

Spatial and temporal variability in growth of southern flounder (*Paralichthys lethostigma*)



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ABSTRACT

Delineation of stock structure is important for understanding the ecology and management of many fish populations, particularly those with wide-ranging distributions and high levels of harvest. Southern flounder (*Paralichthys lethostigma*) is a popular commercial and recreational species along the southeast Atlantic coast and Gulf of Mexico, USA. Recent studies have provided genetic and otolith morphology evidence that the Gulf of Mexico and Atlantic Ocean stocks differ. Using age and growth data from four states (Texas, Alabama, South Carolina, and North Carolina) we expanded upon the traditional von Bertalanffy model in order to compare growth rates of putative geographic stocks of southern flounder. We improved the model fitting process by adding a hierarchical Bayesian framework to allow each parameter to vary spatially or temporally as a random effect, as well as log transforming the three model parameters (L_∞ , K , and t_0). Multiple comparisons of parameters showed that growth rates varied (even within states) for females, but less for males. Growth rates were also consistent through time, when long-term data were available. Since within-basin populations are thought to be genetically well-mixed, our results suggest that consistent small-scale environmental conditions (i.e., within estuaries) likely drive growth rates and should be considered when developing broader scale management plans.

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1. Introduction

Accurate descriptions of populations and subpopulations are important across all of ecology, but particularly important for commercial fish stocks that experience high amounts of harvest mortality. Methods and descriptions of what make fish stocks unique is an active area of fisheries science owing largely to the fact that ecological groupings can be measured and described in many ways—e.g., spatially, genetically, and phenotypically among others (Cadrin et al., 2013). Although the best stock identification approach involves multiple methods in an interdisciplinary analysis (Begg and Waldman, 1999; Abaunza et al., 2013), such studies are not always feasible. One good starting point, however, is the use of life history traits to begin describing (putative)

populations. Many fishery monitoring programs routinely collect life history data such as age, size, sex, and maturity. These traits often vary across a species range in association with genetic and/or environmental factors, and this variation has important stock assessment and management implications (McBride, 2013).

Life history traits used in stock identification can take a number of forms, but often describe biological processes such as growth, maturation, and fecundity (Pawson and Jennings, 1996; Begg et al., 1999; McBride, 2013). Because these processes occur throughout a population, meaningful comparisons of process rates (or other descriptive parameters) can detect differences that have both ecological and management importance. Numerous studies have investigated life history traits in order to advance the understanding of a specific population of fish. For example, DeVries and Grimes (1997) examined growth of king mackerel (*Scomberomorus cavalla*) over large spatial and temporal ranges to support multiple stocks, and Begg and Marteinsdottir (2002) use sex-specific

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maturity data to evaluate length and age-at-maturity of Atlantic Cod (*Gadus morhua*) over many years.

Although questions of appropriate model use and fit are warranted (Katsanevakis and Maravelias, 2008), many life history relationships are well established. Unfortunately, however, rigorous comparisons of life history parameters are less available, partly due to a lack of well-established methodology. Visual comparison of growth curves to other models certainly has value; however, uncertainty around parameter estimates is often not reported, and in some cases multiple comparisons are subject to questionable post-hoc adjustments (Ruxton and Beauchamp, 2008; Gelman et al., 2012). Few studies have explored hierarchical applications of growth modeling, but Pilling et al. (2002) used a random effects model on back-calculated growth estimates for *Lethrius mahaesena* focusing on parameter correlation. Closer to the multiple comparisons focus, Helser and Lai (2004) used a random effects meta-analysis approach on *Micropterus salmoides*. However, Helser and Lai (2004) used mean lengths-at-age and not individual fish data. Building upon both of these studies, we present an alternative parameter comparison technique that is robust to the Type I error issues inherent to many traditional analyses.

Southern flounder (*Paralichthys lethostigma*) are a recreational and commercial flatfish, primarily distributed in nearshore and estuarine habitats in the Atlantic Ocean from southern Virginia to central Florida, and in the Gulf of Mexico from central Florida to northern Mexico (Gilbert, 1986). Range-wide declines in populations have been independently detected and generally attributed to high long-term fishing mortality (in the Atlantic Ocean [Takade-Heumacher and Batsavage, 2009] and Gulf of Mexico [Froeschke et al., 2011]). Currently, no coast-wide assessment (or stock assessment outside of North Carolina) takes place, which limits spatially-extensive inference that can be made on this species.

Males and females exhibit size dimorphism, with females attaining larger sizes (Wenner et al., 1990), and as a result comprising the majority of the fishery by numbers and weight (Takade-Heumacher and Batsavage, 2009). Growth has been estimated independently in locations (Table 1), although the years and data sources vary considerably and thus prevent a robust comparison. Additionally, little is known about sexual differentiation and sex ratios; however, Luckenbach et al. (2003) suggest that sexual differentiation takes place around 100–120 mm total length (TL), and report sex ratios at midrange temperatures near 1:1, but with higher proportions of males at both high and low temperatures. Between ages 1 and 3 years, southern flounder females mature and then move offshore to spawn (Midway and Scharf, 2012), while patterns of male maturation are undocumented.

Based largely on the wide species distribution (and vicariant separation around southern Florida), unknown offshore habitat use during and after spawning, and the recreational and commercial value of the species, stock structure has recently become an area of interest. Genetic work has established two distinct basin populations—the Gulf of Mexico and southeastern US Atlantic Ocean (Anderson et al., 2012). However, genetic work and otolith morphometrics (Midway et al., 2014) have failed to identify any structuring within basins. Despite lack of genetic structuring within basins, phenotypic differences may exist. Previous growth estimation (Table 1) suggests spatial (or temporal) variation, highlighting the possibilities that (1) these variable parameter estimates are accurate and thus serve as a hypothesis for further examination of stock-specific growth, or (2), these variable parameter estimates are inaccurate, and highlight the need for a more unified, comparable way to evaluate model parameters.

