

# Interactions of dimorphic growth, reproductive behavior, and a size-regulated fishery: a case study using spotted seatrout *Cynoscion nebulosus*

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**ABSTRACT:** Sexual dimorphism occurs in many fishes and is expressed in a range of traits, including growth and reproductive effort. These traits can result in sex-specific fishing mortality in a size-selective fishery. Our goal was to understand the trade-offs between growth, mortality, and reproduction, for a species with sexually dimorphic growth, within a fishery context. We used gill nets and hook-and-line fishing to capture 1957 spotted seatrout *Cynoscion nebulosus* from Tampa Bay, Florida (USA), between 2001 and 2002. Females were significantly larger-at-age than males. This larger female size corresponded to a greater prevalence of females in the fishery, evidenced by an 8:1 ratio of females to males at harvestable size. Despite this female-biased sex ratio in the fishery, the total instantaneous mortalities ( $Z$ ) between the sexes were not statistically different (female  $Z = 0.77 \text{ yr}^{-1}$ ; male  $Z = 0.82 \text{ yr}^{-1}$ ). We developed a conceptual model to explain the trade-offs between reproduction and growth as seen in spotted seatrout. Male reproductive effort, including greater spawning frequency and the production of courtship sounds, is hypothesized to result in lower somatic growth, as well as higher natural mortality from increased predation risk. The contrasting roles of fishing pressure on females and natural mortality in males may have important implications for population productivity and fishery management of this species.

**KEY WORDS:** Sex-specific growth · Life history · Trade-offs · Selective harvesting · Mortality · Reproductive strategy · Sexual size dimorphism · *Cynoscion nebulosus*

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## 1. INTRODUCTION

The energetic balance between growth, reproduction, storage, and maintenance is a critical part of the life-history strategy of an organism. Trade-offs between these different life-history characteristics are required to successfully maximize individual fitness and the rate of population increase (Stearns 1976, Cott et al. 2013, Villegas-Rios et al. 2014). Energetic investment in gonad development results in a direct physiological trade-off between reproduction and growth because the energy invested in the development of gonads detracts from that available for somatic growth (Roff 1983). The amount of energy allocated to different life-history traits can vary be-

tween the sexes. For example, it is generally less costly from an energetic standpoint for males to produce milt than it is for females to produce eggs; however, the total reproductive effort over a spawning season may not differ between sexes because the males may invest increased energy in reproductive behavior in addition to their reproductive output (Stearns 1976, Magurran & Garcia 2000, Villegas-Rios et al. 2014). This disparity in reproductive effort between the sexes can lead to a variety of other sex-based differences in life-history traits (Magurran & Garcia 2000, Cott et al. 2013).

Sexual dimorphism (when physical characteristics differ between sexes) is well-documented in fishes and is often understood in terms of the expression of

male coloration and ornamentation (Magurran & Garcia 2000). However, a specific area of sexual dimorphism that is commonly observed is sexual size dimorphism; this occurs when females and males achieve different mean body sizes at ages (Lande 1980, Rankin & Kokko 2007). Sexual size dimorphism can be driven by genetically determined sex-specific growth or result from sexually dimorphic behaviors, i.e. differential energetic expenditures (Lande 1980). Often males exhibit smaller size-at-age and greater mortality than females. This can be a result of males spending energy on early maturation, in the pursuit of mating opportunities, or potentially feeding less as a result of their reproductive behavior (Roff 1983, Magurran & Garcia 2000).

Female-biased sexual size dimorphism is common in fishes, particularly in species that spawn in groups and do not exhibit male-to-male competition for mates. This observed pattern is assumed to be due to greater reproductive success in larger females given the close relationship between size and fecundity (Reznick 1983, Magurran & Garcia 2000, Henderson et al. 2003, Keyl et al. 2015). Examples of female-biased sexual size dimorphism include the mulloway *Argyrosomus japonicus*, spotfin croaker *Roncador stearnsii*, and the brown meagre *Sciaena umbra* (Silberschneider et al. 2009, Williams et al. 2012, Chater et al. 2018).

A species that exhibits a similar pattern of sexual size dimorphism and sex-specific growth is the spotted seatrout *Cynoscion nebulosus*. Many previous studies have examined the life-history characteristics across the range of spotted seatrout, determining that sexual size dimorphism exists whereby females are larger than males within any estuarine subpopulation (Murphy & Taylor 1994, Nieland et al. 2002, Bedee et al. 2003, Murphy & McMichael 2003, Johnson et al. 2011). Sex-specific growth and trade-offs between investment in reproductive effort and other biologically relevant behaviors are likely at work in this species, but a conceptual model of these energetic constraints and selective pressures has yet to be presented.

Because movement, size, and reproductive behavior can all affect vulnerability to capture, the objective of our study was to assess potential sex-specific differences in reproductive behavior and growth and how they may affect mortality in a fishery with size-based regulations. We modeled growth separately for males and females and tested the hypothesis that growth parameters and mean size-at-age differ significantly with sex. We then estimated if the sex ratio of individuals in the fished population differs signifi-

cantly from 1:1 and if mortality rates differ significantly by sex. We present a conceptual model that integrates results from previous reproductive studies with potential energetic trade-offs as an explanation for the observed growth patterns in spotted seatrout.

## 2. MATERIALS AND METHODS

### 2.1. Focal species

The spotted seatrout is found in most estuarine systems in the US Gulf of Mexico and along the US Atlantic coast (Hendon et al. 2002, Bortone 2003), and it was the top species of fish harvested recreationally in the US Gulf of Mexico in 2016 (3399 t; NMFS 2017). There is essentially no commercial fishery for spotted seatrout in Florida. Following a gill net ban in 1996, the commercial harvest dropped to less than 1% of total landings (Addis et al. 2018). Acceptable commercial gears are now hook and line and cast nets. Current recreational catch regulations have been in place since 2000. Anglers are allowed to keep 4 fish  $d^{-1}$  between the sizes of 381 and 508 mm (15–20 inches), and 1 fish of the 4 kept is allowed to be over 508 mm. The recreational size regulation is hereafter referred to as the slot. Recreational fishery landings are highly skewed towards females, with females making up 80% of the total catch in all Florida bays from 2002–2016, and 79% of the catch in Tampa Bay during the study years (FWC Fishery Dependent Monitoring unpubl. data).

