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ARTICLE

Estimating the Sex Composition of the Summer Flounder Catch using Fishery-Independent Data

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Abstract

Models that account for sex-specific behavior and population dynamics are becoming more common in the stock assessment of sexually dimorphic fishes. However, such models can be data intensive and require some knowledge or assumptions about the sex ratio of fishery landings. A recent stock assessment review of Summer Flounder *Paralichthys dentatus* identified the need to account for sex-specific fishing mortality in the assessment model; however, no data on the sex composition of the catch were available. Fishery-independent, sex-specific information for this species is collected annually by the National Marine Fisheries Service's Northeast Fisheries Science Center during their bottom trawl survey. Sex at age from the survey could be applied to the fishery landings if the probability of landing a given sex at a given age is equivalent for fish collected by the survey and those in the landings. To generate the first regionally comprehensive database on the sex ratio of Summer Flounder landings and to determine the efficacy of using survey sex-at-age keys to estimate the sex of landed fish, we recorded the sex

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composition of the commercial and recreational catches of Summer Flounder ($n = 31,912$) in 2010 and 2011. When (1) trawl survey length data were left-truncated to simulate the minimum retention sizes in the fisheries and (2) age-length keys generated from fishery-dependent data were applied to length frequency distributions from the survey to simulate the growth rates of landed fish, the sex-at-age pattern in the survey-derived data closely resembled the patterns in the catch. However, statistically significant differences in sex at age remained between the catch and the survey-derived data. We hypothesize that these differences are attributable to differences in the spatiotemporal distributions of the sexes and of the survey and fishing effort.

Recent work suggests that the inclusion of sex structure in stock assessment models is important for sexually dimorphic fishes. For example, if growth rates or natural mortality differ between male and female fish (Wang et al. 2005; Su et al. 2013), if sex-specific migratory behavior and fishing effort are not evenly distributed in space and time (Okamura et al. 2014), or if fishery selectivity is sex specific (Myers et al. 2014), then the absence of sex structure in the assessment model can bias biological reference points. In light of these recent findings, sex-structured assessment models are becoming more common in describing the population dynamics of fishes that have sexually dimorphic characteristics and/or behavior (Clark and Hare 2006; Wang et al. 2007; Fenske et al. 2011; Su et al. 2011; McGilliard et al. 2013).

Female Summer Flounder *Paralichthys dentatus* grow faster (Poole 1961; King et al. 2001) and mature at a larger size (Able and Kaiser 1994; Packer et al. 1999) than males. In addition, the sex ratio of young fish is skewed in favor of males, probably due to a complex interaction between temperature and the biochemistry of sex determination (Luckenbach et al. 2009). However, as the cohort ages, the balance in sex ratio shifts toward females (Smith and Daiber 1977; Bonzek et al. 2009), a pattern that indicates a higher natural mortality rate among males (Maunder and Wong 2011). Sexually dimorphic life history characteristics of Summer Flounder suggest that a sex-structured assessment model would be appropriate for this species (Jones et al. 2013; NEFSC 2013), yet the most recent assessment applied a statistical catch-at-age model in which the sexes were combined (NEFSC 2013).

Sex-structured assessment models can be difficult to implement because they are data intensive, requiring either some prior knowledge about the sex composition of the catch or that assumptions be made about the sex-specific selectivity curve and its spatial and temporal stability (Methot and Wetzel 2013; Myers et al. 2014). Sex-specific information is not collected from Summer Flounder landings as part of the annual assessment process because (1) like other flatfishes, Summer Flounder display no external characteristics that can be used to identify sex; and (2) Summer Flounder cannot be dissected by port agents and still retain their market value. However, dissection is used to collect sex-specific data on Summer Flounder that are

captured by the National Marine Fisheries Service's (NMFS) Northeast Fisheries Science Center (NEFSC) during its bottom trawl survey, which is conducted twice annually in the spring and fall (NEFSC 2013).

If fishery-independent survey data are sex specific and if the probability that a fish of a given length or age is female (or male) is similar between the survey and the fishery catch, then a sex-at-length or sex-at-age key developed from survey data might be applicable directly to length or age data from the catch (Clark 2004). However, the sex composition of the fishery catch is influenced by a combination of the following factors: (1) differences in the size-, age-, and sex-specific retention selectivity imposed by the minimum retention size (MRS) in each fishery (Kendall and Quinn 2013); (2) the size-, age-, and sex-specific vulnerability of fish resulting from their interaction with the fishing gears (Ryer 2008; Somerton et al. 2011) and/or their availability to the fishing gears (Okamura et al. 2014; Sampson 2014); and (3) the spatial-, temporal-, and sex-specific growth rates of the fish that are retained by the different sampling gears (Poole 1961; Planes et al. 1999; Wilderbuer and Turnock 2009). For instance, different MRS limits are implemented in the recreational and commercial Summer Flounder fisheries (NEFSC 2013), and some limited evidence suggests that at a given length, males' and females' availability or vulnerability to fishing effort may vary seasonally and between the recreational fishery and the NMFS-NEFSC survey (Morson et al. 2012). These fishery-specific processes can generate differences in the sex composition within the fishery catch and between the catch and the survey; thus, it may be incorrect to assume that the probability of a fish being female (or male) at a given length or age is equivalent between catch data and survey data.

The goal of this work was to test the efficacy of applying NMFS-NEFSC survey-derived sex-at-age keys to fishery catch data, thus allowing the potential implementation of a sex-specific model in the Summer Flounder stock assessment to be examined. We collected sex-specific data from the commercial and recreational fisheries and compared the probability distribution for sex at age from the catch data to probability distributions generated by simulating fishery-dependent processes using the survey data.

METHODS

Data collection.—Summer Flounder along the northeastern USA and the U.S. mid-Atlantic continental shelf were collected in 2010 and 2011 by the NMFS-NEFSC fishery-independent survey (NFS data) and by port sampling of the commercial fishery landings (CFS data) and recreational hook-and-line fishery landings (RFS data; Table 1). For all fish, TL, sex, and catch location were recorded. For a subset of the sampled fish, otoliths and/or scales were removed for use in age determinations (Table 1). Otoliths were removed from carcasses collected from the RFS; for the CFS and the NFS samples, scales were collected from specimens up to 60 cm TL, and otoliths were obtained from fish larger than 60 cm TL. The right-side otolith was selected from each fish and was processed by center alignment in a merchandise tag, embedded in black polyester resin, and then cross-sectioned through the otolith core with a low-speed sectioning saw. After processing, otoliths were examined by using a Leica MZ-6 dissecting microscope with transmitted light at 8–60× magnification. Annuli from otoliths were identified as narrow opaque bands and were counted along the ventral side of the sulcal groove. Scales were processed by selecting five or six samples from each fish and creating impressions on acetate sheets. The scale impressions were examined using a microfiche reader with 20- and 29-mm lenses. Annuli in scales were identified by using established protocols (Pentilla and Dery 1988).

