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Evaluating the impacts of fishing on sex-changing fish: a game-theoretic approach

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Sex change has been widely documented in many commercially and recreationally important fish species, yet the implications of this life history trait are not considered in most stock assessments. This omission can lead to poor estimates of parameters vital to understanding the health of sequentially hermaphroditic stocks. Here, we present a game theoretic approach to model the sex changing behaviour of a stock of protogynous (female first) hermaphroditic fish and produce estimates of maximum sustainable yield (MSY), equilibrium biomass at MSY (B_{MSY}) and sex ratio, then compare these reference points to those from an otherwise identical gonochoristic (non-sex changing) stock. We tested each stock at varying levels of exploitation and with a range of assumptions about how sex ratio impacts fertilization rate. We show that a protogynous hermaphroditic stock with flexible timing of sex change produces similar MSY and slightly higher B_{MSY} than a gonochoristic stock with otherwise identical vital rates. Sex changing stocks were also able to maintain a higher proportion of males in the population than did non-sex changing stocks as exploitation increased. Although sex changing stocks were able to maintain their sex ratio, the age at which females changed sex decreased with increased exploitation, suggesting smaller body size, and presumably lower fecundity, for females in heavily exploited sex changing stocks. Our game theoretic approach to evaluating hermaphroditic stocks can accommodate a wide variety of sex changing cues and behaviours and allows a flexible model for understanding the effects of exploitation on hermaphroditic stocks.

Keywords: black sea bass, exploitation, fisheries, game theory, hermaphroditism, protogyny.

Introduction

The ability to change sex over an individual's lifetime (sequential hermaphroditism) has been widely documented in marine teleost fish, having been confirmed in 48 families from thirteen orders including many recreationally and commercially important species (Sadovy de Mitcheson and Liu, 2008; Erisman and Hastings, 2011). Although hermaphroditism is generally well known by fisheries managers, and some management agencies collect data relevant to management of such species (e.g. sex ratio of the catch), most assessments of hermaphroditic stocks are conducted using the same methods as those which are generally applied to non-sex changing fish (Provost and Jensen, 2015). The failure to tailor assessments to the biology of hermaphroditic stocks may lead to poor estimates of biological reference points, or of the effects of exploitation on the stock, perhaps leading to collapse (e.g. Heppell *et al.*, 2006; Alonzo *et al.*, 2008; Brooks *et al.*, 2008). Long-term failure in monitoring exploitation of such populations may also induce evolutionary changes in age at maturity and energy allocation among many other traits (Sattar *et al.*, 2008).

A common theme emerging from research on sequential hermaphrodites is that the specifics of when and why an individual changes sex are critical to understanding the response of the population to harvest (Alonzo and Mangel, 2005). In many studies on the effects of fishing on protogynous (female to male sex change) populations, it is assumed that a female will change sex at a fixed age or size (Alonzo and Mangel, 2004) or that a female

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will change sex at an age proportional to the average age/size of the population (Armsworth, 2001). Given these assumptions, in a fishery where larger fish (predominately male) are preferentially targeted or retained, the sex ratio can become highly female biased and the population may suffer from sperm limitation (Sato and Goshima, 2006). This effect may lead to rapid population decline in the face of fishery-induced mortality, and eventual collapse (Armsworth, 2001; Alonzo and Mangel, 2004). However, species that show plasticity in the timing of their sex change are in some cases as resilient to fishing as non-sex changing stocks (Alonzo and Mangel, 2005; Molloy *et al.*, 2007; Ben Miled *et al.*, 2010). This resiliency is driven by the ability of the stock to compensate for selective loss of one sex by the other transitioning at an earlier age or size than in the absence of fishing. Even when sex ratios become highly female biased due to size-selective harvest of males, the stock can still maintain resiliency if the fertilization rate remains high (Brooks *et al.*, 2008). Together these results strongly suggest that managers cannot derive simple sustainable harvest rules for all sequentially hermaphroditic fish; in short, the details matter.

We gain some insight into these details from reviewing the evolutionary theory behind sex changing populations. A primary prediction is that a hermaphroditic species will change sex at a size where the reproductive rate of the first sex equals that of the second sex (Warner, 1975). This outcome, however, is not common for many wild populations of hermaphrodites, as many will change sex earlier than predicted under the size-advantage theoretical model, suggesting factors other than size play a role in triggering sex change (Kazancioğlu and Alonzo, 2010; Rogers and Koch, 2011). From empirical tests of sex-change theory, we know that sex change in hermaphroditic fish will depend on a combination of social as well as endogenous cues (Warner and Swearer, 1991; Alonzo and Mangel, 2005; Benton and Berlinsky, 2006). For example, Sakai *et al.* (2002) showed that large females of the protogynous wrasse, *Halichoeres melanuurs*, exhibited male sexual behaviour immediately after male removal and became functionally male within 2–3 weeks of removal. However, when the largest female was relatively small, she was less likely to perform the male role. Reluctance to perform the male role at smaller body size is presumed to be due to strong female mate choice for larger males and male/male competition (Sakai *et al.*, 2002). The existing body of research on this topic thus suggests that sex change is driven by a combination of exogenous (e.g. social) and endogenous (e.g. body size) cues. The implication for stock assessment and management is that population models must be flexible enough to capture the complexities of each species' sex change "rules" (Alonzo and Mangel, 2005).