Spotted seatrout growth is estuary-specific (Murphy & Taylor 1994, Murphy & McMichael 2003) but has not yet been estimated for Tampa Bay. Spotted seatrout in the Gulf of Mexico have closed populations over small spatial scales, and typically remain in their natal estuary (Ault et al. 1999). Individuals rarely make long-distance movements (Iversen & Moffett 1962, Tabb 1966, Baker et al. 1986, Bortone 2003), but can move within an estuary in response to freshwater input (Callihan et al. 2015). Spotted seatrout are highly fecund estuarine spawners, producing multiple batches of eggs from March through September, with a peak in spawning activity during April and May (Lowerre-Barbieri et al. 2009).

Males make courtship sounds, called drumming, associated with spawning aggregations by vibrating sonic muscles against their swim bladder (Mok & Gilmore 1983, Holt et al. 1985, Ramcharitar et al. 2006). These drumming sounds were used to map spotted seatrout spawning sites throughout most of Tampa Bay in relatively shallow water near sea-

grass (Walters et al. 2009). A companion study using capture-based sampling in Lower Tampa Bay indicated 2 types of spawning sites: a high-intensity inlet site where fish moved specifically to spawn (97% of females were actively spawning) and lower-intensity sites within the estuary where fish occurred through the year (Lowerre-Barbieri et al. 2009). A consequent study at the high intensity site using acoustic telemetry demonstrated that males moved to this site to spawn more frequently than females (Lowerre-Barbieri et al. 2013) and that there were slight sex-specific differences in space use (Boucek et al. 2017). The dynamics of the inlet site are such that fish that spawn at this site must be drawn from either the estuary or the Gulf of Mexico; telemetry indicated that the vast majority of fish spawning at this site were drawn from and returned to Tampa Bay (Lowerre-Barbieri et al. 2013).

## 2.2. Sample collection

Field sampling was conducted in Lower Tampa Bay in 2001 and 2002 (Fig. 1). Year-round sampling in 2001 collected 1145 spotted seatrout, while 812 individuals were collected during the spawning season (April–October) in 2002. Details on sampling locations and timing can be found in Lowerre-Barbieri et al. (2009).

Multiple gear types were used to collect spotted seatrout. The primary sampling gear was a 228.6 m long monofilament (104 twine size), multi-panel experimental gill net. It was 3.05 m deep, made up of five 45.7 m panels: 0.98, 1.18, 1.38, 1.58, and 1.77 cm stretched mesh. The different sized panels of the experimental gill net were used in order to collect a representative size distribution of the population. Soak time (from deployment of the net to the start of haul-in) was 20 min. Sampling was also conducted with hook and line; 3 anglers fished on any given date and the duration of hook-and-line fishing was recorded. Collected fish were kept on ice until processed in the laboratory where they were measured for total length (TL, to the nearest millimeter), sexed

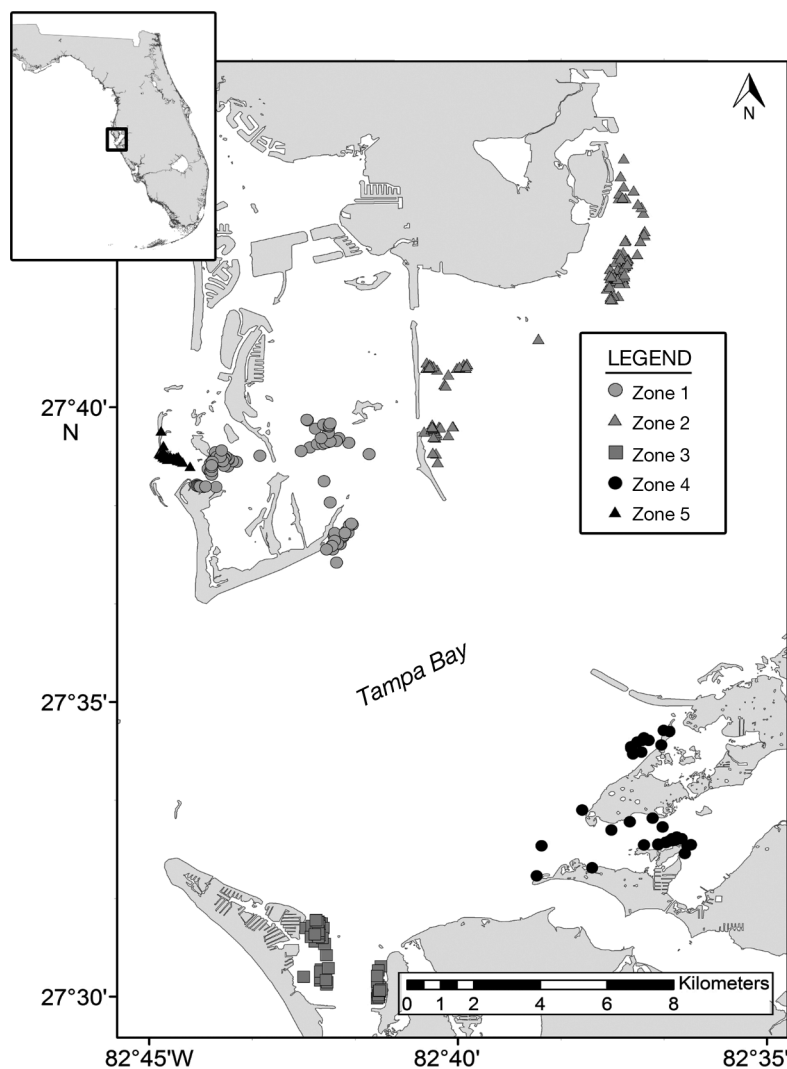


Fig. 1. Sampling sites and zones in Lower Tampa Bay, Florida, USA. Individual sampling locations in the study's 5 zones are denoted by different symbols. The location of Tampa Bay in Florida is indicated in the inset

macroscopically, and had both sagittal otoliths removed. Sex was verified histologically later when the gonads were assessed for development.