Given the genetic difference between Gulf of Mexico and Atlantic Ocean populations, and the fact that growth can be heritable, we hypothesized that growth would differ between basins,

a spatial level at which other stock delineators have found evidence. Mortality (both fishing mortality, F , and natural mortality, M) can impact growth, although in the study areas and over the time we have data, F has likely remained high (Froeschke et al., 2011 in Texas and Takade-Heumacher and Batsavage, 2009 in North Carolina) and M unknown for all stocks; thus, we hypothesize that over time, growth rates have remained relatively stable for southern flounder and any differences in growth reflect environmental or spatial factors. Also, sex ratio data on southern flounder is generally lacking, yet basic biological questions remain about sex differentiation and sex-specific life histories—particularly the disconnect between estimated juvenile sex ratios and the high percentage (80–90%) of females landed in the fishery. We hypothesize that sex ratios at size are consistent across the species range. Thus, the objectives for our work is to both evaluate a new von Bertalanffy parameterization in a Bayesian context, while addressing life history questions for southern flounder.

2. Materials and methods

2.1. Data sources

We used data from fishery-independent sampling programs in North Carolina, South Carolina, Alabama, and Texas in order to evaluate estuarine-specific (spatial), long-term (temporal), and sex-specific differences in southern flounder growth. All four states maintain ongoing fishery-independent sampling programs, and southern flounder data were available for a variety of sampling gears. However, in order to reduce the effect of gear we used only fish collected from fishery-independent inshore gillnet and trammel net sampling. Specifically, we used data from the North Carolina Division of Marine Fisheries (NCDMF) Fisheries Independent Assessment program, which fishes multi-panel gill nets (7.6–16.5-cm stretch mesh in eight 27.4-m sections) in the estuarine waters throughout the state during February–December (see Takade-Heumacher and Batsavage, 2009 for additional programmatic details). South Carolina Department of Natural Resources (SCDNR) data are from their year-round, long-term estuarine trammel net survey that samples with a 183-m long and 2.1-m deep trammel net made up of two 35.56 cm stretch-mesh outer panels and one 6.35 cm stretched-mesh inner panel (Arnott et al., 2010). Gulf of Mexico samples came from the Alabama Department of Conservation and Natural Resources who sample flounder with multi-panel gill nets (6.35–15.24-cm stretch mesh in four 45.7-m sections; John Mareska Personal Communication), as well as the Texas Parks and Wildlife Department estuarine gillnet survey, which uses 7.6–15.2-cm stretch mesh in four 45.7-m sections that are fished for 10-week periods once in the spring and once in the fall (Martinez-Andrade and Fisher, 2012). Sample sizes varied per state as well as differ in the years collected (i.e., in some locations not all sampled fish are aged every year; see Tables 2 and 3 for data summary).

At the time of capture all fish were measured (total length [TL]) and sexed by visual examination of gonads. Otoliths were also extracted, and all ages were estimated by agency biologists using at least one of the sagittal otoliths. North Carolina estimates southern flounder ages using two reads of whole otoliths submerged in water with sectioning as needed. Alabama and Texas biologists sectioned southern flounder otoliths prior to reading (VanderKooy and Guindon-Tisdell, 2003). South Carolina southern flounder otoliths were aged using whole otoliths until 2004, and sectioned otoliths have been used since, although it has been shown (with South Carolina-caught southern flounder) that whole otolith and sectioned otolith ages overwhelmingly agree (Wenner and Roumillat, unpublished data). In general, southern flounder

Table 1

Summary of von Bertalanffy-estimated asymptotic length (L_∞) and growth (K) coefficients for southern flounder from published literature and agency reports. Texas values come from a coastwide analysis (see Stunz et al., 2000). Note: South Carolina and Texas uncertainty is expressed as asymptotic 95% confidence limits in parentheses. NC = North Carolina, SC = South Carolina, LA = Louisiana, TX = Texas.

US state	Sex	n	L_∞ (mm)	K	Gear
NC ^a	Males	1885	381	0.80	Various fishery-independent gears
	Females	7555	699	0.28	
SC ^b	Males	573	518 (360–677)	0.25 (0.10–0.39)	Various fishery-independent gears
	Females	780	759 (658–860)	0.23 (0.18–0.29)	
LA ^c	Males	146	332.5	1.03	Multiple gears; opportunistic sampling
	Females	1202	556.5	0.51	
TX ^d	Males	144	384 (327–441)	0.50 (0.16–0.83)	Various gears
	Females	718	482 (457–509)	0.75 (0.06–0.90)	

^a Takade-Heumacher and Batsavage (2009).

^b Wenner et al. (1990).

^c Fischer and Thompson (2004).

^d Stunz et al. (2000).

accrue well-defined annuli and aging summer and fall-caught fish as described here is considered accurate.

For all data, we excluded fish captured between 1 January and 1 June each year. Southern flounder otolith annuli are generally formed in the late winter and spring, often resulting in an increased possibility for aging error when estimating ages of fish captured prior to summer. For younger ages this is often not a problem as length can inform the age; however, any early-year captures can be problematic and thus were removed from the analysis. Additionally, sampling effort and catch is generally not high during the early-year months, so exclusion of these months did not remove a large amount of samples. All annual ages were then converted to fractional ages based on the completed month prior to capture

(e.g., a November caught fish was given 10 full months, regardless of within-month capture date), as all fish were assumed to have a 1 January birthdate.

2.2. Growth modeling

We evaluated southern flounder growth using a hierarchical Bayesian modeling framework that permitted model parameters to vary spatially or temporally (depending on the analysis). We built upon the Beverton–Holt parameterization (Beverton and Holt, 1957) of the von Bertalanffy model of growth (von Bertalanffy, 1938).

$$y_{ij} = L_{\infty j}(1 - e(-K_j(t_{ij} - t_{0j}))) + \epsilon_{ij} \quad (1)$$

$$\epsilon_{ij} \sim N(0, \sigma^2)$$

$$\log \begin{pmatrix} L_{\infty j} \\ K_j \\ t_{0j} + 10 \end{pmatrix} \sim \text{MVN}(\mu, \Sigma) \quad (2)$$

$$\mu = \log(\bar{L}_\infty, \bar{K}, \bar{t}_0) \quad (3)$$

where y_{ij} is the total length (mm) for fish i from group j , and t_{ij} is the estimated age for fish i from group j . $L_{\infty j}$, K_j , and t_{0j} are the three von Bertalanffy model parameters, representing the asymptotic length (theoretical maximum average size), the growth coefficient (the rate of approaching L_∞), and the hypothetical age at which size equals 0, respectively. The natural log of these three model parameters were assumed to come from a multivariate normal (MVN) distribution with population mean μ and variance–covariance Σ . μ contains L_∞ , K , and t_0 , the population-average parameters, describing the growth curve across all groups. We use the term population-average to refer to the parameters estimated based on all the data and the term group-level to refer to the group-specific parameter estimates, where groups could be, for example, spatial groups (putative stocks) or temporal groups. ϵ_{ij} is the residual error, assumed to be independently and identically distributed as $N(0, \sigma^2)$.