Evolutionary game theory provides a modelling framework in which complex cues of sex change can be represented. Game theory has been used to study hermaphroditic life histories in fishes and many have shown the conditions under which sex change is expected to evolve, and the timing of sex change in such species (Charnov, 1982; Kazancioğlu and Alonzo, 2009; Ben Miled *et al.*, 2010). Game theory is a logical way to represent the life histories of sequentially hermaphroditic species in that it explicitly organizes how costs and benefits to changing sex trade-off against one another to produce net payoffs to the individual. Although other authors have generated model structures that capture these dynamics to a greater or lesser extent (e.g. Alonzo and Mangel, 2005, Molloy *et al.*, 2007), here we formalize its use within a broad and flexible framework to allow its use for many species, rather than a species-specific model. We use our model to determine the maximum sustainable yield (MSY), Biomass at U_{MSY} (B_{MSY}), number of males in the population, number of females changing sex, and average age at sex change. We use as an example black sea bass (*Centropristis striata*), a protogynous hermaphrodite that is the target of important recreational and commercial fisheries throughout much of the Atlantic coast of the United States. We then evaluate how these factors influence estimates of fisheries yield, and compare these estimates to those of an otherwise identical gonochoristic population.

Methods

We chose black sea bass due to its economic and cultural importance throughout the mid-Atlantic coast of the United States. The high exploitation and past overfishing of black sea bass, along with its protogynous mating system make it an ideal species for a modelling approach such as the one presented here (NEFSC, 2012; Provost, 2013). In addition, the most recent stock assessment for black sea bass in the mid-Atlantic region was rejected by the reviewers, in part because it failed to incorporate the protogynous life history of the species within the assessment model. We first built an age and sex-based population projection model and applied it to a non-sex-changing stock. The model included age-specific natural survival (S), age and sex-specific vulnerability to fishing (v), and sex-ratio dependent recruitment (R). Individuals in age-class 2 and above were considered mature. The population model followed the form:

$$\boldsymbol{X}_{t+1} = \boldsymbol{X}_t\boldsymbol{S} - \boldsymbol{X}_t\boldsymbol{U}_x + \boldsymbol{R}_{xt} - \boldsymbol{C}_t$$
$$\boldsymbol{Y}_{t+1} = \boldsymbol{Y}_t\boldsymbol{S} - \boldsymbol{Y}_t\boldsymbol{U}_y + \boldsymbol{R}_{yt} + \boldsymbol{C}_t \quad (1)$$

Where $\boldsymbol{X}_t$ is the total female population vector and $\boldsymbol{Y}_t$ is the male population vector for age classes 1–10 at a given time (t), $\boldsymbol{S}$ is the survival vector consisting of individual annual survival probability estimates for age classes 1–10 calculated as $1-\boldsymbol{M}$ where $\boldsymbol{M}$ is the natural mortality probability vector for each age class. $\boldsymbol{U}$ is the harvest vector of v per age class and is biased toward larger fish and males (Provost, 2013). $\boldsymbol{R}$ is the young recruited into the population for females ($\boldsymbol{x}$) and males ($\boldsymbol{y}$), and $\boldsymbol{C}$ is the number of female fish that become male (set to zero for the non-protogynous population). Age-specific annual natural mortality was estimated using the Lorenzen (1996) model fitted to a power curve (NEFSC, 2012)

$$\mathrm{M} = M_{\mathrm{u}}(\mathrm{age}^b) \quad (2)$$

where M_{u} is the mortality at unit age and b is a scaling factor. Each age-specific mortality value was used to create the mortality vector ($\boldsymbol{M}$). Vulnerability of each sex and age class were estimated from mark-recapture data (Provost, 2013) and used to create the vulnerability vector ($\boldsymbol{v}$).

