

# Demographic Analysis of the Effect of Fishing Mortality on the Red Hind (*Epinephelus guttatus*) Population in Western Puerto Rico

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## ABSTRACT

We used a matrix population model to analyze the effect of fishing mortality on the dynamics, structure and life history traits of the red hind population in western Puerto Rico (PR). The life cycle of the red hind was divided into four stages: (1) eggs-larvae-juveniles, (2) small, (3) medium, and (4) large females. We assumed the population to be close (i.e. no larval input from other stocks), or open, and used published data to parameterize the model. The analysis indicated a population growth rate ( $\lambda = N_{t+1}/N_t$ ) of 0.622 for a close population under the current fishing pressure. The analysis also points towards a significant reduction in the relative abundance of large females. Elasticity analysis of the life cycle transitions (i.e. their proportional effect on  $\lambda$ ) indicates that the most important transitions are the survivorships, specifically that of medium females, while the least important are the fecundities. Analysis assuming an open population suggests that recruits from other populations equivalent to 20% of the contribution made by local females would result in the local population stabilizing at a size 90% smaller than its pre-exploitation size. This result is consistent with the actual behavior of the PR population. If, as this analysis suggests, the PR population is receiving an outside contribution of recruits equivalent to 20% of the contribution made by local females, fishing mortality would need to be reduced from the current 0.31 to 0.02 for the local population to attain its original size. We conclude that the red hind population in western PR is a "sink" (i.e.  $\lambda < 1$ ), and that recruitment from other stocks is keeping it at a relatively small but stable size.

**KEY WORDS:** Matrix population model, fishing mortality, life cycle analysis, source-sink metapopulation, serranid

## INTRODUCTION

The red hind (*Epinephelus guttatus*) is a commercially important species of the reef fisheries of the Caribbean, the Bahamas, and Bermuda. It is taken predominantly by hook-and-line in the insular platforms to depths of up to 80m. In Puerto Rico (PR) it constitute one third of the total grouper landings, and in the U.S. Virgin Islands (USVI) it ranks as one of the top five commercial

species (Appeldoorn and Meyers 1993).

Grouper landings in PR reached a maximum of 1,000,000 pounds in 1979, declined sharply thereafter, and have remained relatively stable at around 100,000 pounds during the last two decades (Sadovy 1993). Because fishing effort has remained relatively constant during the last 20 years (Sadovy and Figuerola 1992), the ten-fold decline in annual catch can be assumed to reflect actual changes in the size of the population. Assessments carried out in the late 1980's on the PR and the USVI populations indicate that red hinds are being growth- and recruitment-overfished (Sadovy and Figuerola 1992).

In addition to their economic importance, groupers, like the red hind, play the important role of demersal piscivores in the coral reef community. The loss of keystone piscivores by overfishing affects the community dynamics of other reef fish populations (Hixon and Carr 1997). Furthermore, the critical overexploitation of reef fish populations which is occurring worldwide may be a significant factor contributing to the degradation of coral reef communities (Bohnsack 1982, 1993; Roberts 1995). Because of these reasons, the effective management of groupers extends beyond fisheries related issues and into more general concerns of biodiversity and ecosystem maintenance.

Our objectives were to develop, parameterize, and analyze a matrix population model of the red hind population in western Puerto Rico with the ultimate goal of developing a scientifically-based management plan. We modeled the red hind population assuming both a "close" (i.e. no recruitment from other stocks) or "open" (i.e. receives recruits from other stocks) structure. In this paper we use the model to address the following questions: (1) What is the effect of fishing mortality on the dynamics and structure of the population? (2) Which life cycle transition has greater effect on the growth rate of the population? (3) To what extent recruits coming from other populations affect the local dynamics?