The von Bertalanffy model often fails to converge when there is limited contrast in ages (particularly a lack of very young or very older ages), in addition to highly variable sizes at younger ages. Southern flounder exhibit both of these characteristics, and in fact during exploratory data analysis, models fit using the *nls* function in R (fit with least squares; R Core Team, 2013) often failed to converge at parameter estimates even when data visually appeared to show an asymptotic growth pattern. In order to improve the model fitting

Table 2

Location, sample size, and years sampled of June–December female southern flounder used in the spatial analysis of 10 locations. NC = North Carolina, SC = South Carolina, LA = Louisiana, TX = Texas.

Abbreviation	Location	Sample size (n)	Years sampled
PS-NC	Pamlico Sound, NC	2537	2002–2012
NR-NC	New River, NC	519	2008–2012
CF-NC	Cape Fear River, NC	169	2008–2012
WB-SC	Winyah Bay, SC	193	1993–1994; 2002–2010
CR-SC	Cape Romain, SC	360	1994–2010
CH-SC	Charleston Harbor, SC	1286	1990–2010
ACE-SC	ACE Basin, SC	222	1991–2010
MB-AL	Mobile Bay, AL	226	1986–2012
CL-TX	Cedar Lakes, TX	130	1999–2001
MB-TX	Matagorda Bay, TX	515	1992–1994; 1999–2000
LM-TX	Laguna Madre, TX	112	1992–1994; 1999–2001

Table 3

Location, sample size, and years sampled of June–December male southern flounder used in the spatial analysis of four locations. NC = North Carolina, SC = South Carolina, LA = Louisiana, TX = Texas.

Abbreviation	Location	Sample size (n)	Years sampled
PS-NC	Pamlico Sound, NC	419	2002–2012
WB-SC	Winyah Bay, SC	86	1993–1994; 2002–2010
CR-SC	Cape Romain, SC	138	1994–2010
CH-SC	Charleston Harbor, SC	414	1990–2010
ACE-SC	ACE Basin, SC	88	1991–2010
MB-AL	Mobile Bay, AL	30	1986–2012
MB-TX	Matagorda Bay, TX	125	1992–1994; 1999–2000

process, we adopted the [Kimura \(2008\)](#) method of estimating the three model parameters on the logarithmic scale, with the addition of 10 to t_0 because negative t_0 values would not be possible, even though it may be negative, when estimated on the log-scale. A value of 10 is subtracted before evaluating the von Bertalanffy parameters on the original scale ([Kimura, 2008](#)).

In addition to evaluating specific estuarine effects on growth, we modeled K based on basin (i.e., Atlantic Ocean vs. Gulf of Mexico) to compare basin average growth rates, as follows:

$$\log \begin{pmatrix} L_{\infty j} \\ K_j \\ t_{0j} + 10 \end{pmatrix} = \begin{pmatrix} \bar{L}_{\infty j} \\ \delta_h \times \text{basin}_j \\ \bar{t}_{0j} \end{pmatrix} \quad (4)$$

where δ_h is a fixed effect representing the estimated mean growth rate (on the log-scale) for each basin ($h=1$ for the Gulf, 2 for the Atlantic). We then calculated the difference in mean growth rates among basins ($\delta_1 - \delta_2$) and examined the 95% credible interval for the difference. Overlap of the 95% CRI with zero would indicate no difference among basins in average growth rates.

For all models, prior probability distributions for σ , μ , and Σ were diffuse; we used a uniform prior for σ , diffuse normal priors for μ , and modeled Σ using the scaled inverse-Wishart distribution ([Gelman and Hill, 2007](#)). We ran three concurrent Markov chains beginning each chain with different values. From a total of 500,000 iterations the first 200,000 iterations of each chain were discarded as burn-in and further thinned by retaining every third value for a total of 100,000 values for analysis. Final posterior distributions were assessed for convergence both visually, as well as with the Brooks–Gelman–Rubin statistic, \hat{R} , with values < 1.1 indicating convergence (although no values > 1.01 were recorded). JAGS (Version 3.4.0) analyses were run using the rjags package ([Plummer, 2013](#)), run from within ([R Core Team, 2013](#)).

The hierarchical Bayesian model fitting approach provided several advantages, particularly in the comparison of model parameters as the models permitted the inclusion of group-level information. The hierarchical approach simultaneously fits a population-level model based on all the data, but also estimates varying parameters, where parameters are treated as random effects. Examples of groups are the putative stocks (unique bay or estuarine systems) from which southern flounder were captured. The treatment of parameters in this hierarchical and Bayesian context both improves model fitting due to shared statistical strength of larger groups ([Kéry, 2010](#)), as well as presents a robust method for quantitative post hoc multiple comparisons that does not rely on traditional ad hoc corrections ([Gelman et al., 2012](#)). We were primarily interested in K_j and $L_{\infty j}$ estimates, the growth coefficient and asymptotic size parameters from the von Bertalanffy growth model, and our analysis will focus on the results of these parameters.

2.2.1. Spatial differences: females

The spatial analysis of June–December gillnet-caught female southern flounder included 10 groups ([Table 1](#)). These groups represented estuarine or bay populations spanning four states and two basins, the Gulf of Mexico and Atlantic Ocean. We assumed that southern flounder—particularly the younger ages dominant in the data—were full-time residents of the estuary or bay in which they were sampled, an assumption supported by high site fidelity from a tagging study of North Carolina southern flounder ([Craig and Rice, 2008](#)). It is also worth noting that here and in other models we separated males and females. Although they could be combined and distinguished by a covariate, sex-specific growth in southern flounder is both distinct and well-documented ([Wenner et al., 1990](#)). For this reason we did not want any growth information from one gender to inform the other, which would happen as a result of

Table 4

Sample size and years sampled of June–December female and male southern flounder for five locations used in the temporal analysis. For all locations, two periods were compared and represented an earlier and later period of the available date. Note that in all cases some years are missing between samples. This buffer period was designed to increase the independence of the samples within each period (and also account for the reason that the combined sample sizes here may not add up to the full location sample sizes in [Table 1](#)). Note: Sample sizes (n) separate females (F) and males (M). NC = North Carolina, SC = South Carolina, LA = Louisiana, TX = Texas.

