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REVIEW ARTICLE

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The status of striped bass, *Morone saxatilis*, as a commercially ready species for U.S. marine aquaculture

Linnea K. Andersen[1] | Jason Abernathy[2] | David L. Berlinsky[3] | Greg Bolton[4] | Matthew M. Booker[5] | Russell J. Borski[6] | Travis Brown[7] | David Cerino[8] | Michael Ciaramella[9] | Robert W. Clark[10] | Michael O. Frinsko[11] | S. Adam Fuller[2] | Steve Gabel[12] | Bartholomew W. Green[2] | Eric Herbst[13] | Ronald G. Hodson[1] | Michael Hopper[10] | Linas W. Kenter[3] | Frank Lopez[14] | Andrew S. McGinty[10] | Barry Nash[13] | Matthew Parker[15] | Stacey Pigg[16] | Steve Rawles[2] | Kenneth Riley[17] | Marc J. Turano[18] | Carl D. Webster[2] | Charles R. Weirich[19] | Eugene Won[20] | L. Curry Woods III[21] | Benjamin J. Reading[1] | StriperHub

[1]Department of Applied Ecology, North Carolina State University, Raleigh, North Carolina

[2]United States Department of Agriculture, Agricultural Research Service, Harry K. Dupree Stuttgart National Aquaculture Research Center, Stuttgart, Arkansas

[3]Department of Agriculture, Nutrition, and Food Systems, University of New Hampshire, Durham, New Hampshire

[4]Department of Bioprocessing & Nutrition Sciences, North Carolina State University, Morehead City, North Carolina

[5]Department of History, North Carolina State University, Raleigh, North Carolina

[6]Department of Biological Sciences, North Carolina State University, Raleigh, North Carolina

[7]Aquaculture and Biotechnology Program, Brunswick Community College, Supply, North Carolina

[8]Aquaculture Technology Program, Carteret Community College, Morehead City, North Carolina

[9]New York Sea Grant, Stony Brook University, New York, New York

[10]Pamlico Aquaculture Field Laboratory, North Carolina State University, Aurora, North Carolina

[11]North Carolina Cooperative Extension, Trenton, North Carolina

[12]North Carolina Cooperative Extension, Edenton, North Carolina

[13]North Carolina Sea Grant, Morehead City, North Carolina

[14]North Carolina Sea Grant, Raleigh, North Carolina

[15]Maryland Sea Grant, Clinton, Maryland

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[16]Department of English, North Carolina State University, Raleigh, North Carolina

[17]National Oceanic and Atmospheric Administration, National Ocean Service, National Centers for Coastal Ocean Science, Beaufort, North Carolina

[18]Nutrition and Technology, Cargill Aqua Nutrition, Minneapolis, Minnesota

[19]National Oceanic and Atmospheric Administration, Oceanic and Atmospheric Research, National Sea Grant Office, Silver Spring, Maryland

[20]Department of Animal Science, Cornell University, Ithaca, New York

[21]Crane Aquaculture Facility, University of Maryland, College Park, Maryland

Correspondence
Benjamin J. Reading, Department of Applied Ecology, North Carolina State University, 100 Eugene Brooks Avenue, Raleigh, NC 27695-7617.
Email: bjreadin@ncsu.edu

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Abstract

Striped bass, *Morone saxatilis*, is an anadromous fish native to the North American Atlantic Coast and is well recognized as one of the most important and highly regarded recreational fisheries in the United States. Decades of research have been conducted on striped bass and its hybrid (striped bass × white bass *Morone chrysops*) and culture methods have been established, particularly for the hybrid striped bass, the fourth largest finfish aquaculture industry in the United States (US $50 million). Domesticated striped bass have been developed since the 1990s and broodstock are available from the government for commercial fry production using novel hormone-free methods along with traditional hormone-induced tank and strip spawning. No commercial-scale intensive larval rearing technologies have been developed at present and current fingerling production is conducted in fertilized freshwater ponds. Larval diets have not been successfully used as first feeds; however, they have been used for weaning from live feeds prior to metamorphosis. Striped bass can be grown out in marine (32 ppt) or freshwater (<5 ppt); however, they require high hardness (200+ ppm) and some salinity (8–10 ppt) to offset handling stress. Juveniles must be 1–10 g/fish prior to stocking into marine water. Commercially available fingerling, growout, and broodstock feeds are available from several vendors. Striped bass may reach 1.36 kg/fish in recirculating aquaculture by 18 months and as much as 2.27 kg/fish by 24 months. Farm gate value of striped bass has not been determined, although seasonally available wild-harvested striped bass are valued at about US $6.50 to US $10.14 per kg and cultured hybrid striped bass are valued at about US $8.45 to US $9.25 per kg whole; the farm gate value for cultured striped bass may be as much as US $10.00 or more per kg depending on demand and market. The ideal market size is between 1.36 and 2.72 kg/fish, which is considerably larger than the traditional 0.68 to 0.90 kg/fish for the hybrid striped bass market.

KEYWORDS

aquaculture, commercial, marine, *Morone*, striped bass

1 | INTRODUCTION

Striped bass, *Morone saxatilis*, are a well-recognized fish native to the North American Atlantic Coast and regarded as the most popular recreational fishery in the United States. Striped bass are euryhaline, anadromous fish and juveniles typically remain in estuaries for 2–4 years prior to migrating to and from the north and south Atlantic Ocean seasonally as adults, ascending to rivers each spring to spawn (Callihan, Harris, & Hightower, 2015). In some cases, such as the Hudson and Cape Fear Rivers and Santee-Cooper reservoir, not all striped bass migrate into the ocean, as some may remain resident in freshwater (Haeseker, Carmichael, & Hightower, 1996; LeBlanc et al., 2020; Waldman, Dunning, Ross, & Mattson, 1990; Wirgin, Maceda, Tozer, Stabile, & Waldman, 2020). The life history and culture of this fish has been researched for decades (Harrell, 1997; Harrell, Kerby, & Minton, 1990; McCraren, 1984), in part due to its use as the progenitor for creation of the original hybrid striped bass cross (striped bass × white bass, *Morone chrysops*; Palmetto bass) for stocking into natural and man-made impoundments for recreational fisheries, and the reciprocal hybrid striped bass (white bass × striped bass; Sunshine bass), which is raised in aquaculture. Hybrid striped bass is the fourth largest finfish aquaculture industry in the nation at a farm gate value of US $50 million when accounting for sales of foodfish as well as fry and fingerling used for commercial growout (Reading et al., 2018; USDA, 2019). A domestic stock of striped bass has been bred for six generations in captivity and distributed across North America as broodfish for hybrid striped bass foodfish production and recreational fishery stock enhancement. However, the establishment of striped bass as a commercial aquaculture industry independent of hybrid striped bass is predominantly stagnant because of several challenges, including inconsistent market demand and lack of supportive regulations and demonstrated sustained market viability.