The NMFS-NEFSC provided NFS data for Summer Flounder sampled from the spring and fall bottom trawl survey cruises at predetermined sampling strata and at depths of 27–365 m from Cape Hatteras, North Carolina, to Nova Scotia, Canada. Detailed descriptions of the bottom trawl survey design are provided by Azarovitz (1981) and NEFSC (1988). To summarize, between 350 and 400 stations were sampled each year with a bottom trawl that had a 1.5-cm stretch-mesh liner and rollers for sampling hard substrate. Tows were conducted for 30 min per station at a tow speed of 6.48 km/h (3.5 knots). The CFS and RFS data were collected by sampling Summer Flounder that were landed at marinas, packing

TABLE 1. Total number of Summer Flounder that were sampled for sex and TL, and the subset of those fish that were also aged via examination of annuli in otoliths and scales (see Methods; NMFS = National Marine Fisheries Service; NEFSC = Northeast Fisheries Science Center).

Data source	Sex and length data	Age data
NMFS-NEFSC bottom trawl survey	4,828	3,935
Commercial fishery port sampling	18,685	11,809
Recreational fishery port sampling	13,232	7,276
Total	36,745	23,020

TABLE 2. Port locations where samples were collected from the recreational (RFS) and commercial (CFS) fisheries for Summer Flounder.

State	RFS port	CFS port
North Carolina		Wanchese
Virginia	Virginia Beach Hampton Buckroe James River Capeville Wachapreague Yorktown Cape Charles Mathews	Hampton Newport News
New Jersey	Cape May Fortescue Barnegat Light Point Pleasant Atlantic Highlands	Cape May Barnegat Light Point Pleasant
New York	Freeport Huntington Captree Port Jefferson Moriches Riverhead Hampton Bays Mattituck Greenport East Hampton Montauk	Point Lookout Hampton Bays Mattituck East Hampton Montauk
Maryland	Ocean City	
Delaware	Lewes	
Connecticut	Niantic	Stonington
Rhode Island	Point Judith	Point Judith
Massachusetts	New Bedford Hyannis	Westport New Bedford Hyannis

houses, and fishing docks from North Carolina to Massachusetts (Table 2).

Sampling of Summer Flounder landings in the commercial fishery occurred year-round wherever the fishery was operational. The minimum mesh size in the commercial fishery was a 14-cm diamond mesh or 15-cm square mesh applied throughout the net body, extension, and cod end. For each visit to a commercial dock, samples of up to 100 fish were collected haphazardly from each market category (medium, large, and jumbo sizes) available from a given fishing trip. The market category was determined by each dock or packing house; generally, small fish ranged from 35 to 45 cm, medium fish ranged from 45 to 55 cm, and jumbo fish were greater than 55 cm. At these sizes, all fish sampled were sexually mature.

Summer Flounder cannot be sexed based on external characteristics; therefore, to avoid reducing the market value of landed fish, we developed a minimally invasive technique for determining sex (Figure 1). On the pigmented side of the fish, an approximately 2.5-cm incision was made in an area halfway between the anterior end of the anal fin and the center of the pectoral fin. Forceps were then used to pull the gonads out through the incision. Orange eggs or empty ovaries were indicative of females; males were distinguished by the presence of white testis tissue. Both males and females were easily identifiable by this method, even for sampling that took place outside of the spawning season.

The RFS ports were sampled once per week during the recreational fishing season (May–September) to collect racks (filleted carcasses) of all Summer Flounder that were caught on the sampling day by all participating boats. Once the Summer Flounder were filleted, the sex organs remained intact and visible on the rack. Boat captains and crews saved fish racks in a bin, and those racks were

collected upon our arrival at a participating dock. To increase the number of fish available for collection, freezers were placed at each dock. Bags and waterproof tags were provided to the boat captains and crews and were made available near the freezers so that samples could be accurately labeled with the date and location of the catch. Participating boat captains were asked to deposit all fish racks from the day's catch into these tagged bags and to place the bags in the freezers. We emptied the freezers upon our arrival at a dock to collect fresh racks. Morson et al. (2012) concluded that the change in Summer Flounder length from freezing was negligible. To ensure that the samples represented the sex, length, and age of harvested Summer Flounder, all fish that were caught during a recreational fishing trip were sampled without regard to size. Sex was determined by macroscopic investigation of exposed gonad on the filleted fish carcass. Over 99% of the fish in the RFS collections had reproductive organs that were intact and readily visible to the naked eye.

For all commercial and recreational samples, records were kept of the NMFS-NEFSC statistical area where the fish were caught (Figure 2; Table 3). The commercial and recreational fisheries operate in different statistical areas, so their fishing locations did not completely overlap. For the NFS, data were collected along transects in a stratified sampling design. To permit spatially similar comparisons between the NFS data and the RFS or CFS data, the latitude and longitude of each NFS tow were used to assign NFS samples to NMFS-NEFSC statistical areas.

Data analysis.—Age was determined for 23,020 of the 36,745 Summer Flounder sampled from the RFS, CFS, and NFS (Table 1). To utilize the full data set for determining how well the NFS sex-at-age data described the RFS or CFS sex at age, it was necessary to generate appropriately partitioned age–length keys (ALKs) for application to fish that lacked empirically determined age data. Age–length data were partitioned by sex, region, and data source (NFS, CFS, or RFS). Region was defined as either “north” (including all fish that were caught or collected north of 40°N) or “south” (including all fish that were caught or collected south of 40°N). To compare ALKs, the age distribution at a given length was modeled using multinomial logistic regression (Gerritsen et al. 2006). The multinomial log-linear models were fitted via neural networks by using the multinom() function in the R package “nnet” (Venables and Ripley 2002). This approach provided a simple, robust method for identifying significant differences between ALKs generated from data partitioned by sex, region, and data source. The best-fitting model identified the most appropriate stratification of the data, and ALKs were generated based on that stratification. For all fish that were not aged empirically, the ALKs were then applied based on the probability of each age given the length of each fish; this was done by using the ageKey function in the R package FSA (Isermann and Knight 2005; Ogle 2014).



FIGURE 1. Photographs showing a technique for determining the sex of a Summer Flounder without dissecting the entire fish: (A) female and (B) male. A small incision was made along the gut cavity, and the gonads were pulled through the incision with a pair of forceps.

