2019

Evaluating Summer Flounder Spatial Sex-Segregation in a Southern New England Estuary

Joseph A. Langan

M. Conor McManus

Adena J. Schonfeld
Virginia Institute of Marine Science

Corinne L. Truesdale

Jeremy S. Collie

Recommended Citation

ARTICLE

Evaluating Summer Flounder Spatial Sex-Segregation in a Southern New England Estuary

Joseph A. Langan*
Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island 02882, USA

M. Conor McManus
Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island 02882, USA; and
Rhode Island Department of Environmental Management, Division of Marine Fisheries, Jamestown, Rhode Island 02835, USA

Adena J. Schonfeld
Virginia Institute of Marine Science, College of William and Mary, Gloucester Point, Virginia 23062, USA

Corinne L. Truesdale
Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island 02882, USA; and
Rhode Island Department of Environmental Management, Division of Marine Fisheries, Jamestown, Rhode Island 02835, USA

Jeremy S. Collie
Graduate School of Oceanography, University of Rhode Island, Narragansett, Rhode Island 02882, USA

Abstract
    Marine fish species can exhibit sex-specific differences in their biological traits. Not accounting for these characteristics in the stock assessment or management of a species can lead to misunderstanding its population dynamics and result in ineffective regulatory strategies. Summer Flounder *Paralichthys dentatus*, a flatfish that supports significant commercial and recreational fisheries along the northeastern U.S. shelf, expresses variation in several traits between the sexes, including growth and habitat preference. To further understand these patterns, 1,302 Summer Flounder were collected and sexed in 2016 and 2017 from fisheries-independent surveys conducted in Rhode Island state waters. Female flounder were more prevalent in shallow waters (≤15 m) through all months, but males had a greater presence in deeper waters (>15 m) from May through September. The probability of a collected flounder being female was evaluated with generalized linear models and covariates representing depth, temperature, month, year, and TL. Summer Flounder were more likely to be female at larger sizes, in shallower waters, and late in the season. When compared with landings data in the recreational fishery over the sampling period, the results suggest

that nearly all flounder harvested in the sector were female. This work provides further evidence for and characterization of Summer Flounder sex-segregation and highlights, for management purposes, the importance of considering fine-scale spatial dynamics in addition to broader distribution patterns. The fitted model represents an effective first step toward understanding the implications of an aggregated fishing effort for disproportionate removals of male or female flounder and for exploring resulting consequences for regional spawning stock biomass and stock resiliency.

Incorporating sex-specific information in fisheries stock assessments can be critical in understanding the structure and resiliency of fish populations. Research on several fish species has indicated that failing to account for sexual dimorphism in fish growth and natural mortality (Swain 1997; Swain and Morin 1997; Wang et al. 2007; Gerritsen et al. 2010; Su et al. 2011; Loher et al. 2016), differing fishery selectivity (Gerritsen et al. 2010; Myers et al. 2014; Loher et al. 2016; Gonçalves et al. 2017), and/or spatiotemporal sex-segregation (Swain 1997; Gerritsen et al. 2010; Loher and Hobden 2012; Okamura et al. 2014; Gonçalves et al. 2017; Haugen et al. 2017) may bias biological reference points and compromise the success of management strategies. Nonetheless, relatively few stock assessments incorporate sex-specific life history characteristics due to the intensive data required (Okamura et al. 2014; Terceiro 2018) and uncertainty in whether local patterns represent stock-wide characteristics. Although some of these data are available from fisheries-independent surveys or landings (Wang et al. 2007; Su et al. 2013; Morson et al. 2015; Loher et al. 2016; Haugen et al. 2017; Terceiro 2018), there is little information characterizing spatial variability or describing the sex-composition of fishery discards, further complicating incorporation of sex-specific information into stock assessments.

Summer Flounder *Paralichthys dentatus* is one of the most commercially and recreationally important finfish species on the northeastern U.S. Continental Shelf (Terceiro 2018). Like many flatfishes (Swain and Morin 1996; Clark 2004; Gerritsen et al. 2010; Loher and Hobden 2012; Loher et al. 2016), this species exhibits sexual dimorphism; females grow larger and faster than males, and sexual differentiation begins between 6 and 12 cm in length or 4.5 to 8 months in age (King et al. 2001). Natural mortality may also differ between male and female Summer Flounder, in that females may have a lower mortality rate (Maunder and Wong 2011); however, this attribute is still debated (Terceiro 2018). Morson et al. (2012) identified a significant relationship between the sex ratio of recreational landings and the port at which Summer Flounder were collected, indicating that this species exhibits spatial sex-segregation. Such spatial differences between the sexes suggest that there is a risk of disproportionately removing female spawning stock biomass if commercial and recreational fishing is localized, which could

alter the population's reproductive capacity (Su et al. 2011, 2013; Loher et al. 2016; Alonso-Fernández et al. 2017; Haugen et al. 2017). A validating example of this concern is seen in the New Jersey recreational Summer Flounder fishery, where the harvest was found to be predominantly female (Morson et al. 2012, 2017). Therefore, it is evident that spatial sex-based population dynamics represent an important consideration in the successful management of this species (Terceiro 2018).

