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Gag grouper, marine reserves, and density-dependent sex change in the Gulf of Mexico

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ABSTRACT

The use of marine reserves for fishery management remains a controversial tool despite evidence of their success. In the Gulf of Mexico (GOM), two marine reserves were put in place in order to protect spawning aggregations of gag grouper, which has experienced a steep decline in the male to female sex ratio since the 1970s. Reserve success is ultimately a function of the total amount of spawning aggregations protected, and fisher response to reserve implementation may have significant influence on the ultimate effectiveness of the reserves. We modeled the GOM gag grouper population under a range of potential reserve sizes and fisher responses. In general, larger reserves resulted in higher adult populations and sex ratio. Fisher response to reserves also had a large impact on reserve success. When we included density-dependent sex change in the model, the results showed a reduction in the sex ratio under high fishing pressure when compared to model simulations when sex change was fixed. While our model suggests that the reserves currently in place should result in a small increase in adult sex ratio given the current level of fishing mortality, such benefits might not be achieved in practice given possible future changes in transition rates or fisher behavior.

1. Introduction

Marine reserves are increasingly used as a tool for managing marine resources, protecting habitat, and conserving biodiversity (Coleman et al., 2004). Evidence from existing marine reserves indicates that reserves can produce rapid positive changes in the biomass and density of fish within them (Halpern and Warner, 2002; Russ et al., 2008) and when properly designed can be an effective tool for promoting recovery of fish stocks and protecting them from overharvest (Claudet et al., 2008; Gerber et al., 2003). These benefits are especially prevalent in older reserves (Edgar et al., 2009; Molloy et al., 2009; Stobart et al., 2009), which are expected to contain more older, larger individuals and also contribute larvae to surrounding areas (Bohnsack and Ault, 1996). Marine reserves nevertheless remain a controversial issue for marine-resource management (Hilborn et al., 2004; Norse et al., 2003), as not all of their anticipated benefits necessarily accrue (Halpern et al., 2004; Hart, 2006).

In the northeast Gulf of Mexico (GOM), the Gulf of Mexico Fishery Management Council (Gulf Council) implemented two experimental marine reserves in 1999 designed to protect offshore spawning aggregations of gag grouper (Fig. 1; GMFMC, 1999). Marine reserves were identified by the Gulf Council as beneficial to management in this case because of the particular life history and behavioral patterns of gag (GMFMC, 1999; Koenig et al., 2000). Gag grouper (*Mycteroperca microlepis*) is a large, long-lived protogynous serranid that experiences a number of ontogenetic habitat shifts during its life: larval gag settle to coastal sea-grass habitat in the spring, where they remain until fall, when they move to nearshore hard-bottom reefs (Koenig and Coleman, 1998). Juvenile gag remain on these nearshore reefs until maturity, when they begin annual spawning migrations to deepwater reefs on the West Florida Shelf (Coleman et al., 1996). Spawning occurs when adult fish create large mixed-sex aggregations on the shelf-edge from December to May, with peak activity during February and March (Domeier and Colin, 1997; Hood and Schlieder, 1992). After spawning, female gag return to the nearshore reefs, whereas males remain offshore (Coleman et al., 1996). This pattern of life-stage separation, migration, and aggregation is well known and exploited by fishers, who fish gag heavily at both nearshore and spawning sites. The most recent stock assessment, completed in 2007 and updated in 2009, determined that the gag population was overfished and undergoing overfishing (SEDAR, 2007, 2009). Perhaps more importantly, the adult gag population has undergone a shift in the adult sex ratio over the last three decades from approximately 20% male in the 1970s to less than 5% male by 2004 (SEDAR, 2006), presumably because of preferential harvest of larger individuals more likely to be male (Coleman et al., 1996; McGovern

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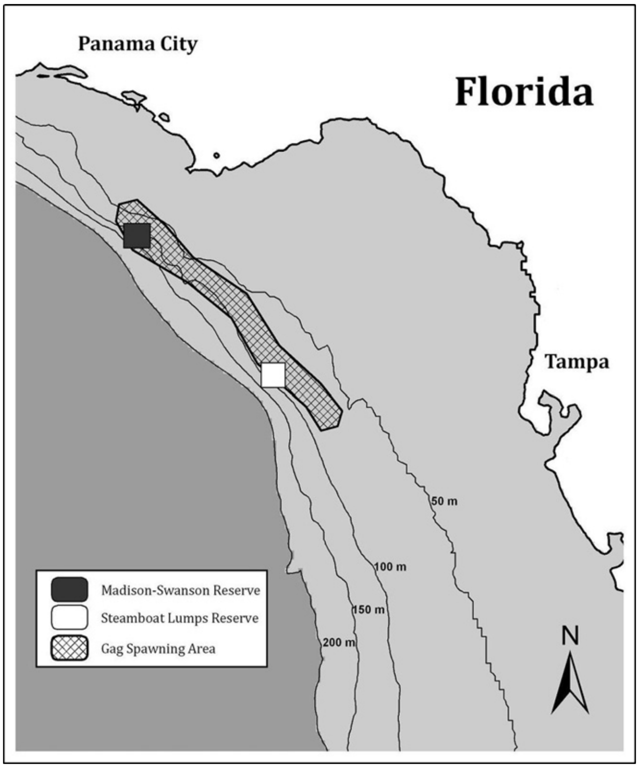