## 2.3. Otolith analysis

The left otolith was processed for age determination unless it was broken through the core, in which case the right otolith was processed. Otolith processing was completed on Buehler Isomet saws, and followed the low-speed multi-blade technique, as described by VanderKooy & Guindon-Tisdell (2003). After processing, sections were mounted on a glass slide with a chemical mounting medium. Otolith sections were examined with a stereo microscope

(20–100× magnification) using transmitted light. Each otolith was read independently by 2 readers without knowledge of fish length or sex; a third read was jointly conducted to resolve discrepancies between the first 2 reads. The number of opaque zones was recorded, along with the degree of completeness of the most distal translucent growth zone (margin) (VanderKooy & Guindon-Tisdell 2003). To assess ageing precision, the average percent error (APE) and percent agreement were calculated between the first 2 reads for each otolith (Campana 2001).

Age class was calculated using opaque zone count, degree of marginal growth, average date of otolith increment deposition, and date of capture. This traditional method of assigning ages is based on a calendar year instead of time since spawning (Jearld 1983, Bedee et al. 2003, VanderKooy 2009). Formation of the opaque zone is complete by late spring to early summer (Murphy & Taylor 1994, Nieland et al. 2002, Murphy & McMichael 2003). Using these criteria, age classes were advanced by 1 yr if a large translucent zone was visible on the margin and the capture date was between 1 January and 30 June. For all fish collected after 30 June, age was assigned to be equal to the opaque zone count because zone formation was considered complete (Murphy & Taylor 1994). The calendar age was used for mortality calculations and for marginal increment analysis. Marginal increment analysis was conducted to indirectly validate the annual formation of an opaque zone on spotted seatrout otoliths. With this method, the amount of translucent growth was measured (in mm) from the end of the last complete opaque zone to the edge of the otolith using Image Pro Plus Version 4.5. These measurement values were then pooled across age classes by capture month and analyzed for annual patterns.

#### 2.4. Modeling and data analysis

Growth modeling was conducted on the Tampa Bay spotted seatrout population using biological ages, calculated using 20 June as the biological birthdate, per the median hatching date as determined by Murphy & Taylor (1994). Fractional ages were calculated based on the relative number of days away from the birthdate and were either added to or subtracted from the opaque zone count based on the time of year the fish was captured (VanderKooy 2009). We evaluated 3 growth models that have been commonly used to describe spotted seatrout growth. The Gompertz growth model:

$$L_t = L_\infty \cdot [e^{-e^{-K(t-t_0)}}] \quad (1)$$

where  $L_t$  is the expected age at time  $t$ ,  $L_\infty$  is the asymptotic length,  $K$  is the coefficient of growth, and  $t_0$  is the age at the hypothetical length 0 (Gompertz 1825, Murphy & Taylor 1994); the von Bertalanffy growth model:

$$L_t = L_\infty \cdot [1 - e^{-K(t-t_0)}] \quad (2)$$

where  $L_t$  is the expected age at time  $t$ ,  $L_\infty$  is the asymptotic length,  $K$  is the coefficient of growth, and  $t_0$  is the age at the hypothetical length 0 (Fabens 1965); and a linear growth model (Olson 1987).

Because spotted seatrout spawn for more than half the year, juvenile fish size varies widely. In the present study, there were fish captured in late fall with no annuli present on their otoliths and whose sizes did not conform to the size of age-0 fish from the growth models. This is due, in large part, to ageing juvenile fish by counting annual opaque zones because there is no means of accurately describing the age of a fish that has not yet deposited its first opaque zone. In this case, these age-0 fish were hatched well before peak spawning and the growth they exhibited far exceeded fish that were spawned during the mid- and late-spawning season. These fish were therefore excluded from the growth analyses.

To ensure that the results from this study were relevant to spotted seatrout management, it was necessary to adopt the approach to the von Bertalanffy growth model used in the last Florida stock assessment (Addis et al. 2018). This approach addresses the poor fit to the lower limb of the growth curve by integrating size-at-daily-age data for age-0 fish from McMichael & Peters (1989). Length-at-age data observed by that study (converted to TL) for 113 unsexed spotted seatrout collected from Tampa Bay, ranging in TL from 9.4 mm (5 d) to 207 mm (225 d), were integrated into the data set to preclude artificially constraining the intercept to 0 mm. This was done to compensate for bias in the early juvenile phase of the growth model due to the exclusion of the large age-0 fish, or gear vulnerability limitations for very small age-0 fish. Using these supplementary daily size-at-age data also allowed for the generation of a von Bertalanffy growth curve that is directly comparable between the sexes.

To compare sexual dimorphism in the life history traits between female and male spotted seatrout, sex-specific growth trajectories were fitted to the von Bertalanffy growth equation using nonlinear least squares regression. Estimates and confidence intervals of  $t_0$ ,  $K$ , and  $L_\infty$  were obtained by bootstrapping

1000 iterations (Kimura 1980, Ogle 2018). Differences between the sexes were assessed by comparing the bivariate 95% confidence ellipses surrounding the estimated  $K$  and  $L_{\infty}$  values, where groups displaying non-overlapping ellipses are considered to have significantly different growth parameters (Kimura 1980, Meekan et al. 2001, Halvorsen et al. 2016).

Total mortality rates were estimated using length-at-age data for the Tampa Bay spotted seatrout population. Observations were pooled by sex across years, sampling zones, and gear types. Sex-specific total mortality rates ( $Z$ ) were estimated using log-linear regression analyses of the age frequency catch curve (Pauly 1983). With this method,  $Z$  is estimated by the slope of the linear regression through the descending right limb of the catch curve. Only fully recruited individuals were used in this analysis, so age-0 and -1 fish from both sexes were excluded because they were not fully vulnerable to the gear types used in this study. Age classes that had fewer than 5 individuals were considered to have too low a sample size for the catch curve analysis and were likewise excluded (female age 8; male ages 7 and 8). Mortality estimates between the sexes were compared using analysis of covariance (ANCOVA).