A recent increased focus on agricultural and coastal development and economic growth in the seafood sector has created an opportunity for establishing the striped bass aquaculture industry. Specifically, the seafood trade deficit in the United States is nearing US $17 billion (NMFS, 2019) and 9 out of 10 seafood products consumed in the United States are of foreign import, half of which are aquaculture products (NMFS, 2020). Although the U.S. aquaculture industry (US $1.52 billion in 2018, USDA, 2019) has grown in recent years, particularly in the production of bivalves such as clams and oysters, it has remained a minor aquaculture producer on a global scale (ranked 17th; NMFS, 2020). Expansion of finfish aquaculture, particularly of striped bass and other species, represents one of the greatest unrealized aquaculture industry growth potentials in the world (FAO, 2018; Lem, Bjorndal, & Lappo, 2014).

Only one-third of global aquaculture products are raised in marine waters, which presents an opportunity for industry expansion as these marine resources and species are currently underutilized in the United States and other countries (Froehlich, Gentry, & Halpern, 2018). The expansion of marine finfish production is hindered by the limited number of appropriate species choices. Atlantic salmon, *Salmo salar* and red drum, *Sciaenops ocellatus* are currently the only finfish species endemic to the United States that are cultured in significant quantities in coastal environments, and presently there is no appreciable aquaculture production of any premium white-fleshed marine finfish species, such as the striped bass, in the country. Candidate aquaculture species identified by the National Oceanic and Atmospheric Administration (NOAA) must command a premium price, have high consumer demand, and successfully adapt to rearing in localized environments for profitable production. The striped bass meets all these criteria and therefore has great potential for commercialization in the United States (Reading, 2017; Reading, Hinshaw, & Watanabe, 2014).

Our purpose is to review the current status of striped bass aquaculture and its potential as a U.S. aquaculture industry, primarily from an Atlantic state perspective. The industry originated and the seminal research was conducted in this region, which is well suited for the culture of striped bass. Section 1 provides an overview of the history and management of the striped bass fishery, the establishment of striped bass culture over time, and the current market opportunity. Section 2 describes the standard methods and tools available for striped bass culture, and Section 3 presents the future directions of the striped bass aquaculture industry, including challenges toward establishment of a culture industry for this species, to be addressed in part through the launch of the new *StriperHub* consortium.

2 | HISTORY OF THE STRIPED BASS FISHERY AND AQUACULTURE AND THE CURRENT MARKET OPPORTUNITY

2.1 | Striped bass fishery status

The endemic range of striped bass stretches from the St. Lawrence River in Canada to St. John's River in Florida and the importance of this fish to commercial and recreational fisheries dates to pre-colonial times (Hill, Evans, & Van Den Avyle, 1989). Overfishing and habitat degradation contributed to the collapse of the striped bass fishery in the 1980s and prompted the development and approval of the Interstate Fisheries Management Plan (ISFMP) for Atlantic Striped Bass by the Atlantic States Marine Fisheries Commission (ASMFC) in 1981 (ASMFC, 1981). Continued decline of striped bass populations led to the passage by Congress in 1984 of the Atlantic Striped Bass Conservation Act (98 Stat. 3187, 16 U.S.C. 5151-5158) that granted the Secretary of Commerce the authority to impose a total moratorium in any state that did not comply with ASMFC management guidelines. To date, the initial striped bass ISFMP put forth by the ASMFC has been amended six times. Notably, striped bass stocks were declared fully recovered in 1995 upon adoption of Amendment 5, which was preceded by the stipulation that focus should be on rebuilding the fishery rather than maximizing harvest yield per Amendment 4 (1989). After the declaration of recovery, per annum commercial striped bass harvest grew from about 1.5 million kg (3.4 million lb) in 1995 to about 2.7 million kg (6.0 million lb) in 2002 (Figure 1a). Atlantic striped bass are currently managed by the ASMFC under Amendment 6 (2003) that established additional biological reference points for management, a commercial quota system, and bag and size limits for recreational fishing.

Although it does not currently have a direct role in managing the striped bass fishery, the NOAA also provides key research and scientific findings to the ASMFC and state agencies that continue to monitor and manage striped bass stocks. Moreover, a series of six addenda to Amendment 6 were implemented beginning in 2007 to address items such as bycatch monitoring, how recruitment failure is considered, commercial harvest tagging, and the modeling of Atlantic striped bass as a single stock. A spawning stock biomass (SSB) assessment for striped bass conducted in 2013 estimated that current fishing mortality rates would reduce SSB below the 90.7 million kg (200.0 million lb) threshold over the next few years (Figure 1b). In response to this 2013 stock assessment, the ASMFC approved Addendum IV in 2014 to reduce harvest levels by 25.0% in coastal states and 20.5% in the Chesapeake Bay. Addendum IV successfully reduced fishing mortality based on stock assessments conducted in 2016; however, striped bass SSB continued to decline. Commercial landings averaged about 3.2 million kg (7.0 million lb) annually from 2003 to 2014, and in 2017 the commercial quota was reduced to approximately 2.3 million kg (5.0 million lb) through Addendum IV (Figure 1a). Recreational landings along the Atlantic coast reported

