NOAA Professional Paper NMFS 22

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U.S. Department of Commerce
Seattle, Washington

Cover photo
Almaco jack (*Seriola rivoliana*) collected by the Northeast Fisheries Science Center 2022 Fall Bottom Trawl Survey aboard NOAA ship *Henry B. Bigelow*. Photograph by Matthew G. Girard and Katherine E. Bemis.

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Abstract— Accurate identification of species is essential to understand their biology and management. Some species of fishes, such as amberjacks (genus *Seriola*) are difficult to identify in the field, including the four species that occur in the western North Atlantic: greater amberjack (*Seriola dumerili* (Risso, 1810)), lesser amberjack (*Seriola fasciata* (Bloch, 1793)), almaco jack (*Seriola rivoliana* Valenciennes, 1833), and banded rudderfish (*Seriola zonata* (Mitchill, 1815)). All four species are caught by standardized Spring and Fall bottom trawl surveys (BTS) from Cape Hatteras to the Gulf of Maine conducted by the National Oceanic and Atmospheric Administration's Northeast Fisheries Science Center; historical records of captures since 1963 are maintained in a database. At sea, captured fishes are assigned to taxa; specimens that are difficult to assign are retained for further study in the laboratory at Woods Hole, Massachusetts. In the laboratory, we identified 105 specimens of the four species of *Seriola* collected by the BTS from 2006-2019 using morphological characters and Cytochrome Oxidase subunit I genetic barcodes to understand rates of at-sea misassignments. We found that at-sea assignments were ≥91% correct for *S. fasciata*, *S. rivoliana*, and *S. zonata,* but only 24% correct for *S. dumerili*. We then applied our analysis of at-sea assignments to evaluate 1218 historical records of *Seriola* caught by the BTS from 1963–2006. We conclude that records in the database are likely valid for catches assigned at sea to *S. fasciata*, *S. rivoliana,* and *S. zonata* but not reliable for *S. dumerili*. To facilitate future at-sea assignments of the four species of *Seriola*, we summarize useful field characters and incorporate these into a new identification guide for banded juveniles and adult-coloration individuals. We also provide new data on diets, reproductive condition, spawning periods, sizes (including a new maximum size for *S. fasciata*), historical literature, and seasonal and geographic distributions for the four species of *Seriola* in the western North Atlantic.

Introduction

The genus *Seriola* (family Carangidae) includes nine species of pelagic, epi-benthic reef fishes from a near global distribution in tropical and warm temperate oceans (Smith-Vaniz, 2003; Swart et al., 2015). Four species occur in the western North Atlantic Ocean: greater amberjack (*Seriola dumerili* (Risso 1810)), lesser amberjack (*Seriola fasciata* (Bloch, 1793)), almaco jack (*Seriola rivoliana* Valenciennes, 1833), and banded rudderfish (*Seriola zonata* (Mitchill, 1815)). Although they were described in the 18th and 19th centuries, persisting problems with distinguishing these four species led to confusion about their co-existence in the western North Atlantic until the 1950s (Mather, 1952, 1958). Despite Mather's work, the clear taxonomic status of all four species, and existing recreational and commercial fisheries for *S. dumerili* and *S. rivoliana*, the four species of *Seriola* are still frequently misidentified. All four have similar body shapes; they also overlap in body color, and exhibit extensive intraspecific variation in color patterns, including ontogenetic loss of juvenile banding. The most reliable meristic characters to distinguish among the four species are the number of gill rakers on the first gill arch and the number of spines in the first dorsal fin (e.g., Smith-Vaniz, 2003; Table 1), both of which can be difficult to count in the field. To better understand the biology of these four species, we need first to be able to reliably identify them.

All four species of *Seriola* in the western North Atlantic are caught during Spring and Fall bottom trawl surveys (BTS) conducted by the Ecosystems Surveys Branch of the National Oceanic and Atmospheric Administration's Northeast Fisheries Science Center (NEFSC) from Cape Hatteras to the Gulf of Maine (Fig. 1; Grosslein, 1969; Azarovitz, 1981; Despres-Patanjo et al., 1988; Link

Table 1

Diagnostic characters from the literature for four species of *Seriola* collected from bottom trawl surveys in the western North Atlantic from 1963 to 2019. Characters are based on key from Smith-Vaniz (2003) and were used to identify the specimens as either greater amberjack (*S. dumerili*), lesser amberjack (*S. fasciata*), almaco jack (*S. rivoliana*), or banded rudderfish (*S. zonata*) based on anatomical structures in the laboratory. FL=fork length.

	Seriola dumerili	*Seriola fasciata*	*Seriola rivoliana*	*Seriola zonata*
First dorsal fin spines	7	8	7	8
First dorsal fin rays	29–34	28–33	27–33	33–39
Gill rakers on first arch (in fishes larger than 20 cm FL)	11–19 total	23–26 total	18–25 total	12–17 total
Supramaxilla	Broad with posterodorsal angle rounded	Supramaxilla relatively slender	Supramaxilla broad with posterodorsal angle acute	Supramaxilla moderately slender

et al., 2008; Politis et al.[1]). Data collected on these surveys since 1963 are maintained in a survey database (SVDBS). Fishes that are hard to identify, such as the species of *Seriola*, are frozen at sea for later, more detailed examination in the laboratory at Woods Hole, Massachusetts.

To understand problems of misidentification of the species of *Seriola,* we distinguish between two types of taxonomic decisions. We refer to taxonomic decisions at sea as assignments; taxonomic decisions made in the laboratory are identifications. The term misassignment means that a fish was incorrectly identified at sea. Using this approach to taxonomic decisions, our first goal was to evaluate the reliability of at-sea assignments for the species of *Seriola*. To do this, we compared at-sea assignments and in-lab identifications for 105 specimens of *Seriola* (14 *S. dumerili*, 28 *S. fasciata*, 21 *S. rivoliana*, and 42 *S. zonata*) captured by the BTS between fall 2006 and spring 2019. We identified fishes in the laboratory using anatomical characters and genetic barcoding of cytochrome oxidase subunit I (COI).

Our second goal was to apply what we learned about problems in at-sea species assignments to evaluate the reliability of historical records in the survey database from 1963–2019. Once we understood which records are likely to be based on reliable assignments, then we could use the reliable records to better understand the biology of *Seriola* in the survey region.

Together, our assessment of problems in identification of the four species of *Seriola* and evaluation of historical records from the BTS provide new insights into the identification, life history, distribution, and ecology of these species in the western North Atlantic, a region where their biology is poorly known. To improve species assignments in the future, we provide an at-sea guide for the four species of *Seriola* in the western North Atlantic (Suppl. 1).

[1] Politis, P. J., J. K. Galbraith, P. Kostovick, and R. W. Brown. 2014. Northeast Fisheries Science Center bottom trawl survey protocols for the NOAA Ship Henry B. Bigelow. Northeast Fish. Sci. Cent. Ref. Doc. 14-06, 138 p. [Available from https://doi.org/10.7289/V5C53HVS.]

Materials and methods

Overview

The 344 catch records in the survey database represent 1323 individuals of *Seriola* collected on Spring (March–May), Summer (June–August), and Fall (September–November) standardized BTS conducted by the NEFSC (Politis et al.[1]). Of these 1323 individuals, we examined in the laboratory at Woods Hole 105 specimens collected between 2006–2019, 92 of which we deposited in permanent natural history collections (Suppl. 2; institutional abbreviations follow Sabaj, 2020). We refer to that subset of 105 specimens as the examined specimens. The other 1218 individuals represent the remaining records in the database collected on cruises since 1963, which we refer to as the historical records. The vast majority of the individuals on which these historical records were based had been discarded at sea after recording basic survey data.

Survey area

The NEFSC BTS began in 1963 and provides the most complete and continuous dataset for fishes of northeast coastal waters of the United States. The survey area extends from Cape Lookout, North Carolina north to the western Scotian Shelf in Canadian waters, including Georges Bank (Fig. 1). In this paper we define 11 regions (Fig. 1): Inshore 1, Inshore 2, Inshore 3, Gulf of Maine, Georges Bank, Southern

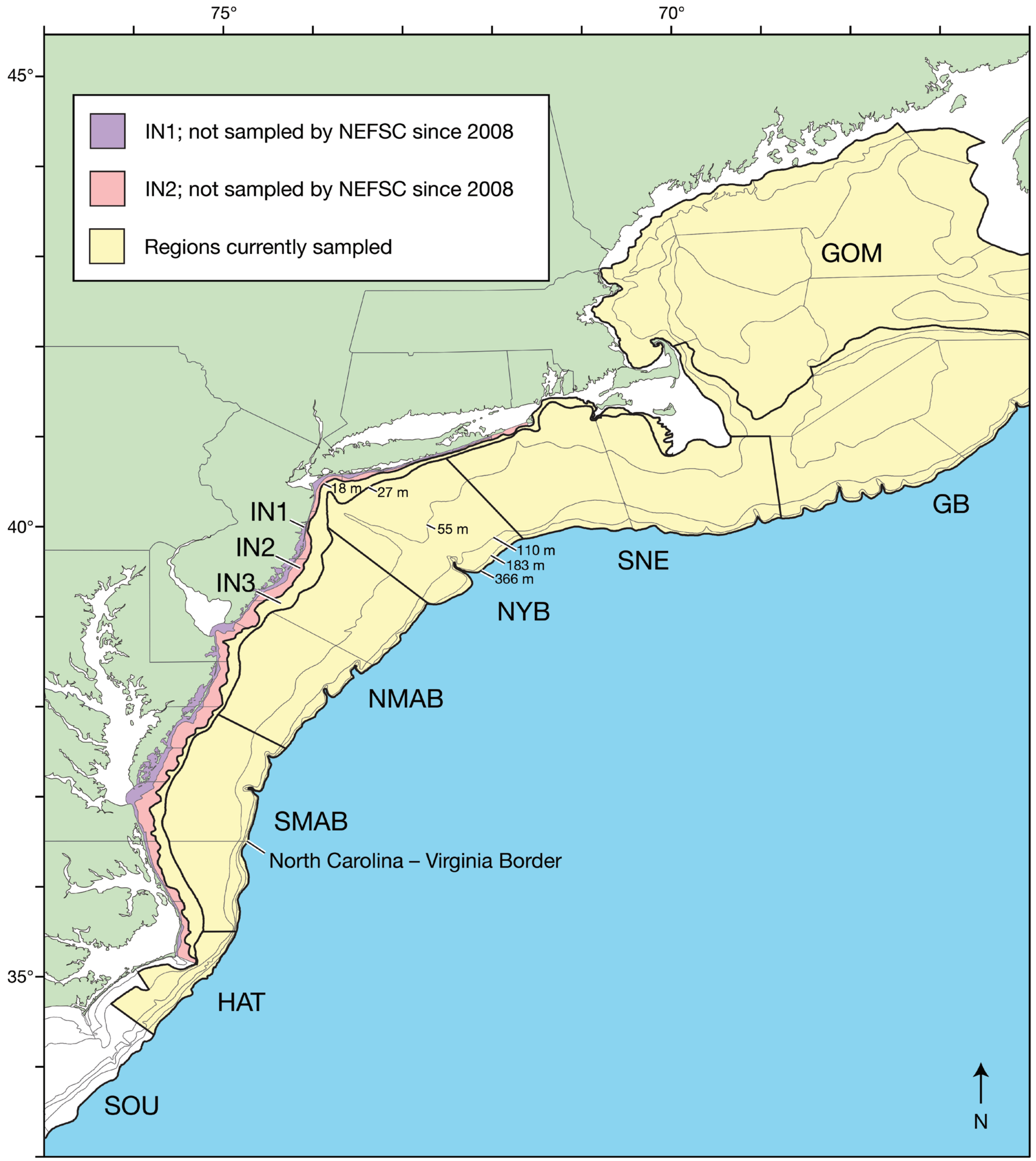


Figure 1

Chart of area sampled by the Northeast Fisheries Science Center (NEFSC) Bottom Trawl Survey (BTS) along the northeast U.S. coast where four species of *Seriola* were sampled between 1963 and 2019. The current survey area (yellow) covers eight of eleven regions recognized in this study: Inshore 3 (IN3), Gulf of Maine (GOM), Georges Bank (GB), Southern New England (SNE), New York Bight (NYB), Northern Mid-Atlantic Bight (NMAB), Southern Mid-Atlantic Bight (SMAB), and Hatteras (HAT). South of Cape Hatteras (SOU), and Inshore regions 1 (IN1, purple) and 2 (IN2, pink) were historically sampled by the BTS. Gray and black lines outline survey strata that are based on bathymetry (meters) and geography.

New England, New York Bight, Northern Mid-Atlantic Bight, Southern Mid-Atlantic Bight, Hatteras, and South of Cape Hatteras. Eight of these regions are currently sampled (all regions except Inshore 1, Inshore 2, and South of Cape Hatteras; Fig. 1). Each region contains strata defined primarily by depth and secondarily by latitude (Politis et al.[1]). Surveys were conducted during Winter (December–February), Spring (March–May), Summer (June–August), and Fall (September–November). Most of the effort summarized in Figure 2 is concentrated in the Spring and Fall bottom trawl surveys, which captures the seasonal distributions of fishes across minimum to maximum water temperatures.

Database, species codes, and queries

Data collected at sea since 1963 are stored in the survey database (SVDBS), maintained in Oracle database management system, Oracle Database 19c Enterprise Edition Release 19.0.0.0.0 (Oracle, Austin, TX) by the NEFSC. More than 45,050 stations have been sampled between 1963 and 2019. Of these, trawls at 344 stations (0.8%) caught one or more species of *Seriola* (Fig. 2). Physical data for each station sampled include geographic location and depth, and, typically, bottom temperature, surface temperature, and salinity.

From 1963–1999, the BTS used paper logs and a three-digit species coding system. From Fall 2000 to Spring 2011, a data entry software system designed by the Office of Aviation and Marine Operations and the NEFSC, Fisheries Scientific Computer System (vers. 1.6), replaced paper logs and used the same three-digit species codes. The three-digit coding system included categories for the four species of *Seriola* known from the western North Atlantic ("*Seriola dumerili*," "*Seriola fasciata*," "*Seriola rivoliana*," and "*Seriola zonata*") and "Carangidae." From Fall 2011 through Spring 2019, a new software implementation, Fisheries Scientific Computer System 2.0, was used. The Fisheries Scientific Computer System 2.0 incorporates a species coding system with links to the Integrated Taxonomic Information System (available from https://www.itis.gov/) and an expanded list of species from the western North Atlantic. The updated coding system made it possible to assign individuals to a genus while at sea if the species assignment could not be determined. Thus, after 2011, "*Seriola*" was a category for specimens that scientists at sea could use when they recognized a specimen as a species of *Seriola*, but could not determine which species. Accordingly, to recover all data for historical records (1963–2006) and examined specimens (2006–2019), we queried the survey database using codes for the four *Seriola* species in the region, "Carangidae" and "*Seriola*."

Laboratory processing

We examined 105 specimens of species of *Seriola* collected at sea between 2006–2019, tagged with computer-generated labels, frozen, and subsequently stored in the NEFSC laboratory freezer in Woods Hole, Massachusetts. Supplement 2 lists all specimens examined. We identified each specimen using anatomical keys and measured standard length (SL), fork length (FL), and total length (TL). We present information based on FL because this is the measurement used at sea for the species of *Seriola*. We recorded meristic data for elements of the median fins (number of dorsal fin spines, dorsal fin rays, anal fin spines, and anal fin rays), and counted gill rakers on the first arch (excluding gill raker rudiments, which are tubercles or short rakers with the diameter of their bases greater than their height following Smith-Vaniz, 2003). We also made a series of morphometric measurements (Table 2) previously used in identification. We examined the shape of the supramaxilla, and based on Smith-Vaniz (2003), expanded descriptions of the width and posterodorsal angle for each species. We added additional supramaxilla descriptions for the four species of *Seriola*: dorsal profile, anterodorsal profile, and anterior transition in width. We define the anterior transition in width as the degree of narrowing, from posterior to anterior, of the supramaxilla. We weighed specimens, stomach contents, and gonads using calibrated precision balances (either 16 kg capacity and 0.1 g resolution or 3200 g capacity and 0.01 g resolution). Specimens collected earlier in the study period (2006–2019) were stored for a longer time in the freezer and may have been more desiccated (and thus weighed less) than those collected later. We preserved a muscle tissue sample from the right caudal peduncle in 95% ethanol for genetic analysis. Using a digital single-lens reflex camera and a photocopy stand with daylight fluorescent lights, we photographed each specimen.

Coloration

We distinguished specimens with juvenile coloration (banded) from those with adult coloration (without bands); note that the presence of adult coloration does not mean that the specimen is a sexually mature adult, merely that it has lost its bands. We used laboratory photographs to categorize background body colors (yellow-olive, reddish-purple, or silver) and scored the presence or absence of a yellow lateral stripe (present, absent), the presence of banding (banded, not banded) and presence of a nuchal stripe (present, absent). We counted bands, excluding the one on the caudal peduncle. We present logistic regressions of banding (binary response; yes/no) versus FL for each species and report the values for lengths at which the proportion

Figure 2

Heat map showing the density of stations sampled (red) by season in each of 11 regions recognized in Figure 1 from 1963 through 2019 along the northeast U.S. coast. Black numbers in red cells represent distinct stations that captured one or more species of *Seriola* (a total of 344 stations). Small gaps in coverage (white) are related to weather or vessel problems (e.g., Southern Mid-Atlantic Bight [SMAB] and Hatteras [HAT] in Spring 2014). Blue represents periods when no sampling vessels were at sea. The survey regions are as follows: Inshore 1 (IN1), Inshore 2 (IN2), Inshore 3 (IN3), Gulf of Maine (GOM), Georges Bank (GB), Southern New England (SNE), New York Bight (NYB), Northern Mid-Atlantic Bight (NMAB), Southern Mid-Atlantic Bight (SMAB), Hatteras (HAT), and South of Cape Hatteras (SOU).

Table 2

Morphometric measurements based on Smith-Vaniz (2003) recorded for the 105 specimens of *Seriola* collected from bottom trawl surveys in the western North Atlantic from 2006 to 2019 and identified to the species level in the laboratory. Data in this table are used for plots in Figure 6 and the principal component analyses shown in Figures 7 and 8.

Measurement	Resolution	Description
Fork length	1 mm	Length from tip of upper jaw to fork of caudal fin
Body depth	1 mm	Deepest vertical length of body, usually near first dorsal fin base
Head length	1 mm	Length from tip of upper jaw to posterior tip of operculum
Eye diameter	0.1 mm	Greatest horizontal diameter of the eye
Upper jaw length	0.1 mm	Length from tip of upper jaw to lower corner of maxilla
Height of 2nd dorsal fin	1 mm	Length from tip of longest ray to its base
Length of 2nd dorsal fin base	1 mm	Length along base of second dorsal fin
Height of anal fin	1 mm	Length from the tip of longest ray to its base
Length of anal fin base	1 mm	Length along base of anal fin not including free spines
Length of pelvic fin	1 mm	Length from tip of longest ray of pelvic fin to base of first pelvic spine

with adult coloration is 5%, 50%, and 95% (L_5, L_{50}, and L_{95}, respectively).

X-rays

To study the anatomy of the first anal pterygiophore, we prepared x-ray images of 14 specimens (three specimens each of *S. dumerili* 19.3–46.7 cm FL; *S. fasciata* 15.5–75.5 cm FL; and *S. rivoliana* 7.6–39 cm FL; and five specimens of *S. zonata* 7.1–26.5 cm FL) using the digital X-ray machine at the NEFSC Woods Hole Aquarium.

Other specimens and photographs

In addition to the 105 examined specimens, we studied 12 other specimens captured on BTS from September 1981 to September 1999 that were deposited at the Museum of Comparative Zoology, Harvard University (Museum records, Suppl. 2). We examined archived cruise images from NEFSC BTS (Suppl. 3). We also examined photographs of carangids caught by recreational anglers fishing in the summer for tuna near the edge of the continental shelf in Southern New England (Fig. 1; Suppl. 3; Historical photographs, Suppl. 2). For comparative identification purposes we examined five specimens of species of *Seriola* collected from Raleigh Bay, North Carolina by colleagues at North Carolina State University. These five specimens were not included in the data or analyses because they were not collected on the NEFSC BTS.

In-lab identifications

We used the key by Smith-Vaniz (2003) to identify to species each of the 105 examined specimens based on anatomical characters (105 examined specimens, Suppl. 2). Diagnostic characters from the literature for four species of *Seriola* in the western North Atlantic are shown in Table 1. To corroborate our identifications based on anatomical characters, we subsequently sequenced COI (approximately 612 bases) for a subsample of 70 specimens (Suppl. 2). From the preserved muscle samples, we extracted DNA using DNeasy Blood and Tissue kits (Qiagen, Hilden, Germany) following the manufacturer's protocol, and amplified sequences using polymerase chain reaction and primers from Integrated DNA Technologies (Coralville, IA). Sequencing primers (5′ to 3′ orientation) used for COI (modified from Ivanova et al., 2007) were:

FishF2_t1 1 TGTAAAACGACGGCCAGT
CGACTATCATAAAGATATCGGCAC

FishR2_t1 1 CAGGAAACAGCTA
GACACTTCAGGGTGACCGAAGAATCAGAA.