### 3. RESULTS

A total of 1957 spotted seatrout were sectioned and examined for age analysis. The precision of independent otolith readings was very high, with a 96.5% agreement between reads, and an APE of 1.1% (Campana 2001). Marginal increment measurements were consistent with other studies, revealing 1 opaque zone deposited each year in early spring (Murphy & Taylor 1994, Nieland et al. 2002, Murphy & McMichael 2003). The range of ages sampled for this project did not differ between sexes. Female seatrout ( $N = 1075$ ) ranged from 0.58 to 7.9 yr of age, and male seatrout ( $N = 882$ ) ranged from 0.57 to 7.8 yr.

The mean TL of females for each age class (Fig. 2) was significantly larger than that of males (ANCOVA:  $df = 1, 13$ ;  $F = 42.17$ ;  $p = 2.02 \times 10^{-5}$ ; Table 1). The overall sex ratio in this study, and the sex ratio of fish captured from the inlet site (i.e. from within a spawning aggregation), was 1.2:1 females:males. For the largest

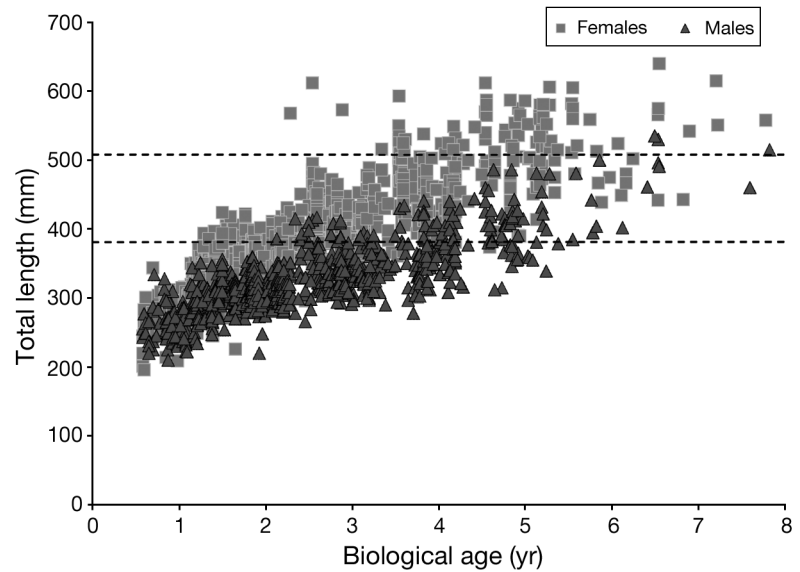


Fig. 2. Observed total length-at-age for female ( $n = 1075$ ) and male ( $n = 882$ ) spotted seatrout *Cynoscion nebulosus*. Dashed lines represent the recreational slot size regulation of 381–508 mm (15–20 inches)

size classes, however, the sex ratio was strongly biased toward females (Fig. 3). Within the recreational slot, the sex ratio of our samples was 8.2:1 females:males, with females accounting for 89% of the fish. In contrast, 88% of the sampled males fell below the minimum slot size, 12% were within the slot size, and only 3 individuals were larger than the upper slot limit (vs. 81 for females). Females and males also differed in relation to the age at which they entered the slot; female spotted seatrout reached the minimum threshold at an earlier age (1.59 yr) than did males (2.5 yr).

All 3 growth models indicated differences in growth between female and male spotted seatrout (Table 2, Fig. 4). Although the Gompertz growth model fit for both sexes, it resulted in a virtually linear relationship for the males and thus an unrealistically large estimate of male asymptotic mean length, roughly twice that of the maximum observed size (1059 mm TL). In contrast, the von Bertalanffy growth model resulted in asymptotic lengths considerably smaller than maximum observed length in both sexes. The non-overlapping 95% confidence ellipses around the von Bertalanffy growth model parameter estimates highlight that males grow significantly faster but have significantly smaller asymptotic lengths than females (Fig. 4).

The total instantaneous mortality rates ( $Z$ ), as calculated by catch curve analysis, were  $0.77 \text{ yr}^{-1}$  for females, and  $0.82 \text{ yr}^{-1}$  for males. Mortality rates were not statistically different between the sexes (ANCOVA:  $df = 1, 8$ ;  $F = 1.003$ ;  $p = 0.346$ ; Fig. 5).



Table 1. Observed and predicted total length (TL)-at-age for female and male spotted seatrout *Cynoscion nebulosus* from Tampa Bay, Florida, USA. Sample size (n) is the number of measured specimens; CV is the coefficient of variation of the observed length-at-age. CV was not computed for female age class 8 due to low sample size and is designated with a dash (-). Predicted TLs are calculated using the Gompertz, von Bertalanffy, and linear growth models

Age (yr)	n	Mean TL (mm)	CV (%)	Range (TL, mm)	Predicted TL (mm)		
					Gompertz	von Bertalanffy	Linear
<b>Females</b>							
1	269	302	12.9	196–424	294	262	307
2	309	357	9.3	226–568	362	378	357
3	244	407	9.8	315–612	419	434	408
4	152	459	9.5	301–593	464	461	459
5	75	510	10.6	374–612	499	473	509
6	17	512	9.7	439–605	525	479	560
7	8	547	13.2	442–640	543	482	611
8	1	558	-	558–558	557	484	661
<b>Males</b>							
1	207	281	10.8	210–356	278	248	278
2	293	312	7.7	220–415	310	328	310
3	209	340	7.6	290–417	341	354	342
4	100	365	9.8	278–444	373	362	374
5	59	402	9.7	312–486	406	365	406
6	9	445	11.9	385–535	438	366	438
7	3	506	4.2	491–530	470	366	469
8	2	488	8.0	460–515	501	366	501