Recruitment (R) is calculated as:

$$R = Ef\ S_{\mathrm{e}} \quad (3)$$

where E is recruitment at maximum fertilization, f is the probability of an egg being fertilized and S_{e} is the probability of an egg surviving to hatch. Alternatively, this could be written in terms of a marriage function (e.g. Iannelli *et al.*, 2005). The recruits are

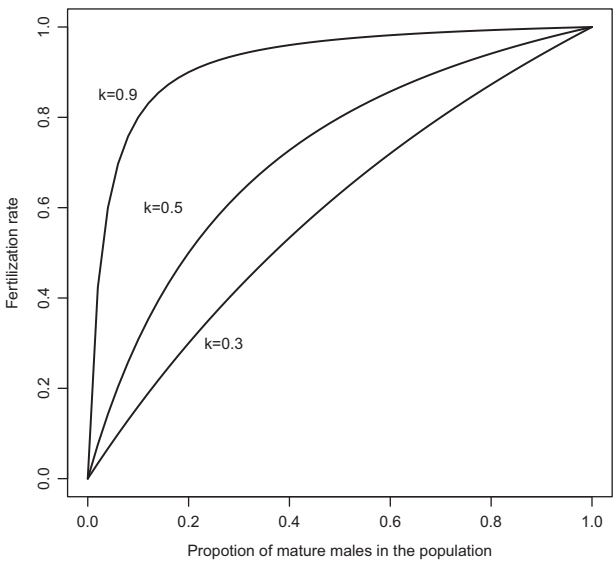

Figure 1. Fertilization rate as a function of the proportion of mature males in the population at varying levels of *k*, a stock specific parameter controlling the ability of the population to compensate for loss of males (equation 5). $k = (0.3, 0.5, 0.9)$.

added to the first age-class of the female population vector ($\boldsymbol{X}$) with probability (p_x) or male population vector ($\boldsymbol{Y}$) with probability ($1 - p_{xy}$). E follows the Beverton-Holt model (Hilborn and Walters, 1992):

$$E = \frac{\alpha F_{\mathrm{m}}}{\beta + F_{\mathrm{m}}} \tag{4}$$

where α is the maximum number of eggs produced by the population, F_{m} is the number of mature females in the population, and β is the value for F_{m} when $E = \frac{\alpha}{2}$.

Fertilization (f) was modified from Brooks *et al.* (2008) so that

$$f = \frac{4km}{(1-k) + (5k-1)m} \tag{5}$$

where m is the proportion of mature males in the population and k is a stock specific parameter controlling the ability of the population to compensate for loss of males, which can range from 0.2 to 1.0. (Brooks *et al.*, 2008). At high values of k, a population can maintain its fertilization rate when there are few males in the population. One would expect species that spawn in groups to have high values for k. At low values of k, losing one male can have detrimental effects on the reproductive output of a population (Figure 1). Species that spawn in pairs are expected to have low values for k.

We started with 100 000 individuals in the population and ran the model under no fishing mortality until the population stabilized. The resulting stable age and sex distributions were used as the initial age and sex distributions for the model under fishing pressure. The model was run with mortality rates of $0.75 \times \times \boldsymbol{M}, \boldsymbol{M}$, and $1.25 \times \boldsymbol{M}$; however, our results did not vary across these levels of natural mortality; all results presented are for models run where **M** is the natural mortality rate. We then estimated MSY, B_{MSY}, and male/female ratios for the population across varying values of k. These values were all estimated numerically by varying exploitation rate ($\boldsymbol{U}$) proportionally in 5% increments and summing total catch over 20 years. The value of U that maximized the catch over this time period was taken to be U_{MSY} and the associated annual catch and abundance at age vector were MSY and N_{MSY}, respectively. Total equilibrium biomass summed across all age classes of N_{MSY} (B_{MSY}) was calculated by multiplying N_{MSY} by the average weight at age (w_{a}) from the following allometric relationship

$$w_{\mathrm{a}} = v_1 l_{\mathrm{a}}^{v_2} \tag{6}$$

where l_{a} is length at age a and v_1 and v_2 are species specific parameters. Length at age was modelled via the von Bertalanffy (1938) growth equation:

$$l_a = L_\infty(1 - e^{-K(a-t_0)}) \tag{7}$$

Parameters were estimated from lengths, weights, and ages of black sea bass collected off of New Jersey (Provost 2013). We caught 1762 males and 1931 females over two study seasons (2011–2012) and we used these to estimate sex-specific length at age. We fit parameters L_∞, K, and t_0 by non-linear regression. All parameter values to initialize the model and their sources used can be found in Table 1.

We then calculated MSY, B_{MSY}, and male/female ratios for a protogynous stock using the same population model described above, but also allowing females to change sex. Sex change occurred according to a game theoretic payoff defined by the fitness and energy loss associated with the decision to change sex or not following a size dependent dynamical game (Kebir *et al.*, 2015). We are focused on protogynous species; therefore size is used as a proxy for reproductive value as size is strongly related to male reproductive value in protogynous species (e.g. Zabala *et al.*, 1997; Munday *et al.*, 2006). As such, the decision to become male will occur when the reproductive value of becoming male is greater than reproductive value of being female.