## METHODS

### **Life Cycle of the Red Hind**

Very little is known about the early stages of the life cycle, except that eggs and larvae are planktonic and have a combined duration of between 4 and 6 weeks (Colin *et al.* 1987). Juveniles start maturing into females during their second year, when they reach a fork length of about 200mm. This is also the size and age at which individuals enter the fishery (Sadovy 1993). Small females are typically found in inshore reefs, while large females and males are more common in offshore reefs (Burnett-Herkes 1975; Garcia-Moliner 1986). Adults are demersal predators with a diet consisting of crustaceans, fishes, and cephalopods (Randall 1967). Large females can have fork lengths greater than 400mm, and be older than 12 years (Sadovy 1993). Von Bertalanfy growth curve

parameters for red hinds from western Puerto Rico are:  $L=514.5\text{mm FL}$  (SE = 6.29),  $K = 0.1013$  (SE = 0.003765), and  $t_0 = -2.944$  (SE = 0.1357), Sadovy et al. 1992. Instantaneous rates of natural mortality (M) and fishing mortality (F) for adult red hinds (females and males) from western Puerto Rico equal 0.23 and 0.31, respectively (Sadovy 1993).

Red hinds are protogynous hermaphrodites (Shapiro et al. 1993). Sex change can occur in individuals as young as 2 and 3 years old, but most males are at least six years old and greater than 300mm (Shapiro et al. 1993). In Puerto Rico reproduction occurs during the full moon of January and February, with individuals forming discrete spawning aggregations, at generally consistent locations, along the shelf edge (Shapiro et al. 1993, Sadovy et al. 1994). Egg production increases exponentially with size, with small females producing in the order of 200,000 and large ones in excess of 1,000,000 (Sadovy 1993). Table 1 presents a compilation of the known demographic information for the PR red hinds.

**Table 1.** Life history parameters of red hinds from western Puerto Rico.

| Stage        | Habitat  | Size     | Age       | M(F)*      | Fecundi   |
|--------------|----------|----------|-----------|------------|-----------|
| Egg          | Pelagic  | 0.5-1.0  | 1 week    | ?          | 0         |
| Larvae       | Pelagic  | 2.0      | 4-6 weeks | ?          | 0         |
| Juvenile     | Inshore  | 10.0     | 0.75-2yrs | ?          | 0         |
|              | Offshore | 200-250  | 2-4 yrs   | 0.23(0.31) | 250,000   |
| Medium       | Offshore | 251-400  | 4-12 yrs  | 0.23(0.31) | 400,000   |
| Large Female | Offshore | >400     | >12       | 0.23(0.31) | 2,000,000 |
| Male         | Offshore | 200->400 | 3-17 yrs  | 0.23(0.31) |           |

\* M - Natural mortality, (F) - Fishing mortality

### Matrix Model

If no sperm limitation is assumed and all the unknown early transitions of the life cycle are combined into a single transition, the life cycle of the red hind can be divided into four stages (Figure 1): Pre-Adults (A0), small (A1), medium (A2), and large (A3) females.

The "pre-adult" stage includes the egg, larvae and juvenile stages, plus all the transitions between them.  $P_i$  is the probability that an individual in stage  $i$  will survive and remain in stage  $i$  between  $t$  and  $t+1$  (one year).  $G_i$  is the probability that an individual in stage  $i$  will advance or grow into the next stage.  $F_i$  is the number of eggs contributed by a female in stage  $i$  during one year.

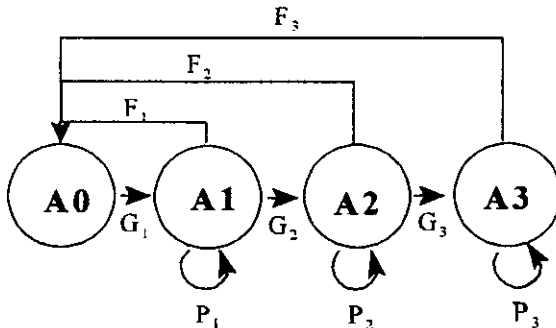
$P_i = \alpha_i (1 - \gamma_i)$  and  $G_i = \alpha_i \gamma_i$ , where  $\alpha_i$  is the annual survivorship in stage  $i$ , and  $\gamma_i$

the probability of growing into the next stage. ( $\gamma_i$  equals:

$$\gamma_i = \frac{(\sigma_i/\lambda)^{T_i} - (\sigma_i/\lambda)^{T_{i-1}}}{(\sigma_i/\lambda)^{T_i} - 1} \quad (1)$$