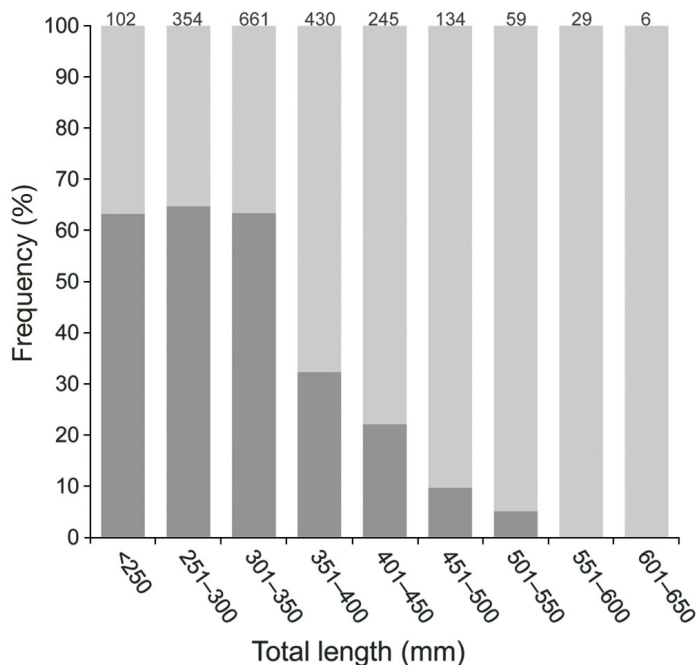


Fig. 3. Sex ratio of spotted seatrout by size category. Females are represented by light gray columns, males by dark gray columns. Bin sample sizes are indicated at the top of each column

## 4. DISCUSSION

### 4.1. Sexual size dimorphism and growth

This study supported the hypothesis of sexual size dimorphism and sex-specific growth in spotted seatrout. Female spotted seatrout were significantly larger-at-age than males and reached longer mean asymptotic lengths. The reproductive demographics of the study population also support this hypothesis because female seatrout matured at a larger size class than males: 320 and 300 mm TL, respectively (Lowerre-Barbieri et al. 2009). These growth and reproductive dynamics are in accordance with the characteristics of a species that exhibits sexual size dimorphism. In this case, females are the larger sex; because fish exhibit indeterminate growth, and size is positively correlated with fecundity, a population with larger females is likely to have greater fecundity and reproductive success (Reznick 1983, Magurran & Garcia 2000, Henderson et al. 2003). Lowerre-Barbieri et al. (2009) found that older and larger females had a higher probability of spawning, and the mean size of actively spawning females was significantly larger than that of spawning-capable females. In contrast to females, males allocate less energy to somatic growth and, in turn, invest more energy into reproduction and repro-

Table 2. Parameter estimates for Gompertz, von Bertalanffy, and linear growth models estimating the mean length-at-age for spotted seatrout *Cynoscion nebulosus*.  $L_{\infty}$ : asymptotic length (mm);  $K$ : coefficient of growth;  $t_0$ : age (yr) at the hypothetical length 0;  $b$ : y-intercept;  $m$ : slope

Parameter	Females	Males
<b>Gompertz</b>		
$L_{\infty}$	589	1059
$K$	0.36	0.08
$t_0$	-0.02	4.49
<b>von Bertalanffy</b>		
$L_{\infty}$	485	365
$K$	0.73	1.15
$t_0$	-0.05	0.02
<b>Linear</b>		
$b$	256	246
$m$	50.66	31.85

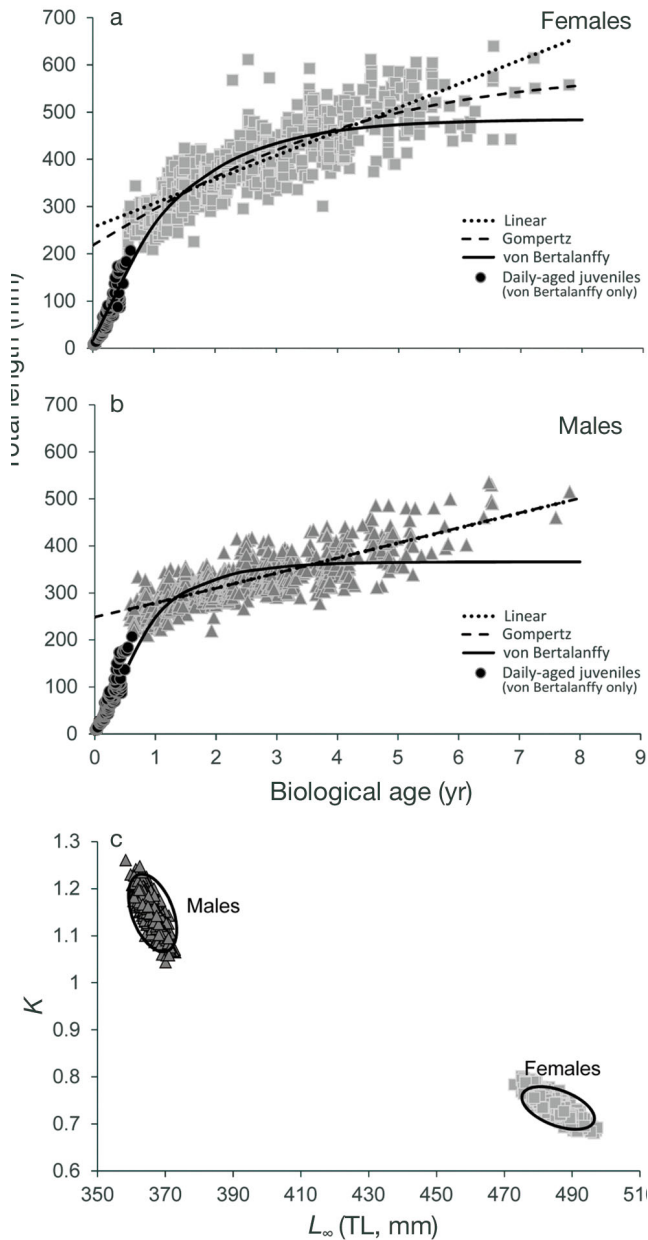


Fig. 4. Growth curves for (a) female and (b) male spotted seatrout. Squares represent females; triangles represent males. In both panels, circles represent supplemental unsexed juveniles from McMichael & Peters (1989) and were only used for the von Bertalanffy growth model. (c) Estimates of von Bertalanffy parameters  $L_{\infty}$  and  $K$  from non-linear least squares regression bootstrap for female and male spotted seatrout. Solid lines represent 95% confidence intervals around parameter estimates

ductive behaviors (Reznick 1983, Magurran & Garcia 2000, Henderson et al. 2003). The prevalence of larger females and smaller males in the study population may indicate interactions of sex-specific growth with mortality.