We performed polymerase chain reactions in 10µL reactions with 1.5 µL of DNA and reagents at the following concentrations: 5.85 µL water, 2 µL 5×ABI buffer, 0.4µL of forward and reverse primers (10µM), 0.2 µL dNTPs, and 0.05 µL One*Taq* enzyme (OneTaq DNA Polymerase, New England Biolabs, Ipswich, MA). We used an initial denaturing step at 95°C for 5 min followed by six cycles of denaturing at 95°C for 40 s, annealing at a graded series of temperatures from 56-51°C for 45 s each with extension at 68°C for 1 min; 23 additional cycles of denaturing at 95°C for 40 s, annealing at 50°C for 45 s and extension at 68°C for 1 min were followed by a final step of 5 min at 68°C. Polymerase chain reaction products were purified using 0.15 µL Antarctic Phosphatase (New England Biolabs) and 0.15 µL Exonuclease 1 (New England Biolabs). Cycle sequencing was performed using the Applied

Table 3

Contingency table developed to explain how at-sea assignment and in-lab identification relate to false positive and false negative assignments.

	Assigned at sea to species A	Not assigned at sea to species A
Identified in lab as species A	Assignment and identification match; specimen is species A	False negative (misassignment)
Identified in lab as not species A	False positive (misassignment)	Assignment and identification confirm that specimen is not species A

Biosystems BigDye Terminator Cycle Sequencing Kit (Thermo Fisher Scientific Inc., Waltham, MA) and recommended cycling conditions. We reviewed and edited sequences in Sequencher, vers. 5.1 (Gene Codes, Ann Arbor, MI).

We compared our 70 sequences with existing data in GenBank (available from https://www.ncbi.nlm.nih.gov/genbank/) and the Barcode of Life Database (available from http://www.boldsystems.org/) using the National Center for Biotechnology Information Basic Local Alignment Search Tool (available from https://blast.ncbi.nlm.nih.gov/Blast.cgi). We downloaded COI sequences from GenBank for each of the four species of *Seriola* that we studied and two potential outgroups for the genus, rainbow runner (*Elagatis bipinnulata*) and pilotfish (*Naucrates ductor*) (Smith-Vaniz, 1984; Reed et al., 2002). We used Clustal Omega, vers. 1.2.4 (Sievers et al., 2011) to align our sequences with those from GenBank and construct a neighbor-joining tree for 113 sequences (3 GenBank sequences for *E. bipinnulata*; 3 GenBank sequences for *N. ductor*; 6 sequences+20 GenBank sequences for *S. dumerili*; 23 sequences+1 GenBank sequence for *S. fasciata*; 10 sequences+11 GenBank sequences for *S. rivoliana*; 31 sequences+5 GenBank sequences for *S. zonata*; Suppl. 2 and Suppl. 4). Sequences for specimens examined in this study are available in GenBank (accession numbers are provided in Suppl. 2).

Terminology for identification

We developed terminology for describing identification. An "assignment" occurred at sea when an individual fish was "assigned" to a species (or higher taxon). In the laboratory at Woods Hole, we "identified" specimens to the species-level. A "misassignment" represents a fish that was not correctly assigned to species at sea. This can only be discovered by confirming at-sea assignments through in-lab identification of the same specimen.

In this system, identifications are never wrong, but assignments can be (Table 3). A correctly assigned fish could either be species A (correctly assigned at sea; Table 3, green cell), or a species that is not species A (assigned at sea to another species; Table 3, white cell). Specimens can be misassigned in two ways. A false negative occurs when species A is misassigned to another species (Table 3, yellow cell). Note that a specimen may be assigned at sea to a higher taxonomic level, which is not technically a false negative, but has the same effect on data. False negatives result in missing data for species A but have no effect on the validity of existing data in the database for that species, provided there is no assignment bias (e.g., against certain life stages, color patterns). In the second type of misassignment, a false positive, specimens of another species are misassigned to species A (Table 3, red cell). Such false positives are erroneous records for species A that could lead to conclusions based on biological information for a different species.

We compared at-sea assignments to in-lab identifications to calculate two rates. The first, recognition rate, is the percentage of specimens correctly assigned to a specified taxonomic level at sea for each species (i.e., percentage of total number of taxonomic level A correctly assigned to A). The second is the identification rate, which is the percentage of at-sea assignments to each species that matched the in-lab identifications (i.e., out of the total specimens assigned to species A, how many were actually species A).

Age, growth, and maturity

Direct age estimates were not obtained for specimens; however, based on available literature for size at age-1 for *S. dumerili* (~50 cm FL at age-1, Thompson et al., 1999; ~15 cm SL at 100 d, Wells and Rooker, 2004; ~50-60 cm FL at age-1, Harris et al., 2007) and evaluation of seasonal length frequency modes, we assumed all individuals ≤35 cm FL in summer and fall were young-of-the-year (YOY). The rapid growth rates have led to interest in aquaculture of *Seriola* (Mazzola et al., 2000; Sicuro and Luzzana, 2016); reported growth rates in captivity support our assumed sizes for YOY

(*S. dumerili* 40 mm TL at 40 d, Papandroulakis et al., 2005; *S. dorsalis* 30 cm at 150 d and 35 cm at 200 d, Schwebel, 2017; *S. rivoliana* growth in weight from 2.5–80.0 g in 9 weeks, Kissinger et al., 2016).

Sex and maturity of fish were assessed macroscopically from frozen specimens following methods of Burnett et al. (1989). Gonad mass was recorded, and gonadosomatic index (GSI) calculated as *GSI*= 100×(*gonad weight*/(*body weight*–*gonad weight*)). For a subset of specimens (sample size [*n*]=26) a portion of the gonad was fixed in 10% buffered formalin for histological analysis. Fixed samples were dehydrated in EtOH, embedded in paraffin, thin sectioned, and stained with periodic acid Schiff-Mallory trichrome (Massachusetts Histology Services, Worcester, MA). Gonad histology (oocyte stages and the presence and stage of post ovulatory follicles in females; spermatogonia, spermatocysts, spermatozoa, and spermatids in males) was evaluated following Brown-Peterson et al. (2011) and Smith et al. (2014) to differentiate immature, resting, and spawning-capable individuals.

Stomach contents

We examined and weighed stomach contents (in kilograms) for 77 of the 105 specimens examined and identified the contents to lowest possible taxonomic level.

Data analyses and software

We plotted and analyzed data in R, vers. 3.5.1 (R Core Team, 2020) and prepared maps using ArcMap vers. 10.3 (Esri, Redlands, CA). We used software included in Adobe Creative Cloud 2020 (Photoshop, Illustrator, and InDesign) (Adobe Inc., San Jose, CA) to edit and prepare photographs and line art.

We performed logistic regressions using a logit link in R to model the onset of adult coloration. We used glm in the base package of R for *S. zonata*, and for all others we used the package brglm (Kosmidis, 2021), which used a maximum penalized likelihood method to account for complete separation in the data.

We used the packages FactoMineR (Lê et al., 2008) and factoextra (Kassambara and Mundt, 2020) in R to perform a principal component analysis of log transformed data for variables included in Table 2 to study morphometric variation within and among species.

Results

Results are organized in two sections. First, we discuss work on 105 specimens examined in the laboratory. We defer treatment of distributions, seasonality, temperature and salinity, and sizes to the second section, which includes historical records for the four species of *Seriola* in the survey database.

In-lab identifications

All laboratory identifications of *S. dumerili*, *S. fasciata*, *S. rivoliana*, and *S. zonata* based on anatomical characters agreed with our identifications based on COI barcoding and comparisons with sequences from GenBank (Suppl. 2).

Accuracy of at-sea assignments Of the 105 examined specimens, 99.04% were correctly assigned to family Carangidae at sea (Table 4; one specimen of *S. fasciata* was assigned to "unknown" at sea) and 82.86% were correctly assigned to the genus *Seriola*. No specimens assigned at sea to the genus *Seriola* were identified as belonging to a different genus. Two specimens were incorrectly assigned at sea to *Caranx*, but laboratory identification confirmed that they were *Seriola*.

At the species level, however, only 37.14% of the 105 examined specimens were correctly assigned at sea (Table 4). Three of the four species were correctly assigned at sea ≥91.67% of the time (*S. fasciata*, 100%; *S. rivoliana*, 100%; *S. zonata*, 91.67%; Table 4) but the accuracy of at-sea assignments was poor for *S. dumerili* (24.0%; Table 4). At-sea assignment of *S. dumerili* resulted in the most false positives (19/25 false positives; Table 4). There were only two false positives for *S. zonata* (identified in the laboratory as *S. rivoliana*), and no false positives for *S. fasciata* or *S. rivoliana* (Table 4).

Lengths and weights of examined specimens Table 5 summarizes lengths and weights of the 105 examined specimens. Most specimens were juveniles, resulting in low mean lengths for *S. dumerili*, *S. rivoliana*, and *S. zonata*. Our examined specimens included eight unusually large specimens of *S. fasciata*, but no large adults for the other three species. Mean weight was also low for *S. dumerili*, *S. rivoliana*, and *S. zonata*, but higher for *S. fasciata* because of the large adult specimens examined.

Coloration Coloration varies interspecifically and species of *Seriola* undergo dramatic ontogenetic changes in body color and banding patterns. Results below are based on the 105 examined specimens and therefore do not include observations of large adults for all four species (Table 5). We photographed banded juveniles and adult-coloration specimens (Fig. 3) and considered four aspects of color and pattern for each species: body color, yellow lateral stripe, banding, and nuchal stripe.

Banded juvenile specimens of *S. dumerili*, *S. fasciata*, and *S. rivoliana* have a yellow-olive body color with or-

Table 4

Comparison of at-sea assignments to laboratory identifications for 105 specimens of four species of *Seriola* collected from bottom trawl surveys in the western North Atlantic from 2006 to 2019. Specimens were identified as either greater amberjack (*Seriola dumerili*), lesser amberjack (*S. fasciata*), almaco jack (*S. rivoliana*), or banded rudderfish (*S. zonata*). Green shaded boxes indicate the number of specimens that were correctly assigned at sea. Light green boxes indicate assignments that were correct at higher taxonomic levels (i.e., genus *Seriola*, family Carangidae) but not identified at the species level. Red boxes indicate the number of specimens with a false positive assignment to species. Yellow boxes indicate false negative assignments. Identification rates represent the percentage of specimens assigned at sea to species that later were confirmed during laboratory examination. Species, genus, or family recognition rates summarize the percentage of specimens recognized at sea.

		In-lab identification				Identification rate: specimens assigned at sea to A that are A
		Seriola dumerili	*Seriola fasciata*	*Seriola rivoliana*	*Seriola zonata*	
At-sea assignment	unknown		1			
	Caranx	1				
	Caranx crysos		1			
	Carangidae	2	8	5		
	Seriola	5	1	6	15	
	Seriola dumerili	6	12	2	5	6/25 = 24%
	Seriola fasciata		5			5/5 = 100%
	Seriola rivoliana			6		6/6 = 100%
	Seriola zonata			2	22	22/24 = 91.67%
Species-level Recognition Rate: specimens of A successfully assigned to species A at sea		6/14 = 42.86%	5/28 = 17.86%	6/21 = 28.57%	22/42 = 52.38%	Average: 39/105 = 37.14%
Genus-level Recognition Rate: specimens of A successfully assigned to *Seriola* at sea		11/14 = 78.57%	18/28 = 64.29%	16/21 = 76.19%	42/42 = 100%	Average: 87/105 = 82.86%
Family-level Recognition Rate: specimens of A successfully assigned to Carangidae at sea		14/14 = 100%	27/28 = 96.43%	21/21 = 100%	42/42 = 100%	Average: 104/105 = 99.04%

Table 5

Mean lengths and weights for 105 examined specimens of four species of *Seriola* collected from bottom trawl surveys in the western North Atlantic from 2006 to 2019. The four species that were identified include greater amberjack (*S. dumerili*), lesser amberjack (*S. fasciata*), almaco jack (*S. rivoliana*), and banded rudderfish (*S. zonata*). *n*=sample size. Standard deviations (SD) are given in parentheses.

Species	*n*	Total length, cm (SD)	Fork length, cm (SD)	Standard length, cm (SD)	Weight, kg (SD)
Seriola dumerili	14	33.1 (± 11.4)	28.5 (± 9.6)	26.7 (± 9.1)	0.53 (± 0.43)
Seriola fasciata	28	45.8 (± 24.2)	39.8 (±21.5)	37.6 (±20.0)	2.30 (± 3.03)
Seriola rivoliana	21	38.5 (± 13.2)	33.3 (±11.4)	30.9 (± 10.5)	0.85 (± 0.59
Seriola zonata	42	26.4 (± 4.5)	23.1 (±3.9)	21.8 (±3.6)	0.24 (± 0.11)

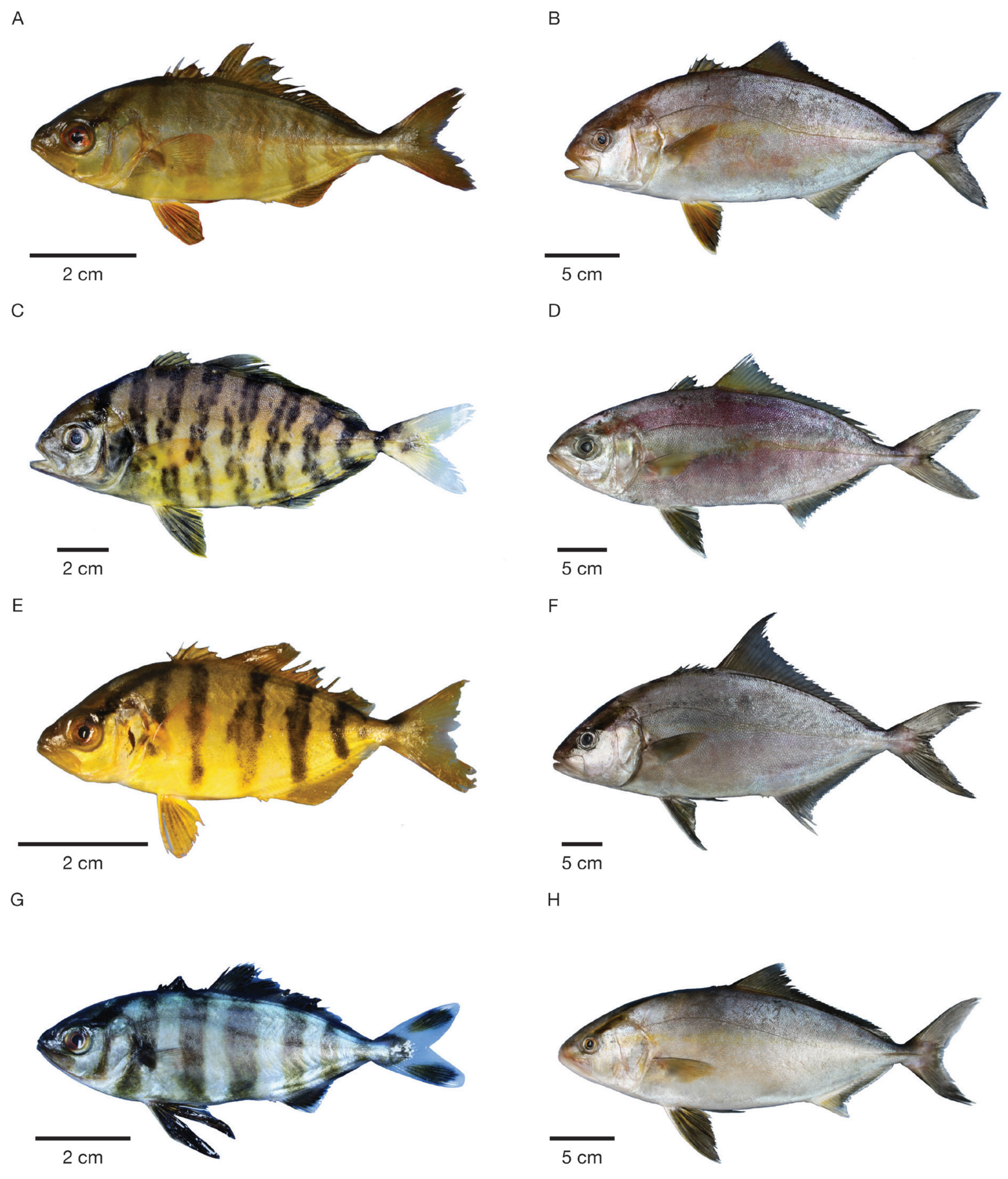


Figure 3

Photographs of banded juvenile and adult-coloration specimens of *Seriola* collected in the western North Atlantic from 2006 to 2019. (A) Banded juvenile greater amberjack (*S. dumerili*) (7.18 cm fork length [FL], VIMS 42095). (B) Adult-coloration *S. dumerili* (25.1 cm FL, CUMV 99124). (C) Banded juvenile lesser amberjack (*S. fasciata*) (14.1 cm FL, CUMV 99154). (D) Adult-coloration *S. fasciata* (28.9 cm FL, CUMV 99155). (E) Banded juvenile almaco jack (*S. rivoliana*) (6 cm FL, uncataloged). (F) Adult-coloration *S. rivoliana* (34.4 cm FL, CUMV 99125). (G) Banded juvenile banded rudderfish (*S. zonata*) (8.0 cm FL, uncataloged). (H) Adult-coloration *S. zonata* (30.2 cm FL, CUMV 99122).

Figure 4

Size record for lesser amberjack (*Seriola fasciata*) (76.0 cm fork length, CUMV 98739) collected in the western North Atlantic on 14 September 2012.

ange fins (Fig. 3, A, C, E). Adult-coloration specimens of *S. dumerili* are silver-gold (Fig. 3B); adult-coloration specimens of *S. fasciata* frequently are reddish-purple (Figs. 3D and 4); most adult-coloration specimens of *S. rivoliana* are silver-olive (Fig. 3F). Both juvenile and adult coloration specimens of *S. zonata* have a silver body color (Fig. 3, G and H).

Juveniles differ from specimens with adult coloration primarily in the presence of dark bands on the body (Fig. 3, A, C, E, G). There are five wavy brown bands in juvenile *S. dumerili* (Fig. 3A), seven to nine wavy brown bands in *S. fasciata* (Fig. 3C), and six in juvenile *S. rivoliana* (Fig. 3E). In contrast, juveniles of *S. zonata* have six relatively straight black bands easily distinguished against the background coloration (Fig. 3G). For *S. fasciata*, *S. rivoliana*, and *S. zonata*, we found that banding intensity fades as size increases; fading of band intensity also likely occurs in *S. dumerili*, but we had only one banded specimen.

Logistic regressions (Fig. 5) show that bands are lost at different lengths: L_{50}=11.7 cm FL for *S. dumerili*; L_{50}=22.9 cm FL for *S. fasciata*; L_{50}=18.7 cm FL for *S. rivoliana*; and L_{50}=25.5 cm FL for *S. zonata*. For *S. zonata*, L_5=22.8 cm FL and L_{95}=28.2 cm FL, indicating that 90% of individuals lose juvenile bands within a 5.4 cm window of FL. For the other three species, a lack of banded juvenile specimens (*S. dumerili*, *S. rivoliana*) and separation in the data (*S. dumerili*, *S. fasciata*, *S. rivoliana*) result in wider confidence intervals than in *S. zonata* (Fig. 5).

The relationship between species identification rates, sizes, and coloration of individuals revealed several points (Fig. 5). Incorrect assignment at sea of specimens as *S. dumerili* (false positives) occurred across species, size ranges, and coloration patterns. Most large specimens of *S. fasciata* with adult coloration were misassigned to *S. dumerili* at sea. Although most *S. rivoliana* with adult coloration (and characteristic tall dorsal and anal fins) were correctly assigned at sea, none of the smaller specimens with juvenile coloration were correctly assigned at sea. In contrast, most of the smaller specimens of *S. zonata* with juvenile coloration were correctly assigned, but none of the larger specimens of this species with adult coloration were correctly assigned at sea.

A yellow lateral stripe is variably present in all four species in both juvenile and adult-coloration specimens (Fig. 3). For example, in an adult-coloration specimen of *S. dumerili* (Fig. 3B), the yellow lateral stripe extends from the operculum mid-way along the body to below the insertion of the soft dorsal fin. Large adult-coloration *S. fasciata* had a prominent yellow stripe (Fig. 4).

All examined specimens of *S. dumerili* had a brown nuchal stripe. All banded specimens of *S. fasciata* had a dark brown nuchal stripe; two other small but not banded specimens (258 mm and 319 mm FL) had a nuchal stripe, but the nuchal stripe was absent in 21 of the 28 specimens, including large individuals. All examined specimens of *S. rivoliana* had a dark brown nuchal stripe. All examined specimens of *S. zonata* had a prominent, black nuchal stripe. In general, banded specimens had more prominent nuchal stripes than larger specimens where bands were absent.