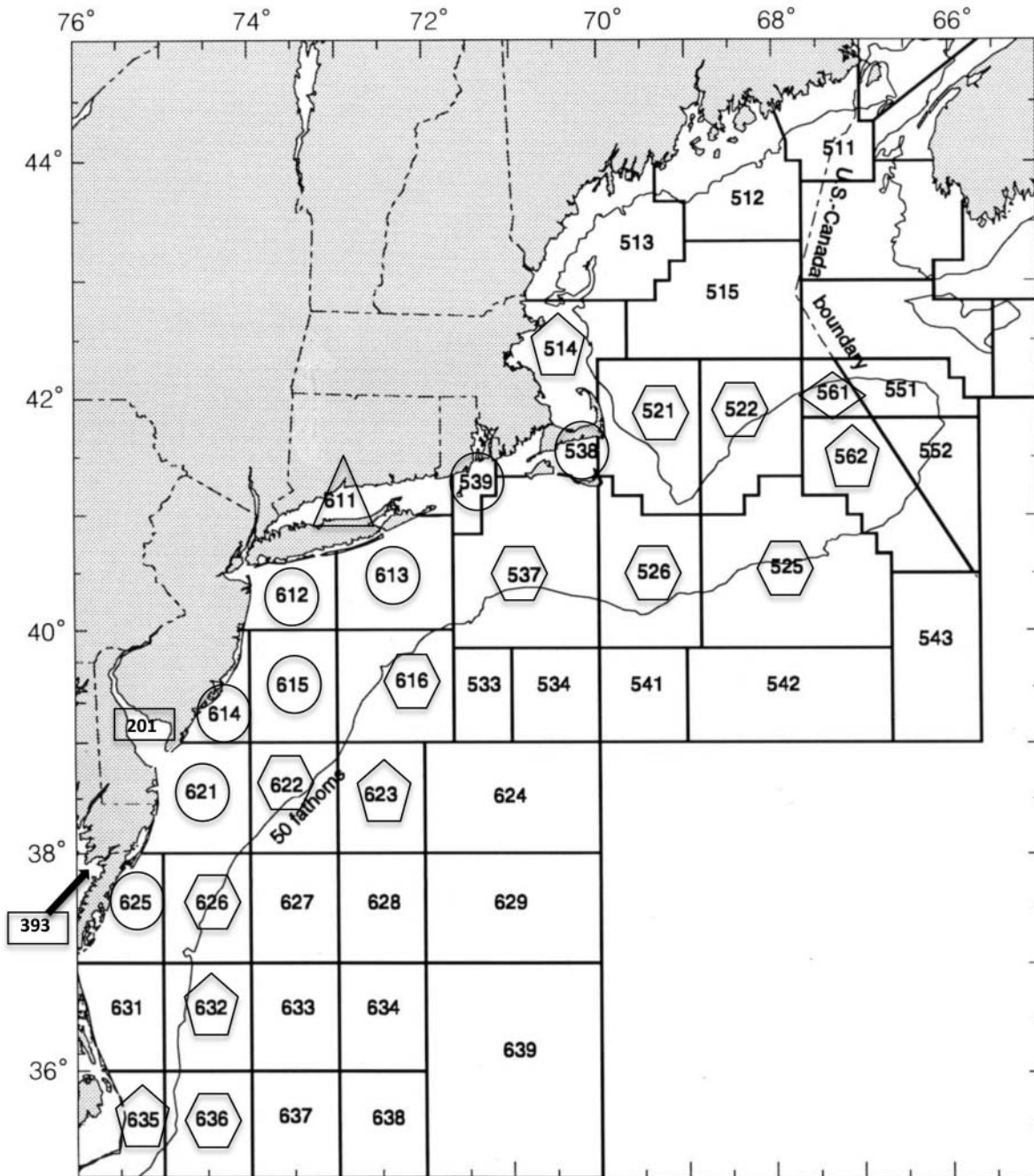


FIGURE 2. Map showing the National Marine Fisheries Service (NMFS) Northeast Fisheries Science Center's (NEFSC) statistical area units along the north-eastern USA and the western mid-Atlantic continental shelf (NEFSC 1997). The shape enclosing each statistical area's number indicates the data source as the NMFS-NEFSC bottom trawl survey (NFS), commercial fishery port sampling (CFS), recreational fishery port sampling (RFS), or some combination thereof (rectangles = RFS only; diamonds = CFS only; pentagons = NFS only; triangles = RFS and CFS; hexagons = NFS and CFS; circles = RFS, CFS, and NFS).

We used logistic regression to evaluate the efficacy of applying a sex-at-age key developed from NFS data to the CFS and RFS age data. The probability of landing a female Summer Flounder at a given age was modeled as the dependent variable, and data source (NFS, CFS, or RFS) was modeled as the independent variable (Wilson and Hardy 2002;

Morson et al. 2012). Significant differences between the NFS data source and both fishery data sources suggested that the sex-at-age key developed from raw NFS data would not be appropriate for describing the sex composition from either fishery. We hypothesized that the variability in sex at age among the data sets could be explained by (1) the size-, age-,

TABLE 3. Total number of Summer Flounder sampled from each National Marine Fisheries Service (NMFS) Northeast Fisheries Science Center (NEFSC) statistical area (see Figure 2). Samples were obtained by the NMFS-NEFSC bottom trawl survey (NFS), commercial fishery port sampling (CFS), and recreational fishery port sampling (RFS).

Statistical area	NFS	CFS	RFS
201			930
393			419
514	12		
521	3	40	
522	14	120	
525	71	401	
526	230	157	
537	741	1,596	
538	5	454	1,278
539	270	2,558	1,065
561		39	
562	27		
611		2,028	1,078
612	7	842	3,454
613	658	3,985	839
614	112	687	45
615	262	3,343	40
616	441	822	
621	421	434	4,080
622	289	508	
623	18		
625	178	176	22
626	493	488	
631	141		15
632	114		
635	293		
636	44	15	

and sex-specific retention selectivity imposed by the MRS of 35 cm for the commercial fishery and the MRSs of 46–53 cm for the recreational fishery; and (2) the differences in growth rates among fish collected from the three data sources. Therefore, the effects of these fishery-specific processes on the fishery-independent survey data were simulated separately for the CFS and RFS, and the resultant sex ratios at age were re-analyzed.

First, to simulate the length-specific retention selectivity of the recreational and commercial fisheries, the NFS data were left-truncated at the MRS for each fishery. This approach provided an NFS-derived measure of Summer Flounder sex at age that was comparable to the left-truncated sex composition in each fishery-dependent data set. The 35-cm MRS was implemented coastwide in the commercial fishery during the sample collection period, so NFS and CFS data were left-truncated at 35 cm for the CFS comparison. The MRS for the recreational fishery varied from 46 to 53 cm depending on the

landing year and the state. To avoid too many pairwise comparisons based on too few data, we left-truncated the NFS and RFS data at 46 cm and at 53 cm in two separate comparisons that together encompassed the full range of potential comparisons.

To simulate the observed growth rates in the commercial and recreational fisheries, sex- and region-specific ALKs generated from the CFS and RFS data were applied to the left-truncated sex- and region-specific NFS length data. This allowed us to assign age to the left-truncated distribution of lengths in the NFS data as if the NFS Summer Flounder had grown at the same rates as the fish in each respective fishery.

Finally, as a proxy for evaluating the length-specific vulnerability of the sexes to the commercial and recreational fisheries, the left-truncated, NFS-derived sex ratio at length was compared with the measured sex at length from the CFS and RFS data. The NFS utilized a smaller mesh size than the regulation size for the commercial fishery, and the MRS for the recreational fishery is set higher than that for the commercial fishery; therefore, all left-truncated NFS data in these comparisons originated from fish that were fully recruited to the survey. For each pairwise comparison, a logistic regression model was fitted to estimate the probability that a landed fish of a given length was female.

All statistical analyses were conducted in R version 3.0.3 (R Development Core Team 2014). Model selection was based on Akaike's information criterion (AIC). In evaluating two competing models, a model with an AIC score that was at least 2 units lower than the other model's AIC was accepted as the better-fitting model (Arnold 2010).

RESULTS

Summer Flounder from 27 different NMFS-NEFSC statistical areas were sampled during the NFS, CFS, and RFS programs (Table 3). The CFS samples were distributed inshore and offshore across similar statistical areas as the NFS samples, whereas the RFS samples were limited to statistical areas located inshore (Figure 2; Table 3).

The probability that a Summer Flounder of a given length was a given age depended on the sex, region of capture, and data source (Table 4). Sex was the most important effect in the model, followed by data source and region.