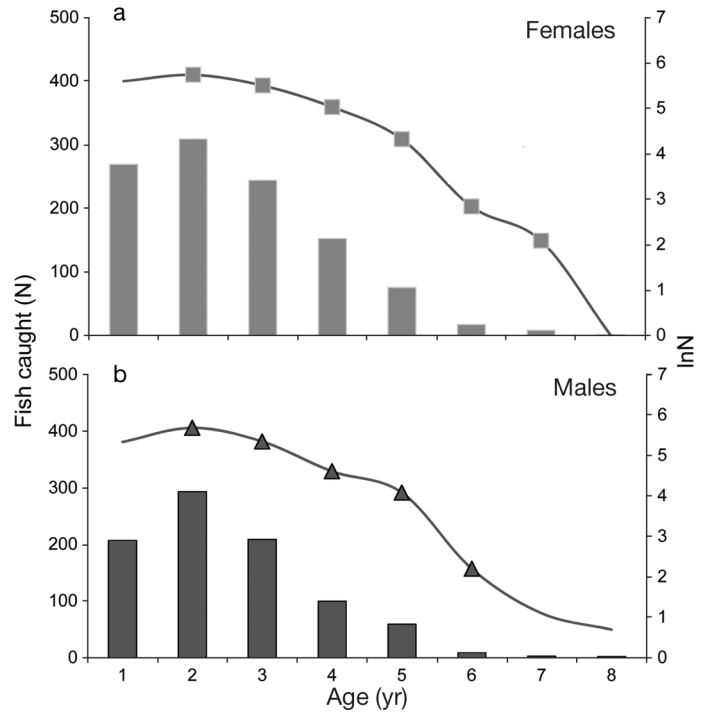


Fig. 5. Age-based catch curve analysis for (a) female and (b) male spotted seatrout. Length frequency is on the y-axis, and natural log-transformed frequency is on the right-hand y-axis. Age classes with symbols were fully recruited with a sample size larger than 5, and were included in analysis. The slope of the linear regression is the estimate of total instantaneous mortality. Female regression:  $y = 6.94 - 0.77x$  ( $r^2 = 0.94$ , 95% confidence interval  $\pm 0.10$ ). Male regression:  $y = 6.85 - 0.82x$  ( $r^2 = 0.90$ , 95% confidence interval  $\pm 0.09$ )

It should be noted that the observed sexual size dimorphism is not a result of sampling bias. Spotted seatrout have a demonstrated pattern of sexual size dimorphism (Murphy & Taylor 1994, Nieland et al. 2002, Bortone 2003, Johnson et al. 2011), which is corroborated by the female-skewed sex ratio of recreational fishery landings (FWC Fishery Dependent Monitoring unpubl. data). In terms of size differences, the gill nets in this study caught large fish that turned out to be females. More males were caught by hook and line because this gear was biased towards smaller fish. This gear bias was acknowledged by Lowerre-Barbieri et al. (2009). The issue in question is not that we failed to catch larger individuals, but that those individuals were not male. For our sampling to have missed large males, an alternative hypothesis would be that the large males exhibited unique behavior to avoid the nets, or that they occupied different space than females. We are not aware of any unique behavior associated with male spotted seatrout that would lead to gear avoidance. In terms of spatial use by the sexes, acoustic tagging by

Boucek et al. (2017) found that the most important receivers for both male and female spotted seatrout were located within seagrass habitat and that there were only slight differences in the way male and female spotted seatrout used the entire acoustic array. Thus, we must conclude that the observed female-biased size dimorphism is the best explanation for this pattern within the population.

Dimorphic growth can result in greater fishing mortality in females than males because size regulations require that anglers target larger individuals, and those larger individuals are more likely to be females. Samples for this study were collected in the same locations used by recreational anglers, so the sizes of the fish caught in this study represent those encountered by anglers in the fishery. The demographics exhibited by the sex ratios within the slot reveal that female seatrout were more vulnerable than males to being captured because they recruit to the fishery at an earlier age and are more prevalent in the slot than males. This increased vulnerability to harvest should be apparent in the mortality values for the species.

#### 4.2. Mortality

Several assumptions were made in order to use a catch curve analysis for this study. The spotted seatrout population in Tampa Bay was assumed to be closed. This assumption is supported by movement and life history literature (Tabb 1966, Baker et al. 1986, Ault et al. 1999). We assumed the combination of hook and line and experimental gill net sampling provided representative samples of adult size and age, as the ranges observed are similar to past studies (Murphy & Taylor 1994, Bedee et al. 2003). The maximum sampled age of 8 is presumed to be due to the age truncation effects of a fishery rather than sampling bias, and not unexpected given a maximum biological age of 12. Finally, the population was assumed to have constant annual mortality and recruitment, which we feel is reasonable given the long-term stability of the population (Murphy et al. 2011, Addis et al. 2018). These assumptions allow for an estimation of the overall mortality of spotted seatrout in accordance with our objectives.

We hypothesized that females would have a higher overall mortality because of the differential fishing pressure exerted on them from the recreational fishery, but no such sexual differences were observed. The total instantaneous mortality rates ( $Z$ ) were not statistically different between the sexes, and rates for males were slightly higher than those for females.

