 1996; Olsen et al. 2008; Hu and Wroblewski 2009). Regardless of genetic structure, preserving phenotypic stock or contingent structure can enhance stock productivity, resilience, and stability (Secor et al. 2009; Petitgas et al. 2010; MacCall 2012).

In response to the increasing demands for identifying stock units, development of pertinent methods has steadily progressed (Cadrin et al. 2005, 2014a). Traditional methods, such as the use of life history parameters, morphometrics, or parasites as natural markers, are still part of the toolbox (Baldwin et al. 2012; McAdam et al. 2012; Zischke et al. 2013; Cadrin et al. 2014a). New technologies, such as otolith microchemistry, single-nucleotide polymorphisms, or electronic tags, have greatly expanded the toolbox (Hodgins-Davis et al. 2007; Rooker et al. 2007; Walther et al. 2008; Cadrin et al. 2014a). Experimental methods investigating reaction norms are becoming more feasible (Swain et al. 2005; Conover and Baumann 2009; Heino 2014), and a suite of methods exists for analyzing mixed-stock fisheries data (Prager and Shertzer 2005). In a growing

number of cases, an interdisciplinary set of methods or simulation modeling has improved confidence in our understanding of stock structure (Coyle 1997; Abaunza et al. 2008, 2014; Cadrin et al. 2014b; Kerr and Goethel 2014).

Herein, I review the marine stock portfolio managed by the Atlantic States Marine Fisheries Commission (ASMFC) (ASMFC 2013a, 2013b, 2013c). The ASMFC operates under the authority of the Atlantic Coastal Fisheries Cooperative Management Act to develop fishery management plans (FMPs) for 25 invertebrate and finfish species that reside in coastal waters along the U.S. east coast from Maine to Florida (e.g., Richards and Rago 1999; Table 1; Figure 1; Table A.1 in the Appendix). Both traditional and advanced stock identification methods have been applied to this marine stock portfolio. Initial FMPs of these species-based stock structure determinations were developed from extensive literature reviews, and the ASMFC continues to recognize the importance of this information by requesting and incorporating new research into stock structure determinations. Several types of stock structure are evident within this species portfolio. Most of these species are distributed across more than one major biogeographic region (Acadian, Virginian, and Carolinian; Briggs 1974; Ayvazian et al. 1992; Gabriel 1992) among a mosaic of bottom types or within a hydrodynamic milieu. These distributions may either induce connectivity between regions or promote disjunct stock structure along a latitudinal cline. Conversely, many ASMFC-managed species spawn in the open ocean, migrate seasonally in marine waters, and show little or no evidence of genetic structure. In over a third of the cases, these conditions support a single stock unit. Continued research is likely to reveal additional stock complexity, either in the underlying genetic structure or in the make-up of the conditionally based (nongenetic) contingents. Although challenges exist for uncovering and applying such new information into assessment and management, further evolution in research and application is still likely because of ongoing advances in the resolution or cost-effectiveness of stock identification methods, as well as because of our expanding awareness of the genetic and phenotypic complexity of stock structure and its value for the management of sustainable fisheries.

This review addresses these claims in seven sections. The first (Methods) provides an outline of how I reviewed the literature, which is followed with a brief summary of relevant terms and concepts of what stock structure looks like in open marine systems (Background). The largest section (Species Synopses) uses a standard format to state the recognized stock structure, summarize the supporting evidence, and highlight specific issues of each of the 25 ASMFC species. The next three sections are critiques. The first (Review of Methods Used) is of stock identification methods applied to ASMFC species, using the rubric of Cadrin et al. (2005); the second (Stock Structure Types) is of the diversity of stock structure among ASMFC species; and the third (Managing Stock Structure) is a perspective on the accomplishments and challenges ahead for managing these interjurisdictional fisheries. This assemblage provides a dynamic set of



FIGURE 1. The Atlantic coast of the United States. Individual coastal states are outlined and identified (FL, Florida; GA, Georgia; SC, South Carolina; NC, North Carolina; VA, Virginia; MD, Maryland; DE, Delaware; NJ, New Jersey; NY, New York; CT, Connecticut; RI, Rhode Island; MA, Massachusetts; NH, New Hampshire; ME, Maine). Other prominent locations mentioned in the text are identified, and the 50-fathom isobath is drawn to indicate the edge of the continental shelf.

TABLE 1. The interaction between spawning grounds and stock structure for 25 fishery species managed by the Atlantic States Marine Fisheries Commission. See Table A.1 for more complete taxonomic information and supplemental information about species ranges, life cycles, stock structure, methods for stock identification, and research and management status.

Stock structure	Spawning ground habitat		
	Marine	Estuarine	Freshwater ^c
Unit	Northern shrimp ^a Spiny Dogfish ^a American Eel Atlantic Menhaden Bluefish Spot Atlantic Croaker Tautog Spanish Mackerel	Weakfish	
Metapopulation	American lobster Atlantic Herring		
Multiple populations (latitudinal) ^b	Black Sea Bass Scup Red Drum ^d Summer Flounder	Horseshoe crab Spotted Seatrout Winter Flounder ^d	Atlantic Sturgeon American Shad Hickory Shad Blueback Herring Alewife Striped Bass

^aA unit stock in U.S. waters only; managed as separate stocks internationally.

^bMarine spawners have a disjunct stock boundary near Cape Hatteras; the multistock estuarine and freshwater spawners have finer-scale structure (i.e., regional to river-specific).

^cAnadromous fishes.

^dSpawns both in estuaries and nearshore marine.

case studies to explore the continued value of traditional stock identification methods, the uptake of new methodologies, the diversity of stock structure types in marine fishes, and the application of this information to manage these fisheries sustainably. A concluding section (Summary) includes recommendations for future research directions.

METHODS

To write this review, I have relied on my own experience (~30 years) of working with marine and diadromous fishes along the North American east coast, from the Gulf of Maine to the Gulf of Mexico, including experience as a state of Florida representative on ASMFC's technical committees. I also consulted with several others for discussion and feedback (see Acknowledgments).

In searching the literature, I started with the ASMFC website, where I reviewed the materials available under "Fisheries Management" (ASMFC 2013a). I also integrated into this review two recent summaries of stock status and research priorities (ASMFC 2013b, 2013c). The methods used to investigate each species' stock structure have been individually reviewed at one time or another as part of the original FMPs (ASMFC 2013a; MAFMC 2013). These documents are important historical records that provide details, and occasionally corrections, of original studies and changing approaches and interpretations

about stock structure. In a multispecies, multimethod review such as this I can only summarize this information (Tables 1, A.1) and leave the specifics to be found in these supporting documents.

Finally, I reviewed selected examples from related books, namely Cadrin et al. (2005), Kritzer and Sale (2006), and Cadrin et al. (2014a). Some papers were easily found, whether in the gray literature (e.g., Cadrin et al. 2004; NEFSC 2013) or the peer-reviewed literature (e.g., Waldman et al. 1988, 1997; DeCelles and Cadrin 2011). Many papers were only discovered by using an iterative approach with Boolean logic when searching the web (Eells et al. 2012).

BACKGROUND

The species managed under the authority of the ASMFC are distributed across a wide latitudinal range (Figure 1; Table A.1), so they are affected by a range of environmental conditions and geologic history. Average winter (February) temperature increases from 2.8°C (Eastport, Maine; 44.5°N) to 22.8°C (Miami Beach, Florida; 25.5°N), approximately 1°C per 1°N (Figure 2). This temperature gradient is discontinuous, particularly near the coast, where it is disrupted by capes that create biogeographic boundaries (Briggs 1974; Friedland and Hare 2007; Briggs and Bowen 2012). Seasonal temperature fluctuations within the Middle Atlantic Bight are

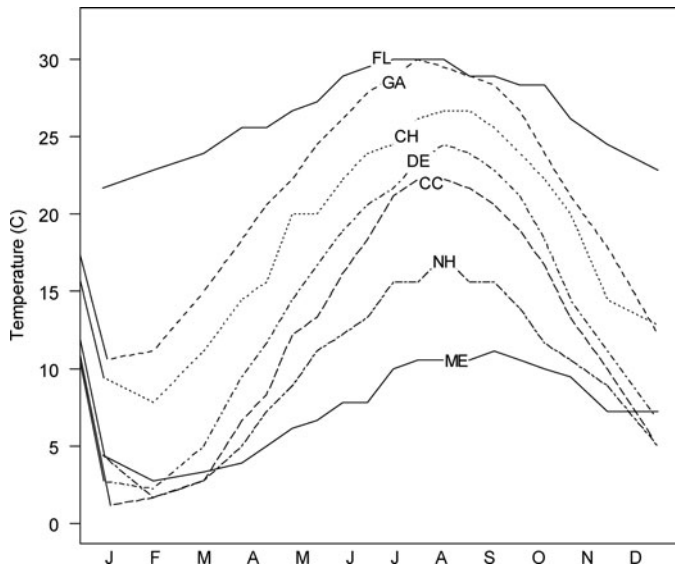


FIGURE 2. Seasonal temperature gradient along the Atlantic coast of the United States. Seasonal temperatures from January (J) to December (D) are plotted for Eastport, Maine (ME); Portsmouth Harbor, New Hampshire (NH); Woods Hole, Cape Cod (CC), Massachusetts; Lewes, Delaware (DE); Cape Hatteras (CH), North Carolina; Savannah Beach, Georgia (GA); and Miami Beach, Florida (FL). See Figure 1 for locations. Data are for 2012, downloaded from <http://www.nodc.noaa.gov/dsdt/cwtg/>.

among the most extreme in the world ($\sim 20^{\circ}\text{C}$; Parr 1933). Finally, this coastal region has experienced several Pleistocene glacial cycles, causing cyclic redistributions, extirpations, and recolonizations of many coastal species (Mach et al. 2011; Anderson et al. 2012).