The potential "Gain" for a female fish (Gain$X$) is simply her potential contribution to recruitment (R) given her size in the next year ($l_{\mathrm{ax}(t+1)}$). The shape of this relationship is given by

$$GainX = 10^{1+l_{\mathrm{ax}(t+1)}/\mu_{l_{\mathrm{ax}(t+1)}}} \tag{8}$$

where $\mu_{l_{\mathrm{ax}}}$ is a weighted average of the sizes of all other females in the current population and t is time. Consistent with the unidirectional nature of sex change in the protogynous black sea bass, male fish cannot change sex in this system. A female fish may change sex or not depending on the relative "Gain" for remaining female or becoming male. Therefore, we computed the potential "Gain" for a male fish (Gain$Y$) similarly to that of the female in order to calculate its potential contribution to R, given the size of the fish.

$$\mathrm{Gain}Y = 10^{1+l_{ay(t+1)}/\mu_{l_{ay(t+1)}}} \tag{9}$$

The "Gain" for a fish that changes from female to male (GainXY) is equivalent to Gain$Y$. The impact of size on the 'Gain' is based on observations in the literature, however, this number is normalized to 1 in order to calculate the payoff (see below), and the impact of numeric values is relative. The only biological relevance

Table 1. Parameter values used in the model and for equations (1)–(6).

Parameter	Parameter value	Source and definition
Mortality		
q	0.694	Parameter for Lorenzen model (NEFSC, 2012)
age	[0.5, 1, 2. . . . . .10]	Age of individual fish
c	−0.417	Parameter for Lorenzen model (NEFSC, 2012)
Exploitation		
U_x	[0, 0.42, 0.54, 0.63, 0.63, 0.63, 0.63, 0.63, 0.63, 0.63]	Maximum exploitation of females. Estimated from mark recapture data on black sea bass (Provost, 2013).
U_y	[0, 0.42, 0.11, 0.28, 1, 1, 1, 1, 1, 1,]	Maximum exploitation of males. Estimated from mark recapture data on black sea bass (Provost, 2013).
Recruitment		
α	2 800 000	Maximum number of eggs that can be produced by the population.
β	50 000	Number of mature females required to produce half of the maximum number of eggs.
F_m	48 040	Number of mature females.
k	[0.2, 0.3. . . . . .1.0]	Steepness parameter for fertilization rate (Brooks *et al.*, 2008)
m	0.34	Proportion of mature males in the population.
S_e	0.05	Survival of eggs.
Biomass		
v_1	0.0649	Species specific parameter for estimating weight at age. (Bohnsack and Harper, 1988)
v_2	2.468	Species specific parameter for estimating weight at age. (Bohnsack and Harper, 1988)