While sexual dimorphism is well documented for Summer Flounder (King et al. 2001; Terceiro 2018), the data needed to construct sex-specific stock assessment models remain scarce. For example, it is unknown whether male Summer Flounder migrate inshore later than females. Such a pattern would shift the sex ratio of the inshore population throughout the season (NEFSC 2013). Although the stock assessment uses trawl surveys covering the latitudinal and bathymetric range of Summer Flounder (NEFSC 2013; Politis et al. 2014; Terceiro 2016), these surveys lack the fine spatiotemporal resolution required to develop a clear understanding of sex-specific distribution patterns in the shallow inshore areas targeted by recreational anglers, who are responsible for a major component of the annual harvest (Terceiro 2016, 2018), and how the sex composition changes throughout the fishing season (NEFSC 2013). To begin addressing these research needs, this work aims to use specimens from two nearshore trawl surveys in Rhode Island waters with the spatiotemporal coverage necessary to evaluate coastal patterns of sex-specific distribution in Summer Flounder. Conducted in the center of southern New England, an area of significant commercial and recreational Summer Flounder harvest (NEFSC 2013; Terceiro 2018), the results of this investigation will help elucidate important spatiotemporal considerations for successful regional fishery management.

METHODS

Sample collection.— Summer Flounder were collected opportunistically in Rhode Island state waters throughout 2016 and 2017 from fish trawl surveys conducted by the University of Rhode Island Graduate School of Oceanography (URI GSO) and the Rhode Island Department of Environmental Management (DEM; Figure 1). Using an otter trawl net with an effective opening of 6.5 m and towed at 2 knots (3.7 km/h) for 30 min, the weekly URI
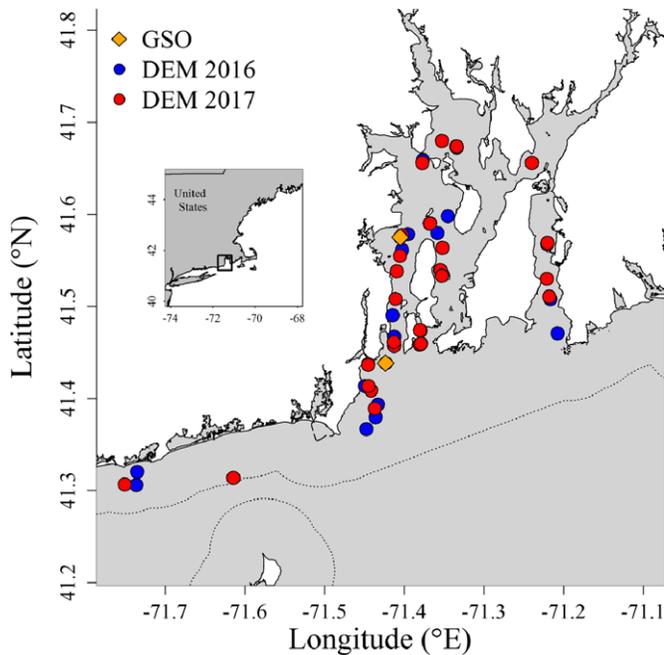
FIGURE 1. Narragansett Bay and the locations from which samples were obtained. URI GSO (orange, diamond) samples were collected in both 2016 and 2017, while DEM samples (circles) were collected over different stations opportunistically in both 2016 (blue) and 2017 (red). The state water boundary is presented as a dotted line.

GSO survey is conducted at two stations in Narragansett Bay: Fox Island, a midbay habitat with a mean depth of approximately 7 m, and Whale Rock, an outer-bay habitat with a mean depth of approximately 22.9 m (Collie et al. 2008). The DEM survey is conducted at 13 set locations in Narragansett Bay monthly and is augmented with additional fixed and randomly chosen stations during the spring (from approximately mid-April to mid-May) and fall (from approximately mid-September to early October) in the Bay, Rhode Island Sound, and Block Island Sound. The DEM survey uses an otter trawl net with a 6.7-m wingspan and tow durations of 20 min traveling at 2.5 knots (4.6 km/h). Accompanying information during the tows, including date, location, depth, and bottom temperature, is recorded for both surveys. A total of 1,328 flounder were collected across the URI GSO and DEM surveys for this analysis. Summer Flounder were measured (TL, cm) and dissected for sexual identification. Dissections occurred within 4 h of capture when collected from the URI GSO survey, and individuals obtained from the DEM survey were frozen and processed at a later date. Previous research has indicated that freezing samples has negligible effect on the TL measurements of the specimen (Morson et al. 2012). Sex was determined by visual inspection of the gonads as in Morson et al. (2015). Small individuals with underdeveloped gonads that were unable to be sexed were excluded from analyses. Because females

were generally easier to distinguish at TLs less than 30 cm, the sex ratio of this small portion of the overall sample may be biased by such exclusions.

Statistical analyses.— The probability of a flounder being male or female was estimated by logistic regression in R (R Core Team 2017). The regression predicted sex as a function of the spatiotemporal capture information (depth, month, year), bottom temperature, and the TL of each individual. Model variants using all combinations of variables considered were compared through minimization of the Akaike information criterion (AIC; Akaike 1973) and maximization of the area under the receiving operator characteristic curve (AUC), a metric describing the statistical power of a model as a function of the type-I error rate of the decision threshold. The classification accuracy, calibration, and bias of the selected model variant were then evaluated via cross-validation analyses (see the Supplement available in the online version of this article).

RESULTS

Nearshore Sex Ratio Description

Of the total 1,328 Summer Flounder collected from the URI GSO ($n = 1,113$) and DEM ($n = 189$) fish trawl surveys, 1,302 could be successfully sexed (Table 1). Despite similar sampling effort between years, approximately twice as many Summer Flounder were collected in 2017 ($n = 889$) than in 2016 ($n = 456$). In the URI GSO survey, the median catch per tow during the study period increased from six individuals in 2016 to 11 in 2017. Further, the proportion of specimens in this survey that were male significantly increased from 46.6% to 54.9% between the sampled years (χ^2 test: $P = 0.0145$).