In terms of life history, species managed by the ASMFC are quite diverse (Table A.1). Six species are anadromous, one is catadromous, and others are estuarine or marine residents, so their collective spawning habitats range from freshwater to marine biomes (Table 1). Philopatry has been demonstrated for the anadromous species, and limited movement (indolence) is evident for some of the estuarine spawners. Two temperate reef fishes are largely sedentary, except for the migratory contingent of Black Sea Bass *Centropristis striata*. Adults of some of these species become more migratory or change their migratory pathways with age. The ability to disperse during early life stages also varies widely. Some broadcast pelagic eggs, with a corresponding widespread dispersal of propagules, while others spawn benthic eggs, and a few carry or bury their eggs.

Given this environmental backdrop and life history variation, several types of stock structure may be expected among these species. The simplest is that of a single or unit stock. A unit stock would be perpetuated by high rates of mixing (i.e., gene flow) within the stock area. This may occur at one life stage, such as by dispersal of an early life stage, or by large home ranges and random mating by adults, or by more than one life stage (Hare 2005; McBride 2014). Dispersal of early

life stages or straying by adults can also lead to vagrancy, an inability to return to spawning grounds to mate (Sinclair 1988; McBride and Able 1998; McBride and Horodysky 2004). Migrants from different stocks may periodically mix, such as on feeding grounds, which may overlap with the fishing grounds and thereby complicate stock identification or assignment of stock-specific landings (McQuinn 1997; Rooker et al. 2007). At a more complex level, a metapopulation may exist, resulting in demographic or phenotypic heterogeneity but genetic homogeneity. In a metapopulation, local populations reside in specific habitat patches and interpatch connections exist but are not so strong as to negate local population dynamics (Sale et al. 2006). Acceptance of a metapopulation structure shifts the emphasis on managing total spawning biomass to maintaining some level of biomass in each spawning component.

Physical barriers within a species' geographic range can lead to stock structure. This can be expected at a macroscale, particularly as related to prominent points along the coast (i.e., capes), which are typically associated with abrupt changes in hydrography and environmental conditions. Along the east coast of the United States, major faunal breaks occur at Cape Canaveral (Florida), Cape Hatteras (North Carolina), and Cape Cod (Massachusetts) (Figure 1). Stock boundaries can also occur at a smaller scale. For example, Cunningham et al. (2009) described an isolation-by-distance pattern among Pacific Cod *Gadus macrocephalus* extending from Washington State to the Aleutian Islands; however, in fjords, which represent sharp barriers to migration and larval dispersal, Pacific Cod were genetically distinct.

Life history or behavioral differences can also contribute to stock structure (Sherwood and Grabowski 2010). When individuals have a strong association with a specific spawning ground, either remaining there (indolence) or returning there after a dispersed or migratory period (philopatry), stocks can arise from reproductive isolation. Philopatry can arise from natal homing, which is caused by imprinting on a specific environmental cue experienced when young, or by repeat homing, which is facilitated by young fish learning spawning routes from older fishes (Fromentin and Powers 2005; MacCall 2012). Differences in spawning location and timing can maintain reproductive isolation even for fish within the same river system. This is evident in the genetic discreteness of nonanadromous and anadromous forms of *Oncorhynchus mykiss* in the same river of Oregon (Zimmerman and Reeves 2000), or between odd and even year spawning stocks of the biennial Pink Salmon *O. gorbuscha* (Beacham et al. 2012). In the open marine environment, subtle behaviors related to depth preferences in spawning habitat can contribute to fine-scale structuring within the spawning ground of Icelandic (Atlantic) Cod *G. morhua* (Grabowski et al. 2011).

These behaviors do not need to be genetically determined (Secor 2005). A conditional response, such as growth rate, may determine whether an individual becomes resident or migratory among diadromous species (Thorpe 1987; Jonsson and Jonsson 2003). Within Chesapeake Bay, the initial physiological

condition of White Perch *Morone americana* had permanent consequences that affected their behavior, growth, and survival as adults, resulting in a portion of the population residing in freshwater and another portion migrating between natal, freshwater habitats and brackish habitats (Kerr et al. 2009). Model simulations revealed that the resident contingent contributed mostly to population stability whereas the dispersive contingent contributed mostly to productivity and resiliency (ability to rebuild from an overexploited state; Kerr et al. 2010a).

Ready solutions to define, identify, and monitor stock structure are much needed for sustainable management. Stock structure can be dynamic, even lost, as many populations become overfished (Ames 2004; Wright and Trippel 2009; Fowler 2011). Stock boundaries may shift in response to environmental change (Nye et al. 2009). Mismatches between genetic units and fishery units persist (Laikre et al. 2005; Reiss et al. 2009), and a better understanding of phenotypic variability within and between stocks is necessary to determine fishery yields, use maturity data to calculate spawning stock size, or understand how conditional or culturally transmitted life history traits contribute to stock productivity, resilience, or stability (Petitgas et al. 2010; MacCall 2012). The following review of species, methods, and patterns of stock structure captures in time the practice of stock structure identification and its application in regard to fishery management of 25 species along the U.S. east coast.

SPECIES SYNOPSES

The following species synopses are in phylogenetic order. Each synopsis briefly describes (1) a species' geographic range, (2) a statement about its stock structure, (3) data supporting its stock structure, (4) how such information affects stock assessment and management, and (5) what research priorities remain in relation to stock structure (see also Table A.1).

Invertebrate Species

Horseshoe crab *Limulus polyphemus* is distributed from the Gulf of Maine to the Gulf of Mexico. Habitat use, genetics, size, and thermal tolerance vary with latitude, and in Atlantic waters, four stocks (southeast, Delaware Bay, New York, and New England) are recognized. Horseshoe crabs reside year-round in estuaries of the Gulf of Maine (Moore and Perrin 2007; Schaller et al. 2010), so they do not migrate out into the gulf (Botton and Ropes 1987). Farther south, horseshoe crabs are distributed both within estuaries and on the continental shelf (Botton and Ropes 1987; Swan 2005). A survey of microsatellite DNA loci reveal an isolation-by-distance pattern (King et al. 2005), with a strong break near northeastern Florida (Saunders et al. 1986). Delaware Bay and the Chesapeake Bay, the two most important spawning areas, are genetically distinct (Pierce et al. 2000). Horseshoe crabs spawn in estuaries, laying eggs in sand (Leschen et al. 2006), and their larvae have limited dispersal even within the estuary (Botton and Loveland 2003). Smaller adults are found at both the northern and southern extremes (Riska 1981; Sekiguchi

and Shuster 2009), and horseshoe crabs from southern Florida cannot survive temperatures typical of Massachusetts, and vice versa (Mayer 1914; Sekiguchi and Shuster 2009). Abundance, harvest pressure, population trends, and regulations vary greatly among the regions (ASMFC 1998b; Smith et al. 2009). The Delaware Bay population is of particular concern because of an ecological link between horseshoe crab spawning and shorebird migrations (Smith et al. 2006), and stock discrimination is an ongoing concern because at least a portion of the landings in several neighboring states can be attributed to this bay (ASMFC 2012b). Sampling near Delaware Bay, Cape Hatteras, and in southern Florida is still a research priority to determine stock boundaries and mixing dynamics (King et al. 2005; ASMFC 2009b, 2013c).

American lobster *Homarus americanus* is distributed as a stock complex in U.S. and Canadian waters, representing a metapopulation (Fogarty and Botsford 2006). Three stocks (Gulf of Maine, Georges Bank, and southern New England) are recognized in U.S. waters, but more are plausible, especially with regard to inshore and offshore components of these populations (ASMFC 2010a). Regulations are applied to nine smaller management areas (ASMFC 2013b). Stocks are defined by migration patterns, location of spawners, and the dispersal and transport of larvae. There is evidence of morphological and genetic differences between stock areas, as well as differences between coastal and offshore areas. In some stock areas, coastal lobsters are smaller (Chen et al. 2006), move less (Haakonsen and Anoruo 1994), have a distinct morphology (Cadrin 1995), and are genetically distinct (Crivello et al. 2005; Hodgins-Davis et al. 2007); these patterns are less evident in Canadian waters (Hare 2005). Patterns of larval dispersal suggest that the coastal and offshore components are not independent (Hare 2005), and there are transient and resident lobsters within stock areas (Geraldini et al. 2009). Fogarty and Botsford (2006) summarized the evidence indicating that inshore areas, where fishing effort is highest, receive recruitment subsidies from offshore areas. Recently, a lower abundance reference point was set for the southern New England stock, because environmental changes in this region are predicted to impede efforts to rebuild this stock to historical levels (ASMFC 2010a, 2013b). One stock-related priority still recognized by the ASMFC is to align the American lobster management areas with the areas used to aggregate landings (ASMFC 2013c).