$\lambda$  is the growth rate of the population ( $\lambda=N_{t+1}/N_t$ ) and  $T_i$  is the number of years it takes an adult in stage  $i$  to grow into the next stage (Caswell 1989). We assumed  $\lambda=1.0$ . Females have to survive order to reproduce. Thus,  $F_i=P_i m_i$ , where  $m_i$  is the number of eggs produced. The number of individuals in each of the life cycle stages at  $t+1$  equals:

$$\begin{matrix} A0 & & 0 & F_1 & F_2 & F_3 & A0 \\ A1 & & G_1 & P_1 & 0 & 0 & A1 \\ A2 & & 0 & G_2 & P_2 & 0 & A2 \\ A3_{t+1} & & 0 & 0 & G_3 & P_3 & A3_t \end{matrix} \quad (2)$$



**Figure 1.** Life cycle of the red hind assuming no sperm limitation, and combining the unknown early transitions into a single one ( $G_1$ ). (A0) Pre-Adults, (A1) small, (A2) medium, and (A3) large females.

By iterating equation 2 one obtains the number of individuals in the different stages through time. In addition, by calculating the eigen values and eigen vectors of the (4x4) projection matrix one obtains the asymptotic growth rate of the population ( $\lambda$ ), the stable stage distribution, the reproductive value of each stage, and the sensitivity and elasticity of  $\lambda$  to variation of each life cycle transition (Caswell 1989).

**Parameterization**

Like in most other organism with planktonic stages, data that would allow estimates of the early transitions of the life cycle is scarce or nonexistent. For example, no information exists about the proportion of fertilized eggs that advance into the larval stage, or the proportion of larvae that successfully settle and metamorphose into juveniles. However, enough is known about the demography of the adult stages to allow good estimates of all the other transitions (Table 2).

Survivorship ( $\sigma$ ) for fished populations equals  $e^{-(F+M)}$  and  $e^{-M}$  for the unfished population (Appeldoorn 1996). Natural (M), and fishing (F) mortality were based on the estimates of Sadovy (1993). She used analysis of catch curves for otolith-aged red hinds to estimate F (Sadovy and Figuerola 1992), and the work of Ralston (1987) to estimate M. Time spent in each stage (T) was calculated using the Von Bertalanffy growth curve for the PR red hinds. Fecundity data (m) was obtained from Sadovy (1993).

**Table 2.** Life cycle transitions for the red hind population in western Puerto Rico with no fishing mortality and with fishing mortality.

| Transition     | No Fishing   | Fishing      |
|----------------|--------------|--------------|
| G <sub>1</sub> | 0.000000675* | 0.000000675* |
| G <sub>2</sub> | 0.335        | 0.145        |
| G <sub>3</sub> | 0.032        | 0.0011       |
| P <sub>1</sub> | 0.435        | 0.315        |
| P <sub>2</sub> | 0.738        | 0.459        |
| P <sub>3</sub> | 0.77         | 0.46         |
| F <sub>1</sub> | 54,380       | 39,380       |
| F <sub>2</sub> | 386,100      | 217,400      |
| F <sub>3</sub> | 1,605,000    | 922,200      |

\* estimated by assuming  $\delta=1.0$  for the unexploited population

RESULTS

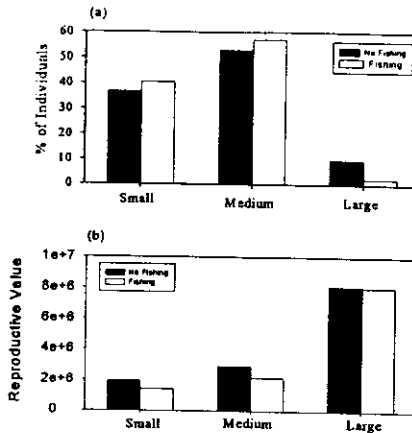
**Close Population**

In a population where adults only suffer natural mortality (M), the probability of an egg making it to a small adult (G<sub>1</sub>) would need to equal

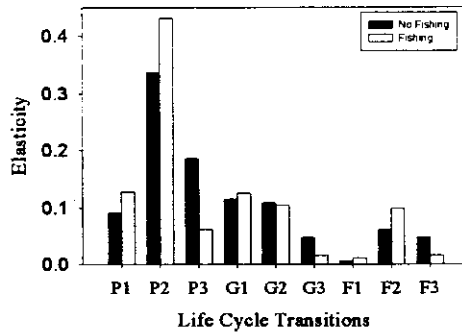
$6.75 \times 10^{-7}$  for the population to be at equilibrium ( $\lambda=1.0$ ). This value is similar to what other investigators have estimated for another serranid of the genus *Epinephelus* in the Caribbean (Doi et al. 1981). To analyze the effect of fishing mortality on the demography and dynamics of the PR red hind population, we assumed  $G_1=0.00000051486$ , and recalculated the life cycle transitions adding fishing mortality (Table 2).

