THE IMPACTS OF FISHING ON HERMAPHRODITIC SPECIES AND TREATMENT OF SEX CHANGE IN STOCK ASSESSMENTS

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Sex-changing fish species present unique challenges for stock assessment and management. Fishing is known to cause size at sex change to decrease and sex ratios to increasingly skew because of sex-selective fishing patterns. We show through a systematic literature review that the effects of fishing on hermaphrodite species can vary widely. Intense fishing has had no detectable effect on sex ratio and size at sex change in some stocks but a clear and dramatic impact on others. There is also substantial variation in the way stock assessments incorporate sex change. Of the 12 stock assessments of hermaphroditic fish stocks in the United States, none evaluate sex-based differences in selectivity, 10 report current sex ratio and estimate size at sex change, and only one tracks changes in both of these critical population characteristics. Despite these challenges, a global comparison of stock status suggests that the status of hermaphroditic stocks is not substantially different from that of gonochoristic species.

Impactos de la pesca en especies hermafroditas y el tratamiento del cambio de sexo en la evaluación de los stocks

Las especies de peces que cambian de sexo, representan retos únicos en cuanto a la evaluación y el manejo de los stocks pesqueros. Se sabe que la pesca reduce la talla a la que los peces cambian de sexo y sesga la proporción de sexos cuando los patrones de pesca son selectivos a esta propiedad. Mediante una revisión bibliográfica se muestra que los efectos de la pesca en especies hermafroditas pueden variar ampliamente. En algunas especies, la pesca intensa ha mostrado no causar efectos detectables en la proporción de sexos ni en la edad de cambio de sexo, pero en otras los efectos son claros y drásticos. También existe una considerable variación en la forma en la que los métodos de evaluación de stocks incorporan el cambio de sexo. De las 12 evaluaciones de stocks de peces hermafroditas en los Estados Unidos de Norteamérica, ninguno consideró diferencias en la selectividad en función del sexo, 10 reportan proporción de sexos y estiman la talla a la cual ocurre el cambio de sexo y sólo en uno se rastrean los cambios en estas dos características poblacionales clave. A pesar de estos retos, una comparación global de los stocks de peces hermafroditas sugiere que su estado de explotación no es distinto que el de las especies gonocóricas.

Les impacts de la pêche sur les espèces hermaphrodites et le traitement du changement de sexe dans l'évaluation des stocks

Les espèces de poissons hermaphrodites représentent des défis uniques pour l'évaluation et la gestion des stocks. La pêche est connue pour causer une diminution des changements de sexe selon la taille et fausser de plus en plus le ratio des sexes à cause des modes de pêche sélectifs en fonction du sexe. Nous montrons à travers une revue systématique de la littérature que les effets de la pêche sur les espèces hermaphrodites peuvent varier considérablement. La pêche intensive n'a eu aucun effet détectable sur le ratio des sexes et le changement de sexe selon la taille dans certains stocks, mais un impact évident et dramatique sur d'autres. Il existe aussi des variations importantes dans la façon dont les évaluations des stocks prennent en compte le changement de sexe. Sur les douze évaluations des stocks de poissons hermaphrodites aux États-Unis, aucune d'elles n'évalue les différences fondées sur le sexe en matière de sélectivité, dix font état d'un ratio des sexes et évaluent le sexe selon la taille et une seule analyse les changements de ces deux caractéristiques principales de cette population critique. Malgré ces défis, une comparaison globale de l'état des stocks suggère que l'état des stocks hermaphrodites ne diffère pas sensiblement de celle des espèces gonochoriques.

INTRODUCTION

Sex change is a life history strategy found in a wide variety of fish species, including many species of commercial and recreational importance. Numerous studies have examined the implications of sex change for fitness (Ghiselin 1969; Warner et al. 1975), but the implications of sex change for stock assessment and fishery management are less clearly understood. Previous reviews of hermaphroditism in fishes have focused on the theoretical advantages of changing sex from female to male (protogyny) and from male to female (protandry; Ghiselin 1969; Ross 1990) and the prevalence of these unique reproductive strategies in different ecological contexts throughout extinct and extant fishes (Smith 1975). Recent studies suggest that the timing of sex change is very flexible; some hermaphroditic species are capable of changing sex earlier or later in response to local fluctuations in the population sex and size ratio, and select species may even change sex multiple times (Munday et al. 2006).