Northern shrimp *Pandalus borealis* is managed as one stock (Gulf of Maine) in U.S. waters (ASMFC 2011a). This is the southernmost stock of a species that is also managed in Canadian waters and throughout the north-central and northeastern North Atlantic Ocean (Fogarty and Botsford 2006; Richards et al. 2012). There is little evidence of genetic structure in Canadian or northeastern Atlantic waters (summarized by Fogarty and Botsford 2006), but the timing of shrimp spawning in different areas suggests local adaptation, because this timing matches the different regional peaks in food suitable for larvae (Koeller et al. 2009). Worm and Myers (2003) reported large-scale coherence

in population biomass trends among northern stock areas, but biomass of the Gulf of Maine stock fluctuates independently of these northern stocks, suggesting a lack of connectivity between the U.S. Gulf of Maine and other stocks. Specific biomass declines in the Gulf of Maine are associated with notably warmer temperatures in the 1950s and in the past decade (Shumway et al. 1985; Richards et al. 2012). Understanding the mechanistic links between climate and northern shrimp recruitment is the focus of most research priorities for this species rather than stock structure (ASMFC 2013b, 2013c).

Dogfish, Sturgeon, Eel

Spiny Dogfish *Squalus acanthias* is distributed worldwide on continental shelves, at boreal and temperate latitudes. In the western North Atlantic Ocean, it is most abundant from Nova Scotia to Cape Hatteras (Stehlik 2007; Veríssimo et al. 2010). The ASMFC comanages Spiny Dogfish as a unit stock together with the Mid-Atlantic Fishery Management Council (MAFMC) and the New England Fishery Management Council (NEFMC; ASMFC 2002a, 2012a). No genetic differentiation is evident along the North American east coast (Annand and Beanlands 1986; Campana et al. 2007; Veríssimo et al. 2010), but the evidence is either restricted to allozymes or to global phylogeographic surveys that have not sampled intensively along the U.S. east coast (McCauley et al. 2004). This suggests that additional work with more information-rich genetic markers at a seascape level is warranted. In an extensive review of tagged fish, Campana et al. (2007) observed a mixing of Canadian and U.S. Spiny Dogfish in the Gulf of Maine. They proposed a metapopulation structure with at least one sink population in Canada. An ongoing mark–recapture study shows extensive mixing of both sexes between the Gulf of Maine, Georges Bank, and the Middle Atlantic Bight (Northeast Fisheries Science Center, National Marine Fisheries Service, unpublished data). Campana et al. (2009) reported that Spiny Dogfish has low reproductive potential in Canadian waters, so ecophenotypic differences along a latitudinal gradient are possible. Continued research of genetic stock structure, migration patterns, and mixing rates remains a high priority research area (ASMFC 2013c).

Atlantic Sturgeon *Acipenser oxyrinchus* is anadromous and spawns in rivers from eastern Canada to Florida (Waldman et al. 2002; McBride and Matheson 2011). Five population segments are presently recognized, but as few as a single to as many as nine distinct population segments have been proposed (ASMFC 1998a; Grunwald et al. 2008; Kocik et al. 2013). There is clinal variation in growth and age at maturity (Smith 1985; Smith and Clugston 1997), and most rivers contain genetically distinct populations (Wirgin et al. 2000; Waldman et al. 2002; Grunwald et al. 2008). They are philopatric, but during the marine phase, tagged fish are known to move considerable distances away from natal systems and straying is evident (Dovel and Bergstrom 1983; ASMFC 1998a; King et al. 2001). All five population segments are listed as endangered or threatened in the USA, and the species is managed under a moratorium on

directed fishing from Maine through Florida (Kocik et al. 2013). Research priorities related to stock structure are focused on regional stock enhancement by aquaculture or discrimination of stocks in nontarget bycatch (ASMFC 2013c).

American Eel *Anguilla rostrata* is catadromous and inhabits aquatic habitats of the North American Atlantic coast from Canada to Florida, as well as Gulf of Mexico drainages (Tesch 1977; Vélez-Espino and Koops 2010; McBride and Matheson 2011). American Eel is managed as a unit, coastwide stock from Maine to southern Florida, with the future potential for joint management with Gulf of Mexico and Canada (ASMFC 2000). Although the classical view is that *Anguilla* species reside in freshwater habitats for many years, there is mounting evidence of contingents arising from partial migration, where a portion of the stock moves between freshwater and estuarine habitats, and other individuals may not even leave marine habitats (Secor 2005; Jessop et al. 2008). There is a latitudinal gradient in size, age, and reproduction (Oliveira 1999), but this appears to be driven by productivity gradients and distance from the spawning grounds (Vélez-Espino and Koops 2010). This species' genetic structure appears to be persistently panmictic (Tseng et al. 2006; Gagnaire et al. 2012), and stock structure research is not listed as a priority (ASMFC 2013c). The chronic, depleted state of this fishery species has led to a petition to list it as endangered, and most research priorities are focused on improving fishery, habitat, and life history information (ASMFC 2013b, 2013c).

Shad and River Herrings

Shad and river herrings (*Alosa* species, subfamily Alosinae) are all anadromous. Data collection and assessment are heavily biased towards American Shad *Alosa sapidissima*, where regional stocks are recognized and state-specific assessments have been completed (ASMFC 2007). Historically, American Shad was found in about 130 rivers, but it is found in only about half (70) of these today as a result of habitat loss (Limburg et al. 2003), and its fishery status is considered depleted (ASMFC 2013b). Interpretation of genetic stock structure of shad and river herrings is confounded by the common, historic practice of stock transfers between rivers and between states. In U.S. waters, genetic structure of American Shad is apparent at only the regional scale (Nolan et al. 2003; Hasselman and Limburg 2012), whereas in Canada, where artificial stock transfers were not common, genetic population structure is evident at the river scale (Hasselman et al. 2009, 2010). American Shad exhibit philopatry (Hollis 1948; Melvin et al. 1986; Walther et al. 2008), which would support river-specific populations. Latitudinal variations in life history characteristics are evident from Canada to Florida (Leggett and Carscadden 1978; Limburg et al. 2003); meristic and morphometric parameters also vary with latitude (Melvin et al. 1992). Research priorities related to stock structure emphasize using native broodstock when restoring stocks by aquaculture to preserve genetic integrity and the potential for stock-specific adaptive phenotypes (ASMFC 2013c).

Hickory Shad *A. mediocris* is distributed from the Gulf of Maine to Florida but appears to spawn only as far north as Maryland (Munroe 2002a; Harris et al. 2007; Murauskas and Rulifson 2011). There are no specific data on genetic structure or philopatry of Hickory Shad, but river-specific stock structure is assumed by proxy. Although there have been anecdotal reports that this species' abundance is increasing (Waldman 2006), no comprehensive, coastwide assessment of Hickory Shad exists, and few states have assessed this species in local waters. River herrings (Blueback Herring *A. aestivalis* and Alewife *A. pseudoharengus*) also appear to be philopatric (Gahagan et al. 2012). They demonstrate genetic structure at least at a regional scale, where three Alewife stock complexes and four Blueback Herring stock complexes are recognized (Palkovacs et al. 2014).

For all Alosinae, concerns about cryptic overexploitation of small populations via ocean fisheries, particularly those targeting Atlantic Herring *Clupea harengus* and Atlantic Mackerel *Scomber scombrus*, has led to modification of the original FMP and reinstated a more river-centric approach to management (ASMFC 1999, 2013c; McBride and Holder 2008; Davis and Schultz 2009; Bethoney et al. 2013; Cronin-Fine et al. 2013). Recently, a determination to list river herrings as threatened failed (NOAA 2013), but concerns continue because river-specific data are not available for all stocks, especially for the smaller stocks (ASMFC 2007, 2009a, 2012c, 2013c). Morphometric analysis appears to be emerging as a promising, readily available tool to discriminate stocks of the river herrings (Cronin-Fine et al. 2013).

Other Herrings

Atlantic Menhaden *Brevoortia tyrannus* is distributed from Canada to southern Florida, and tag returns demonstrate extensive migrations above the Atlantic Continental Shelf (Ahrenholz 1991). As many as three stocks have been postulated based on morphometric and meristic data (Ahrenholz 1991), but these appear to be ecophenotypes. Atlantic Menhaden have a homogeneous genetic population in Atlantic waters (Lynch et al. 2010), and presently, it is managed as a unit stock (ASMFC 2001). Although its larvae and juveniles are strongly associated with estuaries, spawning occurs from estuarine to open-shelf habitats resulting in widespread dispersal of propagules (Ahrenholz 1991; Epifanio and Garvine 2001; Warlen et al. 2002). The fishery was historically distributed coastwide; however, in recent years over half the landings come from Chesapeake Bay, so this region has become the focus of stock assessment and management (ASMFC 2011b; Lynch et al. 2011; Smith and O'Bier 2011). Most research priorities are focused on collecting spatially explicit data within the broad, unit stock area, and using multispecies models to assess this forage species in an ecosystem context (ASMFC 2013c).