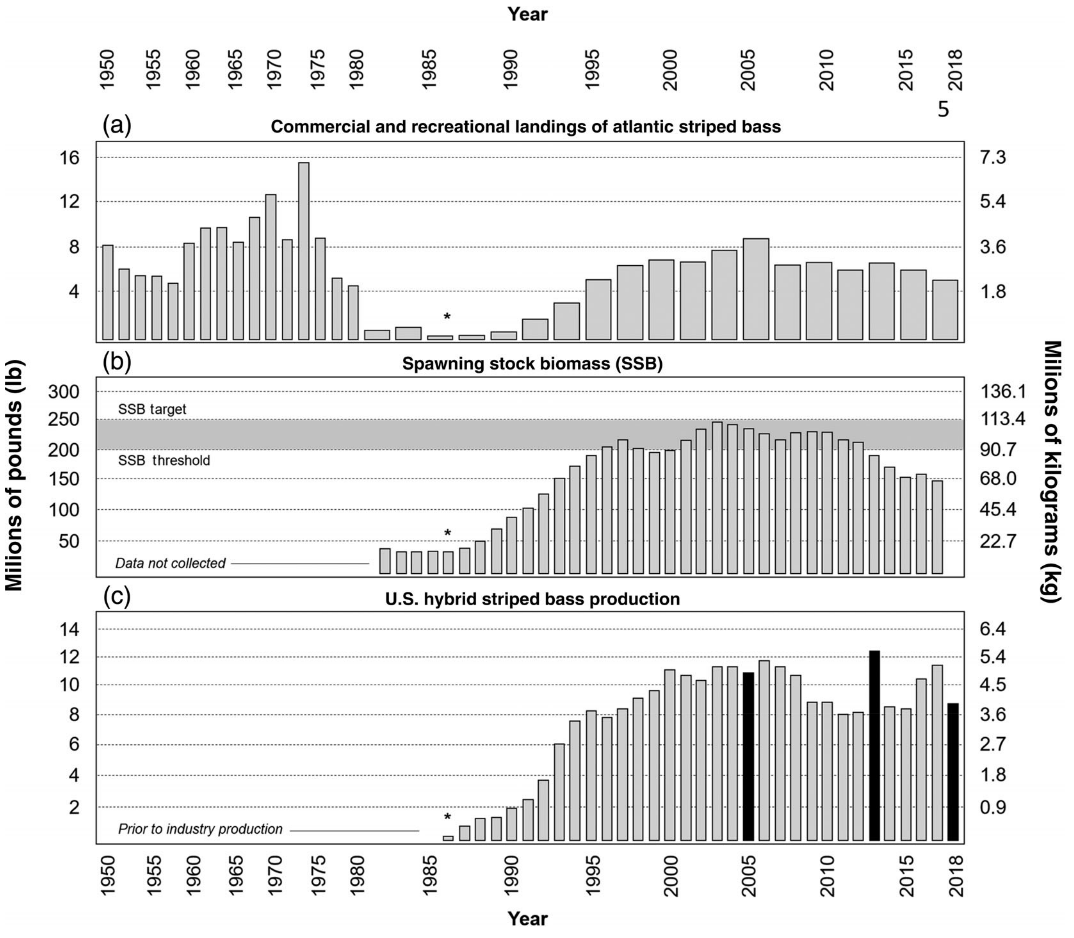


FIGURE 1 (a) Commercial and recreational landings of Atlantic striped bass since the 1950s. Bars indicate the average landings per 2 years from 1950 to 2018. (b) Spawning stock biomass (SSB) of Atlantic striped bass from the 1980s to 2016. (c) Hybrid striped bass production in the United States as reported since industry inception beginning in 1986. Years that aquaculture production volumes were reported in the USDA Agriculture Census are indicated as black bars. Asterisks (*) on all panels mark the year the U.S. hybrid striped bass industry began production (1986). Data for these figures were provided by the Atlantic States Marine Fisheries Council (ASMFC) and National Oceanic and Atmospheric Administration (NOAA) National Marine Fisheries Service (NMFS) (panels a and b), and from Dr. James Carlberg (Kent SeaTech), Dr. Marc Turano (NC SeaGrant), Dr. Anita Kelly (University of Arkansas at Pine Bluff and Auburn University), and the USDA Agriculture Census (panel c)

by the National Marine Fisheries Service (NMFS) Office of Science and Technology (NOAA) were about 11.3 million kg (25.0 million lb) per year from 2007 to 2014 and harvests from 2015 to 2017 were reduced due to implementation of Addendum IV.

As the Albemarle Sound and Roanoke River striped bass stocks contribute minimally to the Atlantic striped bass population in comparison with the Chesapeake Bay and Delaware and Hudson Rivers, Addendum IV deferred management of this stock to the State of North Carolina. In 2017, commercial harvest in the Albemarle Sound and Roanoke River of North Carolina was estimated at 34,375 kg (75,783 lb) and recreational harvest estimated at 45,872 kg (101,131 lb). The North Carolina Division of Marine Fisheries (NC DMF) closed the striped bass season for commercial and recreational fishermen in all internal waters from just south of Oregon Inlet to the South Carolina line in 2019. This is the Central Southern Management Area (CSMA) and includes the Tar, Neuse, Pamlico, and Cape Fear River systems.

A benchmark assessment in 2019 indicated that striped bass SSB was approximately 22.7 million kg (50.0 million lb) below the threshold of 91.6 million kg (202.0 million lb) and determined that the stock had been overfished since 2013. Addendum VI was initiated in 2019 as an adaptive management strategy to end overfishing and bring fishing mortality levels to the target level in 2020. Addendum VI specifically aims to reduce removals along the Atlantic coast by at least 18.0% and mandates the use of circle hooks and a 1-fish bag limit and 28 to 35-in. slot limit for recreational ocean fisheries and an 18-in. minimum size limit for the Chesapeake recreational fishery. States are still permitted to implement alternative regulations through conservation equivalency under Addendum VI. A proposed motion to initiate an amendment that will serve to address stock rebuilding and other management strategies is currently up for review in 2021 by the ASFMC.

2.2 | Early striped bass aquaculture

Practices to culture striped bass were initially developed to improve production of fish for enhancing commercial and recreational fisheries of native Atlantic coastal stocks. This was later expanded to include non-native introduction to the Pacific Ocean in 1879 (Parks, 1978; Stone, 1882) and inland freshwater reservoirs beginning in 1957 (Stevens, 1975, 1984). The first published report of a successful hatch of striped bass eggs under artificial conditions was made in 1874 by Spencer Baird, the first commissioner of the U.S. Commission of Fish and Fisheries, later to become the U.S. Fish and Wildlife Service (USFWS) (Baird, 1874). In 1879, the USFWS hatched striped bass fry at a site located along the Abermarle Sound in North Carolina that had been used as an American shad (*Alosa sapidissima*) hatchery (USFWS, 1882). These fry were sent to Washington D.C. and Baltimore, Maryland (USFWS, 1882). Seven years later in 1884, Stephen G. Worth reported construction of the first dedicated striped bass hatchery on the Roanoke River in Weldon, North Carolina (Worth, 1884). In a subsequent report, Worth (1904) described production of striped bass in that hatchery that included collecting over 2 million eggs and stocking “almost 300,000 fry” into the Roanoke River. The Edenton National Fish Hatchery was then established in North Carolina in 1898 by the USFWS with a similar purpose to Weldon (Woodroffe, 2012).