Abbreviation	Location	n (F/M)	Years sampled
PS-NC-1	Pamlico Sound, NC	606/132	2002–2006
PS-NC-2	Pamlico Sound, NC	1513/202	2010–2012
CR-SC-1	Cape Romain, SC	160/43	1994–1999
CR-SC-2	Cape Romain, SC	117/71	2003–2008
CH-SC-1	Charleston Harbor, SC	537/191	1991–1999
CH-SC-2	Charleston Harbor, SC	351/142	2003–2008
ACE-SC-1	ACE Basin, SC	99/42	1991–1999
ACE-SC-2	ACE Basin, SC	65/27	2003–2008
MB-TX-1	Matagorda Bay, TX	469/70	1992–1994
MB-TX-2	Matagorda Bay, TX	46/55	1999–2000

the partial pooling that occurs during the fitting of the hierarchical models (i.e., model parameters are constrained through their hierarchical distribution and are not estimated independently).

2.2.2. Spatial differences: males

Male southern flounder are captured less frequently than females, which more commonly reach the larger sizes targeted by the fishery. Even in the fishery-independent data we examined, males were much less frequent than females. Due to this lack of male data (frequently in the contrast of ages), we decided not to use the same estuarine framework for spatial analysis and instead pooled males according to state waters in order to increase sample sizes ([Table 3](#)). Less is known about the life history of males and whether they use the same habitats as females at the same sizes and ages; however, assuming the majority of males do not mature in the first year or two of life they are probably remaining in their original inshore systems, much like females.

2.2.3. Temporal differences

Although the above analyses for spatial differences pools samples across years, we also wanted to explore the possibility that growth parameters for spatial groups may have changed over time. For this temporal analysis of von Bertalanffy growth parameters, we split each of the five largest spatial groups of each sex into two subsets ([Table 4](#)). In order to reduce the likelihood of a year-class effect and increase the independence of the sample periods, a minimum of three years worth of data was excluded (or not collected) between the time periods.

2.2.4. Influence of large fish

One concern with the spatial and temporal analysis of females was the presence of older, larger individuals. Although these samples are valuable toward estimating non-linear growth curves, we wanted to explicitly consider this demographic for two reasons: (1) their low numbers can strongly influence the growth curves to the point where a small demographic of larger fish could unduly influence K , which is largely based on younger, smaller fish and (2) our study assumed estuarine exclusivity, yet we know that after age-2 the majority of females have migrated offshore to spawn ([Midway and Scharf, 2012](#)). Although it is possible that older age fish sampled in estuaries could have been juveniles in that same estuary and therefore accurately contribute to estimation of spatially-specific growth, nothing certain is known about the habitats of female southern flounder returning from offshore spawning. Based on these two concerns, we ran a final growth model using the same June–December gillnet caught female

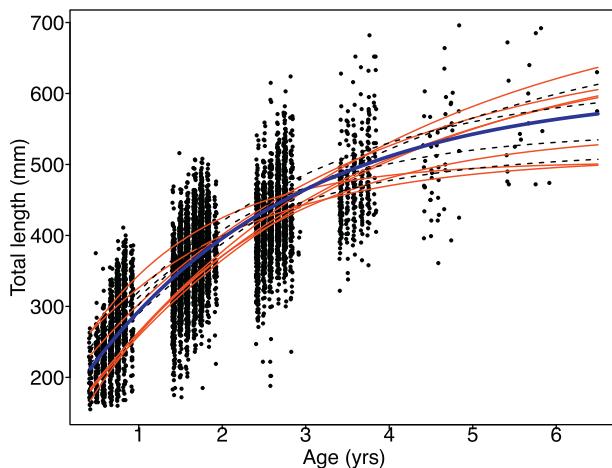


Fig. 1. Age and total length (mm) of June–December female southern flounder are represented by jittered black dots. The lines are posterior mean estimates from a von Bertalanffy model. The thick blue line represents the population-average estimate (all data). The thin solid red lines represent group-level subpopulations (i.e., putative stocks estimated as random effects) for Atlantic estuaries, while the dashed black lines represent group-level subpopulations for Gulf of Mexico estuaries. All estuaries are delineated by separate bay or estuarine systems in which flounder are thought to remain, particularly for younger ages that dominate the data. (For interpretation of the references to color in this legend, the reader is referred to the web version of the article.)

southern flounder in the previous model, but subsetting the data to exclude any fish older than age-2.

2.3. Sex ratio modeling

Due to sexual size dimorphism and females attaining larger sizes than males, we adopted a hierachal Bayesian logistic regression model to describe sex ratios across fish lengths. Sex ratios are more even at smaller sizes, although females dominate with increasing size. Despite this well-known relationship, it has not been quantified or examined among spatial groups. As with our analysis of spatial differences in male growth, we pooled individuals by state in order to increase sample size. The form of the hierarchical logistic model was as follows:

$$y_i \sim \text{Bernoulli}(p_i), \quad \text{for } i = 1, \dots, n \quad (5)$$

$$\text{logit}(p_i) = \alpha_{i[j]} + \beta^{\text{TL}} \times \text{TL} \quad (6)$$

$$\alpha_j \sim N(\mu_\alpha, \sigma^2), \quad \text{for } j = 1, \dots, J \quad (7)$$

Here, y_i represents the gender of an individual fish (1 = female, 0 = male), which is considered a Bernoulli random variable with probability p_i . In the logistic regression (Eq. (5)), p_i 's are modeled with a logit link as a function of total length (TL). The model intercept (α_j) was considered a random variable permitted to vary by group j (here, state), and which was assumed to come from a normal distribution with mean μ_α and variance (σ^2). The logistic regression slope coefficient (β^{TL}) was considered common to all groups. This random intercept and fixed slope framework was based on the idea that sex ratios may be determined at younger ages by environmental variables such as temperature (Luckenbach et al., 2003), and thus the initial ratios may vary among groups. However, whether initial sex ratios differ or not, we assumed the rate at which the females became dominant was common to all groups. Although the comparison of random intercepts may be useful, we decided to take advantage of derived quantities in order to compare the inflection point of the logistic model, or L_{50} value, the length at which the group switches from male-dominated to female-dominated and defined as $L_{50} = -\hat{\alpha}_j/\beta$. Despite this value being somewhat arbitrary, estimation of this point on the curve is well-established in