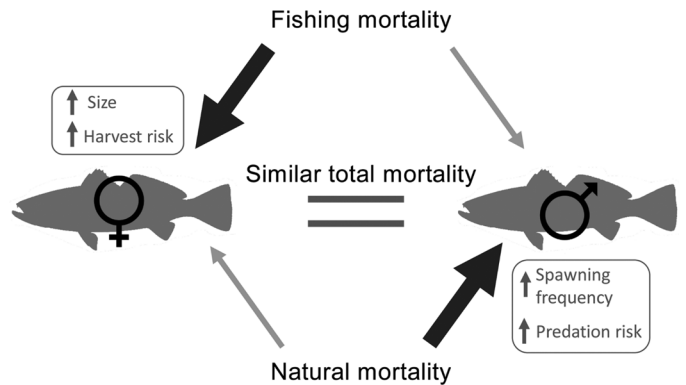


Fig. 6. Primary trade-offs occurring between growth and reproduction, resulting in differential fishing and natural mortality pressures for female and male spotted seatrout. Line thickness represents the proportional force of the differing pressures on each gender

We present a conceptual model representing the biological dynamics and trade-offs that we suggest are occurring within this population (Fig. 6).  $Z$  is the sum of fishing mortality ( $F$ ) and natural mortality ( $M$ ). Given that  $F$  in female seatrout is much higher than that of male seatrout, but that  $Z$  is similar between sexes, other forces must be acting upon the male seatrout that lead to higher  $M$ . Moreover,  $M$  is often inversely related to fish size, which would indicate that the smaller male seatrout may have higher rates of  $M$  (Lorenzen 2000, Powers 2014).

In many contemporary stock assessments,  $M$  is often considered a static parameter and is not directly estimated (Gislason et al. 2010, Maunder & Piner 2015); however, special considerations are necessary in a species that exhibits sex-specific growth, such as spotted seatrout, because the dynamics of the population differ by sex.  $M$  is influenced by individual size, variation in predator and prey interactions, and biological activity (Gislason et al. 2010, Maunder & Piner 2015). As such, we were able to infer some of those interactions using previous research. This study was conducted as a companion study with another that assessed the reproductive dynamics of spotted seatrout in Tampa Bay (Lowerre-Barbieri et al. 2009). Results from that study lend evidence to the trade-offs that may be driving the observed differential mortality and sexual size dimorphism observed in the population examined in the present study.

#### 4.3. Male trade-offs

Selection for small males in the population does not necessarily limit the supply of gametes available for fertilization because reproductive output is not size



dependent for males as it is for females (Henderson et al. 2003, Keyl et al. 2015). Sizes at maturity for females and males from this study were 320 and 300 mm TL, respectively (Lowerre-Barbieri et al. 2009). This indicates that male seatrout recruit to the spawning population, and thus begin to invest in reproduction, at a smaller size than do females. Despite this earlier recruitment to the spawning population, males' direct reproductive investment may not be much more costly, because it takes much less energy to produce milt than eggs (Stearns 1976, Cott et al. 2013, Villegas-Rios et al. 2014). That is not to say, however, that the overall reproductive effort exerted by males is any less costly than that exerted by females because males likely invest heavily in reproductive behavior, in addition to their reproductive output.

One reproductive behavior that may have high energetic costs for male spotted seatrout is the frequency with which spawning occurs. Lowerre-Barbieri et al. (2013) used acoustic telemetry at the high-frequency spawning site in Tampa Bay to determine that male seatrout spawned, on average, every 2.2 d ( $\pm 0.3$  d, SD), while female seatrout spawned, on average, every 9.3 d ( $\pm 1.6$  d). Male seatrout in the study would travel to this nonresident location to spawn at a rate that was more than 4 times the rate of females. Moreover, males were found to commonly spawn on multiple consecutive days, whereas females nearly always spent multiple days between spawns (Lowerre-Barbieri et al. 2013). In a similar acoustic telemetry study, Callihan et al. (2015) reported that male spotted seatrout were 3 times as likely as females to leave the estuary; these emigrations were also highly seasonal and occurred within the summer spawning season. Such sex-specific reproductive movements increase the risk of predation (i.e. natural mortality) for one sex over the other (Magurran & Garcia 2000, Quinn et al. 2001). Males exhibited energetic trade-off patterns typical of sexually dimorphic species in that they maximized mating opportunities (in the form of frequent travels to the spawning site and increased exposure to females) instead of investing in growth (Haugen & Rygg 1996, Magurran & Garcia 2000).

Males of the family Sciaenidae typically make species-specific drumming sounds during the spawning season, expending additional energy in an effort to increase exposure to females (Fish & Mowbray 1970, Sprague 2000). These males have highly vascularized sonic muscles which contract and vibrate the swim bladder and produce the drumming sounds (Ramcharitar et al. 2006). Sciaenid drumming is con-

sidered to have many reproductive functions, such as announcing the male's readiness to spawn, attracting females, facilitating spawning group formation, and synchronizing gamete release (Ramcharitar et al. 2006). The acoustic variables of calls such as call frequency, pulse rate, and duration can play an important role by providing cues for attraction to potential female mates (Connaughton et al. 2000, Parsons & McCauley 2017, Tellechea et al. 2017).

The spotted seatrout exhibits a more diverse drumming range than other sciaenids (Sprague 2000, Ramcharitar et al. 2006). For example, the spotted seatrout has 4 distinct types of calls that are all associated with reproduction, while the blackspotted croaker *Protonibea diacanthus* and meagre *Argyrosomus regius* each have only 2 (Sprague 2000, Lagardere & Mariani 2006, Ramcharitar et al. 2006, Mok et al. 2009). Moreover, the sonic muscles of sciaenids are specialized for speed; sonic muscle twitches in weakfish *Cynoscion regalis* are the fastest of all vertebrate muscle movements (Connaughton et al. 2000). Sonic muscles also change seasonally, seen in the increased vascularization and deepening color of the striped weakfish *C. guatucupa*, or the tripling in size of the sonic muscles in weakfish *C. regalis* (Connaughton et al. 1997, Tellechea & Norbis 2012). These seasonal changes allow for maximized acoustic amplitude and intensity, which is believed to increase the likelihood that females will hear, and mate with, the individuals that exhibit the more intense calls (Connaughton et al. 2002).

Duration of calls is also an important factor when considering the costs of drumming. Lowerre-Barbieri et al. (2013) used passive acoustic listening at the high-intensity spotted seatrout spawning site and determined that spotted seatrout drumming aggregations formed from 15:00 to 02:00 h, with mean peak spawning at 19:20 h. This extended time period during which males were present and drumming on the spawning grounds may illustrate another energetic trade-off. The energetics necessary to build up, maintain, and use sonic muscles for hours at a time, multiple times a week, for months on end is a presumably very costly metabolic endeavor and likely contributes to the sexual size dimorphism exhibited in spotted seatrout.