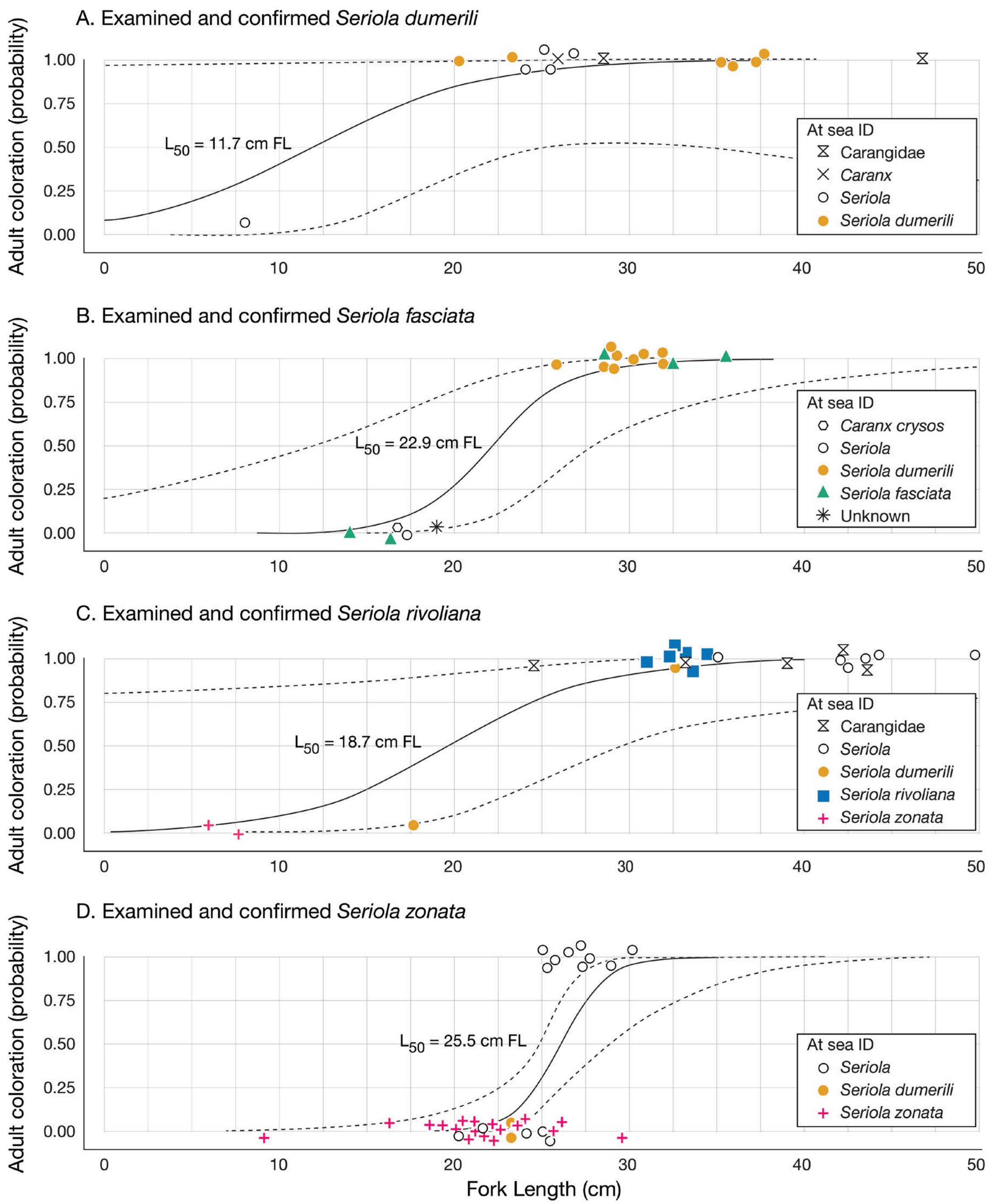


Figure 5

Logistic regression plots estimating laboratory-confirmed (A) greater amberjack (*Seriola dumerili*), (B) lesser amberjack (*S. fasciata*), (C) almaco jack (*S. rivoliana*), and (D) banded rudderfish (*S. zonata*) size at 50% transition (L_{50}) from juvenile banding (0) to adult coloration (1) in the western North Atlantic between 2006 and 2019. Specimens are coded by their at-sea assignment for comparison to the laboratory-confirmed identification. Specimens greater than 50 cm were not plotted. Points are jittered to reduce overplotting. Dotted lines indicate 95% confidence intervals for the logistic regressions. Estimated L_{50} values for each species were as follows: *S. dumerili*=11.7 cm fork length (FL); *S. fasciata*=22.9 cm FL; *S. rivoliana*=18.7 cm FL; and *S. zonata*=25.5 cm FL.

Table 6

Frequency of counts of dorsal fin spines and rays in greater amberjack (*Seriola dumerili*), lesser amberjack (*S. fasciata*), almaco jack (*S. rivoliana*), and banded rudderfish (*S. zonata*) collected from bottom trawl surveys in the western North Atlantic from 2006 to 2019. *n*=sample size.

	1st dorsal fin spines				Attached 2nd dorsal fin spines, 2nd dorsal soft fin rays													*n*
	V	VI	VII	VIII	I,28	I,29	I,30	I,31	I,32	I,33	I,34	I,35	I,36	I,37	I,38	I,39	I,40	
S. dumerili	1	1	12	—	—	—	1	3	3	7	—	—	—	—	—	—	—	14
S. fasciata	—	1	4	23	—	3	9	11	3	1	1	—	—	—	—	—	—	28
S. rivoliana	—	—	21	—	4	8	5	3	1	—	—	—	—	—	—	—	—	21
S. zonata	2	1	2	37	—	—	—	—	—	—	3	6	11	11	7	1	3	42

Table 7

Frequency of counts of anal fin spines and rays in greater amberjack (*Seriola dumerili*), lesser amberjack (*S. fasciata*), almaco jack (*S. rivoliana*), and banded rudderfish (*S. zonata*) collected from bottom trawl surveys in the western North Atlantic from 2006 to 2019. *n*=sample size.

	Free anal fin spines	Attached anal fin spine, anal fin soft rays								*n*
	II	I,15	I,16	I,17	I,18	I,19	I,20	I,21	I,22	
S. dumerili	10	—	—	—	—	—	3	6	1	10
S. fasciata	27	1	—	1	4	12	8	1	—	27
S. rivoliana	20	—	—	—	—	—	13	7	—	20
S. zonata	41	—	—	—	—	9	23	9	—	41

Meristic characters Table 6 reports frequency distributions for spines and fin rays in the first and second dorsal fins. The number of first dorsal fin spines ranged from V to VIII, with modes of VII (*S. dumerili, S. rivoliana*) and VIII (*S. fasciata*, *S. zonata*). To evaluate the number of first dorsal fin spines, it is necessary to closely examine with a probe to be sure that all spines are counted because often spines become embedded and overgrown by soft tissue. Given the overlap in the modal number of spines in the first dorsal fin, this character by itself is not diagnostic for any of the four species but is useful when combined with gill raker counts.

The second dorsal fin in all individuals examined had a single, attached spine preceding the soft dorsal fin rays (Table 6). Counts of second dorsal fin spines and fin rays ranged from I,28 to I,40 with modes of I,33 (*S. dumerili*), I,31 (*S. fasciata*), I,29 (*S. rivoliana*) and I,36-37 (*S. zonata*). This count is most useful for distinguishing *S. zonata* from the other three species.

In all individuals examined there were II free anal fin spines, I attached anal fin spine, and a series of soft rays ranging from 15-22 (Table 7). Anal fin ray modes were 21 (*S. dumerili*), 19 (*S. fasciata*), and 20 (*S. rivoliana*, *S. zonata*). This character was not diagnostic at the species level for any of the species, but *S. fasciata* consistently had fewer anal fin rays than did the other species.

The number of gill rakers on the first gill arch ranged from 14-28 (Table 8). Modal counts were 19 (*S. dumerili*), 24 (*S. fasciata*), 27 (*S. rivoliana*), and 19 (*S. zonata*). Eight specimens of *S. fasciata* that we examined exceeded the previously reported maximum size for the species (see Size, Maturity and Growth) and confirm what Smith-Vaniz (2003) reported regarding gill raker counts decreasing with size for *S. dumerili*, *S. rivoliana*, and *S. zonata*, but not decreasing in *S. fasciata*. Because the number of gill rakers decreases with length for the other three species, and many of our specimens were small, the frequency distributions reported here may not be representative of the species as adults. The combination of this count with counts of first dorsal fin spines is diagnostic for the four species.

Table 8

Frequency of counts of developed gill rakers on gill arch 1 (Smith-Vaniz, 2003) in greater amberjack (*Seriola dumerili*), lesser amberjack (*S. fasciata*), almaco jack (*S. rivoliana*), and banded rudderfish (*S. zonata*) collected from bottom trawl surveys in the western North Atlantic from 2006 to 2019. *n*=sample size.

	Total number of gill rakers on gill arch 1															
	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	*n*
S. dumerili	1	—	1	—	2	3	2	1	—	—	1	—	—	—	—	11
S. fasciata	—	—	—	—	—	—	—	—	—	1	15	8	4	—	—	28
S. rivoliana	—	—	—	—	—	—	—	—	—	—	2	1	7	9	1	20
S. zonata	—	2	5	6	6	8	7	4	2	1	—	—	—	—	—	41

Morphometrics Figure 6 presents bivariate plots of morphometric variables summarized in Table 2 against FL. All characters have been used in previous diagnoses for the four species of *Seriola* in the western North Atlantic (e.g., Smith-Vaniz, 2003). Larger specimens are easier to distinguish using morphometric characters (Fig. 6). Many morphometric characters broadly overlap in the series of 105 examined specimens, however, some are useful for distinguishing species. For example, when compared to the other three species, eye diameter is smaller in *S. zonata* and larger in *S. fasciata* (Fig. 6B). Body depth of *S. zonata* (Fig. 6D) is less than that of the other species, and anal fin base length (Fig. 6G) is smaller in *S. zonata* than the other three species. Second dorsal fin height (Fig. 6F) is greater in *S. rivoliana* than the other three species, as is anal fin height (Fig. 6H).

Results of principal component analyses of 10 morphometric variables listed in Table 2 are summarized in Figures 7 and 8. For principal component 1 (PC1) and principal component 2 (PC2) (Fig. 7), ellipses for each species broadly overlap, indicating that the four species of *Seriola* are difficult to distinguish based on morphometric measurements alone. In particular, the ellipse for *S. zonata* is contained within those of *S. dumerili* and *S. fasciata,* and it contacts the ellipse for *S. rivoliana*. Anal fin height and second dorsal fin height readily separate large individuals of *S. rivoliana* from the other three species. The relatively longer upper jaw, larger eye, and longer head of *S. fasciata* distinguish the largest individuals of this species in our examined specimens. The plot of PC2 and PC3 (Fig. 8) separates *S. fasciata* and *S. zonata* along (increasing) body depth, eye diameter, and anal fin base vectors for *S. fasciata* and (increasing) pelvic fin length, upper jaw length, and head length for *S. zonata*. These characters also separate *S. zonata* from the other two species, and, although there is overlap with *S. dumerili*, they highlight *S. zonata* as the most distinct of the four species. PC2 and PC3 show better separation but account for only 5.4% of the variation among species. As in Figure 7, the ellipse for *S. dumerili* broadly overlaps those of the other three species, reinforcing the similarity of *S. dumerili* to all others.

Shape of supramaxilla Berry and Burch (1979, table 1) described the shape of the upper jaw as diagnostic for the four species. Subsequently, Smith-Vaniz (2003) restricted this character to the shape of the supramaxilla, characterizing each species as follows: *S. dumerili*, broad, with posterodorsal angle rounded (Fig. 9A); *S. fasciata*, relatively slender (Fig. 9B); *S. rivoliana*, broad, with posterodorsal angle acute (Fig. 9C); and *S. zonata*, moderately slender (Fig. 9D). Our observations support these characterizations except in *S. rivoliana*, where we observed variation in the posterodorsal angle, from acutely angled to broadly rounded. *Seriola dumerili* had a broad supramaxilla, with a broadly rounded posterodorsal margin, a pronounced dorsal curvature, a variably concave anterodorsal profile that always formed a concavity in confluence with the maxilla, and a steep anterior transition in width (Fig. 9A, Suppl. 1). *Seriola fasciata* had a slender supramaxilla, with a variably acutely angled to abruptly rounded posterodorsal angle, lacked a pronounced dorsal curvature, with a nearly straight anterodorsal profile, and a slight anterior transition in width (Fig. 9B, Suppl. 1). *Seriola rivoliana* had a broad supramaxilla with a variably acutely angled to broadly rounded posterodorsal profile, a pronounced dorsal curvature, an anterodorsal profile that varied from straight to concave, and a steep anterior transition in width (Fig. 9C, Suppl. 1). *Seriola zonata* had a moderate supramaxilla with a gently rounded posterodorsal angle, a moderate dorsal curvature, a nearly straight anterodorsal profile, and a gradual anterior transition in width (Fig. 9D, Suppl. 1).

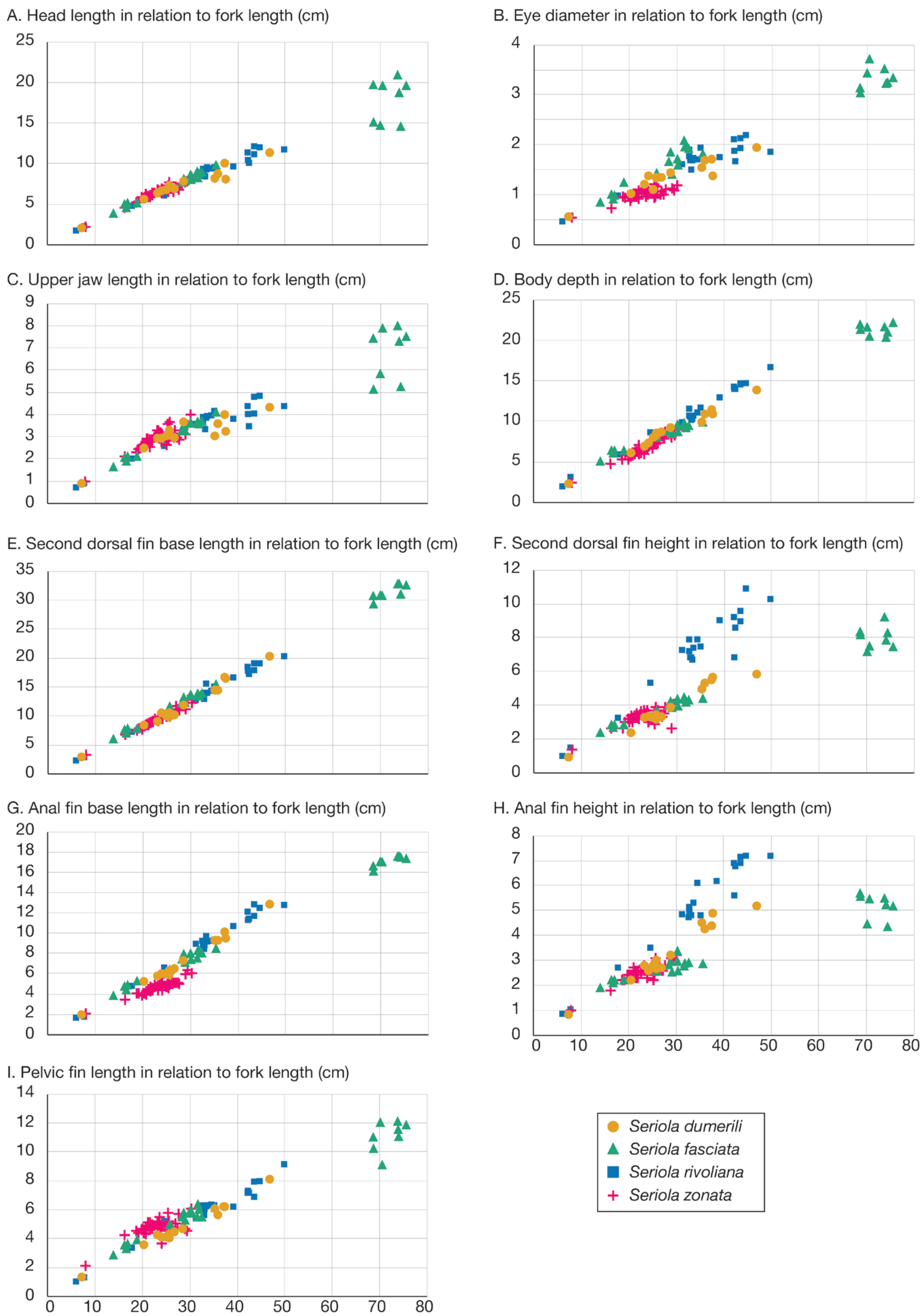


Figure 6

Morphometric measurements in relation to fork length for greater amberjack (*Seriola dumerili*) (circles), lesser amberjack (*S. fasciata*) (triangles), almaco jack (*S. rivoliana*) (squares), and banded rudderfish (*S. zonata*) (crosses) collected in the western North Atlantic between 2006 and 2019. The morphometric measurements documented include (A) head length, (B) eye diameter, (C) upper jaw length, (D) body depth, (E) second dorsal fin base length, (F) second dorsal fin height, (G) anal fin base length, (H) anal fin height, and (I) pelvic fin length.

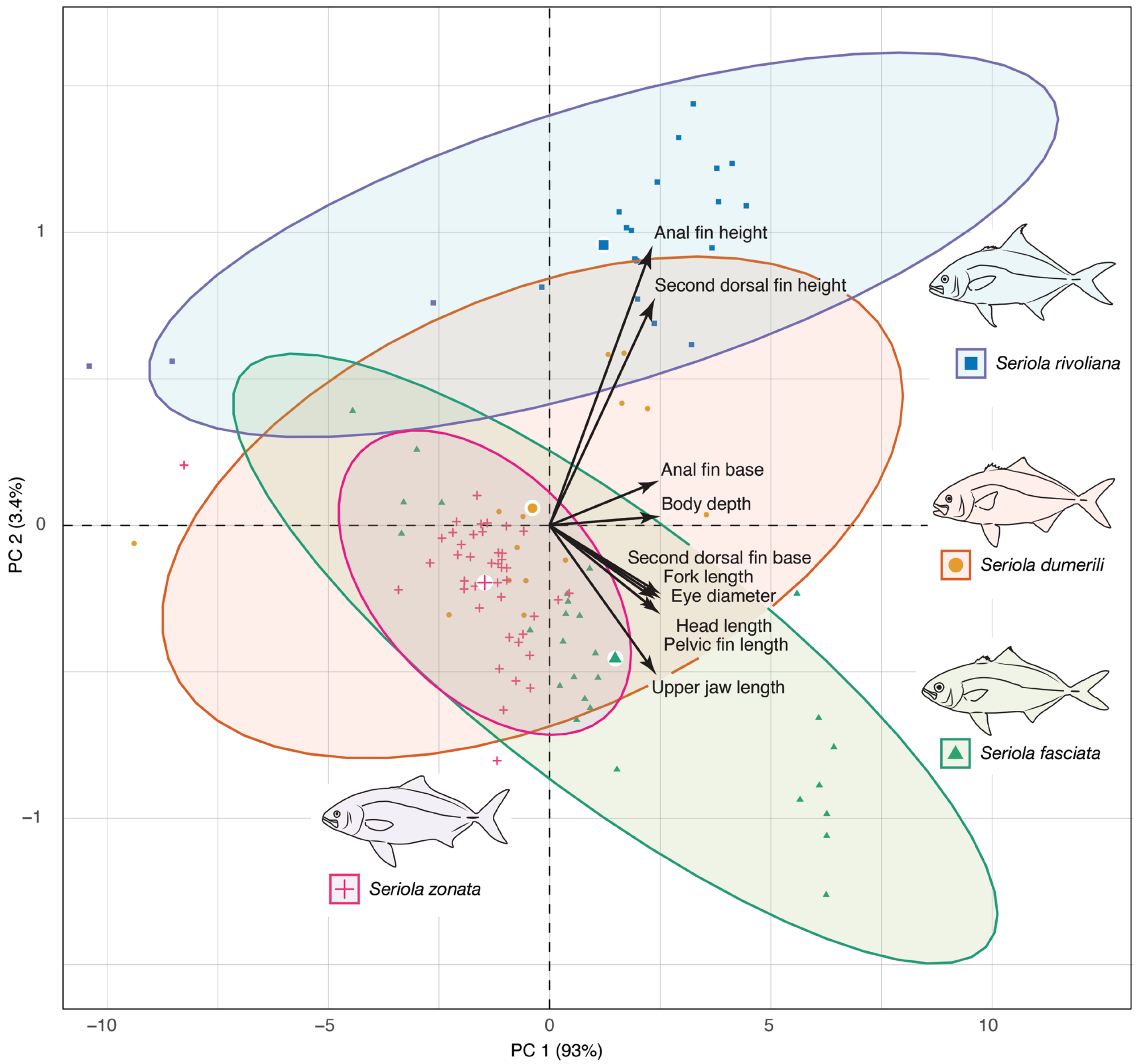


Figure 7

Principal component analysis (PCA) of 10 morphometric variables (see Table 2) in four species of *Seriola* collected in the western North Atlantic between 2006 and 2019: greater amberjack (*Seriola dumerili*) (circles), lesser amberjack (*S. fasciata*) (triangles), almaco jack (*S. rivoliana*) (squares), and banded rudderfish (*S. zonata*) (crosses). Ellipses represent 95% confidence regions. Centroids are indicated with larger symbols. Arrows indicate the correlation of the morphometric variable with the principal components. Percentages refer to the variability explained by the principal component. The 95% confidence ellipse for *S. dumerili* encloses the ellipse for *S. zonata*. *Seriola fasciata* has a comparatively longer upper jaw and larger eye diameter; however, it is morphometrically similar to *S. dumerili* and 50% of their confidence ellipses overlap. *Seriola rivoliana* is relatively well separated by the height of anal and second dorsal fin.