Male Summer Flounder were found to occupy a smaller TL distribution than did females (Figure 2; Kolmogorov–Smirnov [K–S] test: $P < 0.001$). However, male Summer Flounder captured in 2017 spanned a wider range of sizes than those in 2016 (Figure 2; K–S test: $P < 0.001$). In contrast, female Summer Flounder exhibited approximately the same TL distribution in both years (K–S test: $P > 0.05$). While both sexes were prevalent at small sizes, females made up the majority of captured fish larger than the 45.7-cm (93.0%) and 48.3-cm (97.7%) minimum length limits implemented in the Rhode Island recreational fishery in 2016 and 2017, respectively (Jason McNamee, Rhode Island Department of Environmental Management, personal communication) (Figure 2). Specifically, 21.4% and 13.2% of captured females exceeded the 45.7-cm and 48.3-cm minimum length limits, respectively, while 1.6% and 0.3% of captured males were large enough for recreational harvest.

The TL distribution and sex ratio (χ^2 test: $P < 0.001$) of captured Summer Flounder shifted by month (Figures 3, 4).

TABLE 1. Number of Summer Flounder collected and sexed by month and survey (University of Rhode Island Graduate School of Oceanography [URI GSO] and Rhode Island Department of Environmental Management [DEM]) during the study period.

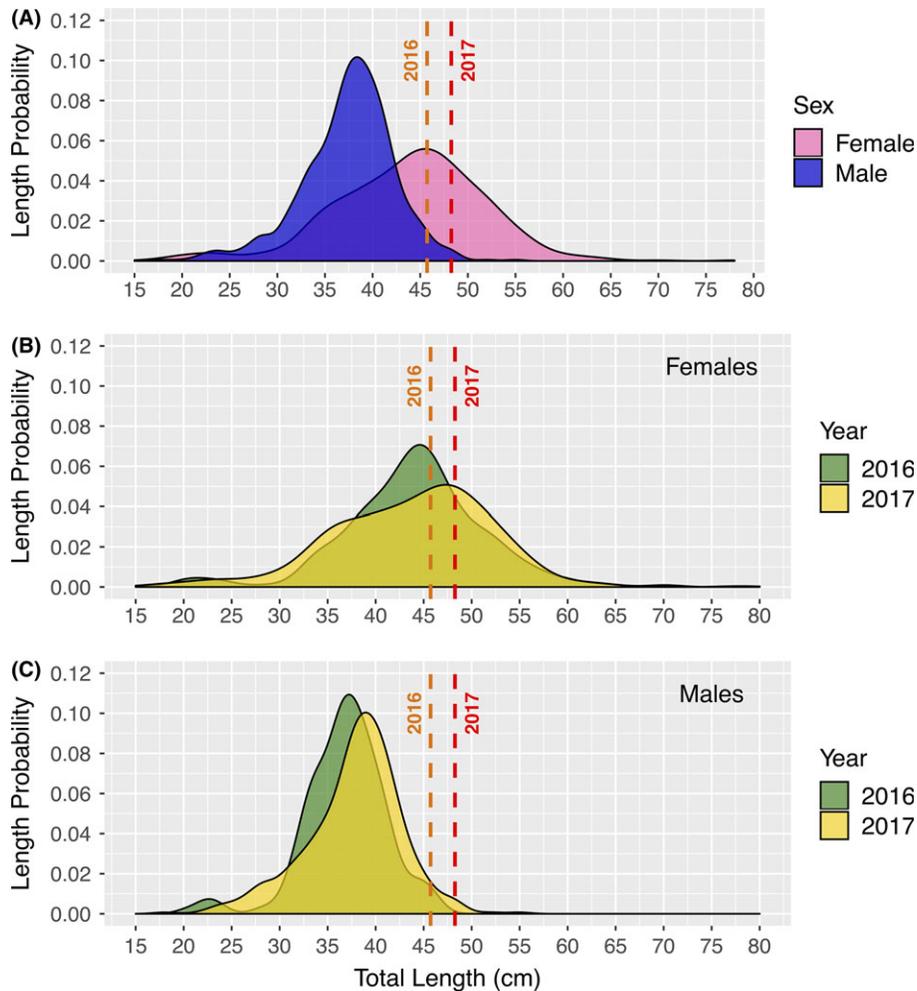| Year	Survey	May	June	July	August	September	October	Total
2016	URI GSO	52	58	73	93	57	17	350
	DEM	6	3	11	25	23	13	81
2017	URI GSO	123	133	168	157	114	68	763
	DEM	21	3	17	15	47	5	108

FIGURE 2. **(A)** The TL distribution of sampled Summer Flounder by sex. **(B, C)** The TL distribution of sampled Summer Flounder by sex and year (B: females, C: males). The 45.7-cm and 48.3-cm minimum lengths used to manage the Rhode Island recreational fishery in 2016 (orange) and 2017 (red), respectively, are demarcated by vertical hashed lines.

Individuals captured in May (median TL = 38.0 cm) tended to be small in size before larger fish arrived in the sampling area in June (median TL = 41.0 cm; K–S test: $P < 0.001$). The TL distribution then remained similar throughout the summer months (K–S test: $P > 0.05$) before again sequentially shifting toward smaller sizes between August (median TL = 40.6 cm) and September (median TL = 39.0 cm; K–S test: $P < 0.001$) and again between September and October (median TL = 38.0 cm; K–S test: $P = 0.004$).