The sex ratio at age in the NFS data was significantly different than those in the CFS data ($P < 0.0001$) and the RFS data ($P < 0.0001$) when comparisons included all NFS data (Figures 3a, 4a). In both fisheries, a higher proportion of the catch at a given age was female (Figures 3a, 4a, 5a). However, fish that were landed under an MRS had a higher mean length at age than fish that were collected by the NFS. The higher the MRS imposed on the landed fish, the higher was the mean length at age (Figure 6). This effect was apparent for all ages that contained the MRS within their length frequency. To account for this,

TABLE 4. Values of Akaike's information criterion (AIC) for eight potential models describing the probability that a Summer Flounder was a given age based on fish length (null model) and fish sex, region of capture (north or south of 40°N), and data source (recreational fishery port sampling, commercial fishery port sampling, or fishery-independent bottom trawl survey). Delta AIC (Δ AIC) is the difference between the specified model and the best-performing model (i.e., the model with the lowest AIC value).

Model	df	AIC	Δ AIC	Residual deviance
Sex, region, data source	65	59,836	0	59,668
Sex, region	56	60,226	390	60,114
Sex, data source	70	60,268	432	60,128
Sex	42	60,605	769	60,521
Region, data source	70	65,590	5,754	65,450
Data source	56	65,949	6,113	65,837
Region	42	66,242	6,406	66,158
Null	28	66,550	6,714	66,494

the NFS data were left-truncated to simulate the MRS values used in the commercial and recreational fisheries; the resulting sex-ratio-at-age pattern more closely approximated the pattern in the data collected directly from the fisheries (Figures 3b, 4b, 5b). The proportions at age in the NFS data shifted dramatically toward females at younger ages (Figures 3b, 4b, 5b). Separate application of sex- and region-specific ALKs generated from CFS and RFS data to the left-truncated, sex- and region-specific NFS length data resulted in a sex-ratio-at-age pattern that further resembled the patterns shown in the CFS and RFS data (Figures 3c, 4c, 5c). The shift in sex ratio at age suggests that the growth differences between Summer Flounder that are landed in the fisheries and those that are collected during the NFS are sex specific. Females that were landed in the commercial and recreational fisheries had grown faster than females that were collected by the NFS, and males that were landed in the fisheries had grown more slowly than NFS-collected males. Thus, the application of fishery-specific ALKs produced a shift in the sex ratio of younger fish further toward females and a shift in the sex ratio of older fish toward males (Figures 3b, c; 4b, c; 5b, c). For example, in the comparison of NFS and CFS data (Figure 3b, c), the survey-derived sex at age 1 increased from approximately 40% female (Figure 3b) to approximately 65% female (Figure 3c), whereas the survey-derived sex at age 6 decreased from approximately 75% female (Figure 3b) to approximately 50% female (Figure 3c). Nevertheless, statistically significant differences remained between the CFS data ($P < 0.0001$) or RFS data ($P < 0.0001$) and the NFS-derived data that were manipulated to simulate the fishery-specific MRSs and growth processes within catches from the two fisheries.

Because accounting for the length-specific retention selectivity and differences in growth rate between Summer

Flounder that were landed in the fisheries and those collected during the survey did not remove all of the variability in sex at age between the NFS data and the catch data, we attempted to estimate the difference in availability of the sexes to the survey and the fisheries. The length-specific vulnerability of the sexes to the gear (modeled as the probability that a landed fish of a given length was female) was similar but statistically different ($P = 0.0037$) between the left-truncated NFS data and the CFS data (Figure 7a). The probability that a landed fish was female was slightly higher for the CFS data than for the left-truncated NFS data (Figure 7a). In addition, the proportion female at length increased at similar rates in both the CFS data set and the left-truncated NFS data set until each reached approximately 45 cm—similar to the smallest MRS for the recreational fishery. At that point, the proportion female at length remained unchanged or increased only slightly from each 1-cm increment to the next until a length of approximately 50 cm was reached, when the rate for both data sets returned to a logistic form (Figure 7). The length-specific probability that a landed fish was female was much higher for the RFS data than for the left-truncated NFS data ($P < 0.0001$; Figure 7b). In fact, for a Summer Flounder landed in the recreational fishery, the probability that the fish was female was 80% at the smallest MRS (46 cm) and rapidly approached 100% with increasing fish size (Figure 7b).

DISCUSSION

To determine whether the sex composition of Summer Flounder from a fishery-independent trawl survey could be used to estimate the sex composition of the commercial and recreational catch without collecting sex-specific data directly from the fisheries, we simulated fishery-specific processes on the survey data, including the MRS in each fishery and the growth rates of fish landed in both fisheries, and we compared the survey-derived estimates to the actual sex composition in the fishery catch.

Summer Flounder that were landed in the commercial and recreational fisheries had grown at different rates than survey-collected fish and at different rates from one another, suggesting that each gear is sampling a different portion of the population. Furthermore, this effect was sex specific: females that were landed in the fisheries had grown faster than those collected during the survey, whereas males that were collected by the survey had grown faster than males landed in the fisheries. This suggests that fisheries are selectively targeting the faster-growing females and slower-growing males. Stari et al. (2010) proposed that sampling location or gear selectivity could explain differences in ALKs for North Sea Haddock *Melanogrammus aeglefinus* collected with different gear types. We propose that the differences among ALKs in the present study could have resulted from (1) the sex-specific spatial segregation of Summer Flounder, as previously suggested by Morson et al. (2012); (2) the influence of