Atlantic Herring is distributed in a complex of spawning populations on both sides of the Atlantic Ocean, representing metapopulation stock structure (McQuinn 1997; Hare and Richardson 2014). In U.S. waters, assessment and allocation of

catch recognizes four management areas comanaged with the NEFMC (Kritzer and Liu 2014). These management areas are defined by spawning, movement of the fish, and harvesting and processing by the fishery: inshore Gulf of Maine, offshore Gulf of Maine, Georges Bank, and a southern coastal stock (i.e., south and west of Cape Cod) (ASMFC 2006). Genetic evidence supports isolation by distance among U.S. and Canadian stocks, but there is little evidence for natal homing and specific evidence of mixing in the Gulf of Maine (Kornfield and Bogdanowicz 1987; McPherson et al. 2001, 2003; Hare 2005). Similar recruitment patterns along the Maine and New Brunswick coasts are evident on the west side of the Bay of Fundy, such that U.S. assessments include these transboundary data (Shepherd et al. 2009). Stocks can be discriminated successfully on a variety of phenotypic characters, including life history characteristics, such as growth, reproductive biology, and geographic distributions, as well as morphometric and meristic characters (Lea 1919; Messieh 1972; Cadrin et al. 2004; Stevenson and Scott 2005). Fishery allocations are distributed by management areas to apportion catch among mixed shoals of herring stocks and to prevent overfishing of discrete, particularly smaller, spawning units (ASMFC 2013b; Kritzer and Liu 2014). Data limitations about mixing rates between spawning components hamper full actualization of policies aimed at managing herring metapopulation structure, so tagging, morphometrics, and related stock identification research remain a priority (Smedbol and Stephenson 2001; Secor et al. 2009; ASMFC 2013c).

Striped Bass and Black Sea Bass

Striped Bass *Morone saxatilis* is anadromous in the northern part of its range, north of the Carolinas (Waldman et al. 1997, 2012; McBride and Matheson 2011). The ASMFC manages Striped Bass as a stock complex, where three primary producer areas (Chesapeake Bay, Delaware Bay, and Hudson River) are distinct stocks contributing to a coastal migratory group (ASMFC 2013b). More stocks are plausible. River-specific stock structure along the U.S. Atlantic coast is documented by both phenotypic and genetic traits (Waldman et al. 1988, 1997; Waldman 2005b). In addition, Secor et al. (2001) identified riverine, estuarine, and coastal contingents in the Hudson River. Thus, there is stock structure between estuaries and substructure (contingents) within estuaries. Estuaries in North Carolina are provisionally considered a fourth source of coastal migrants, both because tagged Striped Bass from North Carolina estuaries make limited movements into coastal waters, and fish tagged in the north foray into coastal waters of North Carolina (ASMFC 2003). The fishery exploits mixed stocks in coastal waters. The composition of landings, even in major producer areas, is not monitored, so the effect is to manage this fishery as a single stock. In the past, when the Chesapeake Bay stock was considered overfished, a coastwide moratorium on fishing Striped Bass was imposed (Richards and Rago 1999). As this stock was rebuilt, the fishing ban was lifted. Special regulations for the Chesapeake Bay region and North Carolina estuaries are

presently in effect as a management equivalency, accounting for a lower size limit in these regions. Tagging methods are still regarded as a research priority to investigate migratory rates and pathways and the resulting stock composition (ASMFC 2013c).

Black Sea Bass spawns on the continental shelf from Cape Cod to the Gulf of Mexico in association with reef structure (Drohan et al. 2007; Fabrizio et al. 2014). Black Sea Bass is considered a unit stock north of Cape Hatteras, where the ASMFC comanages this stock with the MAFMC. Subpopulation structure of this northern stock is unresolved (NEFSC 2012), where several lines of evidence suggest more than one stock: (1) mitochondrial DNA polymorphisms exist within the exploitable stock from North Carolina to Massachusetts (McCartney et al. 2013), (2) ecophenotypes exist and are observable with meristic and morphometric characters (Shepherd 1991), and (3) different migratory contingents exist and either migrate north–south between the northern and southern portions of the Middle Atlantic Bight or undertake shorter, onshore–offshore migrations within the southern portion of the bight (Musick and Mercer 1977; Hood et al. 1994; Moser and Shepherd 2009). Across the species' range, persistent genetic differences are evident between Atlantic populations north and south of Cape Hatteras, as well as between the Atlantic Ocean and Gulf of Mexico (Bowen and Avise 1990; Roy et al. 2012; McCartney et al. 2013). South of Cape Hatteras Black Sea Bass are smaller and nonmigratory (Wenner et al. 1986; Hood et al. 1994); this southern stock is managed by the South Atlantic Fishery Management Council, as part of their snapper–grouper complex (SAFMC 2013). A variety of stock identification approaches are still regarded as research priorities: otolith microchemistry, genetic tools, and tagging (ASMFC 2013c).

Bluefish and Scup

Bluefish *Pomatomus saltatrix* ranges along the eastern coast of North America from the Gulf of Maine to Gulf of Mexico (Shepherd and Packer 2006). In Atlantic waters, Bluefish is comanaged as a single, unit stock with the MAFMC (MAFMC 1998), but historic determinations had suggested that this species has a more complex stock structure. Adults undergo extensive seasonal migrations above the continental shelf, and their spawning produces multiple intraannual cohorts, primarily during the spring and summer, and to a minor extent in the autumn (Kendall and Walford 1979; McBride and Conover 1991; McBride et al. 1993). Two processes appear to create pulses in these Bluefish cohorts: individuals are capable of spawning multiple times in a year (Robillard et al. 2008), and differential larval mortality or vagrancy may occur at certain times of the year (Hare and Cowen 1993). The spring-spawned cohort is typically dominant, and individuals of this cohort attain a larger size by their first winter (McBride and Conover 1991; Munch and Conover 2000). Lund (1961) counted Bluefish gill rakers and concluded that there are multiple phenotypic stocks along the Atlantic coast (Massachusetts–Florida). Tagging data also suggest contingent structure among adult Bluefish, where adults

of different sizes migrate differentially: smaller fish migrate largely north–south in nearshore waters, whereas larger fish migrate more offshore and do not migrate as far south in the winter (Lund and Maltezos 1970; Shepherd et al. 2006). These size-specific migratory patterns are postulated to arise from different physiological conditions among age-classes (Wuenschel et al. 2012). No genetic structure is evident along the U.S. east coast, despite a prolonged spawning season that produces intraannual cohorts of variable abundance, meristics that vary with latitude, and migratory patterns that vary with size-class (Graves et al. 1992a; Graves 1998). However, relative to the attention paid to other ASMFC species, the genetic data available for Bluefish appears rather limited. No research priority directly targets stock structure issues, but the ASMFC prioritizes efforts to improve or coordinate spatially explicit sampling (ASMFC 2013c).

Scup *Stenotomus chrysops* was initially regarded as two species, one each north and south of Cape Hatteras (Steimle et al. 1999). These species have now been combined and the population north of Cape Hatteras, where the fishery is concentrated, is comanaged as a single, unit stock by the ASMFC and the MAFMC (MAFMC 1996). Meristic, morphometric, and tagging data have suggested contingent populations of Scup occupy waters north and south of Cape Hatteras (Mayo 1983; Love and Chase 2009; Chase 2011). The fishery operates in the northern region, where abundance is highest. Coastal spawning and seasonal movements by adults create conditions for gene flow, and there is specific evidence of northern fish migrating south of Cape Hatteras. No stock structure research is identified as a priority (ASMFC 2013c), but Chase (2011) notes that seasonal mixing appears offset from the spawning period, so further investigation of genetic structure appears warranted.

Sciaenids

Spotted Seatrout *Cynoscion nebulosus* spawns in estuaries from Chesapeake Bay to the Gulf of Mexico (Roumillat and Brouwer 2004; Smith et al. 2008). This species is managed by the ASMFC as individual stock units at the state level, from Maryland to eastern Florida, because of an isolation-by-distance genetic structure, estuarine spawning, limited movements outside of estuaries, and differences in growth and mortality (ASMFC 1984a, 2011c). An isolation-by-distance genetic pattern is evident, whether measured with general proteins or allozymes (Weinstein and Yerger 1976; Ramsey and Wakeman 1987) or with microsatellites (Wiley and Chapman 2002; Ward et al. 2007). Spotted Seatrout show limited movements, rarely leaving the estuary. Size and growth rates vary between estuaries but interpretation of stock-specific effects are confounded by different sampling biases, environmental conditions, and fishing mortality rates (Iversen and Tabb 1962; Murphy and Taylor 1994; Murphy and McMichael 2003). Delineation of discrete spawning groups and limited movements of tagged fish have received most attention in the Gulf of Mexico (reviewed by Ward et al. 2007; Lowerre-Barbieri et al. 2009). A recent study that sampled 21 microsatellites from Spotted Seatrout sampled

at 18 sites between Texas and North Carolina identified three genetic stocks in the southeastern United States: (1) from Texas to Apalachicola Bay (western Florida), (2) from Apalachicola to Biscayne Bay (eastern Florida), and (3) from Sebastian Inlet (eastern Florida) to Morehead City (North Carolina; S. Seyoum, Florida Fish and Wildlife Conservation Commission [FWC], unpublished data). Determining mixing rates between North Carolina and Virginia and how hypothermal (winter) mortality may affect genetic diversity are still research priorities (ASMFC 2011c, 2013c).