Beginning in the early 20th century, the USFWS began publishing manuals describing effective techniques for spawning, hatching, and releasing fry of cultured fish, including striped bass (Piper, 1982). By 1910, the basic technology of striped bass aquaculture was in place, but plans to augment marine fishery stocks were inexplicably dropped by the commission (Worth, 1910). Renewed interest in stock enhancement developed in the 1950s after the 1954–1955 discovery that a resident striped bass population had become established in the freshwater Santee-Cooper Reservoir of South Carolina (Scruggs Jr., 1957). The purpose of this new hatchery augmentation program was to establish new populations of striped bass in freshwater rivers and reservoirs throughout the southeastern United States, in states such as Kentucky, Alabama, Georgia, and South Carolina (Geiger & Parker, 1985; Kinman, 1988; Stevens, 1975). Striped bass were also being stocked as part of a fisheries management strategy to help control gizzard shad (*Dorosoma cepedianum*) populations, while providing anglers with a new recreational fishery (Anderson, 1966; Bonn, Bailey, & Bayless, 1976). By the 1980s, striped bass had been introduced into hundreds of reservoirs in at least 36 states (Stevens, 1984).

The first attempts to induce striped bass to spawn using hormones were made by Robert E. Stevens in the 1960s (Stevens, 1966, 1967). Within only a few years, procedures were developed that allowed the two principal hatcheries, the old hatchery established during the earliest years of striped bass culture in Weldon, North Carolina, and the newer hatchery built in Moncks Corner, South Carolina in 1961, to produce millions of striped bass fry annually (Mischke, 2012; Stevens, 1967). The first successful *Morone* hybridization cross was conducted vis-à-vis to the development of procedures to artificially spawn striped bass in captivity in the 1960s. This original cross hybrid, also referred to as the palmetto cross, was made using striped bass eggs and white bass sperm (milt) with the intention of creating a fish that had the hardiness and environmental tolerance of a white bass and would grow to the size of a striped bass, thus appealing to anglers.

Commercial aquaculture of hybrid striped bass began in the 1970s, but it did not gain market footing. It was not until moratoriums were imposed (Maryland 1985–90; Virginia 1989–90) following the collapse of the striped bass fishery in the 1980s (Figure 1a) that the path for commercial hybrid striped bass aquaculture as a means of supplying a replacement product opened (Hodson, 1990; Hodson & Hayes, 1990). The initial pond and small tank aquaculture efforts were pioneered by Theodore I. J. Smith (South Carolina Department of Natural Resources), J. Howard Kerby and Melvin T. Huish (North Carolina State University, North Carolina Cooperative Research Unit), and Ronald G. Hodson (North Carolina State University, NOAA North Carolina Sea Grant), among others. By 1987, the National Coastal Resources Research and Development Institute in North Carolina developed a national research initiative to establish the feasibility of commercial production and profitability of hybrid striped bass reared in ponds. Reginal Harrell (University of Maryland, USDA Northeastern Regional Aquaculture Center) coordinated the summation of these early efforts and methodologies to produce comprehensive reference manuals for culture and propagation of striped bass and its hybrids (Harrell, 1997; Harrell et al., 1990). The first commercial harvest of hybrid striped bass was in 1987 and the industry has since grown to produce 5.4 million kg (12.0 million lb) of hybrid striped bass (white bass eggs and striped bass milt; Reciprocal or Sunshine) annually with a farm gate value of US $50 million (Reading, McGinty, et al., 2018; USDA, 2019) (Figure 1c). Hybrid striped bass foodfish are raised in 19 states of the United States and approximately 50% of the production occurs in Texas, California, and Mississippi with the remaining production largely occurring throughout the Mid-Atlantic and southeast U.S. Commercial fingerling production occurs largely in Arkansas and North Carolina.

2.3 | Current market opportunity

Barring any challenges to the expansion of the U.S. aquaculture industry, the market opportunity for striped bass exists, is strong, and is largely untapped. The seafood trade deficit and growth potential of aquaculture in the United States warrant the development of commercial marine aquaculture and recent evidence from seafood markets along the mid-Atlantic region indicate high demand for larger, white-fleshed marine fish with desired size of 1.36–2.27 kg (3.0–5.0 lb) per fish (Locals Seafood, Raleigh, NC, personal communication and unpublished data from current retail seafood markets). This demand cannot be met by currently available commercial aquaculture species including the hybrid striped bass, whose growth and feed efficiency rapidly decline after the fish reach 0.68 kg (1.5 lb) in size (Turano and Reading, unpublished data). However, some producers in Texas and Mississippi have reported rearing hybrid striped bass to 1.4 kg (3.0 lb) in 18–24 months (Treece and Associates, 2017).

Currently, tilapia (genus *Oreochromis*), pollock (*Gadus chalcogrammus*), cod (*Gadus morhua*), and catfish (genus *Ictalurus*) are ranked fourth, fifth, seventh, and eighth, respectively, among the 10 most popular seafoods in the United States (NFI, 2018). From a culinary perspective, the fillets from these finfishes possess sensory characteristics that are highly valued by professional chefs and discerning home cooks. With their slightly sweet flavor and relatively firm texture once cooked, wild and farmed striped bass can easily be prepared with recipes that have already been crafted for a number of white-meat finfish (NOAA, 2020a, 2020b; SeafoodSource, 2014a, 2014b). Given the mild flavor, the meat of striped bass can easily absorb an assortment of herbs and spices, allowing chefs and home cooks to create a variety of highly flavorful meal preparations. Like cod, pollock, and tilapia, striped bass also is a good source of nutritious, low-fat protein (NOAA, 2020c).

Striped bass, unlike hybrid striped bass, can be grown in "open" marine systems (e.g., coastal areas) or produced in freshwater land-based systems prior to marine transfer. Relative to other marine finfishes, the striped bass is a well-suited candidate to meet the seafood market demand, as the target market size of 1.36 kg (3.0 lb) for striped bass can be attained within approximately 24 months or less of growout. Furthermore, the reproduction, genetics, culture, and feed requirements of striped bass have been studied extensively largely through the development of the hybrid striped bass industry and the potential for striped bass aquaculture is already being established in preliminary small-scale studies in fresh, brackish, and marine environments. The feasibility of commercializing striped bass at a fairly rapid pace is already established as well, to the extent that a single commercial farm in northern Baja California, Mexico (Pacifico Aquaculture), produces enough fish to consistently supply product to various market outlets, including chain-grocery stores.