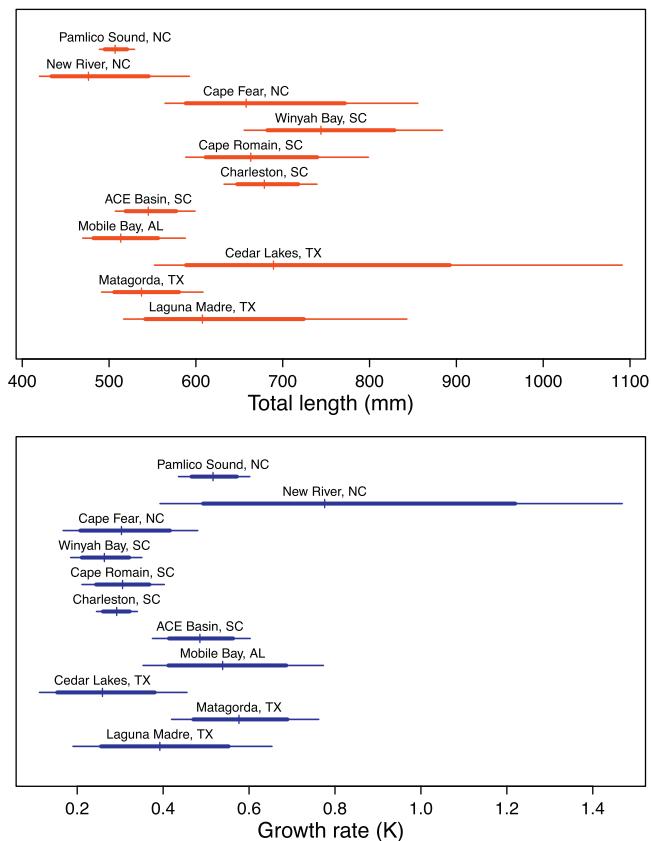


Fig. 2. Group-level estimates of parameters L_∞ (top panel) and K (bottom panel) from a spatially-varying von Bertalanffy model of June–December female southern flounder. The thicker portion of the lines represents the 80% credible interval, the thin portion extends to cover the 95% credible interval, and the median value is indicated by the tick mark perpendicular to the line. These L_∞ and K values are incorporated in the red lines in Fig. 1.

the use of logistic regression, was easily derived in the model, and references a meaningful biological point.

3. Results

3.1. Spatial differences: females

Estuarine-specific growth parameters for female southern flounder varied without a clear spatial pattern. L_∞ posterior means ranged from 484 to 751 mm, and posterior means of K ranged from 0.26 to 0.82 (Figs. 1 and 2; see Online Appendix for full model output). Generally, estuarine groups near each other (e.g., state waters) had overlapping 95% credible intervals, though not exclusively. There was no apparent basin effect on growth, a test for the difference between δ_h (basin growth coefficients), was estimated to be -0.03 (95% credible interval $= -0.32, 0.22$). Although correlation was expected among model parameters, it was generally weak (K and $L_\infty = -0.36$, L_∞ and $t_0 = -0.02$, and K and $t_0 = 0.05$ for the three correlation estimates based on the population-level model).

3.2. Spatial differences: males

Estuarine-specific growth parameter estimates for males varied similarly in magnitude to females; L_∞ posterior means ranged from 407 to 758 mm, and posterior means of K ranged from 0.15 to 0.61 (Figs. 3 and 4)—though they varied considerably less if medians were used to describe the posterior distributions. Unlike females, however, male growth parameters tended to show a

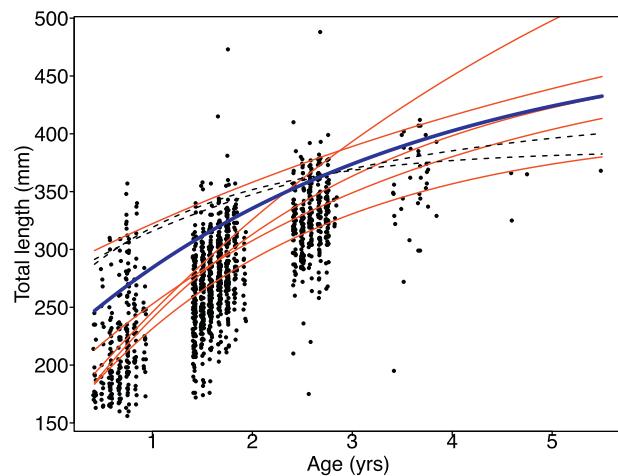


Fig. 3. Age and total length (mm) of June–December male southern flounder are represented by jittered black dots. The lines are posterior mean estimates from a von Bertalanffy model. The thick blue line represents the population-average estimate (all data). The thin solid red lines represent group-level subpopulations (i.e., putative stocks estimated as random effects) for Atlantic estuaries, while the dashed black lines represent group-level subpopulations for Gulf of Mexico estuaries. All estuaries are delineated by separate bay or estuarine systems in which flounder are thought to remain, particularly for younger ages that dominate the data. (For interpretation of the references to color in this legend, the reader is referred to the web version of the article.)

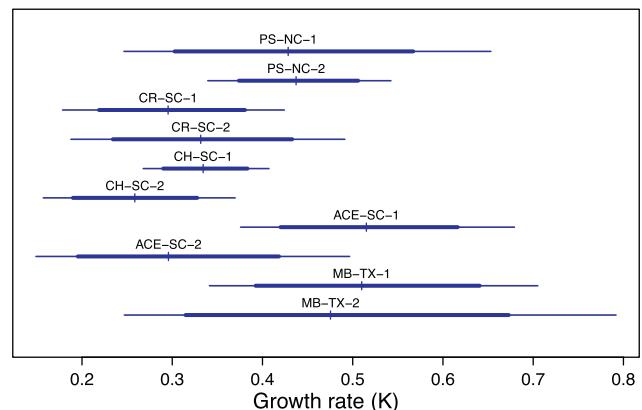
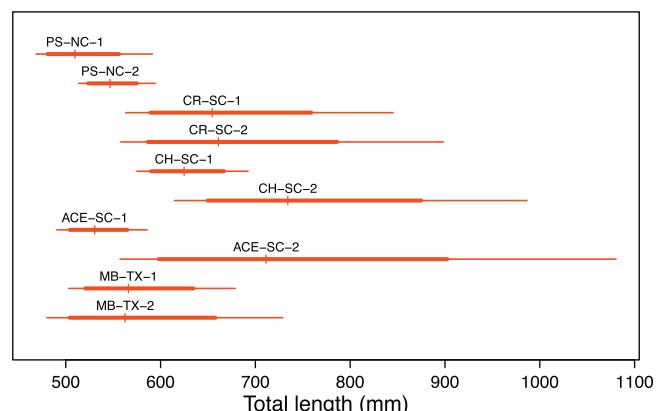