Sex-segregation of Summer Flounder was evident across the sampled water depths. Females were the more prevalent sex in shallow waters (≤15 m) across all months, and across all depths in October (Figure 4). Meanwhile, male Summer Flounder were predominant in the samples from deeper
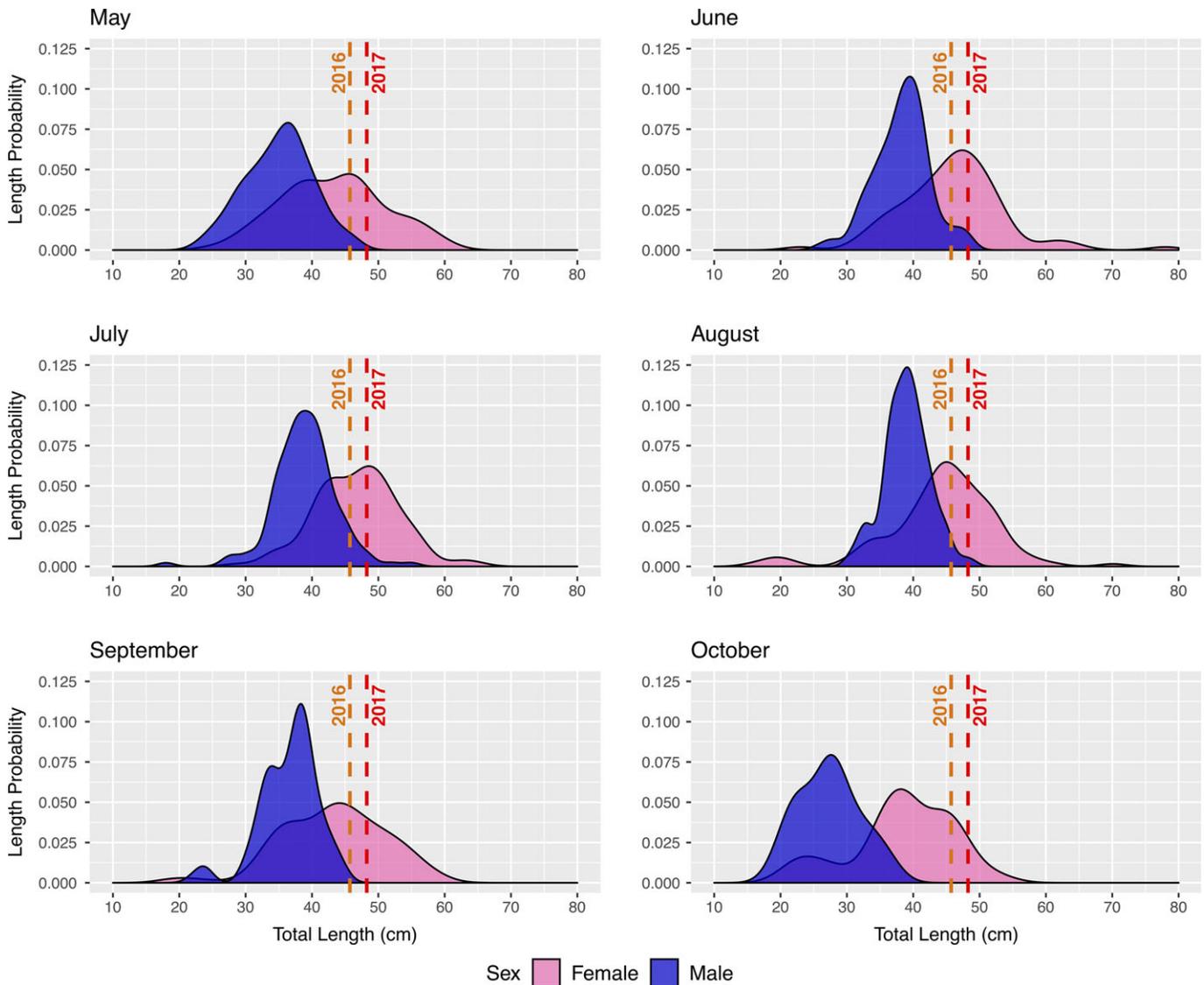
FIGURE 3. The TL distribution (cm) of sampled Summer Flounder by sex and month of capture (May–October) from top left to bottom right. The 45.7-cm and 48.3-cm minimum lengths used to manage the Rhode Island recreational fishery in 2016 (orange) and 2017 (red), respectively, are demarcated by vertical hashed lines.

waters (>15 m) and across all depths combined, from May through September. In collections from sites no deeper than 15 m, the ratio of females to males ranged from approximately 1.25:1 to 6:1 throughout the sampling season (Figure 4). At sizes greater than 30 cm, females tended to be more prevalent in shallow waters (≤15 m) and males more prevalent in deeper waters (>15 m; χ^2 test: $P < 0.05$). However, the overall sex ratio was male dominated across all depths at sizes less than 40 cm TL (Figure 4).