The stock assessment data indicating that the Atlantic striped bass fishery is in decline and the policies that are developing as a response further exacerbate the need to establish commercial aquaculture production of striped bass in the United States. Environmentally conscious aquaculture has a number of potential benefits for the striped bass fishery as it can provide economic development and readily available seafood supply to supplement the current, albeit declining, commercial striped bass fishery. The present-day economic and environmental scenario is very similar to the striped bass fishery decline and moratorium of the 1980s that jump-started hybrid striped bass aquaculture (Figure 1c).

Fisheries data indicate potential market value of aquacultured striped bass. The decline in U.S. wild striped bass fishery landings from approximately 3.4 million kg (7.5 million lb) in 2008 to just slightly over 2.3 million kg (5.0 million lb) in 2017 was coincident with an increase in value from about US $16 million in 2008 to about US $23 million in 2017, indicating a classical supply and demand relationship. Thus, an underutilized current annual market of 1.1 million kg (2.5 million lb) of striped bass appears available along the Atlantic Coast of the United States alone, which cannot be filled by the presently declining commercial fishery. At present, the average dockside or "off-the-boat" price for whole striped bass in the commercial fishing industry is variable; however, the national average is about US $10.14 per kg (US $4.60 per lb) (US $23 million/2.3 million kg). This suggests a farm gate value of at least US $8.82–US $11.02 per kg (US $4.00–$5.00 per lb) for aquaculture striped bass, which closely aligns or may be higher than the current farm gate value of cultured hybrid striped bass (US $8.47 per kg for 0.57–0.91 kg sized fish, or US $3.84 per lb for 1.25–2.0 lb fish; US $9.26 per kg for 1.13 kg or larger fish, or US $4.20 per lb for 2.5 lb or larger fish). Recent retail market prices for striped bass in urbanized areas in North Carolina, New England, and New York ranged from US $26.45 to US $41.89 per kg (US $12.00–US $19.00 per lb) for boneless, skin-on fillets of wild caught striped bass. Market surveys conducted with Locals Seafood in North Carolina found that marketing value-added, boneless, skin-on fillets of aquacultured striped bass in the mid-Atlantic region is feasible even with a final product price of US $39.68 per kg (US $18.00 per lb). Based on these survey data, we estimate the U.S. farm gate value for striped bass can be as low as US $10.14 per kg (US $4.60 per lb) and as high as US $13.23 per kg (US $6.00 per lb) based on a 50.0% to 70.0% mark-up margin. Furthermore, assessments have shown consumer willingness to pay premium prices for striped bass (Quagrainie, 2019). These data show a clear economic and market potential for aquaculture production of striped bass, which already has a wide consumer acceptance and appeal.

3 | STRIPED BASS CULTURE METHODS AND TOOLS

Considerable research on striped bass and its hybrids has been conducted and entire books (Harrell, 1997) and culture method guidelines have been published (Bonn et al., 1976; Harrell et al., 1990). In addition, many studies focusing on striped bass nutrition (Gatlin III, 1997; Small & Soares Jr, 1998; Small, Soares Jr., & Woods III, 2000; Webster & Lovell, 1990; Woods III & Soares Jr., 1996), health (Harms, Sullivan, Hodson, & Stotskopf, 1996; Noga, Kerby, King, Aucoin, & Giesbrecht, 1994; Noga, Wang, Grindem, & Avtalion, 1999; Plumb, 1997; Salger, Reading, & Noga, 2017), pond and recirculating aquaculture system (RAS) culture methodologies (Geiger & Turner, 1990; Geiger, Turner, Fitzmayer, & Nichols, 1985; Harrell, 1997; McGinty & Hodson, 2008; Turano, Borski, & Daniels, 2008), pond fingerling production (Ludwig, 1999, 2004; Ludwig, Perschbacher, & Edziyie, 2010; Ludwig & Tackett, 1991), fingerling production in biofloc production systems (Green, Rawles, Webster, & McEntire, 2018), stress mitigation (Harrell, 1992; Harrell & Moline, 1992; Kenter, Gunn, & Berlinsky, 2019), and high salinity tolerance (Kiilerich, Tipsmark, Borski, & Madsen, 2011; Tipsmark, Luckenbach, Madsen, & Borski, 2007; Tipsmark, Madsen, &

Borski, 2004) have been published and are well known. Therefore, the ability to culture these fish in numerous environments on an experimental scale is not in question and, importantly, the wealth of studies conducted on striped bass has allowed for the development of a captively bred, domesticated broodstock (Garber & Sullivan, 2006; Hallerman, 1994).

3.1 | Domestication

Most cultured fishes in the United States, and the world, originate from wild caught fish or fish that are not domesticated or selectively bred for genetic improvement (Gjedrem & Baranski, 2010; Knibb, 2000; Teletchea & Fontaine, 2014). Domestication is a process by which an organism is taken from its natural environment and then reared in a controlled setting, such as in agriculture. The breeding of these organisms that have been acclimated to and tolerate these culture conditions then produces offspring that are likely to thrive similarly or even better. A domesticated line of striped bass originally obtained from six distinct geographic stocks has been bred in captivity for six generations as part of the *National Program for Genetic Improvement and Selective Breeding for the Hybrid Striped Bass Industry* (Garber & Sullivan, 2006; Hodson et al., 1999; Reading, McGinty, et al., 2018; Woods III, 2001). Except for salmonids, this is the only marine aquaculture finfish species in the United States with an established domestic strain of fish that are available to producers and currently being used for commercial production.

Genetic improvement of finfish broodstock is a critical advancement for aquaculture industry success. Breeding programs provide fish that are selectively bred for optimal culture and performance traits, such as disease resistance, growth rate and efficiency, acceptance of prepared diets, and tolerance to crowding and stress conditions among many others. Performance gains of domesticated fish can be dramatic in comparison to the wild-origin counterparts. For example, gains in body weight at harvest are estimated to be approximately 14% per generation of selectively bred Atlantic salmon (Gjedrem, 2010). Similarly, domesticated strains of striped bass have been shown to have superior performance for some culture traits (Reading, McGinty, et al., 2018).