This review of hermaphroditism focuses on the effect that fishing has had on sex-changing fish species and highlights the variation in how stock assessments currently address sex change. First, we review why hermaphroditic fish species may be especially vulnerable to fishing. Second, we show that fishing can impact hermaphroditic life history and population

structure in two specific ways: fishing can cause a greater skew in sex ratios and/or a decrease in the size or age at sex change. Then, we summarize how sex change is addressed in stock assessments and briefly review the variation in methods for calculating biological reference points in hermaphroditic stocks in the United States. Contrary to concerns in the literature that hermaphroditic fish are particularly vulnerable to fishing, we show that the stock status of hermaphroditic species is not substantially different from the stock status of gonochoristic (non-sex-changing) species and that the effects of fishing on sex ratio and size or age at sex change cannot be generalized to all hermaphroditic fish species.

VULNERABILITY OF HERMAPHRODITIC FISHES TO FISHING

Differences in life history between hermaphroditic and gonochoristic fish species suggest that hermaphroditic species are especially vulnerable to fishing (Alonzo et al. 2008). In stock assessments of gonochoristic fish species, sex ratio is often not evaluated and spawning stock biomass is calculated from mature female biomass alone. This simplification is reasonable if the fishery impacts both sexes equally or if male abundance does not limit fertilization or reproductive output. In sex-changing species, however, there is reason to suspect that fishing mortality does not impact males and females equally. Size selectivity,

either inherent to the fishing gear or a result of management actions such as size limits, translates into sex-based differences in fishing mortality rate for fish species where the sex ratio changes with size. Change in sex ratio with size is a common feature of hermaphroditic fishes and also occurs in gonochoristic species with sexually dimorphic growth; for example, Summer Flounder *Paralichthys dentatus*, (Morson et al. 2012). Size or age selectivity is often accounted for in stock assessments, but selectivity that varies by sex is rarely addressed. Fishing patterns that disproportionately target one sex over the other can potentially have serious consequences for population growth, fertilization, and stability over time (Alonzo et al. 2008) and are important to consider in stock assessments of hermaphroditic fish species. In addition to sex ratios that vary by size, many other characteristics of hermaphroditic fish species suggest that sex-selective fishing is a common occurrence in fisheries of hermaphroditic species.

Differences in sex-specific behavior often cause one sex to be more vulnerable to fishing. Aggressive behavior is known to increase catchability in gonochoristic fish species (Sutter et al. 2012) and will likely have a similar effect in hermaphroditic species. In many protogynous species, male fish exert aggressive behavior while defending territories (Warner et al. 1975; Hoffman 1985) or guarding female mates (Frickle and Frickle 1977; Moyer and Nakazono 1978). Observations by Gilmore and Jones (1992) found that in Scamp *Mycteroperca phenax*, a protogynous hermaphrodite in the Gulf of Mexico, males had greater overall movement, displayed more aggressive behavior (e.g., lunging, attacking), and (anecdotally) had a higher propensity to bite hooks compared to females of a similar length. The authors hypothesized that male Scamp have higher fishing mortality because of their aggressive behavior as seen in underwater videos. Aggression levels also differ between individuals based on social status within social aggregations; in protogynous hermaphrodites, dominant males express the most aggression (Layton and Fulton 2014). There are, however, exceptions such as Red Porgy *Pagrus pagrus*, a protogynous hermaphrodite located in the Gulf of Mexico and South Atlantic. In this species, males show little aggression, and male and female fish appear to be captured proportionally, suggesting that males and females are equally vulnerable to hook-and-line fishing gear (DeVries 2007).

Hermaphroditic fishes may also be vulnerable to fishing because fertilization is dependent upon complex social structures, such as harems, formed during spawning. Social structures help facilitate mate choice during the spawning season (Moyer and Nakazono 1978; Nemtzov 1985; McCormick et al. 2010). Frequent removal of large, dominant individuals by fishing may interrupt these social hierarchies. It is possible that such removal could delay female reproduction and negatively impact fertilization rates, especially in species with a short spawning season and narrow window of opportunity for mating. In Red Hind *Epinephelus guttatus*, for example, small groups consisting of a single male and multiple females come together during a two-week spawning period (de Mitcheson et al. 1994). Exposure to intense fishing pressure during this narrow timeframe could result in rapid removal of large, male individuals. In situations similar to this, females may not have sufficient time to form new spawning groups or, alternatively, reverse their sex and take advantage of mating opportunities with the recently abandoned females.