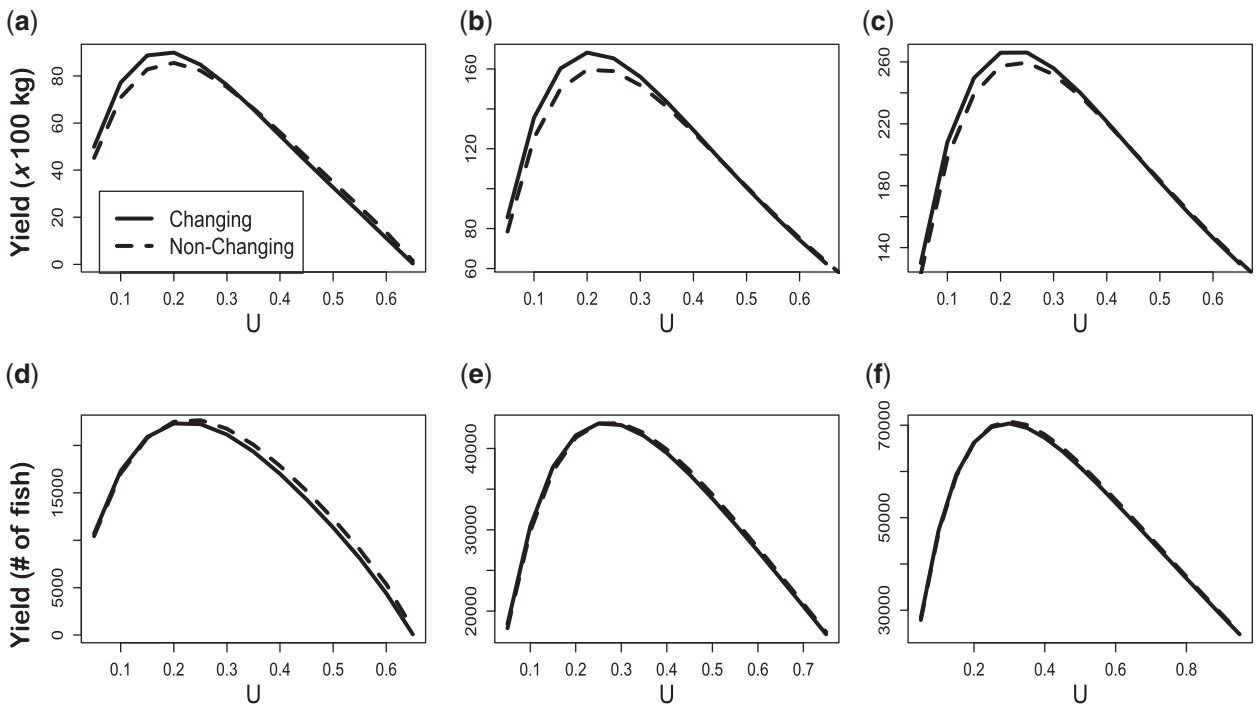

Figure 2. Biomass yield (a–c) and total yield in numbers of fish (d–f) at varying exploitation rates (U) for $k = 0.3$ (a and d), $k = 0.5$ (b and e), and $k = 0.9$ (c and f). The solid line represents the values for the sex changing stock and the dashed line represents values for the non-sex changing stock in all graphs.

in interpretation for the outcome of the model comes from the shape of the curve described. The "Loss" for a female fish in this system (Loss$X$) is set to zero as her contribution to recruitment cannot be any higher or lower than the expected value for a female of a given size; i.e. she will contribute all that she is allowed based on her size, no more or less. The "Loss" for a male fish (Loss$Y$) is the competition for mates, assuming that larger fish in a protogynous species will outcompete smaller ones and have a higher probability of fertilization, particularly for species with a low value for k, given by

Table 2. B_{MSY} and MSY for gonochoristic (G) and protogynous (P) stocks at varying values of *k* (the parameter controlling the ability of the population to compensate for loss of males).

k	B_{MSY} (G)) (× 1000 kg)	B_{MSY} (P) (× 1000 kg)	MSY (G)	MSY (P)
0.2	3645	3672	9404	8786
0.3	8554	8988	22 666	22 317
0.4	12 573	13 287	33 780	33 664
0.5	15 957	16 818	43 092	43 082
0.6	18 906	19 806	51 414	51 212
0.7	21 542	22 378	58 685	58 433
0.8	23 873	24 619	65 109	64 768
0.9	25 951	26 540	70 833	70 379
1	27 817	28 401	75 970	75 388

$$LossY = \text{Gain}Y\left(1 - \left(1 + \frac{l_{ay(t+1)}}{\mu_{l_{ay(t+1)}}}\right)\right) \quad (10)$$

The "Loss" for a fish that will change sex from female to male is calculated similarly, however, there is a growth penalty to changing sex.

$$LossXY = \text{Gain}Y\left(1 - \left(1 + \frac{l_{ax(t)}}{\mu_{l_{ay(t+1)}}}\right)\right) \quad (11)$$

The female fish is not allowed to grow during the year it undergoes the sex change to account for the energetic cost of sex change (e.g. Hamaguchi *et al.*, 2002). Kebir *et al.* (2015) showed that size dependent models of sex change alone may not be sufficient to accurately characterize the timing of sex change, and that the penalty of changing sex must be included. Therefore, sex change will occur, or not, based on the reproductive output at her current size rather than her size in the next year.

The "Payoff" for each sex is simply the "Gain–Loss".

$$\text{Payoff}X = \text{Gain}X - \text{Loss}X \quad (12)$$

$$\text{Payoff}Y = \text{Gain}Y - \text{Loss}Y$$

$$\text{Payoff}XY = \text{Gain}XY - \text{Loss}XY$$

If Payoff*X* is greater than or equal to Payoff*XY*, the fish will remain female. If not, she will change sex.

Finally, we removed those individuals that changed sex from the female population vector and added them to the male population vector. This allowed us to calculate the average age at which the protogynous population was expected to change sex across varying fishing pressures and values of *k*. By considering many values of *k*, we tested the effects of fishing at various levels of male/male competition and across many fertilization rates. We then compared MSY, B_{MSY}, and male/female ratios for the gonochoristic and sex changing stocks.

Results

Gonochoristic stocks produced a slightly higher MSY for all values of *k* (Table 2; Figure 2). MSY for the gonochoristic[MSY(G)] stock ranged from 9404 individuals to 75 970 while MSY for the sex changing [MSY(P)] stocks ranged from 8786 to 75 388 (Table 2). Each stock produced the lowest MSY when $k = 0.2$ and the highest MSY when $k = 1$. The highest difference (as a percent) in MSY between stock types was at $k = 0.2$ where MSY of the gonochoristic stock was 7% higher than that of the sex changing stock. The lowest difference (as a percent) was at $k = 0.5$ where the difference was 0.02% (Table 2).