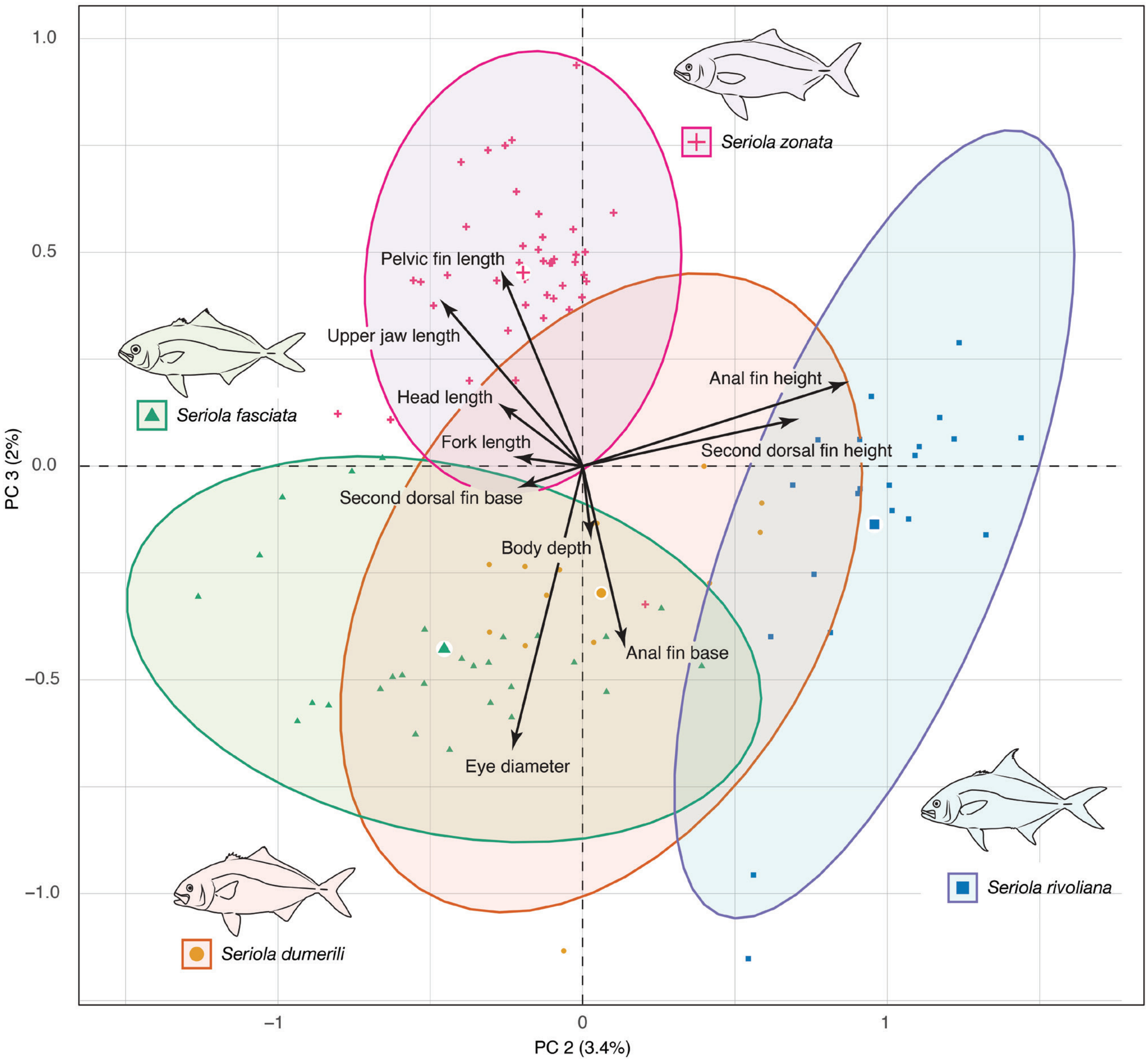


Figure 8

Principal components 2 and 3 from principal component analysis (PCA) of 10 morphometric variables (see Table 2) in four species of *Seriola* collected in the western North Atlantic between 2006 and 2019: greater amberjack (*Seriola dumerili*) (circles), lesser amberjack (*S. fasciata*) (triangles), almaco jack (*S. rivoliana*) (squares), and banded rudderfish (*S. zonata*) (crosses). Ellipses represent 95% confidence regions. Centroids indicated with larger symbols. Arrows indicate the correlation of the morphometric variable with the principal components. Percentages refer to the variability explained by the principal component. The 95% confidence ellipse for *S. dumerili* overlaps the other three species. There is more separation of *S. zonata* in these dimensions than in Figure 7.

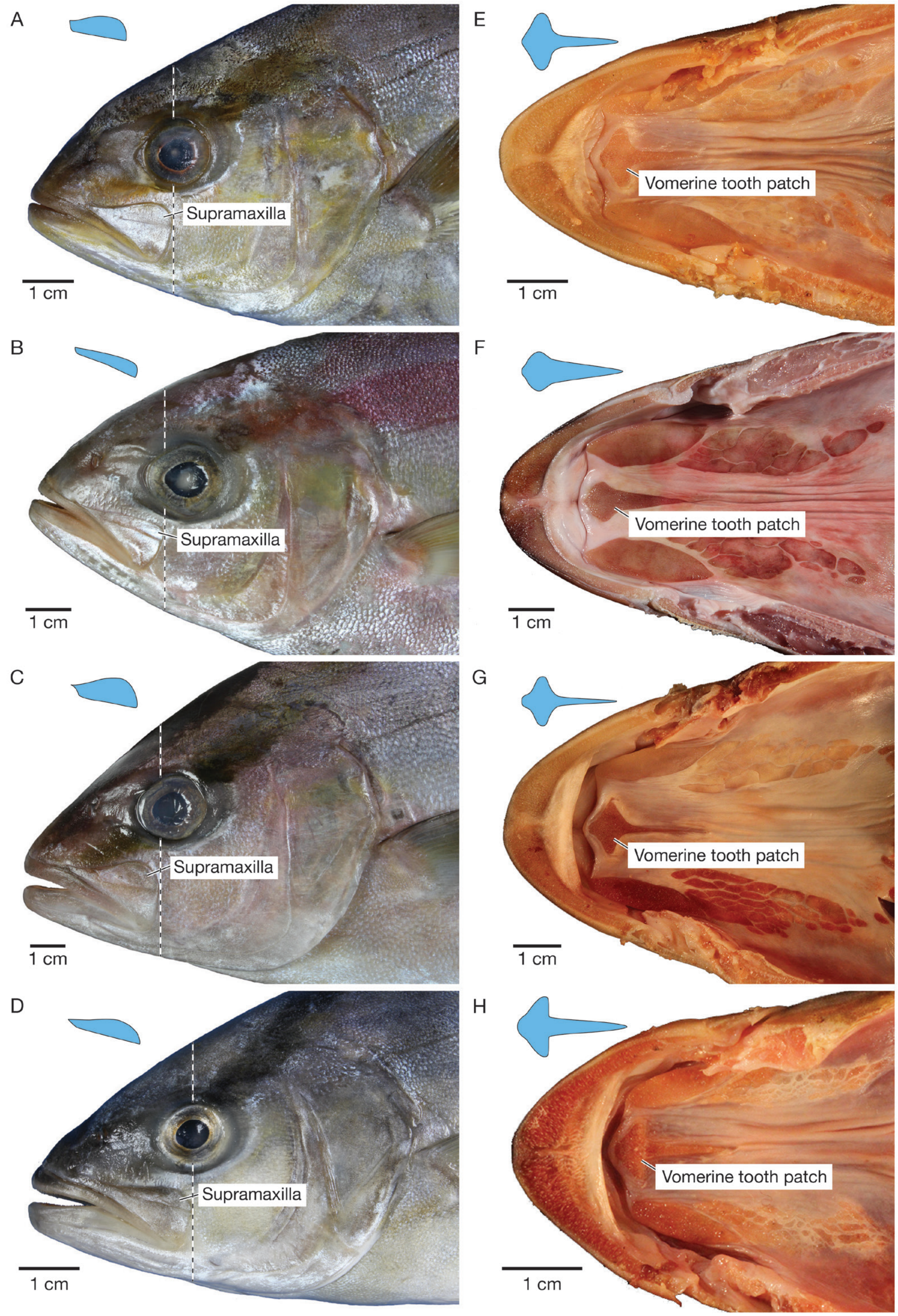


Figure 9

Photographs showing shape of the supramaxilla with dashed lines indicating position of the posterior margin of the supramaxilla in relation to the pupil (left panels) and the shape of vomerine tooth patches (right panels) in four species of *Seriola* collected in the western North Atlantic between 2006 and 2019. (A) Broad supramaxilla of a greater amberjack (*S. dumerili*) (25.5 cm fork length [FL], CUMV 99121) showing a broadly rounded posterodorsal margin, pronounced dorsal curvature, concave anterodorsal profile (variable) forming concavity with maxilla, and steep anterior narrowing. The posterior tip of the supramaxilla extends to the middle of the pupil. (B) Slender supramaxilla of a lesser amberjack (*S. fasciata*) (28.9 cm FL, CUMV 99155) showing the posterodorsal margin abruptly rounded (variable), lack of pronounced dorsal curvature, anterodorsal profile nearly straight, and slight anterior narrowing. The posterior tip of the supramaxilla extends to the anterior margin of the pupil. (C) Broad supramaxilla of an almaco jack (*S. rivoliana*) (34.4 cm FL, CUMV 99125) showing the posterodorsal margin broadly rounded (variable), pronounced dorsal curvature, anterodorsal margin concave (variable), and steep anterior narrowing. The posterior tip of the supramaxilla extends to just beyond the anterior margin of the pupil. (D) Moderate supramaxilla of a banded rudderfish (*S. zonata*) (20.4 cm FL, CUMV 99144) showing a gently rounded posterodorsal margin, moderate dorsal curvature, nearly straight anterodorsal profile, and gradual anterior narrowing. The posterior tip of the supramaxilla extends to the middle of the pupil. The right panels show photographs of vomerine tooth patches in (E) *S. dumerili* (38 cm FL, CUMV 99131), (F) *S. fasciata* (70.1 cm FL), (G) *S. rivoliana* (49.0 cm FL, CUMV 99130), and (H) *S. zonata* (25.9 cm FL, CUMV 99132).

Table 9

Summary of stomach contents for greater amberjack (*Seriola dumerili*), lesser amberjack (*S. fasciata*), almaco jack (*S. rivoliana*), and banded rudderfish (*S. zonata*) collected from bottom trawl surveys in the western North Atlantic (*n*=77) from 2006 to 2019 and examined in the laboratory. Prey constituting noteworthy components are indicated in parentheses.

Species	Stomachs with contents/ stomachs examined	Number of stomachs with fish	Number of stomachs with squid	Number of stomachs with shrimp	Number of stomachs with crabs	Number of stomachs with animal remains
S. dumerili	7/7	3	3	–	–	1
S. fasciata	21/26	1	21 (8 *Illex*, 9 *Loligo*)	1	–	–
S. rivoliana	16/19	10 (3 with flatfishes)	5	5	6 (4 galatheids; 3 portunids)	–
S. zonata	23/25	19 (3 with *Sardinella*, 7 with *Anchoa*)	3	3	–	3

Supramaxilla shape is most useful for distinguishing *S. fasciata* from the other three species. This character can be evaluated at sea and has potential to improve recognition of *S. fasciata*.

Position of supramaxilla Mather (1958, p. 11) described the position of the posteriormost margin of the supramaxilla relative to the pupil as useful for distinguishing the four species. In *S. dumerili* and *S. zonata*, the posteriormost margin of the supramaxilla reaches farther, to the middle of the eye, whereas in *S. fasciata* and *S. rivoliana*, the posteriormost margin of the supramaxilla reaches only to the anterior margin of the pupil (Fig. 9, A–D). In *S. zonata* the supramaxilla sometimes reaches to the posterior of the eye, as reported in Smith-Vaniz (2003). Although the position of the supramaxilla is variable, it can be evaluated at sea.

Shape of vomerine tooth patches Berry and Burch (1979, table 1, fig. 3) showed that the shape of the vomer could be used to distinguish the four species of *Seriola* in the western North Atlantic and figured vomerine tooth patches of each species. They described the vomerine tooth patches as follows: *S. dumerili*, elliptic head, long shaft (Fig. 9E); *S. fasciata*, hastate head, long shaft (Fig. 9F); *S. rivoliana*, elliptic head, short shaft (Fig. 9G); and *S. zonata*, chevron head, long shaft (Fig. 9H). Our observations partially support these characterizations. We could not distinguish between the "long shaft" in *S. dumerili* compared to the "short shaft" in *S. rivoliana*. This character is most useful in distinguishing *S. fasciata* from the other three species, however, the location of the vomerine tooth patch inside the mouth makes it a difficult character to evaluate, particularly if comparative materials for the other species are not at hand.

Shape of first anal fin pterygiophore Smith-Vaniz (2003, p. 1435, fig. 28) described the shape of the first anal fin pterygiophore in the four species of *Seriola* from the western North Atlantic (Fig. 10). The pterygiophore is curved in *S. dumerili* (Fig. 10A), *S. fasciata* (Fig. 10B), and *S. zonata* (Fig. 10D) whereas in *S. rivoliana* it is straight (Fig. 10C). We found this feature to reliably distinguish *S. rivoliana* in the series of specimens that we x-rayed (*n*=14; 7.1–75.5 cm FL). In a 7.6 cm FL specimen of *S. rivoliana*, the first anal pterygiophore is straight, whereas it is curved in the smallest x-rayed specimen of *S. dumerili* (19.3 cm FL), *S. fasciata* (15.5 cm FL; we also confirmed that it is curved in a 9.2 cm FL specimen [MCZ 158099] not collected by the BTS), and *S. zonata* (7.1 cm FL). Thus, the first anal pterygiophore is a good character for distinguishing *S. rivoliana* at small and large sizes. However, x-ray or dissection is needed to evaluate the shape of the anal fin pterygiophore and external characters (e.g., dorsal and anal fin height) readily separate *S. rivoliana* from the other species, so this character is not useful at sea.

Stomach contents We examined stomachs of 77 specimens in the laboratory, of which 67 had stomach contents, summarized in Table 9 into broad categories (full data are provided in Suppl. 2). Stomachs of *S. dumerili* included fish and squid. All 21 stomachs of *S. fasciata* that contained food had squid, and, in the larger specimens examined, these were primarily large northern shortfin squid (*Illex illecebrosus*) (105-145 mm mantle length), a squid not present in stomachs of the other three species of *Seriola*. The stomachs of

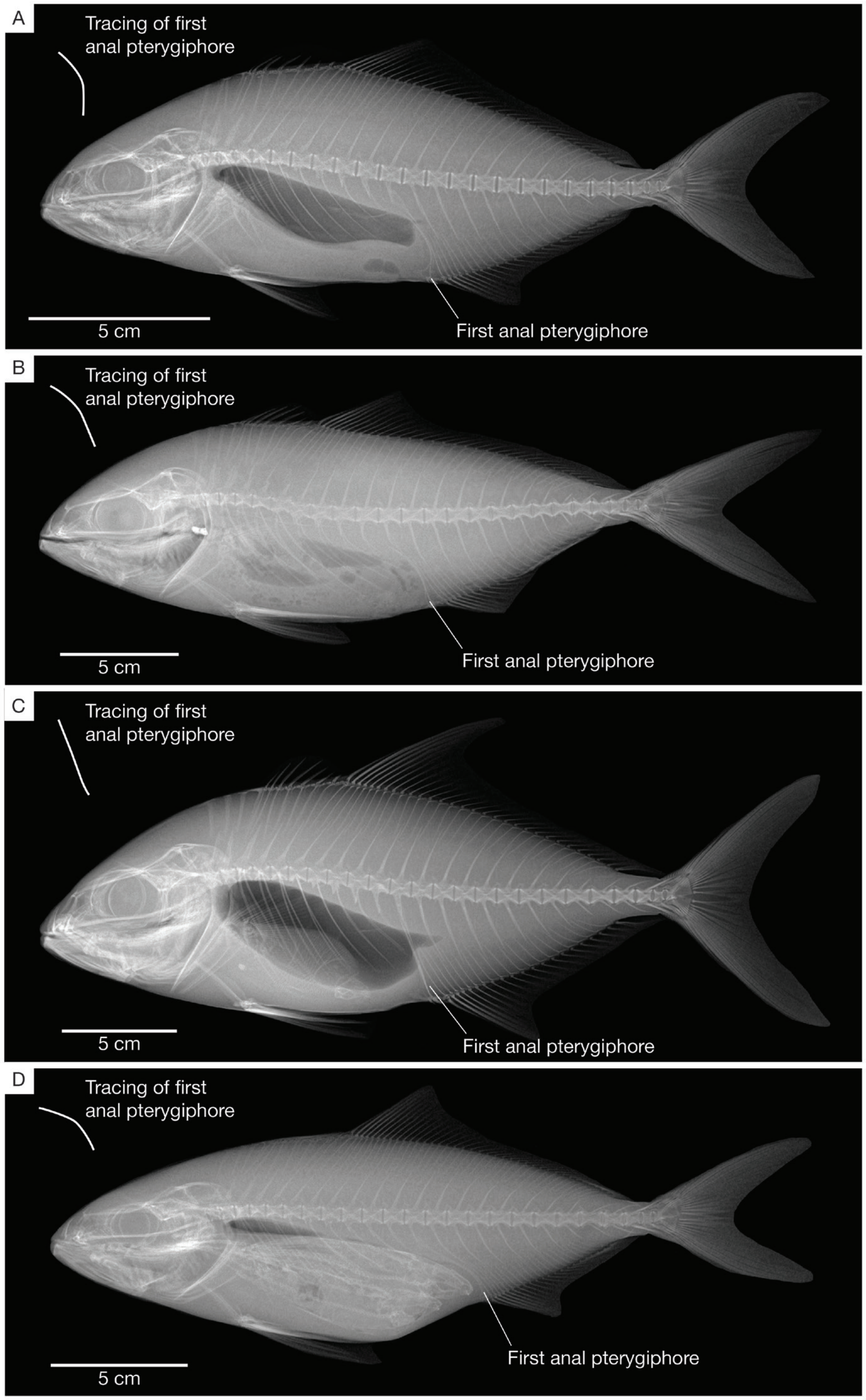
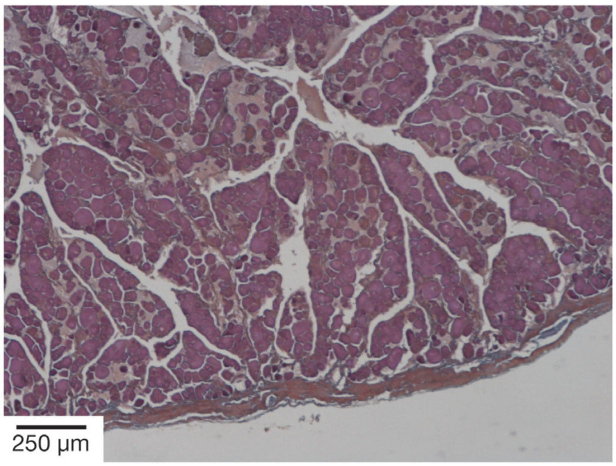


Figure 10

X-rays showing the shape of the first anal fin pterygiophore of four species of *Seriola* collected in the western North Atlantic between 2006 and 2019. (A) Greater amberjack (*S. dumerili*) (19.3 cm fork length [FL], CUMV 99136) with a curved first anal fin pterygiophore. (B) Lesser amberjack (*S. fasciata*) (28.9 cm FL, CUMV 99147) with a curved first anal fin pterygiophore. (C) Almaco jack (*S. rivoliana*) (30.5 cm FL, CUMV 99126) with a straight first anal fin pterygiophore. (D) Banded rudderfish (*S. zonata*) (25.3 cm FL, CUMV 99141) with a curved first anal fin pterygiophore.



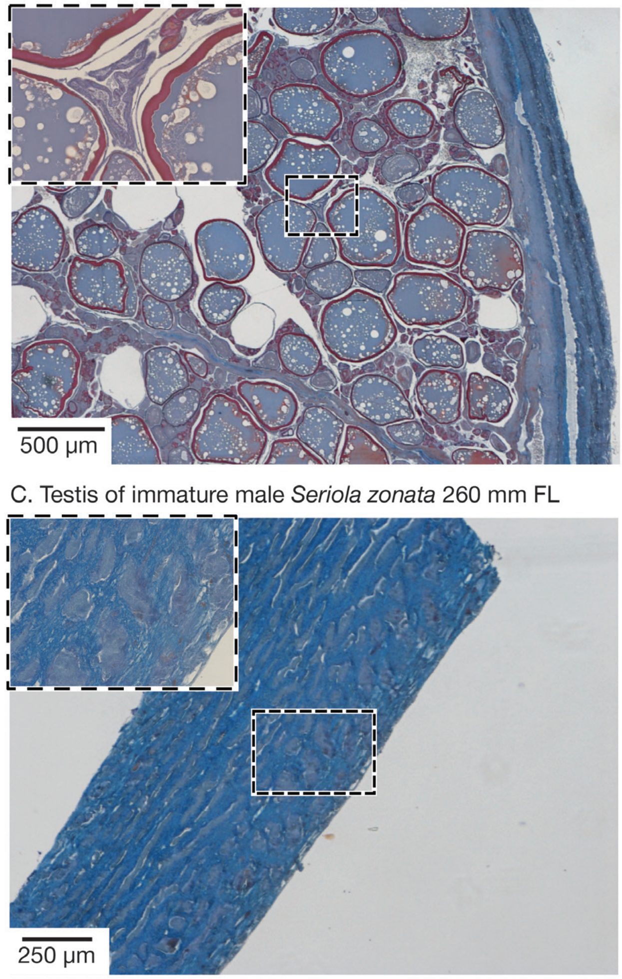


Figure 11

Photographs of the gonads of three species of *Seriola* at various stages of reproductive development collected in the western North Atlantic in the Fall of 2012. (A) The ovary of an immature female greater amberjack (*S. dumerili*) (46.7 cm fork length [FL], CUMV 99160) with only primary growth oocytes and a thin gonad wall. The gonad of the specimen weighed 0.0014 kg (gonadosomatic index [GSI] 0.08). (B) A spawning-capable female lesser amberjack (*S. fasciata*) (75.5 cm FL, CUMV 98739) with vitellogenic oocytes. The gonad of the specimen weighed 0.2127 kg (GSI 2.78). The inset shows a postovulatory follicle and a multilayered and thick gonad wall. (C) The testes of an immature male banded rudderfish (*S. zonata*) (26.0 cm FL, CUMV 98811) with small crypts and a thin gonad wall. The gonad of the specimen weighed 0.000156 kg (GSI 0.05).