Sexually dimorphic growth, a characteristic of some gonochoristic and many hermaphroditic fishes, likely increases

fishing vulnerability for two reasons. First, faster-growing fish grow into vulnerable size ranges more quickly than slow-growing individuals; therefore, they are more susceptible to being captured (Sinclair et al. 2002). Individuals of hermaphroditic species typically experience a burst in growth rate immediately after sex change; for example, parrotfishes (family Scaridae; Munday et al. 2004) and Circle-Cheek Wrasse *Halichoeres miniatus* (Munday et al. 2009). It is hypothesized that this burst in growth increases their ability to compete with existing males. Faster growth rate may push transitioning individuals into size classes vulnerable to fishing (such as a legal catch size) more quickly than non-sex-changing individuals. Second, faster-growing fish have greater energy requirements and must forage more aggressively than slow-growing fish and, therefore, are expected to bite baited hooks more frequently (Sutter et al. 2012).

Although the exact mechanism is unknown, there is evidence that hermaphroditic species that aggregate during spawning tend to have increasingly skewed sex ratios after prolonged periods of fishing (Carter et al. 1994; de Mitcheson et al. 1994; Coleman et al. 1996). Gag *M. microlepis* and Scamp, both protogynous hermaphrodites that form large spawning aggregations, demonstrated a precipitous drop in the proportion

Differences in sex-specific behavior often cause one sex to be more vulnerable to fishing.

of males (from 17% to 1% and 36% to 18%, respectively) over a span of 25 years of exploitation in the Gulf of Mexico (Coleman et al. 1996). In contrast, Red Grouper *Epinephelus morio*, a nonaggregating protogynous hermaphrodite with an overlapping range, showed little change in sex ratio over the same time period and under similar fishing conditions. There are many reasons that may explain this phenomenon; for example, behavior could be sex-specific in spawning aggregations (e.g., Taborsky 1994), lending one sex to be more vulnerable to capture, or spawning aggregations could be predominately composed of a single sex (de Mitcheson et al. 1994) so that only the aggregating sex is exposed to intense fishing.

Changes in cohort strength may also play an important role in sex ratio fluctuations over time. If fishing disproportionately removes the terminal sex—that is, males in protogynous fish species and females in protandrous species—leading to an increasingly skewed sex ratio, then a large cohort entering the population as the initial sex will push the skewed sex ratio even further. Variability of cohort size could translate to variability in recruitment because highly skewed sex ratios may lead to lower fertilization rates.

Effect of Skewed Sex Ratios and Decreases in Size or Age at Sex Change on Fertilization Rates

Increasingly skewed sex ratios will, at some point, result in reduced fertilization rates and, consequently, slow population growth. Though the impact of incremental changes in the sex ratio on fertilization rates is not well understood in fish, there are several examples of reduced fertilization rates in marine invertebrates. A heavily male-biased fishery for blue crab *Callinectes sapidus* in the Chesapeake Bay is thought to have resulted in decreased fertilization rates because of sperm limitation (Hines et al. 2003). Similarly, in a population

of Caribbean sea urchin *Diadema antillaru*, sex ratios were dramatically skewed after a severe mortality event (Lessios 1988). Although female urchin body size and egg production per female greatly increased because of low population density after the die-off, the number of fertilized zygotes produced per female did not increase because female fertilization was drastically reduced in the absence of sufficient numbers of male sea urchins (Levitan 1992). Severe reductions in the proportion of male fish in populations of protogynous hermaphrodites may have similar effects (Alonzo and Mangel 2004), and the impact of sex ratio on fertilization rate remains one of the critical uncertainties in understanding the population dynamics of hermaphroditic fishes (Brooks et al. 2008).

One potential side effect of male scarcity in protogynous species is reduced genetic diversity (Chapman et al. 1999) and possible Allee effects: the phenomenon of negative population growth at low population size (Allee 1931). Even if fertilization rates remain high during times of male scarcity, the bottleneck of genetic material through a relatively small number of males will decrease the population's overall genetic diversity and may reduce the population's ability to adapt to environmental variability and novel pathogens. These less visible genetic bottleneck effects can occur even while fertilization rates remain high (Levitan 1992).