The growth rate of the "fished" population declined substantially, from the assumed equilibrium condition of the unexploited population, to 0.7292 (i.e. equivalent to an annual reduction in population size of 27%). Analysis of the  $\lambda$  "fished" vs. "unfished" matrices show significant changes in the stable stage distribution and reproductive values of fished vs. an unexploited populations (Figure 2a,b). The size structure of the fished population is characterized by the disappearance of large females and an increase in the relative abundance of small females. For all size classes the reproductive value of the exploited population is lower than for the unexploited one. Small and medium females suffered a proportionally greater decline in reproductive value (21.7% and 25.7%, respectively) than the large ones (1.9%).

Elasticity analysis of the life cycle transitions (Horvitz et al. 1997) indicates that the most important transitions (in terms of their relative effect on  $\lambda$  are the survivorships, specifically  $P_2$ , while the least important are the fecundities (Figure 3). Fishing mortality has the effect of increasing the relative importance of the transitions associated with small and medium females ( $G_1$ ,  $G_2$ ,  $P_1$ ,  $P_2$ ,  $F_1$ ,  $F_2$ ), while decreasing the importance of the transitions associated with the large females ( $G_3$ ,  $P_3$ , and  $F_3$ ).



**Figure 2.** Effect of fishing mortality on (a) the size structure and (b) the reproductive value of adult female red hind from western Puerto Rico.



**Figure 3.** Proportional effect on the population growth rate (i.e. elasticity) of the life cycle transitions (see Fig. 1) for exploited and unexploited red hind population in western Puerto Rico.

### Open Population

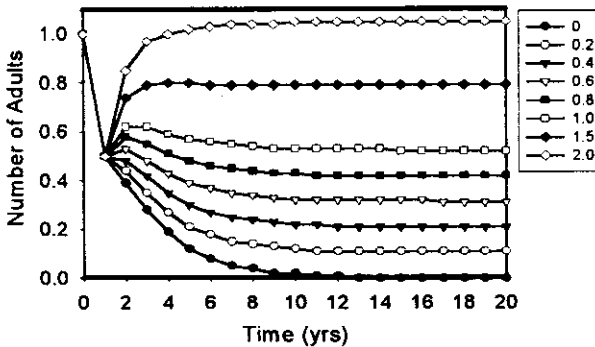
Given a  $\lambda = 0.606$  one could predict that the PR red hind population would have gone locally extinct. However, this has not been the case. Landings have remained relatively low, but stable for the last 20 years. This suggests that the red hind population in western PR is a “sink” (i.e.  $\lambda < 1$ ), and is being “rescued” to some extent by recruits coming from other populations.

To explore this scenario, we modified equation (2) to include a number of females from “other” populations ( $A_4$ ) contributing an  $F_4$  number of recruits to the red hind population in western PR. The matrix equation for this open population equals:

$$\begin{array}{l}
 A_0 \quad \quad \quad 0 \quad F_1 \quad F_2 \quad F_3 \quad F_4 \quad A_0 \\
 A_1 \quad \quad \quad G_1 \quad P_1 \quad 0 \quad 0 \quad 0 \quad A_1 \\
 A_2 \quad = \quad 0 \quad G_2 \quad P_2 \quad 0 \quad 0 \quad A_2 \\
 A_3 \quad \quad \quad 0 \quad 0 \quad G_3 \quad P_3 \quad 0 \quad A_3 \\
 A_4 \quad_{t+1} \quad 0 \quad 0 \quad 0 \quad 0 \quad 1.0 \quad A_4 \quad_t
 \end{array} \quad (3)$$

Equation (3) assumes that the number of females from other populations is at equilibrium ( $A_{4,t+1}/A_{4t}=1.0$ ), and that the local population has no effect on the other populations. By varying  $A_4$  relative to  $A_1+A_2+A_3$  it is possible to analyze the relative effect of recruits from other populations on the local one.