Predicting Male–Female Probability

Upon reviewing the tested variants, the selected logistic model to explain patterns in the observed sex ratio included depth, month, and TL. While the inclusion of the year in which a Summer Flounder was captured resulted in a statistically significantly improved fit compared with the selected model variant (likelihood ratio test: $P = 0.0004$), the reduction of the AIC was small compared with that when other covariates were included (Table 2), and the improvement in classification accuracy was statistically insignificant (DeLong's test: $P > 0.05$). The effect of year in the model was attributed to the increased abundance of males, particularly those greater than 40 cm in length (Figure 2), in 2017 and did not have a significant interaction with any of the other included covariates. Given that the inclusion of year did not
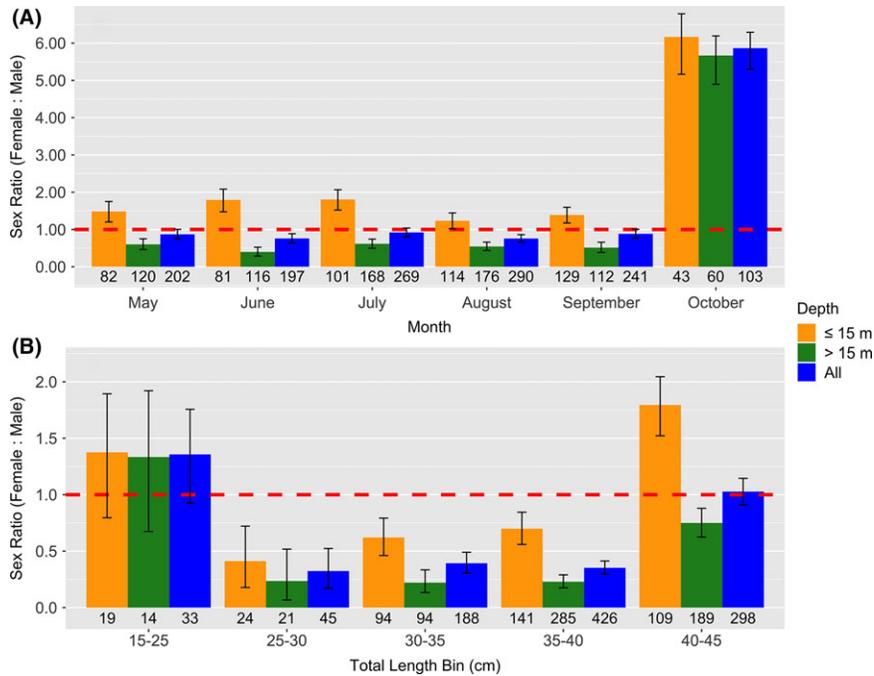
FIGURE 4. Sex ratios of sampled Summer Flounder by **(A)** month and depth categories and **(B)** size bin and depth categories: blue represents all depths, green is depths > 15 m, and gold is depths ≤ 15 m. An even sex ratio (1:1) is demarcated by the red horizontal hashed line. Sample sizes for month and depth category–size bin are labeled under each bar. The error bars represent the 95% CI of each sex ratio estimate. Flounder > 45 cm in length were excluded in (B) due to an extreme female skew.

significantly improve classification accuracy and would inhibit out-of-sample use of the model, this variable was excluded in favor of the selected variant representing the average pattern of sex-segregation between the 2 years in which sampling occurred.

As indicated by the coefficients of the selected regression equation, larger fish and those in shallower water were estimated to have a higher probability of being female (Table 3). Specifically, sites no deeper than 15 m had a 1:1 predicted sex ratio at a TL of 36.5 cm, while predictions at sites deeper than 15 m did not reach an even ratio until 43.2 cm (Figure 5). Further, there was greater predicted probability of a flounder being male from May through September and being female in October (Table 3). Monte Carlo cross-validation indicated that the estimated out-of-sample prediction error rate was minimized at a value of 22.79%, with a decision threshold of a 0.61 probability of being female (Supplement). When applying the 0.61 threshold to the entire data set's predictions, 77.65% of the samples were correctly predicted as male or female (Table 4), and an AUC value of 0.845 was achieved (Table 2). Finally, additional cross-validation procedures indicated that the probabilities that flounder were female predicted by the model were well calibrated and that the unbalanced sampling design between the URI GSO and DEM surveys did not introduce bias into the model fit (Supplement).

TABLE 2. Model variants tested for the logistic regression model predicting the probability of a Summer Flounder being female. Covariates include TL of fish (cm), sample depth (m), bottom water temperature (°C), year, and month. The selected model is in bold text.

Model variant	AIC	AUC
TL + Depth + Month + Year	1257.1	0.848
TL + Depth + Month	**1267.8**	**0.845**
TL + Month + Depth + Temperature	1269.6	0.845
TL + Month + Temperature	1313.9	0.832
Month + TL	1338.6	0.826
TL + Depth	1426.6	0.796
TL	1499.0	0.772
Month + Depth	1650.2	0.682
Depth	1716.0	0.620
Month	1726.5	0.578

Based on the logistic regression predictions, the probability of a collected Summer Flounder being female was greater at smaller sizes in October than in other months at both shallow and deeper depths (Figure 5). At a depth of 7 m (average depth of the Fox Island site), for example, a 50% probability of a captured flounder being female was reached at TLs ranging from 36 to 40 cm between May and September, compared with 21 cm in October. Similarly, at a depth of 22.9 m (average depth of the Whale

Rock site), a 50% probability of a captured flounder being female occurred at a TL of 26 cm in October compared with a range of 41 to 45 cm from May to September (Figure 5). In October, model predictions indicated that Summer Flounder collected at 7 and 22.9 m depths at TLs greater than or equal to 40 and 35 cm, respectively, were expected to be all female. In the other sampled months, flounder between 50 and 54 cm TL caught at 7 m and those between 55 and 59 cm TL caught at 22.9 m were predicted to all be female (Figure 5).

DISCUSSION

The size difference in sampled male and female Summer Flounder agrees with the growth dimorphism reported in previous work (King et al. 2001; Morson et al. 2012, 2015, 2017). Females dominated the captured fish larger than 45 cm (Figure 2), and the sex ratio of observed flounder legal for recreational harvest was more extreme than those reported by the fishery-dependent sampling efforts of Morson et al. (2012, 2015, 2017) and the 2013 Benchmark Stock Assessment (NEFSC 2013). This discrepancy is perhaps due to the greater emphasis on shallower depths in this study. Given that previous results suggest females make up a larger proportion of the recreational catch at a given depth in the mid-Atlantic region (Morson et al. 2017), it is possible that the skewed sex ratios observed here may be less extreme than in other inshore areas to the south. Further, the scarcity of large males implies that these older individuals may stay farther offshore, as has been hypothesized in past work (Morson et al. 2015, 2017). As a result, the habitat preferences of such individuals cannot be characterized by the findings presented here.