HOW DOES FISHING AFFECT HERMAPHRODITIC FISH SPECIES? WHAT HAVE WE LEARNED FROM DECADES OF FIELD OBSERVATIONS?

Fishing is likely to impact hermaphroditic fish species in one of two ways: (1) size or age at sex change will decrease with greater fishing intensity, or (2) sex ratios will become increasingly skewed.

Hypothesis #1: Heavy Fishing Causes a Downward Shift in Age or Size at Sex Change

Alternatively, the sex ratio may change very little or even remain constant under intense fishing conditions because of decreases in size or age at sex change. In some protogynous species, females will compensate for the loss of male individuals by changing sex at earlier ages and smaller sizes. Sex change is often a socially mediated process (Warner and Swearer 1991; Benton and Berlinsky 2006), and the process of sexual transition acts as a compensatory mechanism to maintain an optimal sex ratio (Shapiro 1979). This phenomenon has been observed in laboratory experiments (Benton and Berlinsky 2006) and in multiple field studies (Table 1). Decreases in the size or age at sex change can occur over periods as long as two to three decades; for example, in California Sheephead *Semicossyphus pulcher*, a protogynous hermaphrodite in south-central California, female size at sex change decreased between 72 and 168 mm over approximately 25 years (Hamilton et al. 2007). Decreases can also occur in as short as a few weeks; for example, in a population of protogynous Blue-Headed Wrasse *Thalassoma bifasciatum* in the U.S. Virgin Islands, size at sex change began decreasing within two weeks of heavy exploitation (Warner and Swearer 1991).

Hypothesis #2: Heavy Fishing Results in Increasingly Skewed Sex Ratios

Sex-selective fishing patterns disproportionately target the larger sex—that is, males in protogynous

species—leaving behind a greater proportion of female fish. This phenomenon has been documented in Steentjie *Spondyliosoma emarginatum* (Tunley et al. 2009), Red Hind (Beets and Friedlander 1998), and Snowy Grouper *Epinephelus niveatus* (Wyanski et al. 2000; Table 1).

Literature Review

Based on a review of published literature, we determined the degree of support for each hypothesis regarding the effects of fishing on hermaphroditic fish species. A systematic literature search was carried out using Web of Science (thomsonreuters.com/thomson-reuters-web-of-science) for publications published between 1980 and 2014. There was no restriction of origin and language. Search terms included all combinations of "fish" and ("sex change" or "sex ratio") and ("protogyny" or "hermaphroditism" or "hermaphrodite"). Publications found in Web of Science search results were screened and restricted to studies that measured size or age at sex change and/or the sex ratio in populations exposed to different levels of fishing. Some studies assessed differences among populations that were exposed to different levels of fishing; for example, comparisons between populations inside and outside of a marine protected area (Götz et al. 2008). Other publications may have tracked changes in size or age at sex change and/or the sex ratio within a single population that was exposed to increasing (or decreasing) levels of fishing over a long period of time (e.g., Hamilton et al. 2007). Studies that carried out in situ removal experiments to simulate the process of fishing were

Table 1. Summary of results from the systematic literature review showing the number of publications and species in support of hypothesis 1, size or age at sex change decreases under heavy fishing conditions (H1); hypothesis 2, sex ratios increasingly skew under heavy fishing conditions (H2); both hypotheses 1 and 2 (H1 and H2); and those where fishing had no effect on size or age at sex change and sex ratios (NC).

Hypothesis	Number of publications in support	Number of species examined	References
H1 (size at sex change decreases)	5	5	Mariani et al. (2013), Mackie (2003), Platten et al. (2002), Warner and Swearer (1991), Götz et al. (2008)
H2 (sex ratio changes)	7	10	Coleman et al. (1996), Tunley et al. (2009), Beets and Friedlander (1998), Hawkins and Roberts (2003), McGovern et al. (1998), Wyanski et al. (2000), Buxton (1993)
H1 and H2 (both effects happen)	5	5	S. A. Shepherd et al. (2010), Hamilton et al. (2007), Mariani et al. (2013), Buxton (1993), Harris and McGovern (1997)
NC (no change in sex ratio and size at sex change)	2	6	Hawkins and Roberts (2003), Adams et al. (2000)

also included in this literature review. Reference lists in each publication found through Web of Science and included here were searched to find additional relevant studies. In total, 244 publications were screened from Web of Science search results, and 735 publications were screened from bibliographies of qualifying papers found through Web of Science. Sixteen papers that studied 26 hermaphroditic species presented quantitative estimates of changes in sex ratio or size or age at sex change.