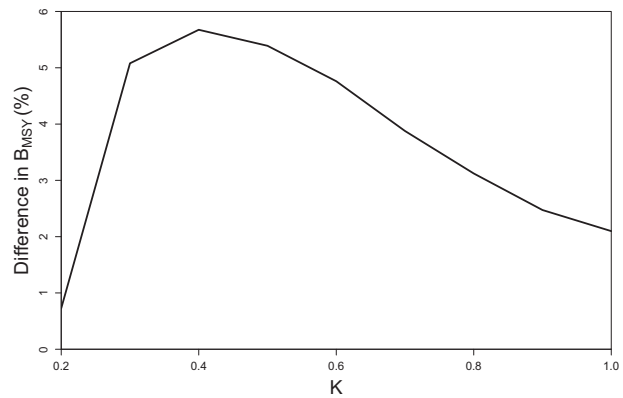

Figure 3. Difference in B_{MSY} as a percent of the total difference between B_{MSY} for a sex-chaning stock and B_{MSY} for the non-sex changing stock at varying values of *k*.

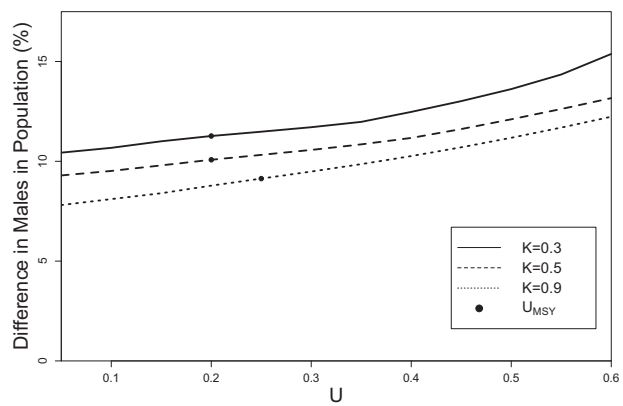

Figure 4. Difference in the proportion of males in the population of the sex changing stock and the non-sex changing stock at varying exploitation rates (U). The solid line is for values when $k = 0.3$, the dashed line represents values when $k = 0.5$, and the dotted line represents values when $k = 0.9$.

Sex changing stocks produced a higher B_{MSY} [B_{MSY}(P)] across all values for *k*, and ranged from 367 to 28 400 (×1000 kg) and the B_{MSY} for the gonochoristic stock [B_{MSY}(G)] ranged from 3645 to 27 817 (×1000 kg) (Table 2; Figure 2). The smallest B_{MSY} for each stock was when $k = 0.2$ and the largest B_{MSY} was when $k = 1$. The greatest difference in B_{MSY} between stocks was when $k = 0.4$ where the difference (as a percent) was 5.7% (Figure 3). The smallest difference in the stocks was when $k = 0.2$ where the difference was 0.74% (Table 2). Although B_{MSY} was still higher for the sex changing population, there was a steep decline in the difference in B_{MSY} between $k = 0.4$ and 0.2 (Figure 3). This result is likely due to the inability of sex changing stocks to effectively compensate for the loss of males when *k* is very low (i.e. where males matter the most).

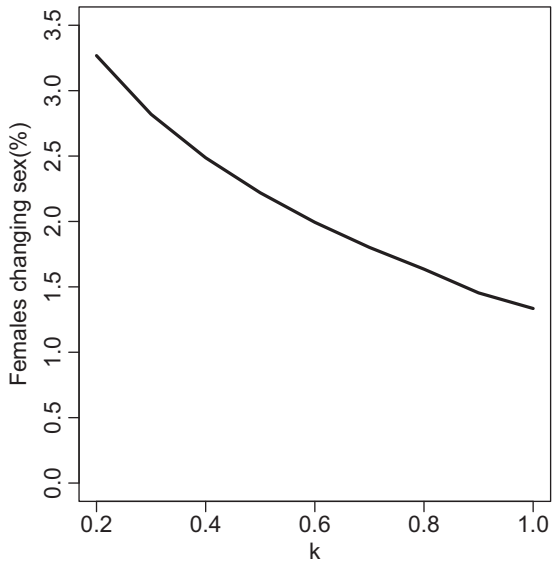

Figure 5. The percentage of females that changed sex in the sex changing population at varying values of *k*, calculated as the number of females that change sex divided by the number of mature females.