Fig. 1. Map of the northeastern Gulf of Mexico showing the main gag grouper spawning area (as identified by Coleman et al., 1996) and the approximate locations of the two gag-specific marine reserves.

et al., 1998). As a result of this observed decline, the gag population might experience sperm limitation and reproductive failure leading to reduced recruitment and continuing population decline (Armsworth, 2001; Bannerot et al., 1987; Beets and Friedlander, 1992; Huntsman and Schaaf, 1994). The importance of including sex change into stock assessment models has been recognized, if not implemented (Alonzo et al., 2008; Brooks et al., 2008), and the importance of sex change in gag was explicitly recognized by the Gulf Council in their decision to utilize spatial closures in the management of the fishery (GMFMC, 1999). Specifically, implementation of the reserves was done to reduce the fishing mortality of older individuals in part to stop the decline in sex ratio observed in the adult gag population and prevent future sperm limitation.

Changes to population structure like the decline in adult sex ratio experienced by gag can have long-term implications for stock health and fishery production. Empirical observations (Molloy et al., 2008) and modeling analyses of harvest strategies for protogynous fishes both support the hypothesis that reducing the fishing mortality of older fish by means of spawning-area reserves can increase the adult sex ratio in a protogynous fish population (Alonzo and Mangel, 2004; Heppell et al., 2006). However, previous studies ignored two potential problems in the case of protogynous fishes: (1) the redistribution of fishing effort after an area closure and (2) possible density-dependent changes in the rate of sex change in adult females.

Following the closure of fishing grounds, changes in allocation of fishing effort and the behavior of fishers can actually lead to an increase in total fishing mortality. For example, the "spillover" effect, which occurs when the density of fish inside a reserve increases to the point where fish preferentially leave the reserve and become vulnerable to harvest, is often a promised benefit of marine reserves and has resulted in the common tactic of "fishing the line" (Kellner et al., 2008). A recent study by Smith et al. (2008) revealed that the actual fisher response to a seasonal closure for grouper increased the total number of fishing days by 5%. Stevenson et al. (2011) found that established fishers increased effort following implementation of marine reserves on the west coast of Hawaii. These results suggest that the assumption that fishing mortality will decline following spatial closures is not necessarily borne out. Even if total fishing effort remains constant, the reallocation of effort may effectively nullify any benefits from the spatial closure if fishers shift their effort to target more vulnerable individuals. Models evaluating management options should consider multiple scenarios for fishing effort changes after management action to account for a range of possible responses to spatial closures.

In gag, the specific mechanism that controls sex change in gag is as yet unidentified. The two main hypotheses for the controlling mechanism of sex change in gag are social cues and size-related cues. Previous analyses have suggested that heavy fishing on spawning aggregations could result in high size-selective mortality and the disruption of social structure, both of which would decrease the proportion of males in a population of protogynous fish (Shapiro, 1987). For gag, the Gulf Council concluded that marine reserves were the preferred management strategy for addressing both issues (GMFMC, 1999), but previous analyses have not considered how density-dependent social processes might affect the rate of sex change in the gag population. The model for socially induced sex change is essentially a density-dependent process: females change sex on the basis of the rate at which they encounter males, which is a function of the adult sex ratio (Ross, 1990). As the number of males in the population declines, the number of males a given female encounters goes down and so the rate at which females change sex should increase. Because the management actions put in place by the Gulf Council are intended to increase the proportion of males in the population, success would result in more males and a corresponding shift in the rate of sex change. Models evaluating management actions that may increase the male proportion of the population should take into account possible changes in the rate of sex change.

In order to evaluate the marine reserves put in place by the Gulf Council in light of effort redistribution and density-dependent sex change, we developed an age- and stage-structured model of the gag grouper population to test a range of marine-reserve options. We were primarily motivated by the question: if a stated goal of a marine reserve is to have a population level effect on adult sex ratio, how much spawning area must be protected in order to observe a population level response? Our model allows for changes in fishing effort after reserve implementation, both in terms of total effort and redistribution following area closures. We also include a density-dependent sex-change process to account for possible changes in the rate of sex-change on population size and sex ratio resulting from management actions. Although a system of marine reserves that provides full protection for gag grouper spawning aggregation sites is unlikely to be implemented and fishers' behavioral responses to closures are uncertain, our model permits comparison of population level responses to different management actions.

Throughout the paper, we use the term "sex ratio" to mean the ratio in numbers of adult males to adult females (expressed as a percentage for discussion in the text), and "marine reserves" to refer specifically to year-round spawning-area closures as a percentage of the total known spawning area.

2. Methods

2.1. Model description

We developed our model on the basis of the age-structured population model described by Heppell et al. (2006), which predicts the sex ratio, adult population size, and fishery yield as