Fig. 5. Group-level estimates of parameters L_∞ (top panel) and K (bottom panel) from a temporally-varying von Bertalanffy model (though accounting for spatial populations) of June–December female southern flounder. Abbreviations indicate the location and time period of the sample (referenced in Table 2). The thicker portion of the lines represents the 80% credible interval, the thin portion extends to cover the 95% credible interval, and the median value is indicated by the tick mark perpendicular to the line.

moderate geographic effect, although we detected no basin effect on growth. The estimated difference between δ_h (basin growth coefficients), was relatively large at 0.52, but with a very wide 95% credible interval ($-0.16, 2.14$). L_∞ tended to decrease and K tended to increase with groups to the south and west. Population-level parameter correlation was again minimal, at K and $L_\infty = -0.38$, L_∞ and $t_0 = -0.03$, and K and $t_0 = 0.25$.

3.3. Temporal differences

Overall parameter estimates did not vary between the time periods for either gender, which supports our approach of pooling sample years. The 95% CI for temporal comparisons of L_∞ and K overlapped (Fig. 5). ACE Basin, SC showed evidence of the greatest temporal differences (non-overlapping 80% CI), with a clear difference of faster growth rates and smaller asymptotic sizes in the earlier period. Parameter correlation for females was minimal, at K and $L_\infty = -0.26$, L_∞ and $t_0 = -0.01$, and K and $t_0 = 0.02$. Parameter estimates for males were even closer than for females.

3.3.1. Influence of large fish

Partly addressing the temporal differences, but also for the purposes of eliminating large old females, we ran an age-truncated model. This analysis predictably increased $L_{\infty j}$ and decreased K_j parameters based on the removal of older and larger fish. Posterior mean parameter estimates more closely resembled neighboring estuaries, although uncertainty increased and created more overlap among all basins (Fig. 6). Focusing primarily on K —which is

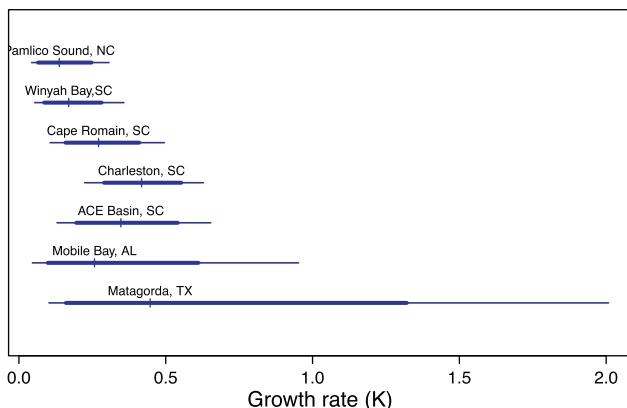
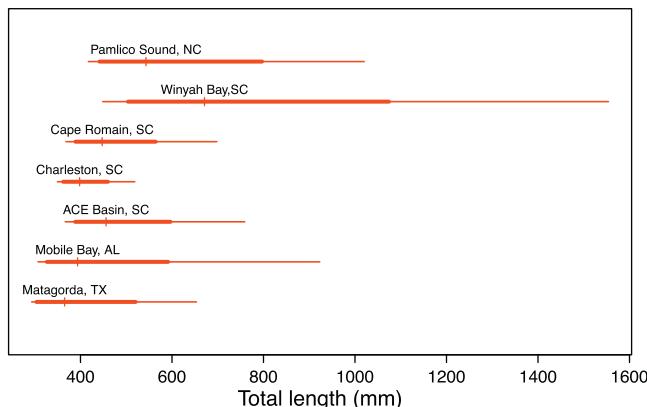


Fig. 4. Group-level estimates of parameters L_∞ (top panel) and K (bottom panel) from a spatially-varying von Bertalanffy model of June–December male southern flounder. The thicker portion of the lines represents the 80% credible interval, the thin portion extends to cover the 95% credible interval, and the median value is indicated by the tick mark perpendicular to the line. These L_∞ and K values are incorporated in the red lines in Fig. 3.

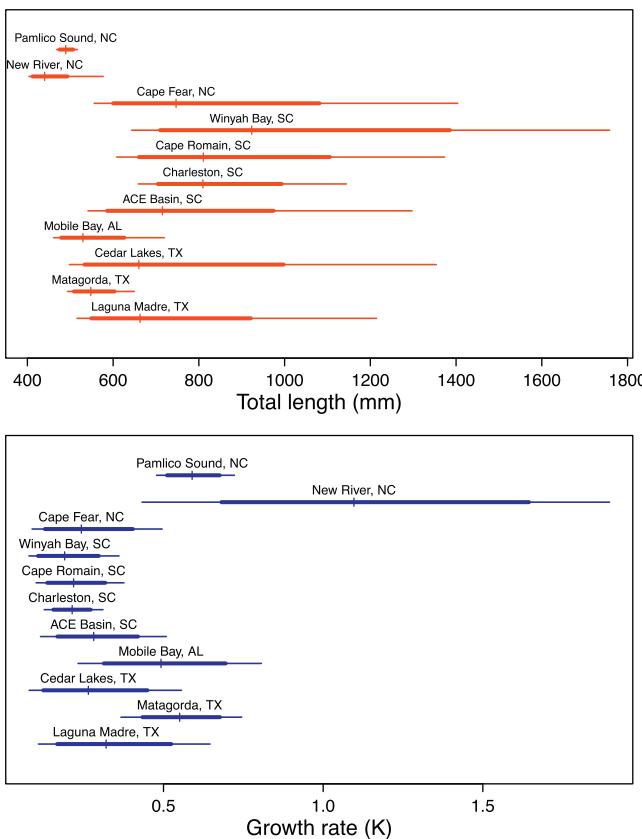


Fig. 6. Group-level estimates of parameters L_{∞} (top panel) and K (bottom panel) from spatially-varying von Bertalanffy model of June–December and age-truncated female southern flounder. These models were run only with individuals captured prior to age-3. The thicker portion of the lines represents the 80% credible interval, the thin portion extends to cover the 95% credible interval, and the median value is indicated by the tick mark perpendicular to the line.

better estimated with younger, smaller fish—there was a general increase in K with groups to the south and west, with the exception of Pamlico Sound and New River, NC. Also noteworthy was the reduction of estimated K for ACE Basin, SC; using the full data this region was previously an outlier to other South Carolina regional estimates (see above), yet under the age-truncated data K was very similar to other South Carolina groups. Correlation between K and $L_{\infty} = -0.56$, which was higher than in other models, although the other correlations were low (L_{∞} and $t_0 = -0.04$, and K and $t_0 = 0.07$).