Sexually dimorphic characteristics are frequently demonstrated in soniferous species. Many soniferous species that exhibit sexual dimorphism are similar in outward appearance but exhibit dimorphism related to the presence and use of sonic muscles (Courtenay 1971, Fine et al. 1990, Nordeide et al. 2008). However, female-biased sexual size dimorphism, as seen

in spotted seatrout, has been documented in sciaenids worldwide, including many with similar habitats and life-history characteristics such as the striped weakfish *Cynoscion guatucupa*, and spotfin croaker *Roncador stearnsii* (Cazorla 2000, Williams et al. 2012). These sexually dimorphic characteristics occur in varying degrees among these soniferous species; however, one commonality they all share is the increased vulnerability to predation resulting from production of acoustic signals.

Soniferous species exhibit a trade-off between the benefits and costs of drumming. These costs are not only metabolic, they are also ecological. The increased risk of predation associated with more frequent spawning movements and with sound production likely contributes to the higher natural mortality of male spotted seatrout. Studies of bottlenose dolphins *Tursiops truncatus* in Sarasota Bay, an estuary near Tampa Bay, found that they were exclusively piscivorous and that their main prey items were seagrass-associated soniferous species (Barros & Wells 1998, Berens McCabe et al. 2010). Furthermore, studies conducted during the same time period as the spotted seatrout spawning season (May–October) found that 52% of the dolphin's total prey comprised soniferous species (Barros & Wells 1998, Berens McCabe et al. 2010).

A similar study conducted on Franciscana dolphins *Pontoporia blainvillei* from Uruguay found that the dolphins' most important prey item was the striped weakfish, and that the most important food group was soniferous teleosts (Tellechea et al. 2017). Dolphins appear to use passive listening while foraging to intercept sounds produced by soniferous fishes and then use echolocation to track and capture prey (Barros & Wells 1998, Gannon et al. 2005, Tellechea et al. 2017). Dolphins increase their capture efficiency of energy-rich prey using this foraging technique because these soniferous species, such as spotted seatrout, drum only during the spawning season. As such, male spotted seatrout drumming coupled with frequent reproductive movements lead to a higher predation risk and subsequent higher natural mortality.

#### 4.4. Management implications

The high estimates of fishing mortality, combined with an estimated natural mortality of  $0.3 \text{ yr}^{-1}$ , indicate that the spotted seatrout population in Tampa Bay is fully exploited (Stokes & Law 2000, Addis et al. 2018). Thus, the largest and oldest individuals are not

abundant. These data are corroborated by the maximum age of the fish in our study, which is less than the species' maximum age of 12, as well as the local maximum age of 9 (Maceina et al. 1987, Addis et al. 2018). While the low abundance of these older and larger individuals may affect the trajectory of this species' growth curves, the contrasting roles of fishing pressure and natural mortality may also have major implications for its stock structure and management. As 89% of our seatrout captured within the recreational slot size were females, the fishery is size-selective. Furthermore, the low rates of inter-estuarine movement by female spotted seatrout may increase their vulnerability to harvest (Callihan et al. 2015). Given these vulnerabilities, the recreational fishery would be expected to disproportionately reduce the number of large females in the population; however, the overall sex ratio of the samples collected for this project was skewed toward females. This dichotomy may suggest that spotted seatrout populations are naturally skewed to be female-biased.

If sexual size dimorphism is a natural part of a fish's life history, then a virgin population would be expected to exhibit higher male natural mortality than female. This pattern has been documented in the blacktail seabream *Diplodus capensis*, which exhibited a female-biased sex ratio and sexual size dimorphism in an unexploited area, but an equitable sex ratio in an exploited area (Richardson et al. 2011). Another example is the boarfish *Capros aper*, which until very recently was unexploited in the Northeast Atlantic, yet its population exhibited female-biased sexual size dimorphism (Hussy et al. 2012). Thus, sexual size dimorphism can occur naturally and may be due to energetic trade-offs with sex-specific reproductive behaviors (Lande 1980, Halvorsen et al. 2016).

The larger female size-at-age pattern seen in spotted seatrout, combined with a slot size management approach, results in females being disproportionately exploited. The net result of this selective harvest is a reduction of large and old individuals, which may have important implications for productivity. This is because big old fat fecund females (BOFFFs) have been shown in multiple species to disproportionately contribute to the reproductive potential (Barneche et al. 2018). An assessment of the relative contribution of BOFFFs to spotted seatrout reproductive potential was conducted by Cooper et al. (2013) and indicated that even relatively low fishing pressure resulted in significant decline in the stock's reproductive potential. However, it appears from spotted seatrout stock assessments that these nega-

tive impacts may not be occurring, indicating that spotted seatrout may have life-history adaptations to high selective fishing pressures (Murphy et al. 2011, West et al. 2014, Addis et al. 2018).

Florida has used size regulations for spotted seatrout since 1969, and the current regulations were enacted in 2000. Under those regulations, despite the selective fishing pressures, populations have remained stable and mostly above the target threshold of 35% transitional spawning potential ratio (SPR) (Murphy et al. 2011, Addis et al. 2018). Similarly, spotted seatrout from Louisiana exhibit sexual size dimorphism as seen in this study and are managed at an 18% SPR threshold but are not overfished nor are experiencing overfishing (Nieland et al. 2002, West et al. 2014). While it appears that the spotted seatrout can withstand the selective fishing pressure exerted on females, assessment models and management efforts must include sex-specific parameters (Su et al. 2013, Keyl et al. 2015). An integral component of successful fisheries management must be understanding the full range of factors affecting population growth and reproductive success. Population dynamics models for sexually dimorphic species should include sex-specific growth parameters, mortality, and catch data. Like sequential hermaphrodites, the integration of data on both sexes in stock assessments is necessary to avoid unexpected long-term consequences to the stock's productivity. Finally, incorporating the behavioral and spatial ecology of a sexually dimorphic species can also be beneficial to understanding the population-level dynamics at play, because fishing is only one of several factors affecting population growth.

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