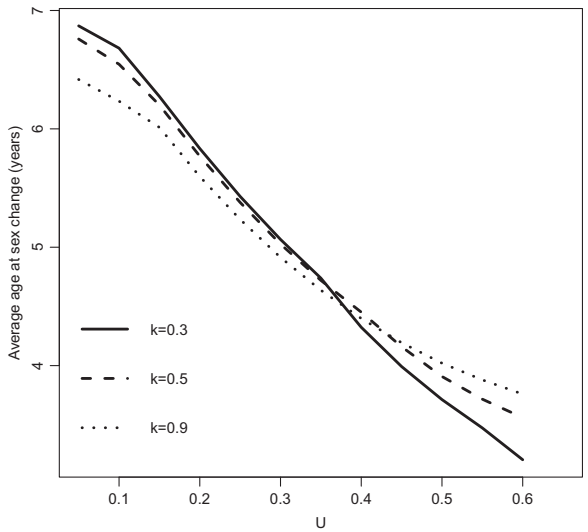

Figure 6. The average age at sex change for the sex changing stock at varying rates of exploitation (U). The solid line is for values when $k = 0.3$, the dashed line represents values when $k = 0.5$, and the dotted line represents values when $k = 0.9$.

The higher B_{MSY}, despite lower MSY, for the sex changing stock reflects the higher proportion of males in that population than in the gonochoristic population; they are larger so the mass per fish is higher (Figure 4). The sex changing stock had a higher proportion of males in the population for all values of *k* and *U* (Figure 4). The difference in the proportion of males in the population increased with an increase in *U* and a decrease in *k*. The number of females that changed sex in the sex changing stock decreased as *k* increased, reflecting the relative importance of males to the fertilization rate as *k* decreases (Figure 5). For low *k* values, more males are required to maintain the fertilization rate, thus females changed sex at twice the rate for the lowest value of *k* than they did at the highest (Figure 5). The age at sex change decreased as the exploitation rate increased, reflecting the population's flexibility in the timing of sex change. As exploitation increased, the relative benefit of changing sex increased, thus, more females changed. As a result, the loss of large males was compensated for by the number of females changing sex. At low values of *k*, the average age at sex change decreased more rapidly as exploitation increased than it did for higher values of *k* (Figure 6).

Discussion

Exploitation of sequentially hermaphroditic fish stocks is common, and these species make up a large proportion of the fisheries serving poorer nation-states (e.g. Carribean; Chiappone *et al.*, 2000; Caballero-Arango *et al.*, 2013). Such fisheries are prone to over-fishing in part due to data scarcity, and the lack of species-specific catch and effort regulations (Chiappone *et al.*, 2000). Methods exist to evaluate the population status of data-poor species (Bednarek *et al.*, 2011), however standard fisheries models cannot account for the effects of sex change in their results. Existing models designed to evaluate the sustainable harvest of sex-changing species (Alonzo and Mangel 2005; Heppell *et al.*, 2006; Molloy *et al.*, 2007) suggest that the impacts of fishing depend heavily on poorly known and likely species-specific parameters like *k*. We developed game theoretic methods to model sustainable yield as a way to flexibly incorporate species' life histories, and illustrated the insights such a model can provide using black sea bass. Our approach considers the size of an individual female relative to the sizes of other fish in the population, the number of individuals at each size in the population, and male/male competition, although other elements of sex change can be incorporated. For example, many species may have endogenous (e.g. hormones regulated by age/size, regardless of the status of others in the population) cues that trigger sex change (e.g. Alonzo and Mangel, 2004; Heppell *et al.*, 2006), and while our example considers only exogenous (size compared with others in the population) cues, endogenous ones could be easily incorporated into the game theoretic framework. Our framework also allows each parameter to be modified or tested over a range of values if the data for a specific species is not available, or if one wishes to weight parameters differently. The flexibility inherent in our model may prove beneficial for species in regions where fishing is especially important, yet where managers lack the resources to perform formal stock assessments.

Our results suggest that a hypothetical black sea bass stock has a slightly lower MSY but a higher B_{MSY} than an otherwise identical gonochoristic stock. This higher B_{MSY} for the sex changing stock is due to the higher numbers of male fish in the population, as male black sea bass are larger than females of the same age (Provost, 2013). As males were fished out of the population, females in the sex changing stock were able to replace them. Females in the sex changing stock replaced males more readily when maintaining the fertilization rate required more males in the population (i.e. low values for *k*, the parameter controlling the ability of the population to compensate for loss of males). Females in the sex changing populations in our model did not replace males lost to harvest nearly as quickly when $k > 0.5$. This finding, along with those of Brooks *et al.* (2008), illustrates the importance of understanding how much males contribute to

reproductive success for a population of concern. We showed that individuals in a protogynous population with low values for *k* would decrease their age-at-sex-change more rapidly than those in stocks with higher values for *k*. This suggests exploitation will affect stocks with a lower value for *k* more drastically than those with a high value.