3.4. Sex ratios

Estimates of proportion of females by total length varied little across the species geographic distribution (Fig. 7). Mean α_f values ranged from -3.01 to 3.58 , and 95% CI all overlapped, suggesting that no intercept was significantly different from another. (Derived L_{50} 's also overlapped at the 95% level, but as the slope [β^{TL}] was common, the L_{50} were perfectly collinear to the intercepts.) β^{TL} was estimated precisely, at 0.015 with high certainty (95% CI = 0.014 – 0.016), further supporting our model specification. Mean L_{50} values ranged from 200 to 238 mm (7.9–9.4 in.), which is well below commercial and recreation size limits across the species (US) range.

4. Discussion

Female southern flounder make up the majority of both commercial and recreational fisheries, and our analysis suggested that variation in growth rates (and asymptotic growth) exists among

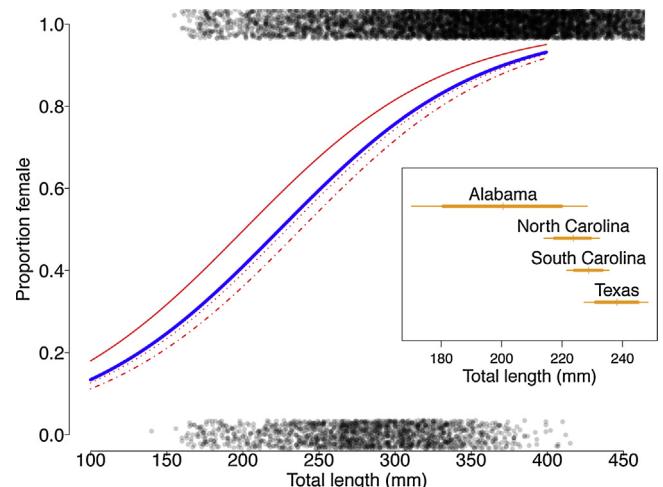


Fig. 7. Proportion of female southern flounder (sex ratios) as a function of total length (based on June–December southern flounder). The thick blue line represents the population-level estimate (all data) and the thin red lines represent state-level subgroups (solid red = Alabama; dotted red = South Carolina; dotted and dashed red = Texas). Note that the apparently missing red line is North Carolina, which is nearly identical to (and covered by) the population-level (blue) line. The jittered gray dots represent individual fish (male = 0, female = 1). The inset plot displays state-specific L_{50} estimates generated as derived quantities. The thicker portion of the lines represents the 80% credible interval, the thin portion extends to cover the 95% credible interval, and the median value is indicated by the tick mark perpendicular to the line. (For interpretation of the references to color in this legend, the reader is referred to the web version of the article.)

estuaries for females. The variation we detected did not adhere to any obvious pattern (e.g., latitudinal variation), and detection of significant female growth differences among some of the estuaries within individual states—regardless of using the full data or age-truncated data—suggests that finer-scale factors may be influencing female southern flounder growth. Males, on the other hand, provided less precise estimates of growth rates due to smaller sample sizes; however, we did detect a weak geographic signal in which growth rates tended to increase with populations south and west. Our analysis did not detect any between basin differences in growth rates for either males or females, which we hypothesized to exist (at least for females) based on previously-established stock differences (genetic [Anderson et al., 2012] and otolith shape [Midway et al., 2014]) at the basin scale.

To the best of our knowledge, there are no published estimates of southern flounder sex ratio variation with size. Our analyses used a logistic model to examine this relationship and found, as expected, female sex ratio increased with size due to sexual dimorphism in growth and body size. However, we were unable to detect any difference in L_{50} (the size at which sex ratio = 50%), despite the fact that southern flounder have temperature-dependent sex determination (Luckenbach et al., 2003), and the populations we studied spanned a fairly wide range of climatic conditions. Another concern with the sex ratio estimation is the lack of life history information for males, and how that might play a role in their selectivity to the sampling gear. For example, conditions where males migrate out of estuaries earlier than females, or do not have the same gear selectivity, or have a higher M (or any combination) could lead to biases in the sampling and subsequent sex ratio estimation.

A number of criteria can be used for determining population structure. Many measures of structure directly or indirectly address genetics, as genetic diversity is important not only for understanding the connectivity of stocks, but also a species' ability to buffer against loss. In addition to genetic structure—or when genetic results are unclear—capture fisheries benefit greatly from knowledge of phenotypic structure. Fisheries management relies

heavily on assessments of biological processes such as growth and maturation, since they directly impact fishery yield (Law, 2000). Size at age is heritable to some degree (Begg, 2005), but may be related only weakly with genetic structure and can certainly be overwhelmed by other growth factors, such as mortality and the environment. For a species such as southern flounder that is relatively well-mixed genetically, fast-growing, and estuarine dependent, we might expect growth in the wild to be closely associated with local environment factors rather than genetic differentiation, at least within each of the Atlantic and Gulf of Mexico regions considered here. Factors such as temperature, productivity, and variable timing of spawning may impact individual and population growth, as might the onset of piscivory (Fitzhugh et al., 1996) in southern flounder, thus prompting our investigation into estuarine-specific growth.