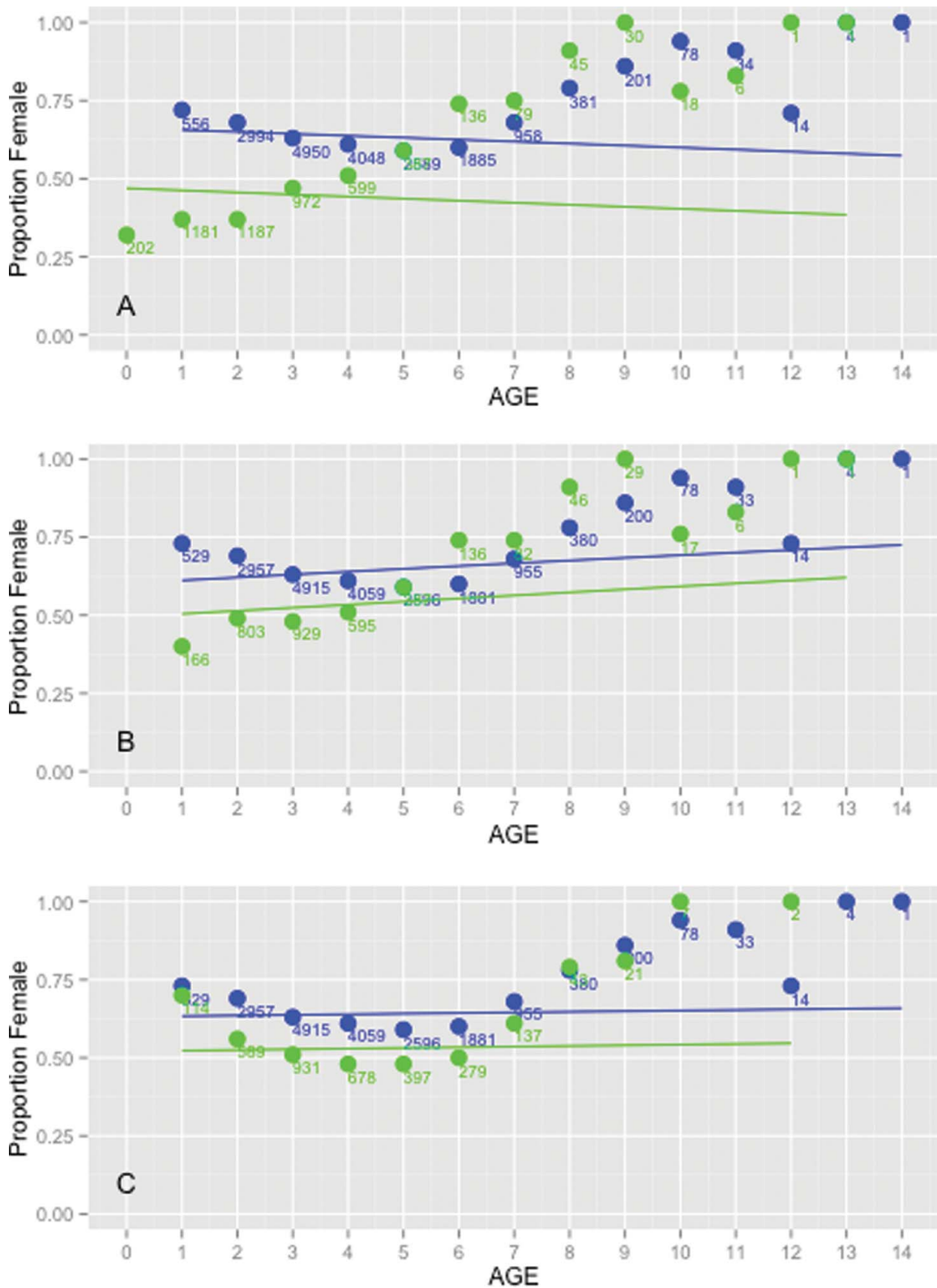


FIGURE 3. Proportion female at age for Summer Flounder sampled in the commercial fishery (blue dots) and the National Marine Fisheries Service Northeast Fisheries Science Center's bottom trawl survey (NFS data; green dots). Lines represent the probability that a landed fish was female, as estimated by logistic regression (see text). Commercial fishery data are compared with the NFS data in the following forms: (A) raw NFS data, (B) NFS data that were left-truncated at 35 cm to simulate the minimum retention size in the commercial fishery, and (C) NFS data that were left-truncated at 35 cm and assigned ages based on age-length keys generated from commercial fishery data. The number of sampled fish is shown next to each data point.

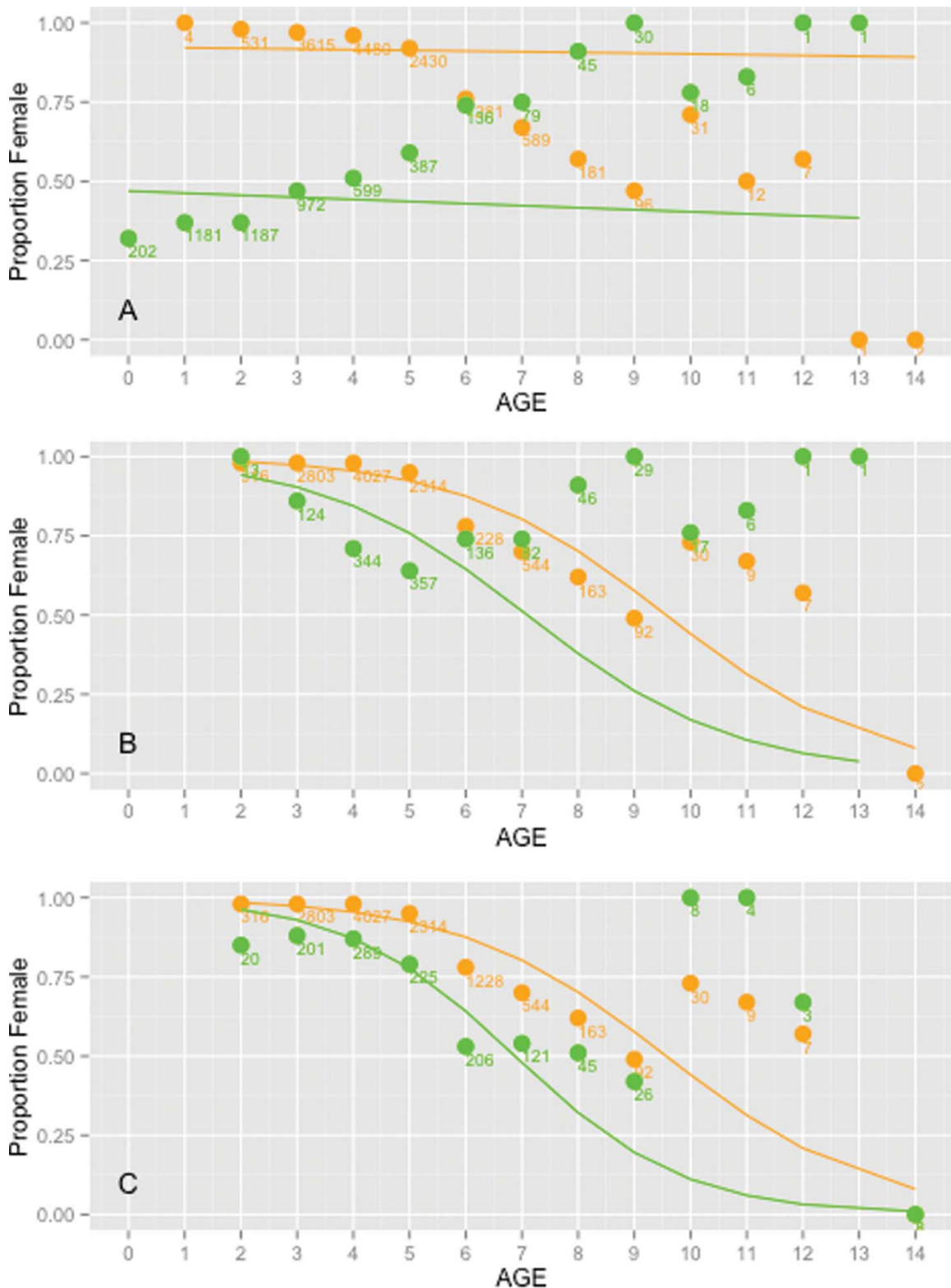


FIGURE 4. Proportion female at age for Summer Flounder sampled in the recreational fishery (orange dots) and the National Marine Fisheries Service Northeast Fisheries Science Center's bottom trawl survey (NFS data; green dots). Lines represent the probability that a landed fish was female, as estimated by logistic regression (see text). Recreational fishery data are compared with NFS data in the following forms: (A) raw NFS data, (B) NFS data that were left-truncated at 46 cm to simulate the smallest minimum retention size in the recreational fishery, and (C) NFS data that were left-truncated at 46 cm and assigned ages based on age-length keys generated from recreational fishery data. The number of sampled fish is shown next to each data point.