S. rivoliana had benthic prey, including flatfishes (Fig. 10C) and crustaceans, not found in the stomachs of the other three species. Finally, *S. zonata* fed on small fishes, such as *Sardinella* and *Anchoa*, which are typical of the inshore habitats occupied by *S. zonata* (Fig. 10D).

Growth and maturity Growth during the first year of life was assessed visually for each season from seasonal progression of length frequency modes. We weighed gonads and determined GSI (n=81), assigned sex and maturity macroscopically (n=96), and verified sex histologically (n=26). The limited histology was used to support our use of thresholds in GSI (sexes combined) to quantify maturity in addition to macroscopic evaluation. All examined specimens of *S. dumerili* were immature (7.2-46.7 cm), with low GSI (mean 0.075, 0.00-0.133; Fig. 11A). The eight large specimens (68.8-75.5 cm FL) of *S. fasciata* were mature with elevated GSI (mean 1.797, range 0.775-2.86), and several of the large females were spawning-capable with advanced oocytes and postovulatory follicles (Fig. 11B). All smaller *S. fasciata* examined (16.4-35.5 cm FL) were immature and had low GSI (mean 0.151, range 0.0009-0.344). All *S. rivoliana* examined were immature (17.5-49.7 cm FL) with low GSI (mean 0.183, range 0.011-0.417). All *S. zonata* examined were also immature (16.2-29.5 cm FL), with low GSI (mean 0.076, range 0.0004-0.175; Fig. 11C). All specimens collected north of the North Carolina-Virginia border were immature.

Combined analyses of examined specimens and historical records Figure 12 summarizes historical records and examined specimens of four species of *Seriola* representing 1323 individuals in the survey database from 1963-2019, at 1 cm FL intervals. Of the 391 records of *S. dumerili*, 14 were examined specimens; of the 46 records of *S. fasciata*, 28 were

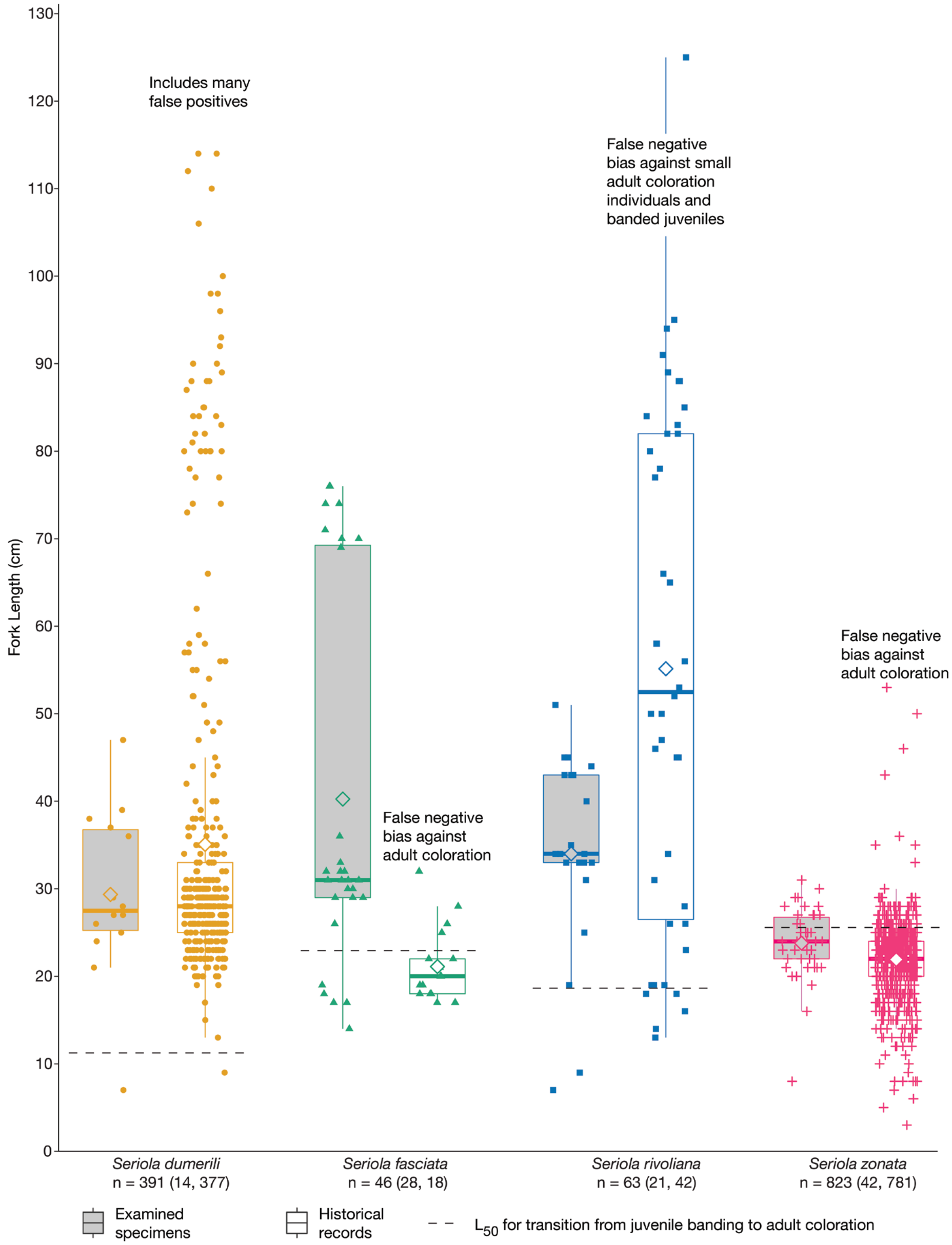


Figure 12

Boxplots comparing the fork length distributions of examined specimens (sample size [*n*]=105, gray boxes) and historical records (*n*=1218, open boxes) of greater amberjack (*Seriola dumerili*) (circles), lesser amberjack (*S. fasciata*) (triangles), almaco jack (*S. rivoliana*) (squares), and banded rudderfish (*S. zonata*) (crosses) collected in the western North Atlantic by the Northeast Fisheries Science Center bottom trawl surveys. Differences in fork length distributions between examined specimens (sampled from 2006 to 2019) and specimens from historical records (collected from 1963 to 2006) highlight biases in at-sea assignments for the four species. The bolded lines represent the median value. The lower and upper hinges of the box plots correspond to the 25th and 75th percentiles. The whiskers extend from the hinge to the farthest value, no more than 1.5 times the interquartile range. Data beyond the end of the whiskers are plotted individually. Open diamond symbols indicate mean fork lengths. Dashed lines indicate the size at 50% transition from juvenile banding to adult coloration.

examined specimens; of the 63 *S. rivoliana*, 21 were examined specimens; of 823 *S. zonata*, 42 were examined specimens. *Seriola dumerili* was the second most abundant species of *Seriola* captured on the BTS based on historical records; however, it was the least abundant species in the examined specimens (Fig. 12). *Seriola dumerili* also had the lowest percentage of correct at-sea assignments, with false positive records from all three other species of *Seriola* (24%; Table 4). The boxplot of 377 historical records for *S. dumerili* (Fig. 12) shows a positively skewed size distribution different from that of the 14 examined specimens. Many individuals <32 cm FL reduce the interquartile range in the historical records; these smaller individuals pull the interquartile range below the mean and shorten the upper whisker, resulting in individuals >44 cm FL plotted as outliers. This pattern is consistent with false positive misassignment of other species of *Seriola* as *S. dumerili*, with a disproportionate contribution from smaller specimens near and below the median value for historical records.

Historical records show *S. fasciata* to be the least commonly captured species of *Seriola* on the BTS; however, they were the second most abundant in our examined specimens (28 examined, 18 historical records; Fig. 12). *Seriola fasciata* was the least recognized at sea of the four species of *Seriola* (17.86%; Table 4). Individuals >32 cm FL are absent from historical records. Nearly 80% of the historical records are below the L_{50} for adult coloration (Fig. 12). Even excluding the eight large *S. fasciata* that we examined, all >65 cm FL, we found twice as many specimens *above* the L_{50} for adult coloration (25-40 cm FL; Fig. 12). This pattern is consistent with a strong false negative bias against recognition of adult-coloration *S. fasciata*.

Historical records show a wide size range of *S. rivoliana* was captured on the BTS (wide interquartile range, extended whiskers, no outliers; Fig. 12). Recognition at sea was low (28.57%, Table 4), but, when assigned, species identifications were highly accurate (100%; Table 4). The size range of the 21 specimens we examined is contained between the median and lower whisker of the 42 historical records, with the exception of two outliers in the examined specimens below the L_{50} for adult coloration (Fig. 12). This pattern is consistent with a slight false negative bias against recognition of small adult-coloration *S. rivoliana*, and a false negative bias against recognition of juvenile coloration *S. rivoliana*.

Seriola zonata was the most abundant species of *Seriola* captured on the BTS (781 of 1218 historical records), and our laboratory work confirmed this (42 of 105 examined specimens, Fig. 12). *Seriola zonata* had the highest recognition rate at sea (52.38%; Table 4), with a high identification rate (91.67%; Table 4). However, none of the adult-coloration *S. zonata* in our series of examined specimens were recognized at sea (Fig. 5D). In addition, Figure 12 shows that examined specimens have an elevated interquartile range, median, and mean with a significantly higher shift in FL from that of the historical records (1.99 cm FL [0.99-2.99], $P<0.001$; Mann–Whitney-U). This pattern is consistent with a strong false negative bias against recognition of adult-coloration *S. zonata*.

Distribution and seasonality Figures 13–16 summarize catch data for the four species of *Seriola* from historical BTS records (including the 105 examined specimens) and select museum records for specimens that we examined.

The combined data of 344 catch records show strong seasonality for all four species of *Seriola* in the survey area (Figs. 1 and 2). Records north of Cape Hatteras are from Summer and Fall surveys, when the water is relatively warm. During these warm water periods, species of *Seriola* were consistently caught as far north as Georges Bank (Fig. 2). No species of *Seriola* were caught north of Cape Hatteras during Spring surveys, when the water is cold (Fig. 2). No species of *Seriola* were captured in the Gulf of Maine in any season (Fig. 2). No specimens of any species of *Seriola* ≥35 cm FL were caught north of North Carolina (Fig. 17). South of the North Carolina-Virginia border, species of *Seriola* were more abundant than they were in the north (853 versus 470 individuals captured; Fig. 17), with higher catch in a single tow (88 versus 46). Most tows that caught any species of *Seriola* collected 1-3 individuals; only three tows north of the Northern Mid-Atlantic Bight (Fig. 1) collected >3 individuals in a single tow (Figs. 13–16). We defer further treatment of the distribution of the four species of *Seriola* to the Discussion, where we provide more context from our analysis of historical records and literature reports.

Temperature and salinity Table 10 summarizes data for bottom temperature, surface temperature, and bottom salinity for catches in three seasons (Fall, Spring, and Summer). Water temperatures and salinity were similar across catch locations, but the trends align with differences in the geography of the four species. Specifically, *S. zonata* occurs in warmer bottom water and lower salinity, which reflects their inshore distribution (Fig. 16), and *S. rivoliana* occurs in higher salinity waters, which reflects their offshore distribution (Fig. 15).

Historical photographs We matched 10 photographs to their corresponding catch records in the database (Suppl. 2 and 3). We found two instances of false positive *S. dumerili* misassignments, one instance

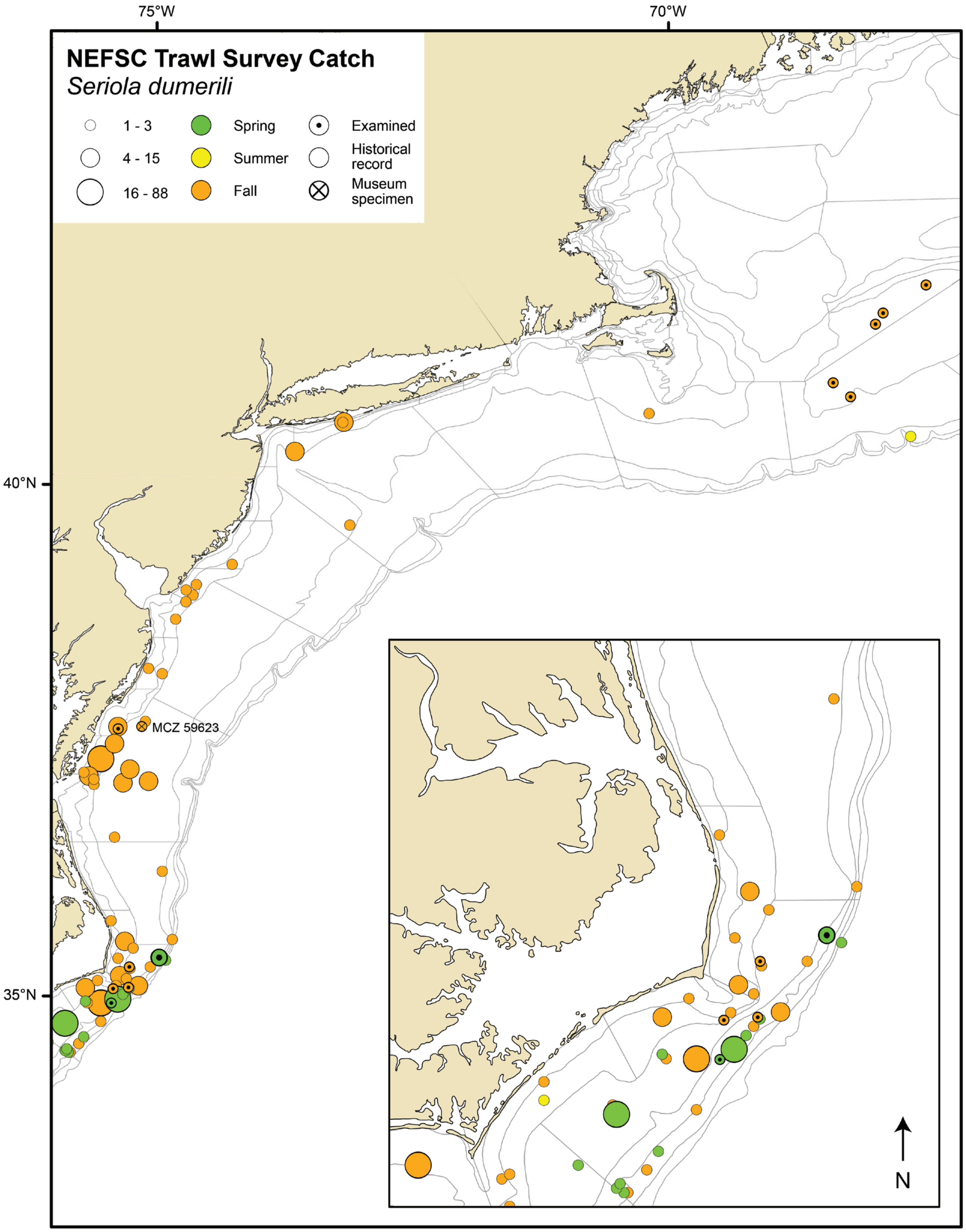


Figure 13

Map showing the size of catch of greater amberjack (*Seriola dumerili*) by season collected during Northeast Fisheries Science Center bottom trawl surveys from 1963 to 2019. Examined specimens are indicated by a dot in the center of the circle. Spring catches are green, summer catches are yellow, and fall catches are orange. A cross in a circle indicates a museum specimen. Sections outlined in gray indicate survey strata, and strata lines that follow the coast indicate bathymetry (see Figure 1). The inset map provides a closer look at catch locations of the southernmost study area.

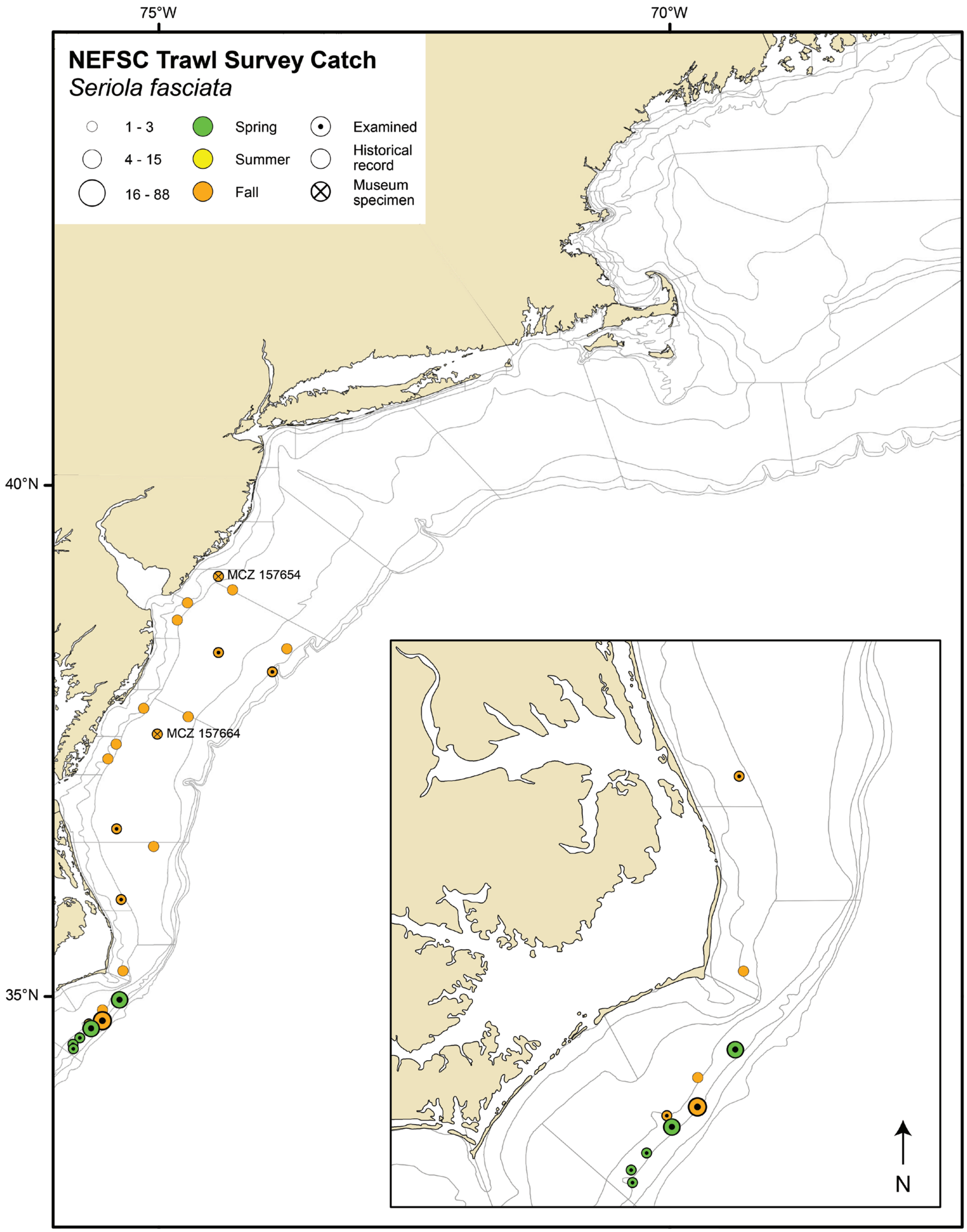


Figure 14

Map showing size of catch of lesser amberjack (*Seriola fasciata*) by season collected during Northeast Fisheries Science Center bottom trawl surveys from 1963 to 2019. Examined specimens are indicated by a dot in the center of the circle. Spring catches are green, summer catches are yellow, and fall catches are orange. A cross in a circle indicates a museum specimen. Sections outlined in gray indicate survey strata, and strata lines that follow the coast indicate bathymetry (see Figure 1). The inset map provides a closer look at catch locations of the southernmost study area.