Weakfish *Cynoscion regalis* spawns in estuaries during summer but migrates offshore during winter (Nye et al. 2008). It is managed as a unit stock from Cape Cod to eastern Florida, and while there is evidence of two stocks, defining a stock boundary has proven elusive (ASMFC 1985; NEFSC 2009). Multiple lines of evidence, such as clinal differences in meristic, morphometric, age, and growth patterns as well as tagging studies, support at least a north and south ecophenotype (ASMFC 1985). No genetic stock structure is evident throughout this range, whether based on allozymes, mitochondrial DNA, or microsatellites (Crawford et al. 1988; Graves et al. 1992b; Cordes and Graves 2003). Thorrold et al. (2001), using otolith microchemistry methods, reported philopatry among a majority of 1- and 2-year-old Weakfish from New York to Georgia. In summary, an isolating effect of philopatry at young ages should create conditions for separate stocks, but mixing among older age-classes appears sufficient to homogenize the genetic structure. Research employing tagging methods is considered a priority to further investigate stock identification, mixing, and overwintering patterns (ASMFC 2013c).

Spot *Leiostomus xanthurus* ranges from the central Middle Atlantic Bight south to the Gulf of Mexico. Spot is considered a unit stock from Delaware to eastern Florida, but this is a particularly data-poor species for assessment (ASMFC 2013b, 2013c). What little is known about Spot includes the following: Spot spawns above the continental shelf and spends its first year in estuaries (Govoni and Pietrafesa 1994); larvae can be dispersed from south to north of Cape Hatteras (Flores-Coto and Warlen 1993); larger and older fish exist in the northern part of their range (ASMFC 1987a). Measuring the extent of stock mixing during autumn with genetic and tagging studies has long been a research priority (ASMFC 1987a, 2011c, 2013c).

Atlantic Croaker *Micropogonias undulatus* is distributed from New Jersey to eastern Florida, and into the Gulf of Mexico. Separate assessments, north and south of Cape Hatteras, were completed until 2003, but have since been done on a coastwide basis (ASMFC 2013b; Munyandorero 2014). Separate assessments were based on life history information that fish north of Cape Hatteras spawn earlier, mature later, grow larger, and live longer than conspecifics south of Cape Hatteras (White and Chittenden 1977; ASMFC 1987b); however, subsequent analyses did not find larger, older fish north of Cape Hatteras (Barbieri et al. 1994). Parasite data also supported existence of two stocks, one north and one south of Cape Hatteras

(Baker et al. 2007), but otolith microchemistry data did not (Thorrold et al. 1997). Lankford et al. (1999) reported evidence of substantial gene flow between these putative stock areas, based on a survey of mitochondrial DNA variations. In addition, Lankford and Targett (2001a) employed the unusual but rigorous approach of a single laboratory experiment to disentangle genetic and phenotypic effects on growth and cold tolerance in young-of-the-year Atlantic Croaker (i.e., a common garden experiment using fish collected from Delaware, North Carolina, and Florida). These results suggest that northern fish have a genetically determined higher capacity for growth or are better able to tolerate colder temperatures, but this variation among individuals does not manifest itself as local adaptation. The temperature-mediated effects expected to affect juvenile survival can indeed predict abundance and distribution (Lankford and Targett 2001b; Hare and Able 2007), but offshore spawning and coastwide movements of adults appear sufficient to mix the genotypes among northern and southern locales. Although collaborative, coastwide studies to examine genetic structure, migration patterns, and mixing rates are still considered high research priorities, the main source of uncertainty in this fishery assessment is the high but difficult-to-measure bycatch rates of Atlantic Croaker in the penaeid shrimp fishery (ASMFC 2010b, 2013b, 2013c).

Red Drum *Sciaenops ocellatus* spawns in estuaries and coastal habitats from Chesapeake Bay to Gulf of Mexico drainages (Johnson and Funicelli 1991; Murphy and Crabtree 2001). The Atlantic stock of Red Drum is managed as two units, north and south of the North Carolina–South Carolina border. This split is based largely on life history differences (e.g., maximum age), an isolation-by-distance genetic pattern, and tagging data. Red Drum in North Carolina grows longer and lives longer than conspecifics to the south (Ross et al. 1995). Atlantic and Gulf populations are genetically distinct, whether based on allozymes, mitochondrial DNA, or microsatellites (Gold et al. 1994; Seyoum et al. 2000; Gold and Turner 2002); this pattern was also evident with otolith microchemistry (Patterson et al. 2004). Genetic structure follows an isolation-by-distance pattern from Florida to North Carolina (Gold et al. 1999). Specific evidence for the stock boundary comes in the form of tagging data. Adults move well out into the coastal environment, and although little mixing of tagged fish occurs between neighboring states, mixing occurs at higher rates in the northern part of the range, specifically between North Carolina and Virginia (ASMFC 1984b, 2002b; Bachele et al. 2009). Continued tagging studies are considered a research priority to clarify how movements affect abundance, mortality, and mixing of Red Drum stocks (ASMFC 2013c).

Tautog and Mackerel

Tautog *Tautoga onitis* ranges from Canada to the Carolinas but is most abundant from Cape Cod to Chesapeake Bay (Steimle and Shaheen 1999). This species is managed as a unit stock (ASMFC 1996) based on data showing restricted

movements by adults and genetic homogeneity. Tautogs reside year-round in association with deeper (<75 m) hard-bottom habitat, but individuals also move inshore (<10 m) seasonally (Hostetter and Munroe 1993; Arendt et al. 2001; Munroe 2002b). Orbacz and Gaffney (2000), using mitochondrial DNA and nuclear (intron) DNA, found no significant genetic differentiation to support more than a unit stock. Tuckey et al. (2007) reported lower mortality rates offshore of the Chesapeake Bay than farther north in the mid-2000s, but these lower mortality rates did not persist and have not changed the status of a unit stock. Stock structure research regarding this data-poor species is not considered a priority (ASMFC 2013c).

Spanish Mackerel *Scomberomorus maculatus* ranges from New York to Florida and throughout the Gulf of Mexico (Collette 2002). The Atlantic stock is assessed and comanaged with the South Atlantic Fishery Management Council (SAFMC) as a unit stock from New York to eastern Florida (ASMFC 1990, 2011c). Spawning is protracted, from May to September, in depths < 40 m above the continental shelf (Collins and Stender 1987). No genetic structure has been detected across this geographic range using mitochondrial DNA and nuclear (intron) DNA (Buonaccorsi et al. 2001), but stock identification research is still regarded as a priority research area for this species, specifically to explore finer-resolution genetic structure (ASMFC 2011c, 2013c).

Flounders

Summer Flounder *Paralichthys dentatus* spawns above the continental shelf from Georges Bank to Florida (Able et al. 1989; Packer et al. 1999). The ASMFC comanages Summer Flounder with the MAFMC as a unit stock from North Carolina northward, where over 70% of the harvest is landed in New York and New Jersey (ASMFC 1982; MAFMC 1991; Terceiro 2011). The issue of stock structure has focused on populations north and south of Cape Hatteras, where broad evidence, including larval distributions, meristic and morphometric data, and movements inferred from tagging, suggested ecophenotypes exist. In a common garden experiment, Burke et al. (2000) reported some physiological differences in larval growth between fish from south and north of Cape Hatteras, but these differences were not consistent across temperatures or relative to predictions. In another laboratory experiment using juveniles, Malloy and Targett (1994) reported higher growth rates and higher growth efficiencies, but decreased tolerance to cold temperature for Summer Flounder from North Carolina compared with fish from Delaware Bay. Kraus and Musick (2001) summarized additional evidence for possible spawning groups above the shelf, latitudinal variation in growth rates, and movement patterns to suggest that at least two stocks exist coastwide. Although some adults returned to their tagged area between years (Caposela et al. 2013), fish leaving estuaries also disperse broadly in shelf habitats (Henderson 2012), and Jones and Quattro (1999) report no genetic structure north or south of Cape Hatteras. Stock-structure-related research priorities are now focused on

approaches that could identify mixing rates around Cape Hatteras (ASMFC 2013c).

Winter Flounder *Pseudopleuronectes americanus* exhibits dramatic life history variability throughout its range, from Labrador to North Carolina. In the United States, three stocks are assessed, but this number has been higher in the past and life history variations exist within the coastal stocks. DeCelles and Cadrin (2011) summarized interdisciplinary evidence supporting stock structure, including meristic and morphometric data, parasite markers, little movement—particularly north to south—inferred from tagging, and differences between growth and maturity. Common garden experiments demonstrate genetically based growth rate differences between stocks (Butts and Litvak 2007). Analysis of microsatellite characters demonstrates genetic differences between Georges Bank and the other Canadian stocks (McClelland et al. 2005; Wirgin et al. 2014). Recently, McElroy et al. (2013) documented temporally stable differences in productivity (i.e., annual fecundity) between all three U.S. stocks, and McBride et al. (2013) and Winton et al. (in press) demonstrated inter- and intrastock variation in age at maturity. Historically, the ASMFC managed three of four U.S. stocks: the Gulf of Maine, southern New England, and the Mid-Atlantic stocks (ASMFC 1992). The last two stocks were combined (ASMFC 2005) into a southern New England stock which appears to have two contingents: estuarine residents and estuarine-nearshore migrants (Sagarese and Frisk 2011). An early analysis of microsatellite loci suggest fine-scale stock structuring of Winter Flounder at this southern range (Crivello et al. 2004), but a more recent analysis using microsatellite and single-nucleotide polymorphic loci did not find support for more than three U.S. stocks (Wirgin et al. 2014). In the Gulf of Maine, coastal spawning is increasingly recognized but the effects of mixing between spawning groups within this region are unclear (DeCelles and Cadrin 2010; Fairchild et al. 2013). The Georges Bank stock, found offshore, is managed by the NEFMC; the phenotype of this offshore stock is so different from the coastal stocks that it was once proposed as a separate species (Chase 2014). Continued investigation of stock structure, particularly for the coastal stocks, remains a research priority (ASMFC 2013c).