There are marked improvements in domestic striped bass growth performance between filial generations captively bred over the last 17 years as evaluated by weight at age. For example, sixth-generation captive-bred domestic striped bass (F6) are about twice the size of third-generation fish (F3) by Age 2 and fifth-generation (F5) female striped bass are about 46% larger than F3 female striped bass at age of 4 years (Figure 2). When considering the average improvement in domestic striped bass growth performance for each captive bred generation, we see 33.8% growth gain between F3 and F4, 26.9% growth gain between F4 and F5, and 24.0% growth gain between F5 and F6. These are fish reared in outdoor tanks and pools at semi-commercial density. The timeframe required for domestic striped bass to grow to about 1,000 g (2.20 lb) in these conditions, which is the desired market size for the hybrid striped bass, has been dramatically reduced by 69% through breeding between the F3 and F6 generations (Figure 3). Furthermore, the time to grow to the desired market size of 1.36 kg (3 lb), which was identified as a target for white-fleshed marine fish such as striped bass, is about 32 months for F3 generation, 29 months for F4 generation, 28 months for F5 generation, and 24 months for F6 generation fish. Thus, selective breeding has taken the F3 generation fish, which were not economically feasible to grow to this market size over a 32-month timeframe, to within the economically feasible timeframe of 24 months or less by the F6 generation of breeding. Overall, this is a 75% reduction in the growout time to market obtained through just three generations of selective breeding. The F7 generation of domestic striped bass, first created in 2020, will likely have further improved growth performance over the next 4 or so years (Figure 2).

Recent studies have demonstrated that female reproductive potential in the domesticated striped bass is superior to that of equal-sized females captured from the wild using a manual strip spawning method (Locke, Sugg, Sullivan, & Turano, 2013). Additionally, domestic striped bass have an improved dress-out weight (0.5–4.0% increase compared with wild-origin fish (Reading, McGinty, et al., 2018), and, importantly, a 13–25% significantly better feed conversion efficiency ($p < .05$), with feed conversion ratio (FCR) values <1.1 (Kenter, Kovach, Woods III, Reading, &

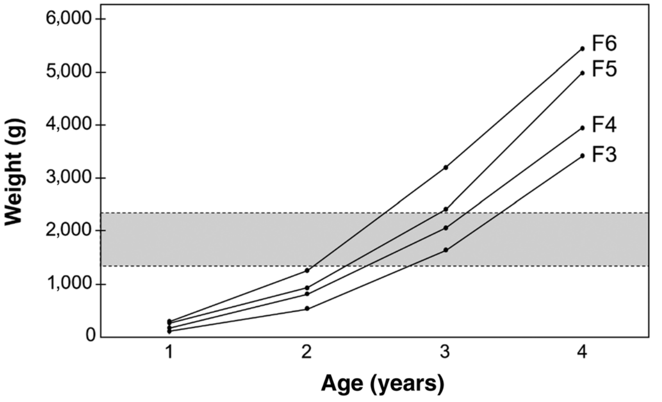
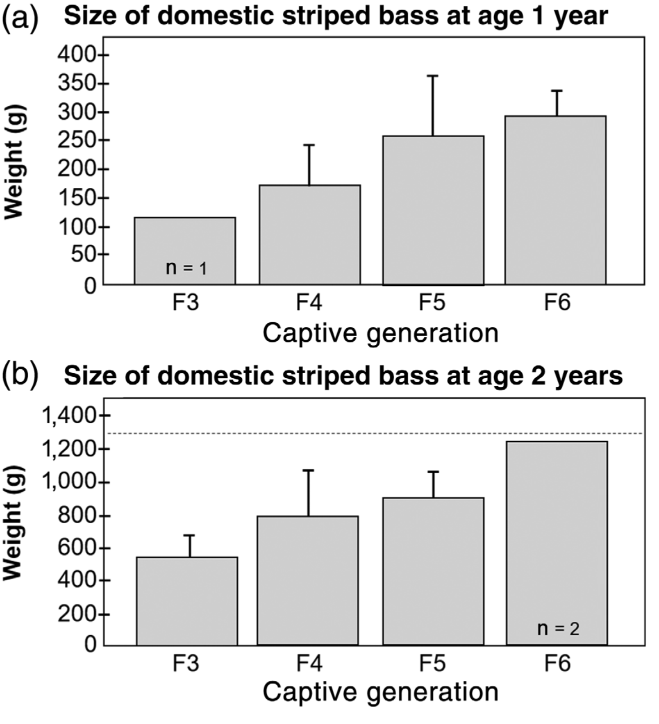


FIGURE 2 Domestic striped bass broodstock performance data collected for different age classes and generations (collected between March and June of each year, 2005–2020): Year 1 (45–60 weeks of age), Year 2 (80–104 weeks of age), Year 3 (136–154 weeks of age), and Year 4 (197–209 weeks of age). The *x*-axis is the age class grand mean and the *y*-axis is weight (g). The filial generation of captive breeding is indicated for the periods of 2004–2007 (F3), 2008–2011 (F4), 2012–2015 (F5), and 2016–2019 (F6). Gray shading indicates the target striped bass market size at between 1.36 and 2.27 kg (3.0 and 5.0 lb). Each datapoint for F3, F4, F5, and F6 represents a grand mean value of 3 or 4 different age class cohorts and hundreds of fish were measured for each age class per annum with the exceptions of F3 age class 1 (a single cohort), F6 age class 2 (2 cohorts), F6 age class 3 (2 cohorts), and F6 age class 4 (a single cohort)

FIGURE 3 Domestic striped bass age class performance data (collected between March and June of each year, 2005–2020): (a) Year 1 (45–60 weeks of age) and (b) Year 2 (80–104 weeks of age). The filial generation of captive breeding is indicated for the periods of 2004–2007 (F3), 2008–2011 (F4), 2012–2015 (F5), and 2016–2019 (F6). Bars indicate grand mean values and error bars indicate standard deviation where there were three or four age class observations (annual performance data of hundreds of fish) for each filial generation; error bars are omitted where there were only one or two annual observations indicated as $N = 1$ or $N = 2$. The dashed line indicates target market size for striped bass at 1.36 kg (3.0 lb)



Berlinsky, 2018). The presumed FCR for striped bass raised at commercial density is approximately 1.5 or slightly higher. Collectively, this domestic striped bass broodstock program has produced a fish suitable for commercial growout economics. However, the use of wild-origin striped bass stocks may be critical for offshore culture in some regions due to escapement concerns (e.g., Northeast Atlantic and Gulf of Mexico), and as such, it is important to extend reproduction and larviculture technology of these fish to those regions as appropriate for the U.S. striped bass aquaculture industry to thrive.