Publications found through the systematic literature review measured fishing pressure in a variety of ways. For example, Hamilton et al. (2007) verified that there were changes in exploitation level by comparing estimates of annual survivorship between historical and recent samples, and Tunley et al. (2009) were able to approximate fishing intensity by landings from recreational boats and shore anglers. For the purpose of this literature review, the type of fishing pressure reported in each study is not relevant, only that size or age at sex change and/or sex ratios were assessed at different levels of fishing. The phrase "fishing intensity" is used throughout this article to reference the general fishing level and covers such terms as exploitation, harvest, and fishing mortality.

Each eligible study was identified as showing support for either one of the two aforementioned hypotheses or for neither hypothesis: size at transition decreases under high fishing intensity (H1) or sex ratios shift—that is, in favor of females in protogynous species and males in protandrous species—while under intense fishing pressure (H2; Table 1). For some species, fishing led to changes in both the sex ratio and size or age at sex change (H1 and H2). Lastly, some studies found that fishing had no effect on the sex ratio and size or age at sex change (no change, NC).

We found more studies documenting shifts in the sex ratio under intense fishing (H2, 7/16) and slightly fewer studies showing fishing caused decreases in size or age at sex change (H1, 5/16; Table 1). The seven publications in support of H2 reported that sex ratios were increasingly skewed in 10 hermaphroditic species. Five publications found in support of H1 showed that size or age at sex change decreased in five hermaphroditic species. There were five publications that showed both sex ratios and size or age at sex change shifted with increasing fishing intensity in the same species (H1 and H2, 5/16). Two of the 16 publications specifically documented that fishing pressure did not affect sex ratio or size or age at sex change in six species (NC).

It should be noted that not every study found through the literature review assessed both sex ratio and size or age at sex change. A lack of support for one hypothesis by one study for a certain species should not be interpreted as evidence against that hypothesis. For example, Coleman et al. (1996) tracked changes in sex ratio over time in three groupers in the Gulf of Mexico. The authors found that sex ratio changed for two of the three species but reported no information on changes in size or age at sex change for all three species; therefore, we cannot make any conclusions regarding the support for H2 for each species. Even though each study did not fully address both sex ratio and size or age at sex change, the results in Table 1 show that fishing has not had a uniform effect on hermaphroditic fish species.

HOW DO STOCK ASSESSMENTS ACCOUNT FOR SEX CHANGE?

The effect of skewed sex ratios and decreases in the size or age at sex change on fertilization rates pose specific challenges for stock assessment. First, protogynous fishes could spend considerably less time reproducing as females if male fishing mortality is disproportionately high because females may undergo sex reversal earlier than usual. Without accounting for the accelerated loss of female biomass to sex change, population dynamics models may overestimate spawning stock biomass (Alonzo et al. 2008). Second, the potential for lower fertilization rates during times of male scarcity complicates recruitment calculations in population dynamics models (Brooks et al. 2008). If the potential for sperm limitation is unknown, which is likely true for most managed hermaphroditic stocks, then estimates of biological reference points (e.g., B_{MSY}) are better predicted when recruitment is measured as a function of both male and female spawning stock biomass (Brooks et al. 2008) rather than just female biomass. Ultimately, however, the effects of fishing on hermaphroditic population dynamics depends on the disproportionate fishing mortality rate of males and how strong of an effect male removal has on female sex change and fertilization rates (Alonzo and Mangel 2005).

We reviewed the treatment of sex change in stock assessments for nine hermaphrodite fish species consisting of 12 different stocks in the Mid-Atlantic, South Atlantic, and Gulf of Mexico and one species from California. Species included Black Grouper *M. bonaci*, Black Sea Bass *Centropristis striata*, Gag, Hogfish *Lachnolaimus maximus*, Red Grouper, Red Porgy, Snowy Grouper, Yellowedge Grouper *Epinephelus flavolimbatus*, and California Sheephead (Table 2). In all of these fisheries, fish are primarily captured by hook-and-line gear or traps. Overall, we found that there is considerable variation in the data reported that is needed to assess the impact fishing has on size or age at sex change and sex ratio.