In agreement with Morson et al. (2017), females were found to prefer shallower habitats at all sizes greater than 30 cm and to dominate the sex ratio of these areas. The consistency of these patterns throughout the sampling season, in addition to recreational fishing data collected in
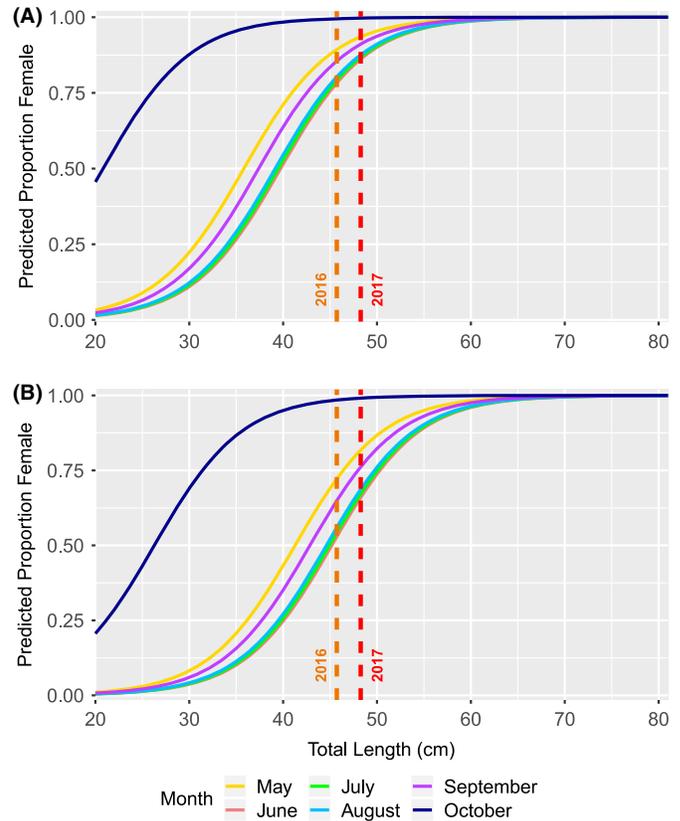

FIGURE 5. Predicted probabilities of a Summer Flounder being female by size and month normalized to depths of **(A)** 7 m and **(B)** 22.9 m, representative of the two stations in the URI GSO fish trawl survey. The 45.7-cm and 48.3-cm minimum lengths used to manage the Rhode Island recreational fishery in 2016 (orange) and 2017 (red), respectively, are demarcated by vertical hashed lines.

TABLE 4. Confusion matrix describing the selected male–female model validation results (decision threshold of 0.61). True male and female predictions comprised 77.65% of the samples.

	Observed male	Observed female
Predicted male	46.93%	17.97%
Predicted female	4.38%	30.72%

Rhode Island waters over the study period (Table 5) and coupled with the logistic model predictions, suggests that inshore fishing efforts in this region will be targeting a female-dominated population segment. Commercial fishing effort focused in deeper coastal habitats, operating under a 35.6-cm minimum length limit, is expected to have an increased catchability of male Summer Flounder.

Suggested causes for spatiotemporal sex-segregation in flatfishes have included depth-specific preferences (Swain 1997; Swain and Morin 1997; Gerritsen et al. 2010), temperature selection (Swain 1997; Swain and Morin 1997),

TABLE 3. Regression summary of the selected logistic model to highlight the influence of the selected covariates on the probability of a Summer Flounder being female.

Covariate	Coefficient	SE	P-value
Intercept	−7.177	0.558	<0.001
TL (cm)	0.215	0.014	<0.001
Depth	−0.074	0.009	<0.001
June	−0.841	0.255	<0.001
July	−0.788	0.239	<0.001
August	−0.716	0.229	0.002
September	−0.341	0.237	0.151
October	3.219	0.403	<0.001

and sex-specific feeding and/or life history strategies (Swain and Morin 1996; Gerritsen et al. 2010). This analysis revealed that the addition of bottom water temperature did not improve the logistic model fit when depth was already included (Table 2). Recorded temperature measurements during sampling efforts ranged between 8°C and 24°C, yet the sex ratio of captured Summer Flounder did not appear to track this pattern throughout the season (Figure 4). While shallower sampled sites were indeed warmer than deeper areas throughout the summer months, the sex ratios in each location were not found to follow monthly changes in temperature. Therefore, as observed in American Plaice *Hippoglossoides platessoides* by Swain and Morin (1997), documented patterns of sex-specific habitat selection in Narragansett Bay Summer Flounder could not be characterized by temperature alone, but rather were best explained by water depth.

Similar to findings reported in New Jersey by Morson et al. (2012), the sex ratio of sampled Summer Flounder varied significantly by month of the year (Figure 4). Controlling for the effects of the TL of the catch and sampling depth, the fitted logistic regression indicated that significantly more females were present in May before the sex ratio shifted toward males during the summer months (Figure 5). As the offshore migration began in August (Packer et al. 1999), the observed sex ratio shifted back toward females in September and October. This pattern suggests that male Summer Flounder migrate into inshore areas later and move offshore considerably earlier than females. Counter to what would be expected in a more female-dominated regime, the Summer Flounder captured in May tended to be smaller than in the following 3 months (Figure 3). Further, the samples had a higher proportion of smaller fish in September and October, despite the increased share of female fish. These patterns were somewhat in contrast to reported recreational catch data from Rhode Island, where the TL frequencies of captured flounder were similar from May to August before increasing at the end of the season (Table 5). While further study is required to understand these trends, we

hypothesize that smaller, immature females that were not actively spawning migrated to inshore sampling areas earlier in the spring and remained there longer into the fall. Additionally, the emergence of flounder less than 25 cm in TL in July and growing in prevalence through the fall (Figure 3) suggests that young-of-the-year individuals (NEFSC 2013) migrating from shallow nursery habitats (Taylor et al. 2016) appeared in the survey samples and also remained present after larger flounder had migrated offshore. If these hypotheses are correct, the observed increased size of recreational landings late in the season could be due to anglers targeting larger female fish as they migrate offshore.