3.2 | Reproduction and larviculture

A major constraint to the culture of any marine fish species is the complexity of larval rearing and ability to produce a reliable source of juveniles for culture (Planas & Cunha, 1999). However, this bottleneck has already been addressed in the culture of striped bass, which have comparatively simple requirements for larviculture and are similar to that of salmonids, one of the only successful marine finfish aquaculture industries in the United States. Early research was conducted to understand the female striped bass reproductive cycle (Berlinsky & Specker, 1991; Swanson & Sullivan, 1991; Tao, Hara, Hodson, Woods III, & Sullivan, 1993; Woods III & Sullivan, 1993) and endocrine events that occur during ovary maturation (King et al. 1994,b; Zohar, 1989). These studies were followed by others that employed environmental (temperature, photoperiod) manipulation to phase-shift the reproductive cycle in order to induce out-of-season spawning (Blythe et al. 1994,b; Clark, Henderson-Arzapalo, & Sullivan, 2005) and to better understand egg quality and reproductive performance (Chapman, Reading, & Sullivan, 2014; Reading et al., 2014, 2018; Reading, Hiramatsu, & Sullivan, 2011; Reading, Williams, Chapman, Islam Williams, & Sullivan, 2013; Schilling et al., 2014; Sullivan, Chapman, Reading, & Anderson, 2015; Williams et al. 2014,b). Both hormone-induced and nonhormone-induced tank spawning of striped bass has been achieved (Andersen et al., 2021; Smith & Whitehurst, 1990; Woods III, Woiwode, McCarthy, Theisen, & Bennett, 1990), although considerably more attention has been focused on inducing ovulation and manual strip spawning for in vitro fertilization (Hodson & Sullivan, 1993; Mylonas et al., 1993; Woods III & Sullivan, 1993). We recently described commercially scalable methods to batch spawn domestic striped bass en masse in tanks without any hormone applications, and these procedures can be used to produce many millions of larvae necessary for commercial production (Andersen et al., 2021; Reading et al., 2016, 2018b, 2018c, 2018d, 2019). Sperm cryopreservation and storage has also been characterized (Frankel, Theisen, Guthrie, Welch, & Woods III, 2013; He & Woods III, 2004; Jenkins-Keeran & Woods III, 2002; Woods III et al., 2018). Additionally, the osmoregulatory apparatus that enables striped bass to be euryhaline is highly geared for life in seawater even as a resident in freshwater environments (Kiilerich et al., 2011; Tipsmark et al., 2004). As such, striped bass larvae are tolerant to half-strength seawater as early as 1 day post-hatch (dph), and growth and survival of 5 dph larvae raised in 20, 40, and 60% seawater was found to be as great as those raised in freshwater (Lal, Lasker, & Kuljis, 1977).

Larval striped bass can be raised to fingerlings at a commercial scale in earthen ponds using natural productivity through fertilization (Harrell, 1997; Ludwig, 1999). This infrastructure is currently in place at many aquaculture operations utilizing pond systems, in particular at commercial hybrid striped bass fingerling operations. Pond sizes for larviculture are typically smaller than for growout and therefore not available at all commercial hybrid striped bass rearing facilities. Intensive larval rearing for fingerling production in tank systems is generally constrained to the use of live feeds, and challenges are not as well described as compared to other life stages. Further research on commercially scalable methods of intensive larval rearing is needed and currently being conducted. Collectively, the larval and juvenile seed-stock supply for striped bass is presently achievable at commercial scale in the United States.

3.3 | Rearing and growout

Striped bass have been shown to adapt well to and exhibit high survival in both RAS technologies and cages. Laboratory-scale RAS studies show that striped bass exhibit equivalent growth performance in freshwater, brackish, and saltwater environments (Kenter et al., 2018). Experimental-scale studies of striped bass in cage culture show that fish grow better than hybrid striped bass in brackish water with little impact on survivorship (Woods, Kerby, & Huish, 1983). Significant progress has been made on growth biology in striped bass including seasonally based feeding protocols; characterization of growout temperature (Harrell, 1992); demonstration that a range of salinities are equally effective in regulating growth (Harrell, 1992; Kenter et al., 2018); nutrient requirements, endocrine and growth physiology (Picha et al., 2009, 2014; Picha, Turano, Beckman, & Borski, 2008; Picha, Turano, Tipsmark, & Borski, 2008; Won & Borski, 2013); and experimental scale studies suggesting a potential for culture of 1.36–2.27 kg (3.00–5.00 lb) fish. However, none of this research has provided insight into commercial scaling or use of stocking densities typical of intensive culture requirements or economic analyses for the full production cycle from egg to plate of domestic or wild striped bass. Currently, data suggest that striped bass can be grown in cages and under RAS at different salinities. Despite this work, one major constraint has been a lack of demonstration that striped bass can be economically cultured at commercial scale.

3.4 | Genomic resources and tools

The striped bass is a priority species for the United States Department of Agriculture (USDA) National Animal Genome Research Support Program (NRSP-8) and as such considerable progress in establishing genomic resources for striped bass has been accomplished. The striped bass genome assembly was recently updated (2019) through a combinatorial approach of short-read sequencing (Illumina, San Diego, CA), long-read sequencing (Pacific Biosciences, Menlo Park, CA), and Chicago® and Dovetail™ Hi-C + HiRise™ scaffolding (Dovetail Genomics, Scotts Valley, CA). This genome assembly (NCSU_SB_2.0) is publicly available under GenBank accession GCA_004916995.1 and is currently in the annotation pipeline. This genome assembly has a total sequence length of 598,109,5477 base pairs and consists of 629 scaffolds (Abdelrahman et al., 2017; Andersen, Baltzegar, Fuller, Abernathy, & Reading, 2019; Reading, McGinty, et al., 2018).