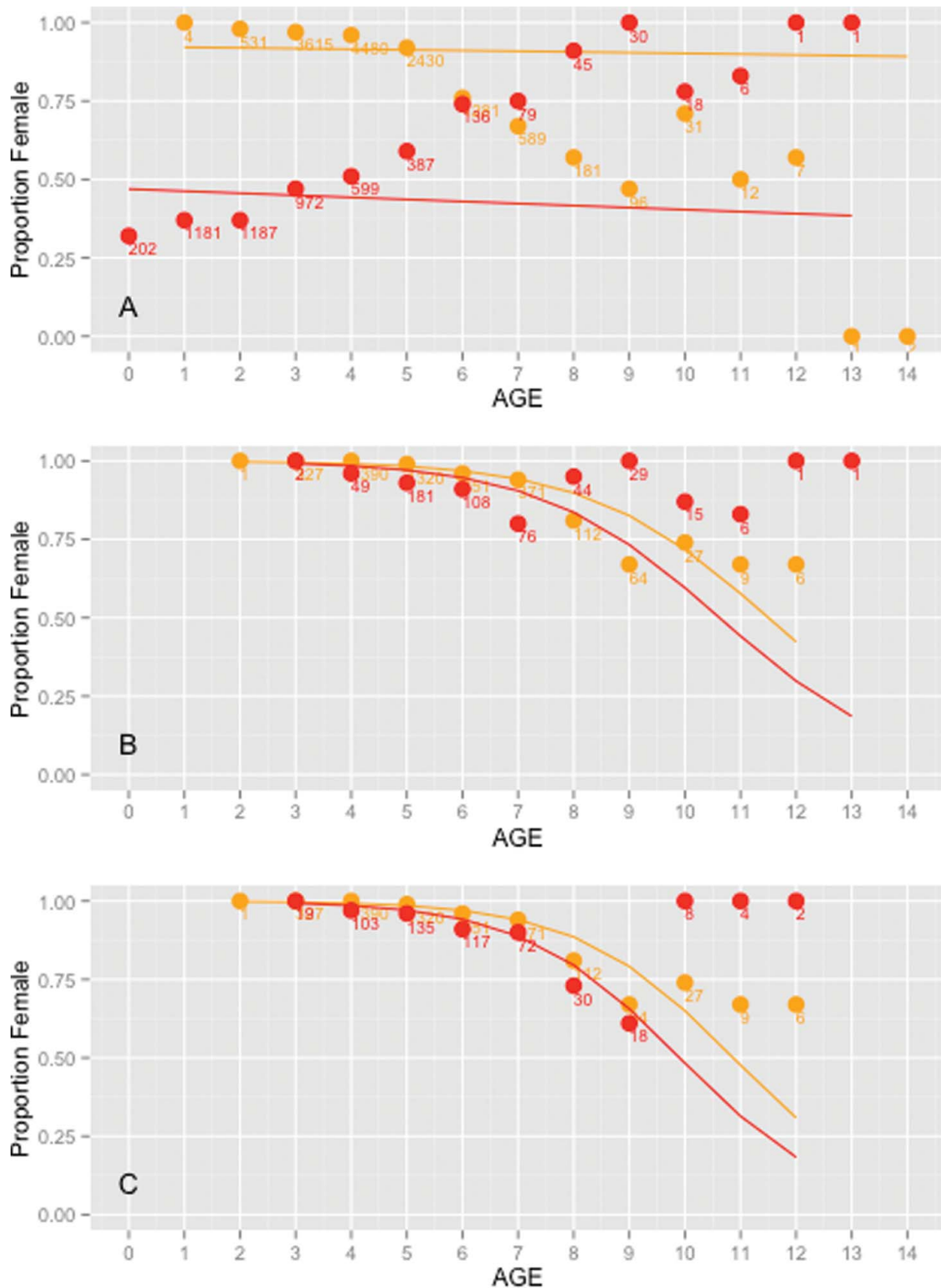


FIGURE 5. Proportion female at age for Summer Flounder sampled in the recreational fishery (orange dots) and the National Marine Fisheries Service Northeast Fisheries Science Center's bottom trawl survey (NFS data; red dots). Lines represent the probability that a landed fish was female, as estimated by logistic regression (see text). Recreational fishery data are compared with NFS data in the following forms: (A) raw NFS data, (B) NFS data that were left-truncated at 53 cm to simulate the largest minimum retention size in the recreational fishery, and (C) NFS data that were left-truncated at 53 cm and assigned ages based on age-length keys generated from recreational fishery data. The number of sampled fish is shown next to each data point.