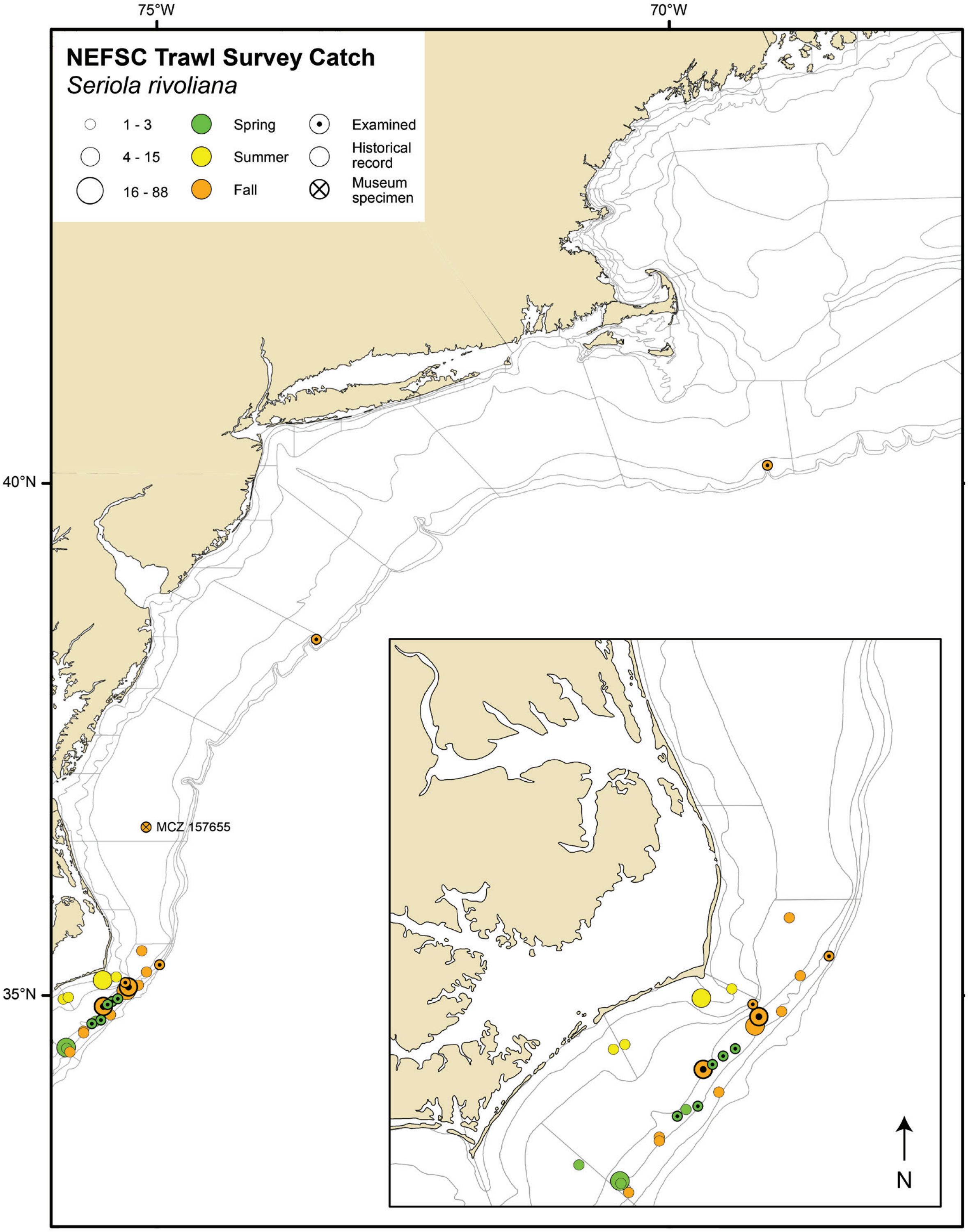


Figure 15

Map showing size of catch of almaco jack (*Seriola rivoliana*) by season collected during Northeast Fisheries Science Center bottom trawl surveys from 1963 to 2019. Examined specimens are indicated by a dot in the center of the circle. Spring catches are green, summer catches are yellow, and fall catches are orange. A cross in a circle indicates a museum specimen. Sections outlined in gray indicate survey strata, and strata lines that follow the coast indicate bathymetry (see Figure 1). The inset map provides a closer look at catch locations of the southernmost study area.

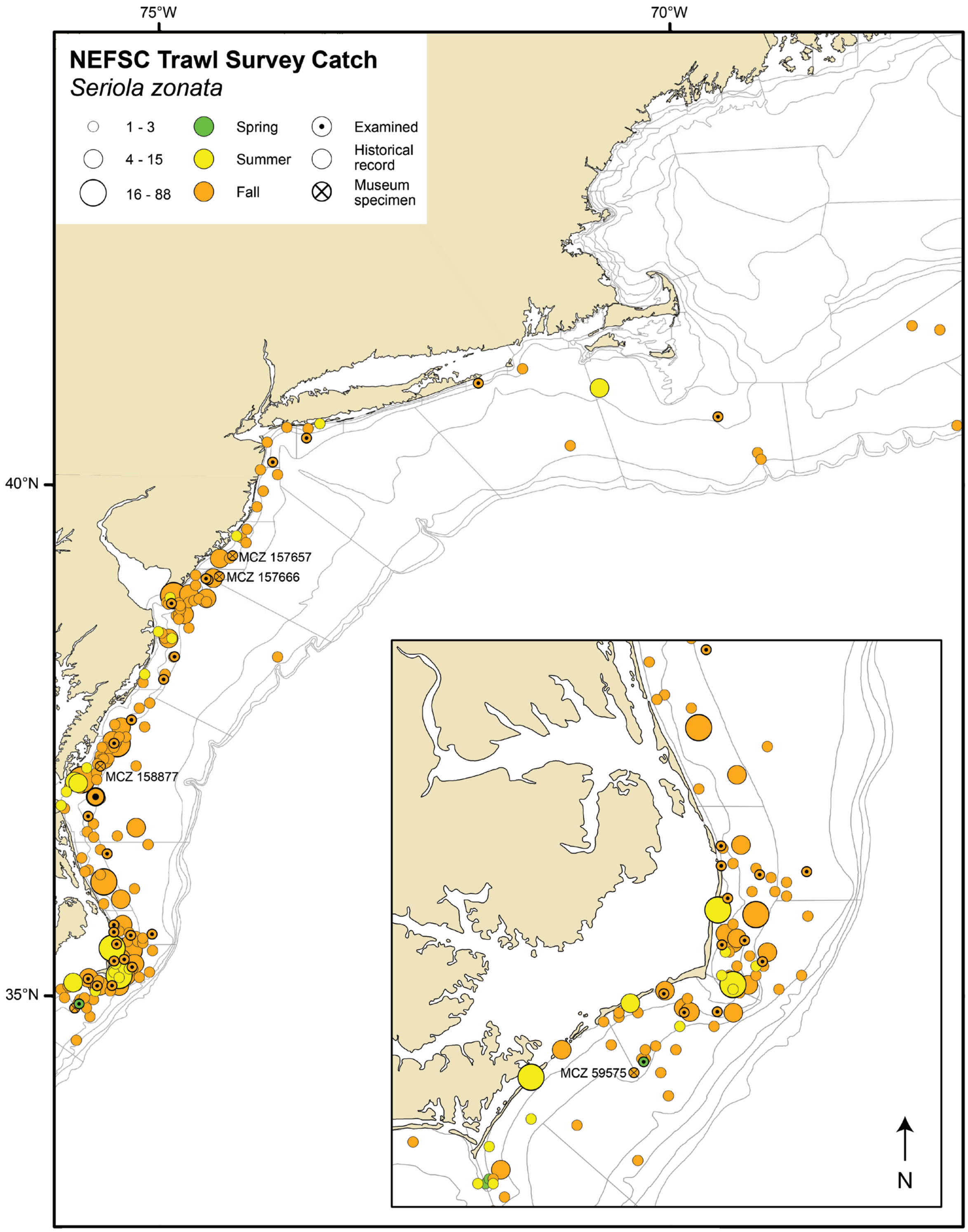


Figure 16

Map showing size of catch of banded rudderfish (*Seriola zonata*) by season collected during Northeast Fisheries Science Center bottom trawl surveys from 1963 to 2019. Examined specimens are indicated by a dot in the center of the circle. Spring catches are green, summer catches are yellow, and fall catches are orange. A cross in a circle indicates a museum specimen. Sections outlined in gray indicate survey strata, and strata lines that follow the coast indicate bathymetry (see Figure 1). The inset map provides a closer look at catch locations of the southernmost study area.

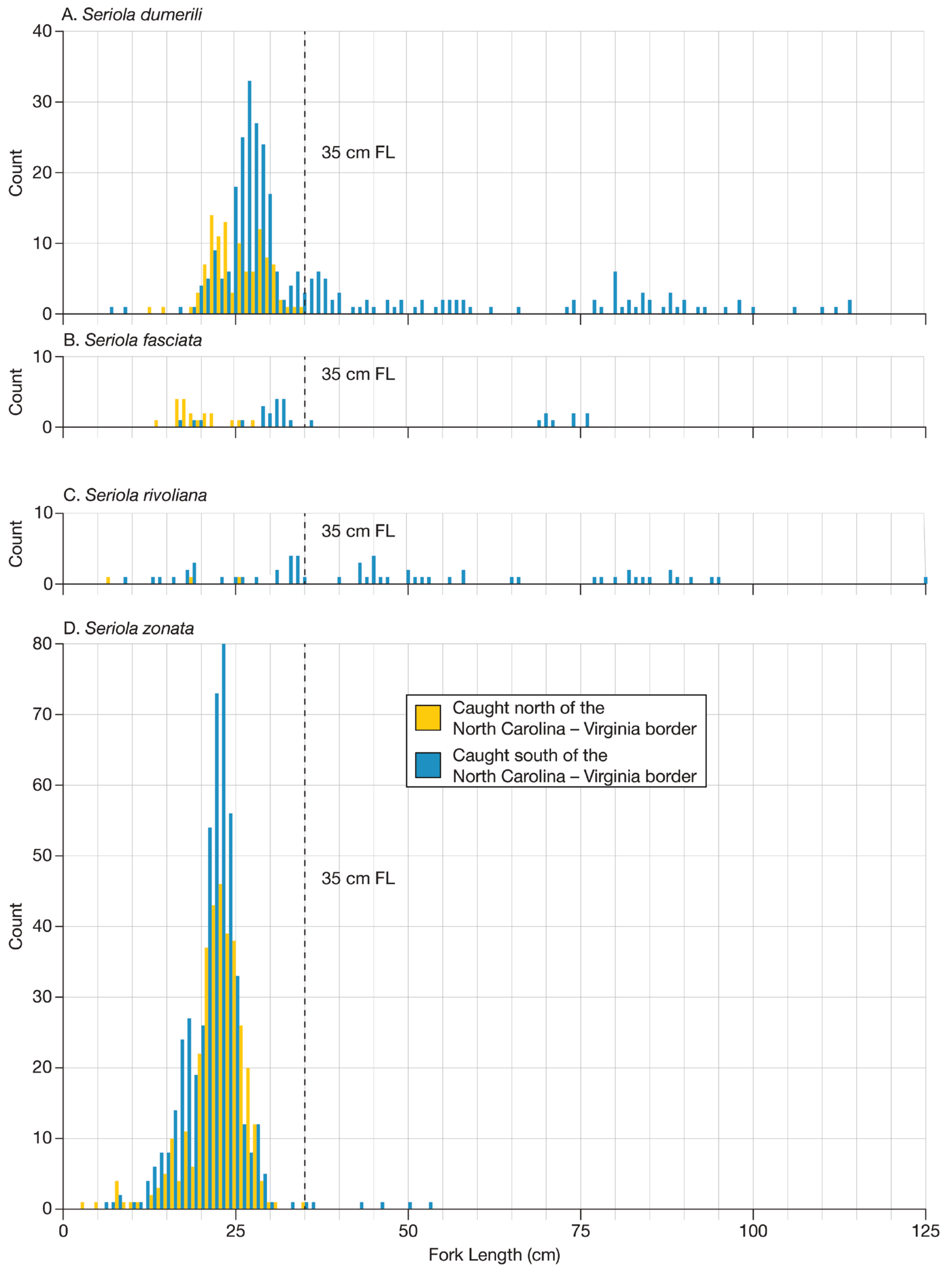


Figure 17

Length frequencies for (A) greater amberjack (*Seriola dumerili*), (B) lesser amberjack (*S. fasciata*), (C) almaco jack (*S. rivoliana*), and (D) banded rudderfish (*S. zonata*) caught north (yellow) and south (blue) of the North Carolina-Virginia border by Northeast Fisheries Science Center bottom trawl surveys from 1963 to 2019. All specimens caught north of the North Carolina-Virginia border were ≤35 cm fork length (FL, vertical dashed line). Fish were binned into 1-cm-FL increments rounded to the nearest whole centimeter.

Table 10

Physical parameters (surface temperature, bottom temperature, and bottom salinity) summarized by season for capture locations of greater amberjack (*Seriola dumerili*), lesser amberjack (*S. fasciata*), almaco jack (*S. rivoliana*), and banded rudderfish (*S. zonata*) in the western North Atlantic between 1963 and 2019. SD=standard deviation, *n*=sample size.

Species	Season	Avg bottom temp °C ± SD	Bottom temp range °C (*n*)	Avg surface temp °C ± SD	Surface temp range °C (*n*)	Avg bottom salinity ppt ± SD	Bottom salinity range (*n*)
Seriola dumerili	Fall	21.7 ± 3.9	13.2–28.1 (*n*=99)	23.8 ± 3.9	15.0–28.9 (*n*=98)	34.07 ± 2.17	30.93–36.36 (*n*=36)
	Spring	18.0 ± 2.3	15.1–20.4 (*n*=35)	15.8 ± 7.3	5.7–23.6 (*n*=36)	36.11 ± 0.34	35.84–36.85 (*n*=22)
	Summer	No data		No data		No data	–
Seriola fasciata	Fall	18.7 ± 3.5	10.9–24.7 (*n*=27)	23.9 ± 2.3	20.9 – 27.0 (*n*=27)	33.89 ± 1.95	30.93–36.00 (*n*=24)
	Spring	16.3 ± 0.8	15.14–17.48 (*n*=15)	15.1 ± 5.9	5.7–19.7 (*n*=15)	36.10 ± 0.18	35.84–36.33 (*n*=15)
	Summer	No data		No data		No data	
Seriola rivoliana	Fall	20.7 ± 4.7	12.6–28.3 (*n*=27)	26.3 ± 2.0	22.4 – 29.0 (*n*=26)	36.00 ± 0.39	34.80–36.45 (*n*=22)
	Spring	18.9 ± 1.4	15.1–21.2 (*n*=18)	20.6 ± 3.8	5.7–23.1 (*n*=18)	36.30 ± 0.14	35.84–36.41 (*n*=16)
	Summer	24.7 ± 1.1	22.6–25.3 (*n*=5)	26.1 ± 0.7	25.5–27.3 (*n*=5)	No data	–
Seriola zonata	Fall	22.4 ± 3.0	11.5–27.6 (*n*=272)	23.4 ± 2.2	16.8–28.7 (*n*=267)	32.31 ± 1.78	28.93–36.30 (*n*=166)
	Spring	17.8 ± 3.1	16.0–21.4 (*n*=3)	17.8 ± 3.1	16.0–21.4 (*n*=3)	36.42 ± 0.00	36.42–36.42 (n=1)
	Summer	23.2 ± 4.2	10.3–27.3 (*n*=59)	25.3 ± 2.2	20.0–27.8 (*n*=59)	No data	–

of correct assignment only to the family level, and seven instances of correct assignment to the species level.

Maximum sizes in the trawl survey database Records for the largest individuals in the survey database are: 114 cm FL for *S. dumerili* (not examined by us, but confirmed by photograph); 76 cm FL for *S. fasciata* (examined; Fig. 4); 125 cm FL for *S. rivoliana* (not examined); 53 cm FL for *S. zonata* (not examined). The 76 cm FL specimen of *S. fasciata* is a length and weight record (7.95 kg) for the species (Table 11).

Discussion

Between 1963 and 2019, the NEFSC BTS captured 1323 specimens of the four species of *Seriola* in the northernmost portions of their ranges in the western North Atlantic. We evaluated the accuracy of at-sea assignments using 105 individuals collected between 2006-2019. We then used this analysis to interpret the historical records in the survey database to better understand the life history of the four species of *Seriola* in the western North Atlantic.

Recommended field characters

The species of *Seriola* in the area surveyed by the BTS differ subtly, and identification requires knowledge of field characters for all four species in two life stages: banded juveniles and adult coloration. Many characters used to identify the species of *Seriola* are relative, such as eye size or heights of dorsal and anal fins. Individuals of *Seriola* are rarely caught by the BTS, making

Table 11

Summary of size and maturity data for greater amberjack (*Seriola dumerili*), lesser amberjack (*S. fasciata*), almaco jack (*S. rivoliana*), and banded rudderfish (*S. zonata*) collected in the western North Atlantic from 1963 to 2019. FL=fork length, TL=total length.

Species	Max size	Max age	Size at 50% maturity	Age at 50% maturity
Seriola dumerili	Maximum reported size 188 cm TL[1,2] (= ~162 FL based on conversion[3])	17[3,6] 13[3]	64.4 cm FL in males[7]	All males > 72 months mature[7]
	Common to 70-110 cm FL[1]		73.3 cm FL in females[7]	15 months in females
			78.8 cm FL[6]	27 months[6]
Seriola fasciata	76.0 cm FL[4]	10.2[6]	37.9 cm FL[6]	27 months[6]
Seriola rivoliana	Maximum reported size 155 cm FL[5] Common to 55-80 cm FL[1]	22.2[6]	81.1 cm FL[6]	53 months[6]
Seriola zonata	Maximum reported size 69 cm FL[1] Common to 47 cm FL[1]	10.3[6]	41.5 cm FL[6]	27 months[6]

[1]Smith-Vaniz (2003), western North Atlantic.
[2]Smith-Vaniz et al. (1999), Bermuda.
[3]Manooch and Potts (1997), North Carolina to Florida Keys.
[4]This study, western North Atlantic. The previous record was reported by Berry and Burch (1979) at 67.5 cm FL and 4.6 kg taken from Beaufort, North Carolina; Claro (1994) lists a *S. fasciata* of the same length and weight, which we suspect is the same record.
[5]International Game Fish Association records.
[6]Farmer et al. (2016), Gulf of Mexico.
[7]Harris et al. (2007), North Carolina to Florida Keys; note: original data for *S. dumerili* provided in years; here converted to months for comparison.

it difficult for at-sea personnel to become familiar with each of the species. It is even rarer to catch more than one species of *Seriola* in the same tow, which prevents direct comparison of specimens and their characters at sea. In contrast, more common species that can be distinguished by relative characters, such as the several species of *Alosa* in the western North Atlantic, can be accurately assigned to species at sea because greater numbers of co-occurring species are often collected simultaneously.

Diagnostic meristic differences among the species of *Seriola* are difficult to study at sea. For example, *S. zonata* has eight dorsal spines versus seven in *S. dumerili* (Table 6); however, dorsal spines are frequently damaged and spines in adults can become embedded beneath the skin, rendering them difficult to count (Smith-Vaniz, 2003, p. 1428, 1434). When combined with counts of dorsal fin spines, counts of gill rakers are informative at the species level (Table 8), however, gill rakers are hard to count accurately without using a microscope. Below, we briefly summarize important field characters based on our synthesis of literature and new observations reported in the Results; see also Suppl. 1.

Seriola dumerili *Seriola dumerili* has a mid-sized eye diameter, a relatively short anal and second dorsal fin height, short pelvic fins, and a short upper jaw with a broad supramaxilla that is broadly rounded posterodorsally (Fig. 9A). The anterodorsal margin of the supramaxilla is variably concave, but in confluence with the maxilla forms a distinct concavity near the anterior suture. Adult coloration is silvery without red or olive hues, and a yellow body stripe is variably present (Fig. 3B). In our sample of 105 examined specimens, the only banded juvenile (<10 cm FL) had five bands (Fig. 3A), which if characteristic of the species, distinguishes juvenile *S. dumerili* from juveniles of the other three species that all have >5 bands (excluding the caudal peduncle band).

Seriola fasciata *Seriola fasciata* most closely resembles *S. dumerili*. Adult-coloration specimens have large eyes, short heads, a short anal and second dorsal fin height, short pelvic fins, and a short upper jaw with a slender supramaxilla that is acutely rounded or angled posterodorsally (Fig. 9B). The supramaxilla lacks a pronounced dorsal curvature compared to the other three species, and the difference in width between the anterior and posterior halves is slight. Adults often have a reddish-purple hue not observed in the other species of *Seriola*. The yellow body stripe is variably present. Banded juveniles are deeper bodied with short heads and seven dark brown bands with wavy margins against an olive body color. The nuchal stripe is present in banded juveniles, but absent in adult-coloration specimens.

The reddish-purple hue of adult-coloration *S. fasciata,* when present, is a useful field character not seen in the other three species. A reliable field character for *S. fasciata* is the narrow supramaxilla (Fig. 9B), which can be seen without magnification. Banded juveniles can be readily identified by the seven or more brown wavy bands (not including the caudal peduncle) which extend onto the fin webs of the dorsal and anal fins. Reports in the literature range from seven to nine bands whereas we counted seven bands in all of our specimens.