4.1. Biological considerations

Describing biological relationships must not only take into account model assumptions, but also the limitations of the samples as they represent the population. Southern flounder have an incompletely sampled and described life cycle, which means that the data we used to evaluate growth and sex ratios may not be a perfect representation of the population. One primary concern is the lack of large, old fish available from sampling. Between ages 1 and 3, females migrate offshore to spawn (Midway and Scharf, 2012), but little is known regarding offshore habitats and any return migrations. Older males are also conspicuously absent from inshore samples, as their maturation and adult habitat use is unknown. Therefore, in our analysis larger fish presented both the concern of violating the assumption of spatial independence, as well as undue influence on L_∞ (which is correlated to K). For instance, we had no way of knowing if a larger proportion of older fish in one sample group was even from that estuary, and whether they significantly impacted the growth estimate. For this reason we ran an age-truncated model—which ameliorated both of these potential issues—and suggested that the parameter estimates were not strongly influenced by older fish.

Juvenile fish (particularly age-0) are another demographic about which our knowledge is incomplete, yet whose dynamics may be strongly represented in the data used to estimate growth. To start, we assume a January 1 birthday and this very well may be imprecise for some fish in some years or regions. However, if timing of spawning is environmentally or latitudinally driven and it fixes growth patterns, we might expect to see that pattern in the data, which we did not. Additional complexities of juvenile habitat use are only now being identified. For example, Nims and Walther (2014) used otolith microchemistry to conclude that post-settlement southern flounder in Texas are split approximately evenly between oligohaline (low-salinity) and marine (high-salinity) environments. Although they detected no growth advantage between the habitats, such spatial separation could be occurring through the species range and be unknowingly reflected in long-term sampling. Perhaps of greater potential influence on juvenile growth is highly variable juvenile abundance. Taylor et al. (2010) present data that show North Carolina southern flounder juvenile abundance varying by an order of magnitude over just a few years. If this abundance impacts density-dependent growth, it could be that southern flounder growth variability is best estimated annually, although we lacked the data to address this. However, if growth variability is annual, it suggests that short-term sampling and pooling of spatial data may more accurately reflect temporal growth than spatial influence. Most of our data spanned several years, and so we are less concerned about this effect driving patterns in our results.

Mortality is another factor that may impact growth (Law, 2000) and obscure interpretation of stock structure. Throughout the species range, natural mortality is largely unknown and not estimated from empirical work. However, if natural mortality is related to density dependence it may also vary annually as described above. Fishing mortality may represent a greater influence on stock size and growth than does natural mortality—largely due to high estimates of harvest mortality and long-term declines in population size across the range (Takade-Heumacher and Batsavage, 2009; Froeschke et al., 2011). For instance, although fishing mortality is not estimated across the species range, North Carolina is the only state in the species distribution with a substantial inshore commercial fishery over the time-series in this study, likely due to extensive estuarine areas in the state and efficient and diverse fishing gears (Takade-Heumacher and Batsavage, 2009). Such great fishing pressure on ages 0–2 may be unique to North Carolina, and it likely removes the larger age 0–2 fish. Although we still observe high growth rates in Pamlico Sound and New River, NC (possibly due to greater resource availability for the remaining fish), this may explain the lack of larger age-1 and age-2 fish, and suppressed estimates of L_∞ .

4.2. Modeling advantages

Life history modeling is vital to fisheries science and the assessment process, yet fitting non-linear models to ecologically variable data can often present difficulties, and subsequent parameter comparisons among models can also be questionable. In many ways, our incomplete biological knowledge of southern flounder is typical of many species. Despite the limitations of our data, management and conservation decisions still need to be made with the best possible information. To this end, we used a hierarchical Bayesian modeling framework that is robust to many of the previous concerns regarding non-linear parameter estimation and comparison. The partial-pooling aspect of the model, where a common prior distribution on model parameter estimates provides a loose constraint that allows regions to share information, allowed for group specific estimates to be possible when sample sizes were small and when group-specific data did not show a strong asymptotic relationship (Gelman and Hill, 2007). Although sensitivity analyses suggested that all our sample sizes were adequate (and not greatly informed by the overall sample), this feature of hierarchical models may be of great use in other fisheries that are data-limited. Additionally, we recognize that our results can be improved with additional data, both temporally and spatially. Future modeling efforts may increase the accuracy of our results, or serve as a reference if growth estimates are hypothesized to have changed. Either way, our posterior estimates should provide useful priors for work that builds on ours.

Additionally, the use of Bayesian estimation provides probabilistic interpretation of results, including parameter estimates, and eliminates the need for post-hoc multiple comparisons corrections (Gelman et al., 2012). In fact, meaningful comparison of parameters was the primary objective of our analysis, yet under multiple, separate models we were unable to generate the same interpretation of parameter uncertainty (and for a smaller number of spatial groups as some models did not have enough data to fit individual models). This clear and direct comparison of parameters—including derived quantities such as the L_{50} in our sex ratio models—may have many uses in fisheries science, and particularly within the field of stock identification.

4.3. Conclusions

Ultimately, life history traits may not be a sensitive enough tool to detect stock differences for some species (Pawson and Jennings, 1996). Lankford and Targett (2001) investigated Atlantic Croaker (*Micropogonias undulatus*) physiological traits from Delaware to Florida, hypothesizing two stocks separated by Cape Hatteras. Ultimately they found no evidence of different physiologies—interpreted as stock structure—and concluded that gene flow from offshore spawning individuals may sufficiently mix the coast-wide stock and “preclude local genetic adaptation.” A similar scenario may be playing out in southern flounder. However, regardless of genetic structure (or lack of), estimates of vital rates are the foundation for assessment and management, and we found strong evidence that growth rates for southern flounder vary at small spatial scales. Currently, North Carolina is the only state to have a stock assessment for this species, although as the fishery expands and additional biological information is needed for regulation, reliable estimates of spatially-varying life history traits will be critical to ensure that the species is optimally managed.

Modeling southern flounder growth and sex ratios is hampered by an incomplete knowledge of the species' life history and subsequent gaps in biological sampling. Despite these limitations, we present a hierarchical Bayesian model that is robust to small sample sizes and accommodates meaningful comparisons among whatever putative groups may be of interest—in our case we were interested in spatial and temporal groups, though the group framework is entirely flexible for the specific question. We acknowledge that certain aspects of southern flounder life history are not well described or sampled, yet with (nearly) standardized fishery-independent gears over four states and many years we were able to derive estimates of growth and sex ratios. In this way, our results may not be directly comparable to previously published growth estimates (which have generally included multiple data sources); however, we see the among group estimates within our results as comparable.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.fishres.2015.03.009>.

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