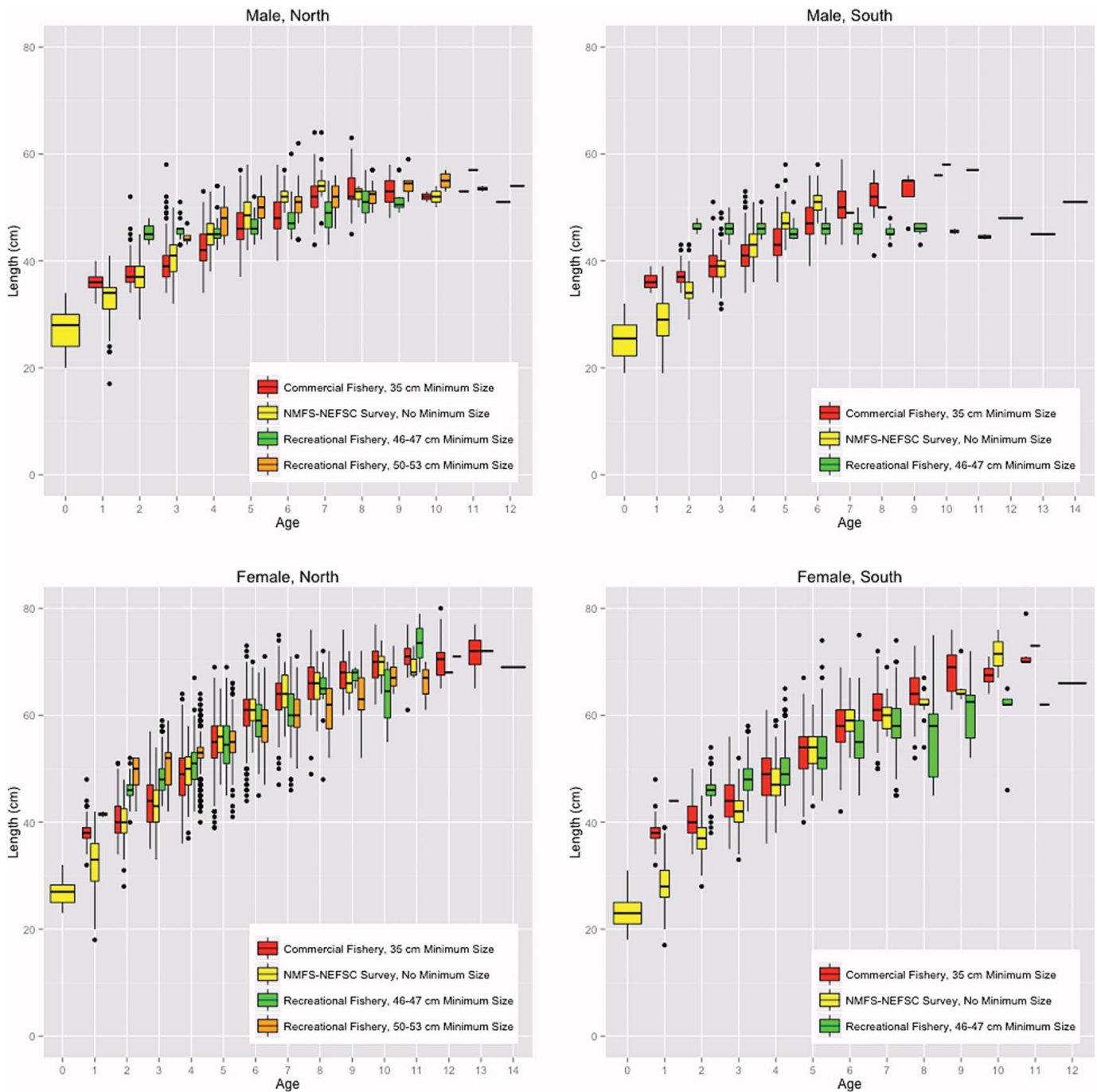


FIGURE 6. Box-and-whisker plots of the mean TL at age for Summer Flounder under different minimum retention size regulations in the commercial and recreational fisheries (NMFS–NEFSC survey = National Marine Fisheries Service [NMFS] Northeast Fisheries Science Center [NEFSC] bottom trawl survey). Plots are organized by region (north and south of 40°N) and sex. The black horizontal line within each box is the mean, the ends of the box represent the interquartile range, the ends of whiskers denote the 5th and 95th percentiles, and the dots are outliers.

region on growth rates, which was previously identified by Kraus and Musick (2001) and further confirmed with this work; and (3) the spatial and temporal distribution of fishing effort, although the influence of age-specific gear selectivity cannot be ruled out. We discuss the spatiotemporal

distributions of the fish and of the fishing effort in more detail below.

The MRS in each fishery, operating on the sex-specific growth rates (Poole 1961; King et al. 2001), forces a higher fraction of females at age in the catch than would be expected

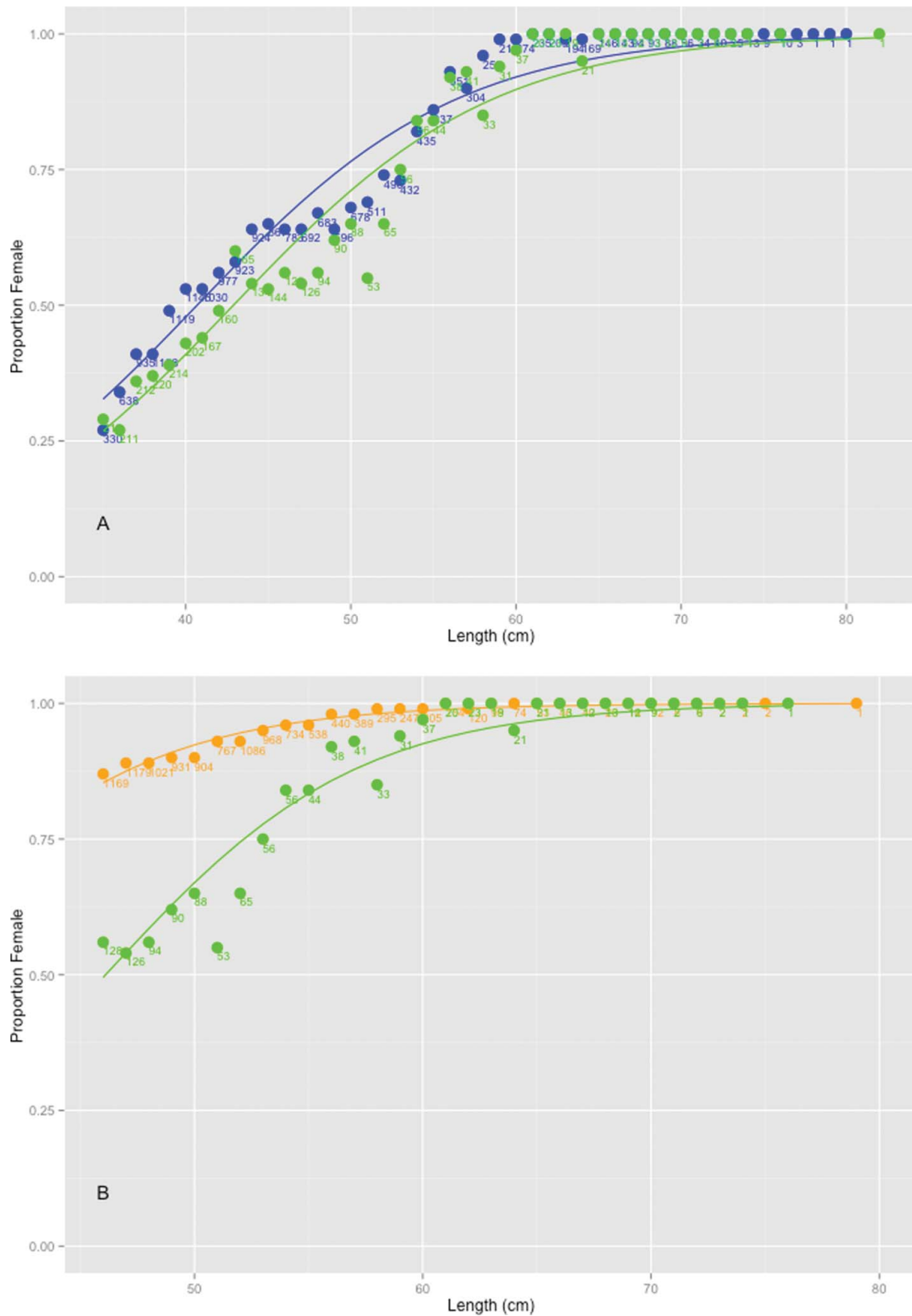


FIGURE 7. Proportion female at length (TL) for Summer Flounder sampled in the commercial fishery (blue dots), the recreational fishery (orange dots), and the National Marine Fisheries Service Northeast Fisheries Science Center’s bottom trawl survey (NFS data; green dots). Lines represent the probability that a landed fish was female, as estimated by logistic regression (see text). The NFS data are truncated according to the minimum retention size in (A) the commercial fishery (35 cm) and (B) the recreational fishery (46 cm). The number of sampled fish is shown next to each data point.

in a non-culled, fishery-independent sample. We were able to largely correct for this by left-truncating the NFS data to mimic the MRS in each fishery; the transformation of the survey data recovered a sex-at-age pattern that more closely resembled the pattern measured directly from the fishery catch. Not surprisingly, when we applied ALKs developed from fishery-dependent data to the left-truncated NFS data, the result was a sex-at-age pattern in the survey-derived data that even more closely resembled the pattern measured directly from the catch.

This stepwise approach to simulating fishery-specific effects on fishery-independent data recovered the sex-at-age pattern observed in the fisheries; such an approach may therefore be applicable to other fisheries for which biological data from the catch are limited and for which the estimation of sex-specific parameters in an assessment is desirable. However, these manipulations did not yield the exact proportions at age measured directly from the catch. We hypothesize that this was due to some difference in the spatiotemporal distributions of stock structure and fishing effort such that the males' and females' availability to the NMFS-NEFSC survey and the fishing fleets was not equivalent. As evidence, we showed that sex at length (used as a proxy for fish availability to the fishing gears) varied slightly between the commercial fishery and the NFS and differed dramatically between the recreational fishery and the survey. The recreational fishery occurs inshore from late spring to early fall and the commercial fishery occurs year-round inshore and offshore, whereas the NFS takes place offshore, once in March and once in September. Because there was no spatial or temporal overlap between the recreational fishery and the survey, we would expect that if there is spatial and temporal structure in the population's sex composition, then differences in the spatiotemporal availability of the sexes to the survey and the recreational fishery will be reflected in the catch. Indeed, this was manifested by the large difference in sex ratio at length between the RFS and NFS data.