Seriola rivoliana *Seriola rivoliana* has a greater body depth than the other three species (Figs. 6–8), elongated anal and second dorsal fin heights (Figs. 6–8), and a broad supramaxilla (Fig. 9C). The posterodorsal angle of the supramaxilla is variably acutely angled to broadly rounded, and the anterodorsal angle is variably straight to concave. Adult coloration is often olive (Fig. 3F), which is not seen in the other three species. A yellow body stripe is variably present as in the other species.

The olive color of adult-coloration *S. rivoliana*, when present, is a useful field character not seen in the other three species. The most useful field characters for *S. rivoliana* are its deep body and tall anal and second dorsal fins. Banded juveniles of *S. rivoliana* most resemble those of *S. dumerili,* but *S. rivoliana* has six wavy brown bands. The brown, irregular wavy bands of juvenile *S. rivoliana* have variable separation zones, making them difficult to count, and reported counts vary. For example, Mather (1958, p. 5) reported: "Both [*S. rivoliana* and *S. dumerili*] usually have 5 split and irregular vertical bands, with a dark area at the base of the caudal sometimes forming a 6th." Walls (1975) reported five to six bands for both species (without mentioning a band on the caudal peduncle); Murdy et al. (1997) reported five bands for *S. rivoliana* and six bands for *S. dumerili* with no mention of a band on the caudal peduncle; Smith-Vaniz (2003) reported six bands for *S. rivoliana* and five for *S. dumerili* (specifically excluding the band on the caudal peduncle for both species); McEachran and Fechhelm (2005) reported seven bands for *S. rivoliana* (without mentioning a band on the caudal peduncle) and five for *S. dumerili* (mentioning a sixth band on the caudal peduncle).

Seriola zonata *Seriola zonata* has the shallowest body depth (Figs. 6–8), making it appear elongate compared to the other three species. The head and upper jaw are long, as are the pelvic fins. Eye diameter is the smallest of the four species. The supramaxilla is moderate in size, with an anterodorsal margin that is usually straight, and a posterodorsal margin that is gently rounded; the difference in width between the anterior and posterior portions of the supramaxilla are slight compared to *S. dumerili* and *S. rivoliana* but greater than *S. fasciata* (Fig. 9D). The yellow body stripe is variably present. Juveniles have six broad, straight, uniformly wide black bands that vary in intensity. Loss of banding in *S. zonata* occurs between 20 and 30 cm FL (Fig. 5). A distinctive black nuchal stripe was present in all banded juveniles and adult-coloration specimens (versus brown in *S. dumerili* and *S. rivoliana*).

Characters for identifying adult-coloration *S. zonata* include: long upper jaw length, small eye diameter, short anal fin base length, and shallow body depth (Figs. 3, G and H, and 6–8). Banded juveniles of *S. zonata* are easily identified based on their black, straight, and uniform bands against a silver body, even if the bands are faint. A solid black nuchal stripe is prominent in both banded and adult-coloration specimens.

Evaluation of historical records

We cannot know the true rate of misassignments in the survey database for species of *Seriola* collected prior to 2006, but our examined specimens allow us to better understand both strengths and limitations of the historical records. For example, high numbers of false positive at-sea assignments, such as we found for *S. dumerili* (Table 4), mean that we must cautiously interpret historical records for *S. dumerili*. In contrast, low numbers of false positive misassignments, such as we found for the other three species (Table 4), mean that records in the survey database for those species have a high probability of being reliably assigned, and that data associated with these records can be used to understand their biology. False negative misassignments do not affect the validity of existing records for the species in question. However, biases in false negative misassignments could affect spatial, temporal and biological conclusions. For example, a strong false negative bias for adult-coloration *S. fasciata* would lead to the incorrect conclusion that adults are absent from the survey area.

Seriola dumerili *Seriola dumerili* has the second highest recognition rate (42.86%; Table 4), but the lowest identification rate (24%, Table 4). This is likely because *S. dumerili*, for which there are commercial and recreational fisheries, is a more familiar species of *Seriola*. Specimens assigned to *S. dumerili* at sea are not recognized by a specific field character, but because they "look like an amberjack." If a distinctive field character is recognized (e.g., height of dorsal and anal fins in *S. rivoliana*), then the fish is not assigned to *S. dumerili*. This conversely explains the higher identification rates for the other three species. Figures 7 and 8 demonstrate this graphically. Personnel at sea who recognize an individual fish as a species of *Seriola* effectively start at the center of each graph; then, they either recognize a character and follow that vector outward to an ellipse for a species other than *S. dumerili*, or they do not, with the result that they default to *S. dumerili* as the assignment. For example, five of 42 specimens of *S. zonata* were false positive assignments for *S. dumerili* (Table 4), and this is not surprising given the overlap in morphometric characters for these two species (Figs. 7 and 8). This pattern of assignment probably has been consistent throughout the survey time series since 1963, and, despite changes in personnel over time, the general pattern for our examined specimens (high recognition rate but low identification rate) likely applies to historical records for *S. dumerili*. Historical records for *S. dumerili* (Fig. 12) show a disproportionate number of small adult-coloration specimens, which skews the size distribution. We interpret that many of these are false positive misassignments of the other three species. This is also consistent with the high recognition rate for the genus *Seriola* (82.86%, Table 4), a low recognition rate for individual species of *Seriola* (37.14%, Table 4), and a greater contribution from fish ≤35 cm FL (Fig. 17), which come from both sides of the North Carolina-Virginia border (whereas all individuals >35 cm FL are from south of the North Carolina-Virginia border). Larger specimens of the other three species undoubtedly also contribute to misassignments, and this is easily seen for *S. fasciata* (Table 4, Fig. 12). Although this is not as obvious for *S. rivoliana* and *S. zonata*, misassignment of larger specimens might occur by the same principle. We conclude that survey database records for *S. dumerili* should be interpreted cautiously given that many of the records likely represent false positive misassignments from the other species.

Seriola fasciata *Seriola fasciata* has the lowest recognition rate of the four species (17.86%; Table 4), but a 100% identification rate (Table 4), although the sample size was small. Our interpretation is that *S. fasciata* is the least familiar species of *Seriola* captured on the BTS, which is why it has a low recognition rate. High identification rate is driven by the distinct banding pattern of juveniles (Fig. 5). Adult-coloration *S. fasciata* resemble *S. dumerili* (Figs. 3, 7, 8). Only four individuals of *S. fasciata* in the historical records are $>L_{50}$ for the transition from juvenile banding to adult coloration. One of those four likely had adult coloration (e.g., its size placed it at L_{100}), but the other three may have been banded juveniles (Fig. 12).

There are no records of *S. fasciata* in the survey database earlier than 1991. Therefore, we conclude that *S. fasciata* was an overlooked species in the early decades of the BTS, with adult-coloration specimens misassigned and banded juveniles only recently identified. Historical records are trustworthy but artificially sparse due to low recognition rates overall, combined with a strong false negative bias against recognition of adult-coloration specimens.

Seriola rivoliana *Seriola rivoliana* has the second lowest recognition rate (28.57%; Table 4), but a 100% identification rate (Table 4), although the sample size was low. The low recognition rate suggests that survey scientists are not familiar with *S. rivoliana*, but that its characters allow successful assignment when it is noticed as different. The tall second dorsal and anal fins (Figs. 3, 7, 8) distinguish this species, and are particularly apparent in large individuals. In contrast, all three banded juveniles of this species in our examined specimens were misassigned. Historical records for *S. rivoliana* are trustworthy but artificially sparse due to low recognition rates and a false negative bias against small adult-coloration individuals and banded juveniles.

Seriola zonata *Seriola zonata* has the highest recognition rate of the four species (52.38%, Table 4) and a high identification rate (91.67%; Table 4). We interpret that the high identification rate is due to the combination of the distinctive juvenile banding and juvenile color (Fig. 3), and because it is more abundant than the other three species, personnel at sea are more familiar with this species (Figs. 16 and 17). Our examined specimens showed that false positive misassignment of banded juveniles only occurred for individuals <10 cm FL (Fig. 5D). No adult-coloration specimens of *S. zonata* were recognized at sea in our examined specimens; however, some historical records are for specimens >35 cm FL, which is above the L_{100} for the transition between juvenile banding and adult coloration (Figs. 5D and 12). Historical records are artificially sparse due to false negative bias against recognition of adult-coloration individuals. Historical records for banded juvenile *S. zonata* are trustworthy, except for specimens <10 cm FL.

Given the similarities in bands and coloration of *Naucrates ductor*, there is potential for confusion with *S. zonata*. Although we found no direct evidence that the two species have been confused at sea (Table 4), we also found the majority of historic records of *S.*

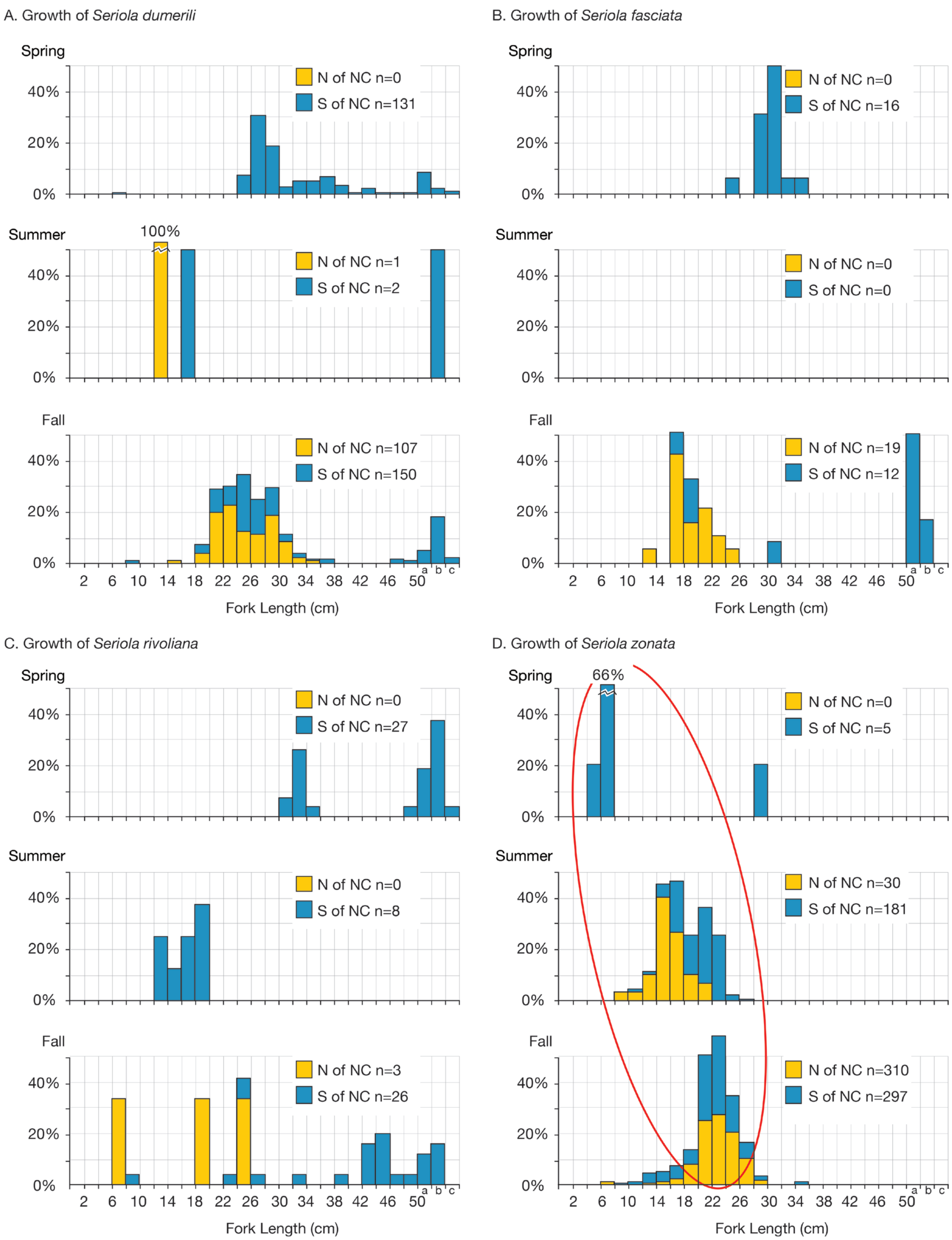


Figure 18

Seasonal length frequencies for (A) greater amberjack (*Seriola dumerili*), (B) lesser amberjack (*S. fasciata*), (C) almaco jack (*S. rivoliana*), and (D) banded rudderfish (*S. zonata*) caught north (yellow) or south (blue) of the North Carolina-Virginia border by Northeast Fisheries Science Center bottom trawl surveys from 1963 to 2019. Older fish show larger size distributions and are thus contained in three size bins: (a) 51–75 cm FL, (b) 76–100 cm FL, and (c) 101–125 cm FL. The red oval highlights growth during the first year of life for *S. zonata*. For all but *S. zonata,* the smallest fish in spring are age-1 fish that overwintered. n=sample size.

zonata occur inside the 27 m depth zone, and no confirmed specimens beyond the 55 m depth zone (Figs. 1 and 16). We found small numbers overall of *S. zonata* records ≤10 cm FL, which we attribute to consistent seasonal growth (Fig. 18D). The lone examined specimen of *S. zonata* ≤10 cm FL was an inshore spring capture (south of Cape Hatteras; Fig. 16, Suppl. 5). Historical records of *S. zonata* ≤10 cm FL, captured near the continental shelf edge in fall, therefore look suspect. The two examined specimens fitting this description were actually *S. rivoliana* (false positive *S. zonata*, Suppl. 5). The proximity of similar *N. ductor* records make them, along with *S. rivoliana*, a possible source for false positive *S. zonata* (≤10 cm FL, fall season, continental shelf edge; Suppl. 5).

Historical photographs documenting misassignments Two photographs in BTS records from 1979 show individuals that had been assigned as *S. dumerili* at sea but that we identify as large *S. rivoliana* (48 and 92 cm FL). These historical photographs support two conclusions: 1) historical misassignment of other species of *Seriola* to *S. dumerili* has occurred; 2) there have been low recognition rates for *S. rivoliana*. We also found one photograph of an adult-coloration *S. zonata* corresponding to a 1997 record assigned to Carangidae (50 cm FL). This photograph supports a third conclusion that records of adult-coloration *S. zonata* are likely under-represented in the survey database due to false negative assignment of larger specimens of this species.

Size, maturity, and growth

Large specimens of *S. fasciata* are uncommon in museum collections. The largest individual *S. fasciata* in our series of specimens (CUMV 98739) increases the maximum recorded length for this species from 67.5 cm FL to 76.0 cm FL and increases the weight record from 4.60 kg to 7.95 kg (Berry and Burch, 1979; Claro, 1994; unknown if record is a museum specimen or tackle record). Large *S. fasciata* might be inadvertently caught by the recreational fisheries for *S. dumerili* and *S. rivoliana*. Future studies could examine the frequency with which *S. fasciata* is caught in the recreational fishery because of differences in its life history compared to other species of *Seriola*.

Some information is available on size and age at maturity for *S. dumerili* (e.g., Burch, 1979; Beasley, 1993; Manooch and Potts, 1997; Thompson et al., 1999; Harris et al., 2007). For example, Harris et al. (2007) estimated size at 50% maturity to be 64.4 cm FL (mature individuals as small as 46.4 cm FL and one year old) for male *S. dumerili* on the southeast coast of the United States. For females, the size at 50% maturity was estimated to be 73.3 cm FL (mature individuals as small as 51.4 cm FL). The age at 50% maturity was estimated to be 1.3 years in females, while males were >50% mature at age one. Similarly, Harris et al. (2007) reported GSI >0.5 peaking at 3.5 for female *S. dumerili* during the spawning season and declining below 0.5 thereafter. Comparable information is not available for other species of *Seriola* that occur in the survey area, but our observations provide preliminary insights. All 105 examined specimens, except for the eight largest specimens of *S. fasciata,* were immature; these observations agree with available maturity estimates from the Gulf of Mexico for all four species (Farmer et al., 2016, table 1). Lack of samples across a complete range of sizes precludes estimation of maturity at length.

Available data suggest that species of *Seriola* grow very quickly. For example, in the Gulf of Mexico, growth rates for YOY *S. dumerili* are 1.65-2.00 mm/d (Wells and Rooker, 2004). Size at age-1 for *S. dumerili* off the southeastern United States coast is >45 cm FL (Harris et al., 2007). We used 35 cm FL as the cut-off between YOY and older individuals (Fig. 17). Seasonal length frequencies demonstrate growth of the YOY cohort in the first year (Fig. 18), which was more evident for *S. zonata* than the other species that had higher seasonal variation and low samples sizes. BTS historical records include a wide range of sizes, indicating vulnerability to the gear, and therefore breaks between modes in the length frequency (absence of certain sizes) are informative. Species of *Seriola* grow rapidly during their first summer, similar to growth rates observed in other carangids (crevalle jack [*Caranx hippos*]) (McBride and McKown, 2000).

The early life history of *S. zonata* resembles that of bluefish (*Pomatomus saltatrix*) spawned in the early spring south of Cape Hatteras (Able et al., 2013). Larvae of *P. saltatrix* are advected northward, then seasonally exploit temperate nearshore habitats North of Cape Hatteras during their first year of life, where they feed on small fishes before migrating south in the fall (Juanes and Conover, 1994, 1995; Wuenschel et al., 2012). Among the four species of *Seriola* studied, only *S. zonata* consumed small, nearshore fishes such as anchovies (Table 9). Based on sizes attained by YOY *S. zonata* in the Mid-Atlantic Bight (which are larger than the YOY of *C. hippos* and *P. saltatrix*), and their absence in the spring BTS, it is likely that YOY *S. zonata* move south in the fall and recruit to populations south of Cape Hatteras. In contrast to *P. saltatrix*, *S. zonata* seasonally exploits temperate waters only in the first year of life, as evidenced by the lack of specimens >35 cm FL north of the North Carolina-Virginia border (Fig. 17).

The lower absolute abundance of northern juveniles of *S. dumerili, S. fasciata,* and *S. rivoliana* suggests northern habitats are less important nurseries for these species, but future tagging studies and population genomics (e.g., Boehm et al., 2015) are needed to evaluate this.

Spawning, reproduction, and seasonal movements

Harris et al. (2007) collected *S. dumerili* in spawning condition from North Carolina to the Florida Keys from January to June. They indicated that spawning was concentrated off south Florida and the Florida Keys in April and May. A similar spawning period (March-May) was reported for *S. dumerili* in the Gulf of Mexico (Smith et al., 2014). Larval collections in the Mid-Atlantic Bight (Fahay, 2007) suggest that: *S. dumerili* spawn through winter into spring; *S. fasciata* spawning possibly peaks in summer; and *S. rivoliana* probably spawn spring through fall. In a study conducted in the Gulf of Mexico and Atlantic coast of the southeastern United States, Aprieto (1974) reported larval *S. zonata* nearly year-round, but collections were too sporadic to determine if spawning occurred year-round or was split into two periods: one in the winter-spring and another in fall. Annually, the Spring BTS occurs before or coincides with spring spawning periods, so it is not surprising that YOY, except for a few *S. zonata,* are not caught in the spring, even south of the North Carolina-Virginia border (Fig. 18). By summer, the YOY cohorts have recruited to the bottom trawl sampling gear (especially *S. zonata*). Seasonal length frequencies from historical records (Fig. 18) suggest spawning of *S. dumerili* occurs earlier than that of *S. fasciata*, and that *S. rivoliana* has a more protracted spawning season. Our observations of spawning-capable *S. fasciata* in September indicate their spawning may be either protracted or bimodal; however, based on YOY length frequencies it is uncertain whether such late summer-fall progeny survive. The richer historical records for *S. zonata* (Fig. 18D) show a first appearance of YOY at southern stations in spring (indicating winter-early spring spawning), widespread occurrence at both north and south stations in summer, with larger fish in the south at this time, and with similar size individuals distributed at both north and south stations in the fall.

Relevant literature

Prior to the start of the BTS in 1963, all four species of *Seriola* treated here had been described from the western North Atlantic. Particularly in reports from the 19th century, synonyms for the four species were in use. There remains uncertainty about species identifications in some older literature when specimens were not kept, but in most cases, we could refer such reports to a valid species following synonymies in Fricke et al. (2021), which we provide in parentheses after the name referenced in older reports. The following review is organized by publication years, and treats only literature records from the BTS survey area (Fig. 1). It is not a complete review of literature from the region, and focuses on relevance to the study.

The type locality of *Scomber zonatus* Mitchill, 1815 (=*Seriola zonata*) is New York Bay. Mitchill (1815, p. 427, plate IV, fig. 3) stated: “Taken from the bay of New York, occasionally, during the warm season. One that was taken at a city wharf, on the 26th of August, 1814, was seven inches and a half long [19.05 cm], rather more than two deep [5.08 cm], and somewhat above one [2.54 cm] in thickness. I have known of one of nine inches long [22.86 cm], that weighed rather more than half a pound [0.227 kg].”

De Kay (1842, p. 128–129), in the fishes volume of *Zoology of New York* listed “*Seriola zonata”* as being taken by hook and line in Long Island Sound and “usually caught in August, September, October.” He listed “*Scomber zonatus* Mitchill 1815” as a synonym. De Kay (1842, p. 129) refers to four other *Seriola* species from Volume 9 of Cuvier and Valenciennes (1833) as “extra limital” to the region: “*S. boscii,*” “*S. fasciata,*” “*S. leiarchus,*” and “*S. cosmopolita.*”

Storer (1867, p. 81, plate XV, fig. 5) in *A History of the Fishes of Massachusetts* listed two specimens of “*Seriola zonata,* Cuvier” he examined in 1844 and 1849 that were collected off Wellfleet, Massachusetts (on the north side of Cape Cod in the Gulf of Maine, Fig. 1).