REVIEW OF METHODS USED

Methods used to identify stock structure of ASMFC species fell into five broad categories: life history traits, other phenotypic traits, genetic traits, natural marks, and applied marks (Cadrin et al. 2005). All species have not been treated equally in terms of the breadth and depth of methods used to explore stock structure; a few ASFMC species have been investigated rather exhaustively whereas others have received almost superficial treatment. Where more intensive research has been applied, rather complex patterns have emerged, such as in metapopulation structure for American lobster and Atlantic Herring, or contingent structure for American Eel, Striped Bass, and Winter Flounder. Experimental methods, although rarely applied, have

been particularly helpful in teasing apart ecophenotypes from genotypes, such as for horseshoe crab, Atlantic Croaker, and Winter Flounder. Therefore, methods do affect our confidence in identifying and managing stock structure.

Life history characteristics, such as distribution and abundance, age and growth, and reproductive traits, are often the most historically rich kinds of information available because these traits are measured, and sometimes routinely monitored, to estimate vital rates used in assessment (Costello et al. 2012; McBride, 2014). The coarse-scale distribution of spawning grounds is well documented for all ASMFC species (Table 1). At one extreme, marine spawners are associated with a unit stock or metapopulation, and at the other extreme, anadromous species are associated with river-specific genetic units that are treated at least as regional stock complexes. Life history data were typically part of early stock definitions established in the initial FMPs developed by the ASMFC, but such descriptive data can be simply demonstrative of ecophenotypes that no longer justify separate stock status. The use of experimental approaches to test for stock-specific effects of temperature on mortality (horseshoe crab) or growth reaction norms (Atlantic Croaker, Winter Flounder) have been particularly effective for partitioning phenotypic and genotypic sources of stock integrity.

There is also a rich history of using meristic and morphometric methods to define ASMFC and other fishery stocks (Cadrin and Friedland 2005; Waldman 2005b; Cadrin 2014; Chase 2014; Stransky 2014). These methods have waned presumably because of the numerous studies already published, leaving little room for new information to be uncovered, together with the potential for existing variation to be an ecophenotypic signal unrelated to genetic structure or assessment needs. Nonetheless, a truss network approach has been recently fruitful in separating regional stock units for Alewife and Scup (Love and Chase 2009; Chase 2011; Cronin-Fine et al. 2013).

Application of genetic methods is very uneven across ASMFC species. At one extreme, analysis of broad spatial and temporal patterns with a number of different genetic markers has occurred for horseshoe crab, Atlantic Sturgeon, American Shad, Striped Bass, Weakfish, and Red Drum. Still, the genetic structure of some other “data-rich” species, such as American lobster, remain poorly known (Hodgins-Davis et al. 2007), or it appears on the verge of new interpretations from applications of single-nucleotide polymorphisms technology, such as for Atlantic Herring (Helyar et al. 2012; Limborg et al. 2012). In other cases, the evidence rests on a single study for species such as Bluefish, Atlantic Croaker, Tautog, and Spanish Mackerel. No genetic evidence exists for Hickory Shad, Scup, and Spot. Since mechanisms that change gene frequencies can operate on different spatial and temporal scales, management of many of these species could benefit from additional or finer-scale seascape surveys of variation across their range, especially in the vicinity of biogeographic capes. Such approaches are often listed as research priorities (ASMFC 2013c) to either

examine temporal consistency of the number of stocks or stock boundaries, or to compare life history and genetic responses by different species to explore robust mechanics of stock structure (e.g., Gold and Richardson 1998). Genetic studies of the better studied species, such as horseshoe crab and Red Drum, have revealed sex-specific differences in dispersal (Gold et al. 1999; King et al. 2005) and other interesting aspects of animal biology relevant to connectivity.

Allozymes and other related measures of gene expression were pioneering methods, and in select cases, these methods may still contribute to mixed-stock analysis (Koljonen and Wilmot 2005). Still, most recent studies of genetic structure by ASMFC species employ direct measurement of DNA, especially mitochondrial DNA. In at least one case, for Weakfish, the conclusion of a unit stock did not change with increasingly sophisticated markers, from allozymes, to mitochondrial DNA, to nuclear DNA microsatellites (Cordes and Graves 2003). Otherwise the choice of genetic marker can make a big difference, is controversial, or is a work in progress (Waples et al. 2008; Helyar et al. 2011; ICES 2012; Antoniou and Magoulas 2014; Mariani and Bekkevold 2014). Reiss et al.’s (2009) strict focus on genetic interpretation of stock structure exposes these challenges. In their review of 32 managed species in the eastern North Atlantic, they found that genetic data are rarely adequate alone to unequivocally address the stock status of exploited marine fishes. To further clarify the data, they formulated three criteria—temporal replication, sample size, and number of loci—as an operational basis for sorting out weak or conflicting results.

In terms of natural markers, parasites have been used for only a few ASMFC species (Striped Bass, Atlantic Croaker, Summer Flounder, Winter Flounder). This method is used to characterize stock structure in many different regions of the globe (e.g., Moore et al. 2011; Baldwin et al. 2012; Zischke et al. 2013; MacKenzie and Abaunza 2014), and an International Council for the Exploration of the Sea working group is actively exploring and promoting the strategic use of parasite taxonomy and genetics for stock identification (ICES 2012). Fatty acid profiles have been used to identify stocks of Striped Bass (Grahl-Nielsen and Mjaavatten 1992), and such biochemical markers, including amino acids, may hold promise with other species (Riveiro et al. 2011; Grahl-Nielsen 2014). Using otolith chemistry to associate habitat and connectivity of fishes has become more popular recently, contributing to stock identification of several species (American Shad, Striped Bass, Weakfish, and Red Drum). Its increasing cost-effectiveness is promising for continued use, especially in identifying contingents or metapopulation structure, where genetic signals between spawning units are confounded by even low levels of gene flow (Patterson et al. 2004; Kerr and Campana 2014).

Many stock definitions of ASMFC species are based on tag returns, although much of this can only be found in the gray literature or as summarized in the original FMPs. Tag returns often only confirm what can already be inferred from seasonal

distributions, but strategic use of tags to explore connectivity of metapopulations or parallel life histories of contingents is still very relevant today (Secor 1999; DeCelles and Zemeckis 2014). Many recent ASMFC FMPs still prioritize tagging research for investigating mixing at stock boundaries (i.e., for Spotted Seatrout: ASMFC 2011c, 2013c). Cape Hatteras or Cape Cod are routinely used as stock boundaries because of their association with biogeographic patterns rather than with specific evidence, so tagging studies near these locales may be particularly useful. The use of electronic tags is still typically directed at investigating habitat use (Aunins and Olney 2009; Grothues et al. 2009; DeCelles and Cadrin 2010), but as these data accumulate, their use for stock identification is growing (Rooker et al. 2007; Bacheler et al. 2009; DeCelles and Zemeckis 2014).

Simulation modeling is emerging as a complementary tool to understand stock-specific population dynamics (Kerr and Goethel 2014). Fogarty (1998) explored the metapopulation dynamics of American lobster, particularly the role that spawning by offshore populations plays in recruitment to inshore populations. Kerr et al. (2010b) explored a general model for simulating stock structure processes and applied this to a simple metapopulation example of Atlantic Herring. Henderson (2012) used different tagging approaches with Summer Flounder to explore how small-scale behaviors influence large-scale population movements and distributions.

Among the methods outlined in Cadrin et al. (2005), few have not been used repeatedly with different ASMFC species. Marking of otoliths of ASMFC species has occurred but not for stock identification purposes (Volk et al. 2005; Duffy et al. 2012); considering that the mass marking of juveniles has many applications for measuring homing rates and survival (e.g., Keefer et al. 2008), this method has considerable potential. An a priori, strategic, interdisciplinary research program (e.g., Abaunza et al. 2008, 2014) has not been applied directly to any ASMFC species, but Striped Bass and Winter Flounder have received ad hoc interdisciplinary reviews (Waldman et al. 1988, 1997; DeCelles and Cadrin 2011; Cadrin et al. 2014b).

STOCK STRUCTURE TYPES

As expected, a variety of stock structure patterns exist in U.S. waters among these 25 species (Tables 1, A.1). Much of this diversity is easily related to coastal hydrographic and life history processes. Two marine spawners, American lobster and Atlantic Herring, are recognized as metapopulations. This helps integrate the latitudinal and onshore–offshore spawning components with the potential for both larval dispersal and adult movements. Most other marine spawners are recognized as single stocks. Spot is considered a unit stock on very weak evidence. Otherwise, the evidence is fairly robust for Spiny Dogfish, American Eel, northern shrimp, Atlantic Menhaden, Bluefish, Atlantic Croaker, Tautog, and Spanish Mackerel (Table 1). The high number of unit stocks among marine spawners was not entirely expected, since a complex structure exists for many marine spawners in the

North Atlantic (e.g., Ames 2004; Reiss et al. 2009). There is always the suspicion that a lack of evidence for more than one stock leads to an incorrect conclusion of a unit stock (Abaunza et al. 2014), and unresolved issues about contingent structure exist for some of these same species. Nonetheless, the high seasonal variability in temperature, specifically within the Middle Atlantic Bight, is the dominant mechanism that drives large-scale, north–south or onshore–offshore, migrations for many of these species. These movements disrupt conditions for reproductive isolation, particularly in terms of isolation by distance, but may promote conditions for establishing contingent structure, evident in Black Sea Bass, Bluefish, and Scup. Some of these same species have relatively long planktonic larval durations and considerable larval dispersal, which reduces the potential for stock structure even further. Other unresolved questions regarding the marine species generally fall into three categories: continuous or disjunct clinal stock structure, variation in vital rates between Cape Cod and Cape Hatteras, or mixing rates of individuals around capes.