The majority of stock assessments did not track changes in sex ratio or size at sex change, and none reported estimates of sex selectivity in the fishery (Table 2). Of the 12 stock assessments we reviewed, 10 included both male and female biomass in spawning stock biomass calculations, as suggested by Brooks et al. (2008) for more reliable spawning biomass estimates in hermaphroditic species. Most assessments, 10 of 12, also reported the current sex ratio and estimates of size or age at sex change; however, only 4 of these 10 assessments reported whether the size or age at sex change has changed over time, and only 2 of the 10 assessments evaluated changes in the sex ratio over time.

We found there to be some variation in the way reference points were calculated among stock assessments, especially between stocks from different management regions (Table 3). Biological reference points are a critical part of stock assessment because they are used to guide fishery management objectives—that is, how hard to fish—and are calculated based on biological characteristics of the species (Quinn and Deriso 1999). Incorporating a sex change parameter into reference point calculations is expected to lead to more reliable estimates of spawning stock biomass (Alonzo et al. 2008). Most stock assessments from the South Atlantic, specifically Red Grouper, Snowy Grouper, Red Porgy, and Gag, estimated reference points based on maximum sustainable yield (MSY) from the Beverton-Holt stock recruitment model. Transition from female to male was modeled using logistic regression, which was input to the statistical catch-at-age model as proportion female at age. Spawning stock biomass was then computed using both female and male biomass. In the Gulf of Mexico, there was more variation among assessments: reference points for both Red Grouper and Yellowedge Grouper were also based on MSY from a Beverton-Holt stock recruitment model. Reference points for

Table 2. Treatment of sex change in stock assessments of protogynous hermaphrodite fish species in the United States.

Family	Stock and stock locations	Spawning stock biomass (SSB)	Reports sex ratio at age (or size)	Reports change in proportion male	Change in the age (or size) at sex change	Measures or estimates of sex selectivity	Reference
Serranidae	Black Sea Bass *Centropristis striata* South Atlantic	Male + female	Yes	Not reported	Not reported	Not reported	SAFMC (2013b)
	Black Sea Bass *Centropristis striata* Mid-Atlantic	Male + female	Yes	Not reported	Not reported	Not reported	G. R. Shepherd and Nieland (2012)
	Black Grouper *Mycteroperca bonaci* South Atlantic, Gulf of Mexico	Male + female	Yes	Not reported	Not reported	Not reported	SAFMC (2010b)
	Gag Grouper *Mycteroperca microlepis* Gulf of Mexico	Female	Not reported	Not reported	Yes (no decrease reported)	Not reported	GMFMC (2014)
	Gag Grouper *Mycteroperca microlepis* South Atlantic	Male + female	Yes	Not reported	Yes (no decrease reported)	Not reported	SAFMC (2006)
	Red Grouper *Epinephelus morio* South Atlantic	Male + female	Yes	Yes	Yes (no decrease reported)	Not reported	SAFMC (2010a)
	Red Grouper *Epinephelus morio* Gulf of Mexico	Female	Yes	Not reported	Yes (no decrease reported)	Not reported	GMFMC (2009)
	Snowy Grouper *Epinephelus niveatus* South Atlantic	Male + female	Yes	Not reported	Not reported	Not reported	SAFMC (2013a)
	Yellowedge Grouper *Epinephelus flavolimbatus* Gulf of Mexico	Male + female	Yes	Not reported	Not reported	Not reported	GMFMC (2011)
Labridae	California Sheephead *Semicossphus pulcher* California	Male + female	Not reported	Not reported	Not reported	Not reported	Alonzo et al. (2004)
	Hogfish *Lachnoaimus maximus* S. Atlantic, Gulf of Mexico	Male + female	Yes	Not reported	Not reported	Not reported	SAFMC (2004)
Sparidae	Red Porgy *Pagrus pagrus* South Atlantic	Male + female	Yes	Yes	Not reported	Not reported	SAFMC (2012)

Gag were based on yield per recruit, and for Black Grouper they were based on spawning potential ratio.