By adding the fertilization rate to the male/male competition component of the model, we were able to determine how the decision to remain female or become male changes with varying values of *k* in the fertilization rate; where *k* is a proxy for the importance of males to the reproductive output of a population. The impact of sex ratio on the fertilization rate has not been estimated empirically for a real fish population. However, the impact of changing sex ratio on the fertilization rate is essential to understanding population dynamics and the effects of fishing on protogynous species. Even if it cannot be directly measured, these parameters may be inferred from the reproductive behaviour of a species. One would assume species that spawn in large groups would have relatively high values of *k* because losing one male will not be very detrimental to the population (Brooks *et al.*, 2008). One would also assume that species that spawn in pairs would have a very low value for *k* because losing a male could have detrimental effects on the population's fertilization rate. This has been shown in the protogynous reef fish *Thalassoma bifasciatum*, which has two distinct mating systems; group mating and paired mating (Marconato *et al.*, 1997). For high values of *k*, we observed the lowest amount of sex change and for the lowest values of *k* we observed the highest amount of sex change. Understanding the breeding behaviour of a protogynous species will allow researchers to estimate *k* and better understand the impacts of fishing on the fertilization rate and on the stock as a whole.

We found that increased exploitation increased the difference in male proportion of the population between gonochoristic and sex changing stocks, and decreased the average age at sex change for the sex changing stock. This result is due to the compensatory mechanism of flexible timing at sex change. For the species with a relatively fixed age-at-change, the proportion of males drastically declines with an increase in exploitation (Alonzo and Mangel, 2004; Heppell *et al.*, 2006). For species with plasticity in their age-at-change, populations may remain relatively stable under higher rates of exploitation (Alonzo and Mangel, 2005). This stability is due to the flexibility in this life history parameter. In order for gonochoristic species or species with fixed age-at-change to maintain a stable sex ratio, their age-at-maturity and/or age-at-change would have to decrease. These traits could require thousands of generations to respond to exploitation, but a trait such as age-at-change in a species where that trait is flexible may be changed in a single generation (e.g. Sattar *et al.*, 2008). Although adjusting the age at which females can change sex can compensate for lost males, it does create a situation where the average size of individuals in the population decreases with an increase in exploitation. It has been shown for protogynous stocks that populations under heavy fishing pressure may have similar sex ratios to those stocks of the same species under lighter fishing pressure (Götz *et al.*, 2008). However, these studies have also shown that stocks under heavier fishing pressure have a smaller average body size and a smaller size-at-change than those under lighter fishing pressure (Hamilton *et al.*, 2007; Götz *et al.*, 2008). The findings of these studies are reflected in our results as well. Although the sex ratio for our sex changing stock remained fairly constant across varying rates of exploitation, the age-at-change decreased drastically. If fishery managers were to collect data on the age or size-at-change for sex changing stocks, they could alert policy makers to fishing rates that may be dangerously high. Many assessments collect data on sex ratio, however few collect data on age-at-change (Provost and Jensen, 2015). Although sex ratio can allow managers to detect problems in gonochoristic populations or sex changing populations with a fixed age-at-change, it is not as helpful for sex changing stocks with flexible age-at-change.

Our game theoretic approach accommodates stocks with fixed age-at-change and/or stocks that cue on exogenous factors before changing sex. Although there may be other fisheries induced changes to life history traits of hermaphroditic stocks that may affect sex change such as age at first maturity, or energy allocation (e.g. Sattar *et al.*, 2008), we focused on the rapid effects of exploitation on sex change that may be monitored by fisheries managers and included in stock assessments. Our implementation here included competition as a function of the size relative to the population and weighted by the number of individuals in each size class. Some models considering exogenous cues for sex changing fish have simply assumed that a fish will change sex when it reaches a given size relative to the largest in the population (e.g. Molloy *et al.*, 2007). Other models have included expected reproductive output as a cue for sex change (e.g. Alonzo and Mangel, 2005). Although these assumptions may hold true for some species, such a case-by-case approach to examining the effects of exploitation on sex changing fish would not be of broad use. If the assumptions above were true for a species of concern, our game theoretic framework would accommodate that assumption by simply adjusting the "Loss matrix" to fit the assumptions. This framework also provides an opportunity to determine the effects of exploitation on the assumptions themselves. The results of our approach are similar to those produced by more species-specific models in that they both predict that sex changing stocks that use exogenous cues are as robust to exploitation as gonochoristic stocks. Our results also predicted that stocks of sex changing fish, while maintaining similar sex ratios, tend to have smaller individuals and smaller size-at-change. This matches the empirical results observed for sex changing stocks (Hamilton *et al.*, 2007; Götz *et al.*, 2008). Having such a flexible, non-species specific model to examine the effects of fishing may be beneficial to managing sex changing species.

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