The commercial fishery overlapped with the survey both in time and in space, so the expectation is that the sex-specific availability of fish to the commercial fishery and the survey will be similar. Such a finding was also observed as the fairly close match in sex at length between the CFS and NFS data. To our knowledge, the present study provides the first evidence that Summer Flounder exhibit sex-specific segregation spatially and temporally.

Spatial and temporal segregation of fish by sex is a common phenomenon and occurs in other sexually dimorphic flatfishes (Morgan and Trippel 1996; Swain 1997; Swain and Morin 1997; Gorchinsky 1998; Richards et al. 2008; Gerritsen et al. 2010; Sahin and Gunes 2010; Loher and Hobden 2012; Loher et al., in press). Explanations for sex-specific segregation include temperature selection (Swain 1997) and/or depth selection (Swain and Morin 1997), sex-specific life history strategies that promote sexually dimorphic characteristics (Gerritsen et al. 2010), and sex-specific foraging intensity and

the spatial and temporal distribution of the forage base (Swain and Morin 1996). Any of these postulations could be advanced to explain the sex-specific distribution of Summer Flounder in space and time. The importance, however, of estimating and understanding the sex-specific spatial and temporal distribution of Summer Flounder goes beyond these interesting ecological implications. Okamura et al. (2014) showed that biological reference points were highly sensitive to assumptions about effort allocation in space and time when seasonal migrations of offshore Lingcod *Ophiodon elongatus* were sex specific. A similar analysis for Summer Flounder is beyond the scope of this paper, but minimally the application of sex-aggregated ALKs to landings data should result in highly biased estimates of catch at age given that (1) female Summer Flounder grow much faster than males and (2) the recreational fishery lands females almost exclusively. Accounting for the complex spatiotemporal dynamics in the distribution of sex composition and fishing effort will undoubtedly complicate future stock assessments of Summer Flounder.

Given the importance of having an accurate estimate for the sex composition of the catch and given the failure of our method to recover an exact match by applying sex-specific processes to survey data due to what appear to be complex, time- and space-varying sex-specific fishery selectivities, it makes sense to explore other options for collecting sex composition data directly from fishery landings. For the recreational fishery, this would be easy to incorporate into any port sampling program that already collects length frequency data from the catch. We demonstrated that even when Summer Flounder are filleted at sea, the gonad remains intact and readily visible to the naked eye. An observer measuring the length of a Summer Flounder can thus determine its sex macroscopically, with no additional time or cost. Collecting sex-specific information from the commercial fishery may prove more difficult because fish are not filleted at sea to expose the gonads, and the fish are typically sold whole to market, which precludes full dissection of the fish to determine sex. We introduced a method for determining sex by using a small incision in the gut cavity. Although this may still be too invasive for some fishing ports or fish sellers or buyers, we encountered no resistance on the part of the many commercial docks that we sampled. The International Pacific Halibut Commission used microsatellite-based genetic techniques to measure the sex composition of the catch for Pacific Halibut *Hippoglossus stenolepis* (Loher et al., in press). This reduced the influence of spatial and temporal variability in survey and fishing effort when deriving sex composition of the catch using survey data, as it provided a direct measure of sex composition of the catch. A cost-benefit analysis comparing the purchase and dissection of fish versus the development of microsatellite techniques may reveal the most cost- and time-effective method for determining the sex composition of the commercial catch. No matter how the data are obtained, if a program is instituted to collect sex composition data directly from the Summer Flounder catch, that

program would have to mirror the spatial and temporal distribution of the fishing effort since it appears that males and females are disaggregated in time and space.

The trends we observed in the sex, length, and age of the catch may interact with fishing regulations and induce changes in population structure. The mean length at age of individuals in the Summer Flounder population is declining over time, with none of the accompanying changes in length–weight relationship or condition index (NEFSC 2013) that one might expect from density-dependent influences on individual fish growth (Rose et al. 2001). Given the dynamic nature of climate change in the northwestern Atlantic Ocean (Scavia et al. 2002) and its influence on the fish stocks of this region (Rothschild and Jiao 2012; Sparrevohn et al. 2013), a simple, environmentally determined change in growth rate for the Summer Flounder stock cannot be discounted. Nonetheless, we presented a trend of increasing mean length at age with increasing MRS in the fishery landings. The MRS implemented for a fishery is selecting the fastest-growing fish at a given age while leaving behind the slower-growing fish to reproduce another year. A growing body of literature addresses the potential evolutionary effects of size-selective fishing (e.g., Conover and Munch 2002; Law 2007). Varying opinions exist concerning the time scale and fishing pressure that are needed to induce evolutionary change as opposed to simple phenotypic change in a fish population (e.g., Anderson and Brander 2009; Enberg et al. 2009). However, we cannot rule out the possibility that size-selective fishing pressure on the Summer Flounder population is causing a shift in the genetic structure of the stock, favoring slower growth and resulting in a decrease in the mean length at age over time.

Additionally, the proportion female at age is declining in the Summer Flounder population (NEFSC 2013). If an MRS selects the faster-growing fish at a given age in the population, those fish must be disproportionately female because of the difference in growth rates between the sexes. Our sampling found that the sex-at-age relationship from the recreational catch—and, to a lesser extent, from the commercial catch—was skewed toward females in comparison with the sex at age that would be expected from survey data. Simulation of MRS effects showed that this result accrued in part from the implementation of the MRS in each fishery. For example, the proportion of fish that were female increased with increasing TL in the survey as well as in the fisheries. Interestingly, in both the CFS data and the NFS data, the sex ratio remained relatively unchanged at around the 5-cm increment that encompassed the range of MRS values used for the recreational fishery (45–50 cm), despite the expectation that the sex ratio should increase as it did at each length increment before and after the 45–50-cm increment. This observation suggests that the MRSs implemented in the recreational fishery have altered the population sex ratio within this range of sizes. Therefore, one potential explanation for the trend of a decreasing proportion female at age in the population over

the last decade (NEFSC 2013) is the increase in MRSs used to rebuild the stock over that same time period and the associated increases in female-specific fishing mortality. Sex-specific differences in fishery selectivity have been reported for other sexually dimorphic flatfishes that are regulated by MRSs (Briggs 1965; Loher and Hobden 2012). In fact, the sex composition estimates for commercial landings of Pacific Halibut indicate that males may never reach the mean sizes associated with full fishery selectivity at age (Clark and Hare 2006).

If current management strategies are driving changes in the structure of the Summer Flounder stock, it is important for managers to consider the potential adverse effects of those changes. Size-selective fishing can alter the sex ratio of a population (Kendall and Quinn 2013) and can influence the reproductive potential of the stock (Rowe and Hutchings 2003; Claereboudt et al. 2004; Rijnsdorp et al. 2010), and genetic traits that are selected against by implementing an MRS as a management strategy may be difficult to recover (Enberg et al. 2009).

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