Although we expect hermaphroditic fish species to be especially vulnerable to fishing, as discussed previously, hermaphrodite gagstock status, in general, is no better or worse than stock status of gonochoristic stocks (Figure 1). By plotting biological reference points from 189 fish stocks in the RAM Legacy Stock Assessment Database (Ricard et al. 2012), we compared biomass relative to the level of biomass at MSY ($B:B_{MSY}$) and exploitation rate relative to the exploitation rate at MSY ($U:U_{MSY}$) for gonochoristic ($n = 178$) and hermaphroditic ($n = 11$) stocks. California Sheephead were not included in this comparison because reference points have not yet been estimated. The biomass of 8 out of the 11 hermaphroditic stocks (73%) was below B_{MSY} compared to 57% for gonochoristic species, a difference that is not statistically significant ($\chi^2 = 0.53$, df = 1, $P = 0.47$). The current exploitation rate was above U_{MSY} for 5 of the 11 hermaphroditic stocks (45%) compared to 50% for gonochoristic species, a difference that is also not statistically significant ($\chi^2 = 0.01$, df = 1, $P = 0.97$).

One reason why hermaphroditic stocks may not be worse off than gonochoristic stocks could be that some sex-changing species compensate for sex-selective fishing. Hermaphroditic fishes that maintain an optimal sex ratio are expected to be less vulnerable to fishing based on simulation studies (Huntsman and Schaaf 1994). This suggests that when sex change is affected by exogenous social cues, such as the local sex ratio (Munday 2002) or density (Lutnesky 1994), the species may be more resilient to fishing pressure compared to species where sex change is triggered through endogenous cues; for example, size or age of fish (Alonzo and Mangel 2005). In the preceding literature review, it appears that some species are able to compensate for sex-selective fishing (H1), whereas other species are not able to maintain sex ratios (H2). Hawkins and Roberts (2003) found that high fishing intensity did not always lead to skewed sex ratios and smaller size at sex change among different parrotfishes species; similarly, Coleman et al. (1996) showed that fishing lead to highly skewed sex ratios in some Serranidae species but not others. Maintaining optimal sex ratios presumably helps to keep fertilization rates high (Huntsman

Table 3. Summary of the types of stock assessment models, methods for calculating biological reference points, and methods of incorporating sex change into stock assessment for hermaphroditic stocks in the United States. MSY is maximum sustainable yield, and YPR is yield per recruit.

Stock and management region	Assessment model type	Method for estimating reference points	Method of incorporating sex change (if any)
Black Sea Bass, South Atlantic, SAFMC (2013b)	Beaufort assessment model, a statistical catch-at-age model	Benchmarks were calculated based on MSY estimates from the Beverton-Holt stock-recruitment curve.	Sex ratio is estimated using logistic regression; spawning stock biomass is computed using female mature biomass.
Black Sea Bass, mid-Atlantic, G. R. Shepherd and Nieland (2012)	Statistical length-based model (SCALE)	YPR	Spawning stock biomass is computed using both male and female biomass.
Black Grouper, South Atlantic, Gulf of Mexico, AFMC (2010b)	Statistical catch-at-age model (ASAP2)	Benchmarks are based on spawning potential ratio.	Sex ratio is estimated using logistic regression; spawning stock biomass is computed using female and male mature biomass.
Gag, Gulf of Mexico, GMFMC (2014)	Stock synthesis assessment model	Benchmarks are based on YPR estimated from stock synthesis (for females only).	NA
Gag, South Atlantic, SAFMC (2006)	Beaufort assessment model, a statistical catch-at-age model	Benchmarks were calculated based on MSY estimates from the Beverton-Holt stock-recruitment curve.	Sex ratio is estimated using logistic regression; spawning stock biomass is computed using female and male mature biomass.
Red Grouper, South Atlantic, SAFMC (2010a)	Beaufort assessment model, a statistical catch-at-age model	Benchmarks were calculated based on MSY estimates from the Beverton-Holt stock-recruitment curve.	Sex ratio is estimated using logistic regression; spawning stock biomass is computed using female and male mature biomass.
Red Grouper, Gulf of Mexico, GMFMC (2009)	Age-structured forward projection model	Benchmarks were calculated based on MSY estimates from the Beverton-Holt stock-recruitment model.	NA
Snowy Grouper, South Atlantic, SAFMC (2013a)	Beaufort assessment model, a statistical catch-at-age model	Benchmarks were calculated based on MSY estimates from the Beverton-Holt stock-recruitment curve.	Sex ratio is estimated using logistic regression; spawning stock biomass is computed using female and male mature biomass.
Yellowedge Grouper, Gulf of Mexico, GMFMC (2011)	Statistical catch-at-age	Benchmarks were calculated based on MSY estimates from the Beverton-Holt stock-recruitment curve.	Spawning stock biomass is computed using both male and female biomass.
California Sheephead, California, Alonzo et al. (2004)	Stock synthesis length-based model	Benchmarks were based on changes in spawning potential ratio.	Developed two models: (1) Two-sex model—All individuals recruit to population as female, become mature with probability at each length-at-age, then become male with a different probability at each length-at-age. 2) Single-sex model—Only tracks females. The two models differ in the maturity and fecundity functions.
Hogfish, South Atlantic, SAFMC (2004)	REEFS, a sex-differentiated, age-structured, stochastic length-based population simulation model	Reference points are based on YPR.	A parameter representing sex ratio at age is included.
Red Porgy, South Atlantic, SAFMC (2012)	Beaufort assessment model, a statistical catch-at-age model	Benchmarks were calculated based on MSY estimates from the Beverton-Holt stock-recruitment curve.	Sex ratio at age is estimated using logistic regression; spawning stock biomass is computed using female and male mature biomass.