Other genomic resources available for striped bass include a medium-density genetic linkage map of 289 polymorphic microsatellite DNA markers (Liu et al., 2012), 23,000 unigene sequences from a multi-tissue transcriptome (Li, Beck, Fuller, & Peatman, 2014; GenBank accession GBAA00000000), and a well-annotated transcriptome of 11,200 unigene sequences derived from ovary representative of all stages of oocyte growth and maturation (Reading et al., 2012; GenBank accession SRX007394). A number of studies have reported the development of microsatellite DNA markers for striped bass (Brown, Baltazar, & Hamilton, 2005; Couch et al., 2006; Han, Li, Leclerc, Hays, & Ely, 2000; Rexroad et al., 2006; Skalski, Couch, Garber, Weir, & Sullivan, 2006). Epigenetic studies on striped bass are limited to sperm methylation profiles and their correlation to fertility (Woods III et al., 2018). Additional resources are also available for closely related Moronids including a reference genome sequence assembly for white bass (Abernathy et al., 2019), multi-tissue transcriptome of 22,000 unigene sequences for white bass (Li et al., 2014; GenBank accession GAZY00000000), and 1,730 unigene sequences for white perch (*Morone americana*) (Schilling et al., 2014; GenBank accession GAQS00000000).

These resources collectively provide excellent tools for selective breeding, marker-assisted selection, and domestication, as well as for functional studies on the biology and aquaculture of striped bass. For example, the genome and transcriptome data empower proteomic analyses (Andersen et al., 2019; Reading et al., 2012, 2013; Schilling et al., 2014, 2015; Schilling, Loziuk, Muddiman, Daniels, & Reading, 2015; Williams, Reading, Amano, et al., 2014).

4 | FUTURE DIRECTIONS AND CHALLENGES

Striped bass is an aquaculture species that is well positioned for commercial production. The current extent of consumer visibility, established market size and product price-point, knowledge of the biology and culture, and infrastructure for commercial seed production and rearing of striped bass all support the likelihood of its success as an aquaculture industry. Furthermore, the fish is euryhaline, which means it can be reared in fresh, brackish, or marine water in both coastal and inland systems throughout the United States. Culture methods of striped bass are well established and therefore no major hurdles remain regarding the technology to produce the fish. Recent efforts have established a reliable hatchery larval production system, which in the past has been considered a bottleneck to commercial-scale production (McCraren, 1984). One of the only limitations to developing a striped bass industry is the lack of current commercial U.S. producers and data to support the economic viability of commercial production.

4.1 | Barriers and opportunities

Significant barriers remain primarily the full commercial-scale demonstration and detailed economics of production and marketing to show that striped bass aquaculture is solvent. Development and expansion of the striped bass aquaculture industry in the United States has great potential if the following conditions are addressed:

1. Identifying domestic producers for commercial production and providing adequate fish to consistently supply seafood markets;
2. Demonstrating profitability through production, marketing, processing, and economics;
3. Clarification and general reduction of regulatory permitting and licensing procedures; and
4. Promoting comprehensive extension education, technical training, marketing, and product visibility to consumers and stakeholders.

The establishment of a conglomerate group of stakeholders and partners would enable a centralized demonstration of the technologies and outreach necessary to commercialize striped bass production. This would include items such as demonstrating the culture of adequate volumes of fish for commercialization and marketing using diverse aquaculture systems (pond, cage, and RAS or combinations thereof), development of business models for demonstrating profitability, and establishing extension activities to disseminate this information. Current finfish aquaculture infrastructure exists that can provide support for producing and marketing striped bass at commercial scale. Collaboration with social scientists and seafood distributors to better understand seafood marketing, consumer preferences, market depth, supply and demand, retail pricing, and the provision of additional outreach about striped bass aquaculture are also crucial (Pigg & Reading, 2018; Ryan et al., 2018).

Venture capital investment will be required for the next phase of industry development and upscaling once commercial striped bass production and marketing has been demonstrated. Additionally, engagement in extensive outreach, including extension programming and technology transfer, is required to provide the necessary aquaculture and marketing training tools to support the growth of this industry. This would include working with state NOAA Sea Grant programs along with the USDA and state cooperative extension agents at Land Grant Universities in the region to address social, behavioral, economic, and policy priorities associated with striped bass aquaculture.

Clarity on policies relevant to commercial aquaculture (e.g., production, product transport) is also imperative to the development of a striped bass aquaculture industry. Presidential Executive Order 13921, 2020 ("Promoting American Seafood Competitiveness and Economic Growth") was issued in 2020 with the intent to:

> …improve the competitiveness of American industry; ensure food security; provide environmentally safe and sustainable seafood; support American workers; ensure coordinated, predictable, and transparent Federal actions; and remove unnecessary regulatory burdens.

Among the specific actions outlined in the order to achieve these goals is the renewal of a:

> …focus on long-term strategic planning to facilitate aquaculture projects, we can protect our aquatic environments; revitalize our Nation's seafood industry; get more Americans back to work; and put healthy, safe food on our families' tables.

Several of the legislative hurdles hindering development of the U.S. marine aquaculture industry are addressed by the executive order, such as requiring environmental reviews of aquaculture projects to be completed within 2 years.

4.2 | Establishing the StriperHub

The *StriperHub* is a Sea Grant-supported network that formed to facilitate striped bass aquaculture. The aim of the hub is to overcome barriers to industry development and expansion through demonstration and promotion of commercial-level culture, economics, and marketing of U.S. striped bass. North Carolina Sea Grant is leading the initiative and coordinating the *StriperHub* network, which is made up of several Sea Grant programs, USDA and other federal scientists, industry partners, and university researchers focused on consolidating and streamlining commercialization efforts in various culture environments. Detailed analyses of economics and marketing, baseline farm gate value and market depth, estimations of production economics, and demonstration of the potential for commercial culture scaling necessary for adoption and growth of the commercial striped bass aquaculture industry are some of the priorities of the *StriperHub*. The *StriperHub* has been active since 2020 in organizing project meetings, developing a web presence, creating recipes, and conducting research. Activities to date have resulted in successful commercial aquaculture production and the first farmed domestic striped bass will be available in U.S. markets in 2021.

In addition to being identified as a candidate aquaculture species by the NOAA, establishing a commercial striped bass aquaculture industry relies on the continued efforts of stakeholders, scientists, legislators, policymakers and their institutions in conducting research, performing assessments, developing business models and marketing strategies, and adopting clear permitting and licensing procedures for producers and vendors. These goals will be best realized if all of these stakeholder groups are able to synergize in a coordinated effort to serve as a nexus for information that can be disseminated to commercial producers and the public through the additional avenues of communication, outreach, education, and extension created through the *StriperHub*.

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ORCID

Bartholomew W. Green https://orcid.org/0000-0003-3772-9404
Matthew Parker https://orcid.org/0000-0003-1380-8351
Charles R. Weirich https://orcid.org/0000-0001-9555-0096
Benjamin J. Reading https://orcid.org/0000-0002-0778-4069

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