While Morson et al. (2012) found a statistically significant difference in the monthly trend in the sex ratio among the years of sample collection, no such pattern was found here. However, the overall sex ratio did shift between years of sample collection. While incorporating a year effect did not improve the classification ability of the model, this does indicate that there may be year-to-year variability in model accuracy. Further, data from the URI GSO fish trawl survey suggest that the timing of annual Summer Flounder ingress and egress have each shifted significantly in recent decades (J. S. Collie, unpublished data), matching results found for other flatfishes (van Walraven et al. 2017). Therefore, it may be necessary to investigate and monitor such interannual and long-term patterns if the spatiotemporal sex-specific distribution of this species is to be successfully considered in management of the fishery.

The strong diagnostics of the fitted model (Supplement) and use of few covariates highlights the prospective application of this tool in predicting spatial sex ratio patterns in Summer Flounder in southern New England. Month of sampling, depth, and the size of fish are data frequently collected as part of other fisheries-independent surveys (Politis et al. 2014) and may even be available from recreational anglers or party and charter vessels (Morson et al. 2015). Such predictions could provide further insight into the finer spatial characteristics of the species' sex-specific habitat preferences. However, while the reported relationship between the selected covariates and the probability of a given fish being female represents dynamics in Rhode Island waters and is similar to past results (Morson et al. 2015), it is unclear how the model fit corresponds to other regions. Further, while the model is built with a large sample size, many of the specimens come from depths typical of the coastal zone. Thus, predictions at greater depths farther offshore will have greater uncertainty.

The interaction of patterns of sex-segregation and fishing activities in Rhode Island waters could result in the disproportionate removal of Summer Flounder by size and sex, thereby affecting the regional spawning stock biomass or the stock's reproductive potential. While limited

TABLE 5. Marine Recreational Information Program (MRIP) reported FL (cm) quantiles for landed Rhode Island Summer Flounder caught within state waters (ocean and inland) (NMFS FDS 2018). Percentiles are aggregated over years (2016–2017) by the three MRIP waves: May–June, July–August, September–October. Recreational fishing activity included party and charter boats, private or rental boats, and shore fishing.

Wave	0%	5%	10%	25%	50%	75%	90%	95%
May–Jun	42	45	46	47	51	53	57	59
Jul–Aug	33	42	43	47	48	54	58	64
Sep–Oct	39	39	41	47	56	59	59	59

in spatial scope, the patterns characterized by fishery-independent sampling in this work resemble and further elucidate some of those described in the sex ratio of Summer Flounder landings previously (Morson et al. 2012, 2015). As discussed by Morson et al. (2017), the implementation of high minimum length limits may only compound the population impacts of harvest. However, the finding that sex-specific habitat preferences in Summer Flounder are both consistent and predictable suggests that with additional sampling in other regions, management strategies incorporating more targeted spatial considerations in fishing effort are possible. The predictive model proposed here offers a first step toward this goal, but should be further validated and expanded upon by future work. In doing so, the incorporation of spatiotemporal sex-structure into the management of the coastwide Summer Flounder fishery may be successfully achieved.

ACKNOWLEDGMENTS

REFERENCES

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 *in* B. N. Petrov and F. Csaki, editors. Proceedings of the 2nd international symposium on information theory. Akadémiai Kiadó, Budapest.

Alonso-Fernández, A., J. Otero, R. Bañón, J. M. Campelos, J. Santos, and G. Mucientes. 2017. Sex ratio variation in an exploited population of common octopus: ontogenic shifts and spatio-temporal dynamics. Hydrobiologia 794:1–16.

Clark, W. G. 2004. A method of estimating the sex composition of the commercial landings from setline survey data. Pages 111–162 *in* L. Sadorus, editor. Report of assessment and research activities 2003. International Pacific Halibut Commission, Seattle.

Collie, J. S., A. D. Wood, and H. P. Jeffries. 2008. Long-term shifts in the species composition of a coastal fish community. Canadian Journal of Fisheries and Aquatic Sciences 65:1352–1365.

Gerritsen, H. D., D. McGrath, C. Lordan, and X. Harlay. 2010. Differences in habitat selection of male and female Megrim (*Lepidorhombus whiffiagonis*, Walbaum) to the west of Ireland: a result of differences in life-history strategies between the sexes? Journal of Sea Research 64:487–493.

Gonçalves, P., A. Ávila de Melo, A. G. Murta, and H. N. Cabral. 2017. Blue Whiting (*Micromesistius poutassou*) sex ratio, size distribution and condition patterns off Portugal. Aquatic Living Resources 30(1):24.

Haugen, J. B., T. H. Curtis, P. G. Fernandes, K. A. Sosebee, and P. J. Rago. 2017. Sexual segregation of Spiny Dogfish (*Squalus acanthias*) off the northeastern United States: implications for a male-directed fishery. Fisheries Research 193:121–128.

King, N. J., G. C. Nardi, and C. J. Jones. 2001. Sex-linked growth divergence of Summer Flounder from a commercial farm: are males worth the effort? Journal of Applied Aquaculture 11:77–78.