Gill (1873, p. 4, 25) in *Catalogue of the Fishes of the East Coast of North America* documented species of *Seriola* in the Virginian faunal zone (Cape Cod to Cape Hatteras), and the adjacent Carolinian faunal zone (Cape Hatteras south to the northern limits of the coral reefs of Florida). However, Gill introduced the genera *Halatractus* Gill 1863, and *Zonichthys* Swainson 1839, in place of *Seriola*. Gill (1873, p. 25) listed “*Halatractus zonatus* (Mitch.)” (=*Seriola zonata*), with a range from Cape Cod to Florida; he also listed “*Halatractus carolinensis* (Holbr.)” (=possibly *Seriola zonata*) and “*Zonichthys fasciatus* (Bloch)” (=*Seriola fasciata*) as present in the waters of South Carolina.

Many years of sampling by the United States Fish Commission in the waters around Woods Hole, Massachusetts started by Spencer Baird in 1871, and continued over the years by others, including Vinyl Nye Edwards and Tarleton Hoffman Bean, are summarized by H. M. Smith’s (1897, p. 97) Fish Commission Bulletin entitled *The fishes found in the vicinity of Woods Hole*. Smith lists “*Seriola zonata* (Mitchill)” as “common from July to October,” mentioning fish 6-7 in long (15.24-17.78 cm). “*Seriola dumerili* (Risso)” is listed as “rare,” with three specimens from 7.75-13.0 in (19.69-33.02 cm) in the Woods Hole Collection (now at USNM), taken in August and September. Smith also lists "*Seriola lalandi* (Cuvier and Valenciennes)" as rare, but he cites two captures that measured 2.25 ft (68.58 cm; September) and 3.08 ft (93.88 cm; July). Likely, the specimens Smith (1897, p. 97) referred to as *S. lalandi* were *S. dumerili* because *S. lalandi* does not occur in the western North Atlantic (e.g., Martinez-Takeshita et al., 2015).

Jordan and Evermann (1896, p. 902–903) listed "*Seriola zonata* (Mitchill)" as ranging from Cape Cod to Cape Hatteras and stated "banded young rather common northward." However, they also considered it is "represented south of Cape Hatteras by *Seriola zonata carolinensis,* Holbrook" (ranging into the Gulf of Mexico), which is "very similar to *Seriola zonata*, but more elongate and paler in color" with "banded young" and a high soft dorsal ray count (36-37). Jordan and Evermann, (1896, p. 903–904) described "*Seriola lalandi,* Cuvier and Valenciennes" as "in all stages more slender than *Seriola dumerili*" and as common from west Florida to Brazil, ranging occasionally north to New Jersey. They described "*Seriola dumerili* (Risso)" as "very close to *Seriola lalandi* but reaching a smaller size, and with the body deeper and little compressed" and ranging as far north as Pensacola, Florida, but there is no mention of its occurrence on the Atlantic Coast of Florida or farther north. Jordan and Evermann (1896, p. 904–905) described "*Seriola fasciata* (Bloch)" as not very common, ranging from the West Indies to Charleston, and reaching sizes of about one foot. They list "*Seriola rivoliana* (Cuvier and Valenciennes)" and "*Seriola falcata* Cuvier and Valenciennes" (=*S. rivoliana*), as "probably identical" and ranging as far north as the Carolinas.

Sumner et al. (1913) published *A Biological Survey of the Waters of Woods Hole and Vicinity*, a continuation of the work by the United States Fish Commission. Sumner et al. (1913, p. 751) reported "*Seriola zonata* (Mitchill)" as "rather common about piers, pound-net stakes, vessels, and under floating seaweed and eelgrass," and present from July to October. They listed "*Seriola dumerili* (Risso)" as "under the same circumstances as *S. zonata*, but of rare occurrence." Sumner et al. (1913, p. 751) also stated: "Owing to the difficulty with which members of this genus are distinguished from one another, all records of occurrence must be accepted with caution," words still relevant today. Sumner et al. (1913, p. 751) described "*Seriola lalandi* Cuvier and Valenciennes" as "never common" and introduced skepticism regarding the presence of this species in the western North Atlantic, stating: "A specimen which had been so labeled in the local collection is very doubtfully of this species."

Mather (1952) contributed *Three species of fishes, genus* Seriola*, in the waters of Cape Cod and vicinity*. He listed "*Seriola zonata* (Mitchill)," "a more or less regular summer visitor to the southern side of Cape Cod," as being present on the north side of Cape Cod (Gulf of Maine, Fig. 1), in summer and fall 1950-1951. He obtained 12 individuals between 15-23 cm SL, "which is about the size-range of the others I have observed around the Cape." He also stated that a local pound net fisherman reported that *S. zonata* were exceptionally abundant during 1949-1951 in Cape Cod Bay, noting that he had "shipped two barrels of rudderfish to market" from a single day's catch. Mather (1952, p. 209–210) also reported captures of "*Seriola dumerili* (Risso)" and "*Seriola fasciata* (Bloch)" while trolling for tuna roughly 24 km (15 mi) south of Nomans Land (Southern New England, Fig. 1) in September 1951. The 17 specimens of *S. dumerili* (Mather, 1952, p. 210) ranged from 19-23 cm SL; the single specimen of *S. fasciata* was 19 cm SL (MCZ 37167) and represents the northernmost range record for this species. Mather (1952) also reported a specimen of *S. fasciata* (<7 cm SL), identified by Isaac Ginsburg, captured off Long Island (we could not find a record of this specimen at USNM).

In *Fishes of the Gulf of Maine*, Bigelow and Schroeder (1953) added additional but sporadic records of "*Seriola zonata* (Mitchill) 1815", with some reports from the western shore of the Gulf of Maine. They listed *S. zonata* as a rare visitor to the Gulf of Maine and noted the small size and dark bands of specimens. Although Georges Bank (Fig. 1) was included in the area covered, no species accounts were given for any other species of *Seriola*. This status did not change in *Bigelow and Schroeder's Fishes of the Gulf of Maine* (Collette and Klein-MacPhee, 2002), and "*Seriola zonata* (Mitchill 1815)" was again listed as rare, although additional western shore *S. zonata* records were reported.

Mather (1958) wrote *A preliminary review of the amberjacks, genus* Seriola*, of the western Atlantic*. He noted that allometry within the genus makes it important to consider a complete size range of specimens. He stated "in dealing with early descriptions it is important to take into consideration the size of the specimens on which they were based." Mather (1958) concluded that "there are at least four distinct species of *Seriola* in the western north Atlantic. To these I have tentatively assigned the names *dumerili*, *fasciata*, *rivoliana*, and *zonata*." He also examined "another species, which occurs in the western south Atlantic but apparently does not range north of Brazil, I have tentatively called *lalandi,*" obtaining four specimens from the type locality, Brazil, and one from the Cape of Good Hope. Mather concluded that *S. lalandi* is a southern hemisphere species, and can be readily separated from all western North Atlantic species of *Seriola* by its head length. Berry and Smith-Vaniz (1978) and later Smith-

Vaniz (2003) in the FAO series on fishes in the western central Atlantic confirmed Mather's conclusion that only four species of *Seriola* occur in the western North Atlantic.

Occurrences of the species of *Seriola* in the current survey area (Gulf of Maine to South of Cape Hatteras, Fig. 1) do not represent recent shifts in distributions. The northern ranges, size classes, and relative abundances of the four species of *Seriola* were similar in the past (1815-2003) to the patterns we document here for 2006-2019. *Seriola zonata* is the most abundant of the four species with the northernmost distribution, including Southern New England (Fig. 1), with occasional presence of individuals in the Gulf of Maine (Fig. 1). Literature reports of sizes for *S. zonata* in inshore northern waters are consistent with our observations, and what we report as YOY. *Seriola dumerili* had a similar northern distribution in the past, but always with low numbers; reported sizes in the literature are consistent with our findings of YOY in the survey area. In the earliest accounts, both *S. fasciata* and *S. rivoliana* were only recorded farther south (Carolinas). *Seriola fasciata*, probably rarely detected in the past due to problems in distinguishing this species, was verified as far north as Southern New England by Mather (1952), and it is the second most common species of *Seriola* north of Cape Hatteras in our examined specimens. We can confirm based on both literature reports and data from the BTS that *S. fasciata* and *S. rivoliana* do not occur in inshore Southern New England waters except as strays.

One discrepancy between our findings and the literature concerns the presence of large individuals in waters off Southern New England (Fig. 1). Smith (1897, p. 97) reported two large specimens of *Seriola* from the region. He referred those specimens to *S. lalandi*, but they were most likely *S. dumerili* as noted above. Both specimens were >35 cm FL, which is the maximum size that we found for any species of *Seriola* caught north of the North Carolina-Virginia border (Fig. 17). Smith's records for large specimens of *Seriola* are for individuals that were caught during summer, when higher water temperatures allow tropical species to survive in areas north of their typical range. The BTS does not currently sample Southern New England or inshore waters during the summer. We examined the illustration of a 391 mm (unknown if TL, FL or SL) specimen identified as *S. zonata* from Woods Hole (Klein-MacPhee, 2002, fig. 229). The illustration shows seven dorsal spines, 31 soft-dorsal rays, and a broad supramaxilla, characters consistent with *S. dumerili*, not *S. zonata*. Although the size of this specimen is not as large as the *S. lalandi* specimens reported by Smith, it suggests that some of the southern New England records of *Seriola* species >35 cm FL may be *S. dumerili*.

Banded juveniles of *S. fasciata* are the second most commonly encountered juveniles of *Seriola* north of Cape Hatteras, with a northern limit off southern New Jersey. This finding does not match the early literature, in which *S. fasciata* was rarely reported. Mather (1952, p. 210) confirmed *S. fasciata* from off Nomans Land, and later (Mather, 1958, p. 5) described dipnetting post-larval juveniles on the surface in "oceanic" waters (likely off the continental shelf; location is not further specified). We interpret the lack of early records of this species north of Cape Hatteras as a result of incorrect identification. Mather (1958, p. 4) stated that *S. fasciata* "is seldom caught, or at least seldom reported." Early accounts also considered *S. fasciata* to be very small to "about one foot [30.48 cm]" (Jordan and Evermann, 1896, p. 904). Although Jordan and Evermann also reported that juvenile bands disappear with age, 62 years later Mather (1958) was unsure, having examined no specimens >8 in (20.32 cm) and stating that above that size "they may lack bands" (Mather, 1958, p. 8). Mather also considered *S. fasciata* to be small, calling it the "dwarf of the genus" (Mather, 1958, p. 5), and further "as far as I know, the species does not attain a weight of one pound [0.454 kg]" (Mather, 1958, p. 7). Thus it seems clear that banded juvenile *S. fasciata* were historically present yet overlooked north of Cape Hatteras. South of Cape Hatteras, adult-coloration *S. fasciata* were also overlooked, and almost certainly confused with other species. Adult-coloration *S. fasciata* could have fostered some of the confusion that resulted in the description of several nominal species of *Seriola* in early literature.

Distribution

Although there are a few records from Canadian waters (e.g., Scott and Scott, 1988), the BTS samples the northernmost portions of the ranges for all four species.

Seriola dumerili *Seriola dumerili* had the most northern distribution of the four species based on five verified records from Georges Bank, including one taken near the Northern Edge (41°56'45.6"N, -67°28'58.8"W; Fig. 13). Two literature records document this species from off Nova Scotia (20-30 cm TL; Scott and Scott, 1988). North of the North Carolina-Virginia border, *S. dumerili* has an inshore distribution with most captures in Inshore Stratum 3 (9-27 m) and the shallowest offshore stratum (28-55 m). Captures from Georges Bank also occurred in shallow water (30-53 m) with only a single record from the southern side near the edge of the continental shelf. All catches north of the North Carolina-Virginia border are likely YOY fish. South of the North Carolina-Virginia border, there are records from fall surveys of individuals >35 cm FL. We verified large (>35 cm) and small (≤35 cm) specimens south of Cape Hatteras in both Spring and Fall surveys and verified small specimens in Fall surveys between Cape Hatteras and Georges Bank. These captures show that *S. dumerili* is a year-round resident within the current survey area. Our results suggest that many historical records of *S. dumerili* are misassignments, and that this species may in fact be the least numerous *Seriola* captured on the BTS. However, our examined specimens indicate that the range based on historical records accurately represents that of *S. dumerili* within the survey area (Fig. 13).

Seriola fasciata *Seriola fasciata* is the least known of the four species of *Seriola* in the western North Atlantic. Our 28 examined specimens confirm its presence in the survey area (Fig. 14). Juveniles between 14–28 cm FL were encountered across the continental shelf from Inshore Stratum 3 (9-27 m) to shelf edge strata beginning at 183 m, with the northern limit at southern New Jersey. Mather (1952) recorded a single *S. fasciata* off southern Cape Cod in September 1951 and a single specimen from off Long Island, New York. *Seriola fasciata* >28 cm FL have only been captured by the BTS south of Cape Hatteras, during both Spring and Fall surveys. Specimens >35 cm FL were only captured once by the BTS in a single tow of eight specimens 69–76 cm FL in 2012, however many records of *S. dumerili* in the survey database are probably adult-coloration *S. fasciata*. Historical records suggest that, like YOY *S. zonata*, *S. fasciata* may use northern habitats before they migrate south and do not return. Unlike *S. zonata*, YOY and fish >one year, including sexually mature *S. fasciata*, occur year-round south of Cape Hatteras.

There are no records of *S. fasciata* in the survey database prior to 1991 even though the NEFSC species code for *S. fasciata* existed. Museum specimens and Mather (1952, 1958) document that all four species of *Seriola* were recorded in the survey area prior to the start of the survey in 1963. Thus, *S. fasciata* has not recently expanded its range, and its absence in survey records prior to 1991 is probably because individuals were misidentified as *S. dumerili*. Changes in survey personnel and reference materials post 1991 probably resulted in improved awareness of and assignment to *S. fasciata* on the BTS.

Seriola rivoliana *Seriola rivoliana* is the least encountered species north of the North Carolina-Virginia border (Fig. 15). It is a resident species between Cape Hatteras and Cape Lookout, with both Spring and Fall captures spanning a range of lengths. Larger individuals (>35 cm FL) remain off the North Carolina coast at or below Cape Hatteras in strata between 55 and 183 m deep, with only a slightly more southern distribution in the spring. Photographs of adult-coloration individuals captured by rod and reel near the continental shelf edge off Cape Cod in the summer confirm the presence of both banded juveniles and adult-coloration *S. rivoliana* north of Cape Hatteras (Suppl. 3). The rarity of captures by the BTS north of Cape Hatteras likely reflects their infrequent occurrence and preference for warm oceanic waters (Table 10).

Seriola zonata Juvenile *S. zonata* occur inshore north of the North Carolina-Virginia border, where they are part of the summer fauna. This is the most abundant species of *Seriola* captured by the BTS (Fig. 16). It is the least encountered species during Spring surveys, with only five spring captures south of Cape Hatteras (only one of these five individuals was taken in the current survey area, a banded juvenile <10 cm FL). Unlike the other three species of *Seriola*, *S. zonata* does not appear to be a year-round resident between Cape Hatteras and Cape Lookout. However, this may be a result of false negatives in historical records, given that none of the examined specimens of adult-coloration *S. zonata* were correctly assigned at sea. All records in the survey database for *S. zonata* north of the North Carolina-Virginia border were ≤35 cm FL, and likely all were YOY (Fig. 17). Within the survey area, *S. zonata* arrive as YOY in coastal inshore waters, where they appear to stay for a single season before leaving the survey area.

Seriola is a genus that might be expected to expand poleward due to climate change, as has been reported off Tasmania (Stuart-Smith et al., 2018). Our study confirms historical literature reports that as far north as Southern New England, the presence and rough abundance of *S. zonata* and *S. dumerili* (i.e., many *S. zonata* and few *S. dumerili*), have remained consistent for >100 years. Our study also indicates that *S. fasciata* has likely been present in the region as long as *S. dumerili* and *S. zonata;* however, the presence of *S. fasciata* above the North Carolina-Virginia border could otherwise be mistaken as a poleward range expansion. Improved identification is important in understanding range expansions or contractions.

Use of *Sargassum* as juvenile habitat

Differences in captures rates of banded YOY specimens examined (*S. dumerili, n*=1*; S. fasciata, n*=5; *S. rivoliana, n*=3; *S. zonata, n*=23) might relate to differences in juvenile habitats of the different species. For example, Casazza and Ross (2008) reported that juvenile *S. rivoliana* are among the most common *Sargassum*-associated fishes in the Gulf Stream off North Carolina, and that juvenile *S. dumerili* and *S. fasciata* were also more frequently caught in association with *Sargassum* than they were in open water. In contrast, they caught few specimens of *S. zonata* either associated with *Sargassum* or in open water. This apparent species difference in *Sargassum* association could reflect their sampling effort, which included waters further offshore and further south of the area sampled by the BTS. Records for *S. zonata* from the BTS during the months sampled by Casazza and Ross (2008) (July to September) are from more inshore stations (Fig. 16). Along the U.S. east coast, *Sargassum* abundance and extent is low in winter and spring before increasing in summer (Gower and King, 2011), which occurs after YOY *S. zonata* have recruited to the region. Thus, juvenile *S. zonata* may be less dependent on *Sargassum* compared to later spawning species. If *Sargassum* is less important as juvenile habitat for *S. zonata*, then this might explain differences in juvenile coloration. Juveniles of the three *Sargassum*-associated species, *S. dumerili*, *S. fasciata,* and *S. rivoliana*, have yellow-brown background coloration with wavy brown bands (Fig. 3, A, C, E). In contrast, juvenile *S. zonata* have a distinctive silver background, overlain with straight black bands (Fig. 3G).

Diets

Our data (Table 9, Suppl. 2) agree with some observations of Manooch and Haimovici (1983), who studied diets of *S. dumerili* (81 individuals, 39.7-138.6 cm TL) and *S. rivoliana* (49 individuals 27.6-109.4 cm TL) captured in the recreational fishery off North and South Carolina. They found that fishes, including both reef associated and pelagic species, were predominant in their diets in both frequency and volume; large squid (*Loligo* spp.) were secondarily important in the diets of both *S. dumerili* and *S. rivoliana* by frequency and volume. Crustaceans were more common in the stomachs of *S. rivoliana* than those of *S. dumerili*, which we also found. Manooch and Haimovici (1983) also found that stomachs of *S. rivoliana* had a higher percentage of pelagic prey species than did stomachs of *S. dumerili*, suggesting that *S. rivoliana* may forage more frequently in open waters. Our data suggest that *S. rivoliana* targets benthic prey, but because our specimens are smaller than those examined by Manooch and Haimovici (1983), this may indicate ontogenetic differences in foraging strategies.

No published diet information was found for *S. fasciata*. Casazza[2] provided unpublished data for one specimen of *S. fasciata* collected during her diet study of *Sargassum* associated fishes (Casazza, 2008). The specimen was 9.6 cm SL and its stomach contained carangids, monacanthids, unidentified fishes, and animal remains. Our data (Table 9) suggest that *S. fasciata* may be a squid specialist because all 21 stomachs with contents contained squid; only 1 contained fish, and 1 contained shrimp.

Conclusions

- Four species of *Seriola* (*S. dumerili*, *S. fasciata*, *S. rivoliana*, and *S. zonata*) routinely occur in waters north of Cape Hatteras. All four species were recorded prior to the beginning of the BTS in 1963, with variable abundance. In particular, YOY *S. zonata* are most abundant, use inshore waters of the survey area, and feed on small nearshore fishes such as anchovies. *Seriola fasciata* is the second most common species in the region, although it has been historically overlooked.
- Species of *Seriola* can be reliably identified, but this requires careful examination of specimens. In general, characters related to banding are more useful at smaller sizes, and characters such as heights of second dorsal and anal fins, eye size, upper jaw position in relation to eye, and shape of supramaxilla are more useful for identifying larger individuals. For a summary of field characters for banded juvenile and adult-coloration specimens, see Suppl. 1.
- Historical records in the survey database were evaluated and better interpreted with insights gained from analyses of identification rates using current samples. We conclude that historical records for *S. fasciata*, *S. rivoliana*, and *S. zonata* are reliable assignments, and useful for biology if false negatives are taken into account, but that those for *S. dumerili* are not.
- For taxa that are difficult to identify, it is important to validate at-sea assignments in the laboratory and to encourage retention of specimens at sea. For example, the largest BTS catch of *Seriola* (88 specimens; collected 6 March 2010, Hatteras) was assigned at sea to *S. dumerili*, but only five specimens were retained. Upon examination in the laboratory, none of these were actually *S. dumerili*: 4 were identified as *S. fasciata* and 1 as *S. rivoliana*.
- Results of our study will facilitate more accurate at-sea assignments, improve the accuracy of records in the database going forward, and refine our understanding of the distribution, habitat, and life history of each species of *Seriola*. This in turn will improve our understanding of the western North Atlantic ecosystem.
- Procedures outlined in this study can be applied to other groups of species taken by the BTS where taxonomy and identification have been difficult. In turn, this will allow greater reliability and use of historical records in the survey database.

[2] Cassaza, T. L. 2015. Personal commun. National Museum of Natural History, Smithsonian Institution, Washington DC, 20560.

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