Red Drum and Winter Flounder spawn in both estuaries and in the nearshore coastal environment and demonstrate relatively limited coastal movements. Their stock structure is correspondingly more complex than that for strictly marine spawners. Sufficient evidence exists to manage Red Drum as separate stocks north and south of Cape Hatteras (Bacheler et al. 2009). Winter Flounder probably comprises dozens of biological populations in the southern New England region where spawning is concentrated in estuaries, but there are resident and migratory contingents. The spawning groups of Winter Flounder in six New York estuaries are small enough to show symptoms of inbreeding (O’Leary et al. 2013).

Among the strict estuarine spawners there is well recognized stock structure. Horseshoe crab is managed by four latitudinally segmented stocks. This scale of structure is only a problem for the Delaware Bay stock where landings are highest. Fisheries in multiple states harvest individuals of this stock, and there are overlapping ecosystem concerns regarding migratory birds, specifically the red knot *Calidris canutus*. Spotted Seatrout is assessed at the state level because of its limited movements outside estuaries, whereas Weakfish is not, presumably because philopatry and the potential for genetic structure break down when older weakfish migrate offshore.

Anadromous species show stock structure at the river level. Nonetheless, while there is evidence of philopatry for Atlantic Sturgeon, American Shad, the river herrings, and Striped Bass, there is also evidence of straying and the knowledge that much of the fishing mortality occurs on mixed-stock complexes in the ocean. Consequently, stock units have been set at a regional rather than a river-specific scale.

MANAGING STOCK STRUCTURE

The ASMFC incorporate stock structure into the management of these 25 exploited species reasonably well. Implementation of each FMP included a review of research and knowledge

about stock structure (ASMFC 2013a). Further debate about stock structure of individual species takes place largely through peer-review panels and the primary literature (reviewed herein). There are many example of timely uptake of new information, as advocated by Cadrin et al. (2014b).

I found it difficult to develop a simple metric to define success, based on some association between knowledge of stock structure with stock status. This review does summarize the stock structure and status of these 25 species. About one-third (eight) of these species are not overfished and over half (15) are not experiencing overfishing (Table A.1); however, there is marked uncertainty about both stock structure and status for several species. Furthermore, overfishing or an overfished status was evident at the adoption of some FMPs that stated good knowledge of stock structure, and for many species priorities other than stock structure are driving the research needs for assessment and management (ASMFC 2013c). Instead of focusing independently on developing such a metric, I highlight a few issues to guide further consideration of the intersection of research and the application of stock structure in an assessment and management context.

The anadromous fishes, most of which are in a depleted status, show that much more could be done. The concerns about shad and river herrings as bycatch in ocean fisheries are confounded by a lack of real-time methods to discriminate between stocks in the fishery catch. Improved methods that would address these concerns should allow a more nuanced approach in the future for these species (Waldman et al. 2012; Cronin-Fine et al. 2013). Palkovacs et al. (2014) promoted a two-pronged approach of defining river herring stocks with genetic tools and monitoring them by using more traditional demographic traits. In the case of Atlantic Sturgeon, low levels of abundance, a moratorium on directed fishing, and evidence of straying by adults has culminated in managing distinct population segments by region (Grunwald et al. 2008; Kocik et al. 2013). In the case of Striped Bass, where the fishery is largely in coastal waters, stocks are recognized by the FMP, but as no stock is considered overfished and stock composition cannot be managed cost-effectively in real time, the species is managed at a coastwide level. These factors have resulted in managing the fisheries of some anadromous species in a binary regulatory manner (Richards and Rago 1999). Directed fishing is allowed when all stocks are not overfished or overfishing is not occurring—as is presently the case for Striped Bass—but is not allowed (i.e., a fishing moratorium) when these thresholds are crossed for even one stock—as is presently the case for Atlantic Sturgeon and in the past for Striped Bass. Recent efforts to list river herrings or close the stocks to fishing failed; as an alternative, Bethoney et al. (2013) and Cournane et al. (2013) explored an approach that monitors bycatch of depleted stocks of shad and river herrings in real time and develops control rules to stop fishing when bycatch is excessive.

Although metapopulation structure is recognized in American lobster and Atlantic Herring, much remains to be considered

in terms of understanding its dynamics and the effectiveness of area-specific harvest control rules to preserve metapopulation structure. American lobster management is area-specific, taking the form of several coastal areas, where 90% of the landings occur, and an offshore area (ASMFC 1997); however, the management boundaries do not conform precisely with stock boundaries, which complicates data collection and stock assessment (ASMFC 2013c). Similar questions arise for Atlantic Herring (Kritzer and Liu 2014). Reiss et al. (2009) documented the inertia of historical stock designations and noted the tradeoffs between rigid and simple management versus the dynamics of flexible management structures.

The issue of mixing rates is not limited to these two metapopulations. Mixing rates around faunal breaks or between jurisdictional boundaries is a frequently recognized research priority by the ASMFC. Regarding Winter Flounder, the potential for genetic diversity between some individual estuaries, as well as different migratory contingents within estuaries, exceeds the resolutions of fishery data. Defining smaller stock units will have little effect on assessment if monitoring of catch, effort, and other fishery parameters do not occur at a similar scale (Reiss et al. 2009).

Although individual states can often adopt a specific management plan for their coastal waters, including to declare de minimis (exempt from regulations if their state contributes <1% of coastwide landings), each state's harvest policies may also be governed by agencies other than the ASMFC. A state's territorial seas do not typically extend beyond 3 mi (4.8 km) in Atlantic Ocean waters, but many of the species treated here are distributed across the shelf, requiring interaction with the regionally based federal fishery management councils. The NEFMC is the lead council on FMPs for Atlantic Herring and Winter Flounder; the MAFMC is the lead council for Spiny Dogfish, Black Sea Bass, Bluefish, Scup, and Summer Flounder; the SAFMC is the lead council on Spanish Mackerel (ASMFC 2013b).

The distribution of several species extends beyond the ASMFC's range of governance and into the Canadian Maritimes or the Gulf of Mexico as well (Table A.1). In most cases, Canadian populations are considered separate stocks and their assessments are independent of U.S. stock assessments. Notable exceptions are Atlantic Herring, such that data for the west side of the Bay of Fundy are part of the U.S. stock assessment, and as proposed for Spiny Dogfish, which may be a sink population in Canada relative to a larger, possibly metapopulation structure along the North American east coast. Among the several species that are distributed along both the east and west coasts of Florida, fish on each coast are treated as separate populations—some are recognized as subspecies—and are governed by the ASMFC and the Gulf States Marine Fisheries Commission, respectively. Only American Eel has the potential to be comanaged by both commissions as a common species in both regions.

Given this governance framework and the costs of identifying stocks and implementing stock-specific monitoring and management, the ASMFC demonstrates considerable

accomplishment. One measure of success is that almost one-third (seven) of these managed species do not prioritize continued stock research (Table A.1; ASMFC 2013c). For Scup, the temporal allocation of fishing effort is more of a concern than is its spatial allocation (ASMFC 2013b). About half the ASMFC-managed species support active recreational fisheries, and recreational landings can be dominant for a few (e.g., Bluefish, Tautog), such that these species' research priorities are focused on better characterization of the recreational catch. In the case of Atlantic Croaker, for which the ASMFC continues to identify stock structure as a research priority, there are competing priorities, such as discard mortality. There are so little data for Hickory Shad that it could benefit from additional research, not just regarding stock structure, but in nearly all areas related to assessment.

The following trends will increase our confidence in identifying and understanding the value of stock structure to manage sustainable fisheries: (1) strategic integration of methods to disentangle genetic from phenotypic variation; (2) improved cost-effectiveness of advanced methods, notably genetic markers, otolith microchemistry, and artificial tags; (3) simulation models to evaluate the effects of different stock structure types on assessment and management processes. Aside from the concrete concept that stock structure reflects some degree of reproductive isolation, the growing recognition of nongenetic contingent structure, e.g., in American Eel, Striped Bass, Black Sea Bass, Bluefish, Scup, and Winter Flounder so far, is also likely to have broad implications.

SUMMARY

In an attempt to improve our understanding and the application of stock structure in marine fisheries, this review provides a glimpse of how a specific set of species has been treated. It attempts to point out how methods that may be unfamiliar to some researchers could be complementary to those methods that may be more familiar. And it notes the tradeoffs that exist in putting such research into practice by assessment scientists and resource managers. Initial FMPs developed by the ASMFC, often in conjunction with federal management councils, included rigorous reviews of the available stock identification data. These were used to inform stock assessments and management policy, and the ASFMC continues to request and readily incorporate new data and information to manage these coastal fisheries. Marine spawners are treated as a single stock, two stocks, or a metapopulation, whereas estuarine and freshwater spawners are typically assessed and managed at a finer scale. Nonetheless, the stock structure of some species is still poorly known or the available data are conflicting and not resolved. Continued research of this subject should consider (1) research priorities tabulated by ASMFC review panels, (2) strategic use of interdisciplinary stock identification methods, (3) use of experiments or reaction norms to separate phenotypes from genotypes, (4) genetic surveys at a seascape scale, (5) demonstration of contingent (non-

genetic) structure and its implications for management, and (6) simulation modeling. Obstacles to adopting finer-scale structure into management of ASMFC fisheries include: (1) multiple stock units are apparent but boundaries are not clear, (2) monitoring requirements for smaller areas or for mixed-stock catches are not cost effective, or (3) mixing rates within a metapopulation or across biogeographic boundaries are poorly described.