Loher, T., and J. Hobden. 2012. Length and sex effects on the spatial structure of catches of Pacific Halibut (*Hippoglossus stenolepis*) on longline gear. U.S. National Marine Fisheries Service Fishery Bulletin 110:46–51.

Loher, T., M. A. Woods, I. Jimenez-Hidalgo, and L. Hauser. 2016. Variance in age-specific sex composition of Pacific Halibut catches, and comparison of statistical and genetic methods for reconstructing sex ratios. Journal of Sea Research 107:90–99.

Maunder, M. N., and R. A. Wong. 2011. Approaches for estimating natural mortality: application to Summer Flounder (*Paralichthys dentatus*) in the U.S. mid-Atlantic. Fisheries Research 111:92–99.

Morson, J. M., E. A. Bochenek, E. N. Powell, and J. E. Gius. 2012. Sex-at-length of Summer Flounder landed in the New Jersey recreational party boat fishery. North American Journal of Fisheries Management 32:1201–1210.

Morson, J. M., E. A. Bochenek, E. N. Powell, E. C. Hasbrouck, J. E. Gius, C. F. Cotton, K. Gerbino, and T. Froehlich. 2015. Estimating the sex composition of the Summer Flounder catch using fishery-independent data. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 7:393–408.

Morson, J. M., D. Munroe, R. Harner, and R. Marshall. 2017. Evaluating the potential for a sex-balanced harvest approach in the recreational Summer Flounder fishery. North American Journal of Fisheries Management 37:1231–1242.

Myers, R. A., M. W. Smith, J. M. Hoenig, N. Kmeicik, M. A. Luehring, M. T. Drake, P. J. Schmalz, and G. G. Sass. 2014. Size- and sex-specific capture and harvest selectivity of Walleyes from tagging studies. Transactions of the American Fisheries Society 143:438–450.

NEFSC (Northeast Fisheries Science Center). 2013. 57th northeast regional stock assessment workshop (57th SAW) assessment report. NEFSC, Reference Document 13-16, Woods Hole, Massachusetts.

NMFS FDS (National Marine Fisheries Service, Fisheries Statistics Division). 2018. MRIP Summer Flounder fork length (cm) distribution query from 2016–2017 for all waves, modes, and areas in Rhode Island. Available: https://www.st.nmfs.noaa.gov/recreational-fisheries/data-and-documentation/queries/index. (April 2018).

Okamura, H., M. K. McAllister, M. Ichinokawa, L. Yamanaka, and K. Holt. 2014. Evaluation of the sensitivity of biological reference points to the spatio-temporal distribution of fishing effort when seasonal migrations are sex-specific. Fisheries Research 158:116–123.

Packer, D. B., S. J. Griesbach, P. L. Berrien, C. A. Zetlin, D. L. Johnson, and W. W. Morse. 1999. Essential fish habitat source document: Summer Flounder, *Paralichthys dentatus*, life history and habitat characteristics. NOAA Technical Memorandum NMFS-NE-151.

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 Fisheries Science Center, Reference Document 14-06, Woods Hole, Massachusetts.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: https://www.R-project.org/. (January 2019).

Su, N.-J., C.-L. Sun, A. E. Punt, S.-Z. Yeh, W.-C. Chaing, Y.-J. Chang, and H.-Y. Chang. 2013. Effects of sexual dimorphism on population parameters and exploitation ratios of Blue Marlin (*Makaira nigricans*) in the northwest Pacific Ocean. Aquatic Living Resources 26:19–24.

Su, N.-J., C.-L. Sun, A. E. Punt, S.-Z. Yeh, and G. DiNardo. 2011. Evaluation of a spatially sex-specific assessment method incorporating a habitat preference model for Blue Marlin (*Makaira nigricans*) in the Pacific Ocean. Fisheries Oceanography 20:415–433.

Swain, D. P. 1997. Sex-specific temperature distribution of American Plaice (*Hippoglossoides platessoides*) and its relation to age and abundance. Canadian Journal of Fisheries and Aquatic Sciences 54:1077–1087.

Swain, D. P., and R. Morin. 1996. Relationship between geographic distribution and abundance of the American Plaice (*Hippoglossoides platessoides*) in the southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences 53:106–119.

Swain, D. P., and R. Morin. 1997. Effects of age, sex and abundance on the bathymetric pattern of American Plaice in the southern Gulf of St. Lawrence. Journal of Fish Biology 50:181–200.

Taylor, D. L., J. McNamee, J. Lake, C. L. Gervasi, and D. G. Palance. 2016. Juvenile Winter Flounder (*Pseudopleuronectes americanus*) and Summer Flounder (*Paralichthys dentatus*) utilization of southern New England nurseries: comparisons among estuarine, tidal river, and coastal lagoon shallow-water habitats. Estuaries and Coasts 39:1505–1525.

Terceiro, M. 2016. Stock assessment of Summer Flounder for 2016. Northeast Fisheries Science Center, Reference Document 16-15, Woods Hole, Massachusetts.

Terceiro, M. 2018. The Summer Flounder chronicles III: struggling with success, 2011–2016. Reviews in Fish Biology and Fisheries 28:381–404.

van Walraven, L., R. Dapper, J. J. Nauw, I. Tulp, J. I. J. Witte, and H. W. van der Veer. 2017. Long-term patterns in fish phenology in the western Dutch Wadden Sea in relation to climate change. Journal of Sea Research 127:173–181.

Wang, S.-P., C.-L. Sun, A. E. Punt, and S.-Z. Yeh. 2007. Application of a sex-specific age-structured assessment method for the Swordfish, *Xiphias gladius*, in the North Pacific Ocean. Fisheries Research 84:282–300.

SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.