and Schaaf 1994), and it may be that those hermaphroditic fish species able to shift size or age at sex change are better equipped to withstand moderate fishing intensity.

Accurately assessing the impact of fishing will require tracking changes in both male and female biomass over time, because male biomass may be just as important as female biomass in populations of hermaphrodite species (Brooks et al. 2008). Even though overall stock status of hermaphroditic species is not significantly different from that of gonochoristic species, as fishing intensity rises hermaphroditic species may not be able to compensate enough for sex-selective fishing, and stock assessments will need to incorporate not only size and age but also sex into stock assessment models.

In conclusion, it is difficult to generalize the effects of fishing on hermaphroditic species as seen from the literature review. For many hermaphroditic species, fishing has impacted
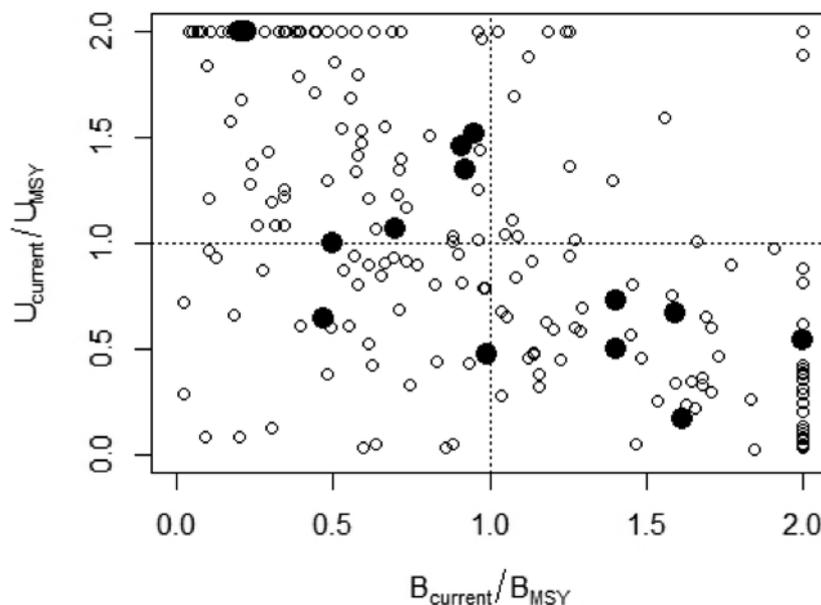
Figure 1. Biomass and exploitation rates relative to levels expected at maximum sustainable yield (B_{MSY} and U_{MSY}, respectively) for hermaphroditic (filled circles, n = 11) and gonochoristic (open circles, n = 178) fish stocks from the RAM Legacy Stock Assessment Database (Ricard et al. 2012).

the sex ratio, size or age at sex change, or both. A lack of consistency in fishing's impact is likely because fishing's influence is highly species specific and in part depends on life history characteristics other than sex change itself. The variation in fishing's influence on sex ratio and size or age at sex change, in addition to the variation in how stock assessments address sex change, may suggest why hermaphroditic species are not significantly worse off than gonochoristic species. A nuanced understanding of the impacts of fishing on sex-changing fishes requires species-specific studies of sex change and life history, time series of sex ratio and size or age at sex change, and estimation of sex selectivity of fishing gear.

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