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Appendix: Supplemental Information on the ASMFC Fishery Species

TABLE A1. Tabulation of species managed by the Atlantic States Marine Fisheries Commission, grouped by order and family, identifying aspects of their natural history and stock identity, and how this relates to their stock status and management (ASMFC 2013a, 2013b, 2013c). Black Drum *Pogonias cromis* was added as a managed species in 2013 but is not included here because the first coastwide stock assessment is not planned until 2015. The ASMFC also manages several coastal sharks as a species complex but these are not considered herein because of data limitations. Life cycle characterizes if a species is resident in marine (Mar), estuarine (Est), or both (Mar-Est) habitats and where its spawns if different (in parentheses); diadromous species are assigned as either anadromous (Anad) or catadromous (Catad), based on whether they spawn in freshwater or marine habitats, respectively. Striped Bass migrates strictly within freshwater (Potamodromous; Pot) in the southern part of its range.

Species ^a	Latitudinal range ^b	Life cycle	ASMFC stocks ^c	Other stocks ^d	Stock identification methods ^e	Overfished ^f	Overfishing ^f	Research priority ^g	Other ^h
Xiphosura, Limulidae Horseshoe crab	21°N–44°N	Mar-Est (Est)	Lat (4)	GoMex	LHda, LHag, LHrn, GEal, GEmo	Unknown	Unknown	Y	
Decapoda, Nephropidae American lobster	41°N–51°N	Mar	Meta (3[9])	Canada	LHda, LHag, LHre, PHmo, GEal, GEmo, AMct, AMet	GOM: N GBK: N SNE:Y	GOM: N GBK: N SNE:N	N	OI
Decapoda, Pandalidae Northern shrimp	42°N–82°N	Mar	Unit	Canada +	LHda, GEal, GEmo	Y	Y	N	Herm
Squaliformes, Squalidae Spiny Dogfish	56°S–73°N	Mar	Unit	Canada	LHda, LHre, GEal, GEmo, AMct	N	N	Y	Vivip
Acipenseriformes, Acipenseridae Atlantic Sturgeon	10°S–56°N	Anad	River (5 DPS)	Canada	LHda, LHre, GEmo, AMct	Y	N	Y	Listed
Anguilliformes, Anguillidae American Eel	7°N–66°N	Catad	Unit	Canada, GoMex	LHda, LHag, LHre, GEal, GEmo	Y	Unknown	N	Cont (Part)
Clupeiformes, Clupeidae Blueback Herring	25°N–41°N	Anad	River	Canada	LHda	Y	Unknown	Y	
Alewife	34°N–55°N	Anad	River	Canada	LHda, PHmo, GEmo	Y	Unknown	Y	
Hickory Shad	25°N–46°N	Anad	River		LHda, LHre	Unknown	Unknown		
American Shad	22°N–61°N	Anad	River	Canada	LHda, LHag, LHre, PHme, PHmo, GEal, GEmo, NMhc, AMct	Y	Unknown	Y	
Atlantic Menhaden	30°N–46°N	Mar-Est (Mar)	Unit		LHda, PHme, PHmo, GEmo, AMct	Unknown	Y	N	
Atlantic Herring	33°N–80°N	Mar	Meta (4)	Canada +	LHda, LHag, LHre, PHme, PHmo, PHhm, GEal, GEmo, AMct	N	N	Y	OI
Perciformes, Moronidae Striped Bass	24°N–51°N	Anad (Pot)	Unit (North [3])	GoMex	LHda, LHre, PHme, PHmo, PHhm, GEka, GEal, GEmo, NMpa, NMhc, NMfa, AMet	N	N	Y	Cont

(Continued on next page)

TABLE A1. Continued.

Species ^a	Latitudinal range ^b	Life cycle	ASMFC stocks ^c	Other stocks ^d	Stock identification methods ^e	Overfished ^f	Overfishing ^f	Research priority ^g	Other ^h
Perciformes, Serranidae Black Sea Bass	25°N–45°N	Mar	Unit (North)	SAFMC, GoMex	LHda, LHag, LHre, PHme, PHmo, GEmo, AMct	N	N	Y	Cont, Herm, Reef
Perciformes, Pomatomidae Bluefish	44°S–45°N	Mar-Est (Mar)	Unit	GoMex	LHda, LHag, LHre, PHme, GEmo, AMct	N	N	N	Cont
Perciformes, Sparidae Scup	25°N–46°N	Mar	Unit (North)		LHda, LHre, PHme, PHmo, AMct	N	N	N	Cont
Perciformes, Sciaenidae Spotted Seatrout	22°N–42°N	Est	Lat (State)	GoMex	LHda, LHag, LHre, GEal, GEmo, AMct	Unknown	Unknown	Y	
Weakfish	27°N–47°N	Mar-Est (Est)	Unit		LHda, LHag, LHre, PHme, PHmo, GEal, GEmo, NMhc, AMct	Y	N	Y	
Spot	19°N–43°N	Mar-Est (Mar)	Unit	GoMex	LHda, LHag, LHre	Unknown	Unknown	Y	
Atlantic Croaker	37°S–43°N	Mar-Est (Mar)	Unit	GoMex	LHda, LHag, LHre, LHrn, GEmo, NMpa, NMhc, AMct	Unknown	N	Y	
Red Drum	0°N–43°N	Mar-Est	Lat (2)	GoMex	LHda, LHag, LHre, GEal, GEmo, NMhc, AMct	Unknown	N	Y	
Perciformes, Labridae Tautog	31°N–46°N	Mar	Unit		LHda, LHag, GEmo	Y	Y	N	Reef
Perciformes, Scombridae Spanish Mackerel	19°N–44°N	Mar	Unit	GoMex	LHda, LHre, GEmo	N	N	Y	
Pleuronectiformes, Paralichthyidae Summer Flounder	29°N–45°N	Mar-Est (Mar)	Unit (North)		LHda, LHag, LHre, LHrn, PHme, PHmo, GEal, GEmo, AMct	N	N	Y	
Pleuronectiformes, Pleuronectidae Winter Flounder	31°N–55°N	Mar-Est	Lat (3)	Canada	LHda, LHag, LHre, LHrn, PHme, PHmo, GEmo, NMpa, AMct, AMet	GOM: U GBK: N SNE: Y	GOM: N GBK: N SNE: N	Y	Cont, OI

^aNomenclature follows Page et al. (2013), McLaughlin et al. (2005), and Sekiguchi and Shuster (2009).

^bLatitudinal range is from FishBase (www.fishbase.org), Shumway et al. (1985), Sekiguchi and Shuster (2009), and Currie and Schneider (2011).

^cASMFC stock structure characterizes how the Commission manages this species: as distinct population segment (DPS; an aggregate of regional spawning groups); river-specific groups (River); at the state level (State); by latitudinally defined groups (Lat); a metapopulation (Meta); or a single unit (Unit). Several species are only managed by the ASMFC north of Cape Hatteras (North), either because that is where the coastal fishery exists (Striped Bass) or is concentrated (Scup, Summer Flounder), or little mixing is apparent north and south of this cape (Black Sea Bass); in such cases, southern stocks are managed by separate authorities. The number of stocks is provided (in parentheses) with an additional number of management units [in brackets], if greater than one or not at the state level.

^dOther regional management agencies responsible for these species are indicated as occurring in the Gulf of Mexico (GoMex), the South Atlantic Fishery Management Council (SAFMC) Canada (Canada), or Canada and other nations in the North Atlantic Ocean (Canada+).

^eCategories of evidence identifying stock structure for each species. Life history evidence is related to distribution and abundance (LHda), age and growth (LHag), reproduction (LHre), and experimental demonstration of a reaction norm (LHrn). Phenotypic evidence is related to meristics (PHme), morphometrics (PHmo), or hardpart morphology (PHm; i.e., scales or otoliths). Genetic evidence is grouped as based on karyotype (GEka), protein allozymes (GEal) or more direct molecular markers (GEmo). Natural markers include parasites (NMpa), hardpart chemistry (NMhc), or fatty acid profiles (NMfa). Applied marks are indicated as conventional tags (AMct) or electronic tags (AMet).

^fIdentifies stock status in terms of overfished and overfishing (Y = yes; N = no; Unknown) as discussed in ASMFC (2013b). Specific stocks are identified as Gulf of Maine (GOM), Georges Bank (GBK), and southern New England (SNE).

^gIdentifies stock structure related research priorities (Y = yes; N = no) as discussed in ASMFC (2013c).

^hSpecial characteristics are identified as: contingents (Cont), hermaphroditic (Herm), listed as threatened or endangered (Listed), offshore–inshore larval source dynamics (OI), partial migration (Part), reef-associated habitat preference (Reef), or viviparity (Vivip).