As already demonstrated by the closed population analysis, if  $A_4=0$  the local population goes extinct in less than 20 years (Figure 4). A recruitment contribution by females from other stocks equivalent to 20% of the contribution made by local females would result in the local population stabilizing at a size 90% smaller than its original size (Figure 4), a result that is consistent with the behavior of the PR red hind population. The analysis also predicts that in order for the PR population to maintain its original size under the current exploitation level, an influx of recruits from other areas equivalent to at least twice the local production would be necessary (Figure 4).



**Figure 4.** Effect of recruitment from other red hind populations on the size of the PR population. Each trajectory assumes an increasing contribution of recruits from the outside populations relative to the contribution from the local one, from 0 to twice the contribution. All simulations assumed a local population size of 1 at  $t=0$ .

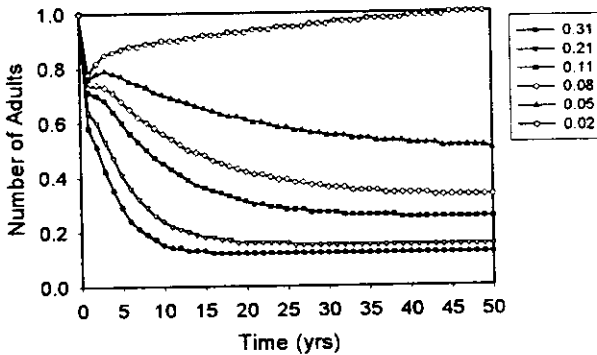
Assuming that, as the above analysis suggests, the western PR population is currently receiving an outside contribution of recruits equivalent to 20% of the contribution made by local females, it is of interest to ask by how much fishing mortality would need to be reduced for the local population to be completely restored? We performed such an analysis, and it indicated that fishing mortality would need to be reduced from 0.23 to 0.02 for the local population to attain its



pre-exploitation size (Figure 5).

DISCUSSION

Our analyzes confirms the conclusion of Sadovy and Figuerola (1992) that the current level of fishing mortality on the PR red hind population is too high, and is having a negative impact on the size and structure of the stock. The model provides two new lines of evidence to support the conclusion that the red hind population in PR is being over-exploited. First, the analysis assuming a close population indicates a growth rate much smaller than the equilibrium condition ( $\lambda=1$ ). Secondly, the elasticity analysis revealed that the growth rate of the population can potentially be most affected by a reduction in adult survivorship (P1, P2 and P3), which accounts for almost half (49%) of the total elasticity. In other words, fishing mortality is directly affecting the most important transitions in the life cycle of this fish.



**Figure 5.** Effect of fishing mortality on the size of the PR red hind population assuming it receives a contribution of recruits from other populations equivalent to 20% of the contribution made by local females. Each trajectory assumes different levels of fishing mortality. All simulations assumed a local population size of 1 at t=0.

High elasticity in the survivorship of adults is not unique to red hinds, but a trait common to long-lived, iteroparous organisms that live in environments characterized by high temporal and spatial variability in recruitment success (Stearns 1992). Under these conditions, it is advantageous to reproduce

repeatedly in order to maximize the likelihood of producing a cohort that will recruit successfully. This will result in selection in favor of an increase in reproductive life span, and thus in adult survivorship (Tuljapurkar 1989). It follows from the above arguments that susceptibility to fishing mortality should be positively correlated with longevity. Which provides an explanation for why the largest and longest-lived of the western Atlantic groupers, the jewfish (*Epinephelus itajara*), was the first to go commercially extinct in the 1960s, followed by the Nassau grouper (*Epinephelus striatus*) in the 1970s (Sadovy 1992). It is unfortunate that the life history trait that allows coral reef fishes to cope with the highly variable recruitment (i.e. longevity), make them so susceptible to fishing mortality.

A generally accepted paradigm among biologists working with marine populations is that the local production of offsprings has little impact on the size or dynamics of local populations (Coley et al. 1996). In our model, this would be equivalent to  $F_4$  being much larger than  $F_1 + F_2 + F_3$ , which is not what we are assuming in our analyzes. However, the fate of locally produced offspring as well as the number and origin of recruits coming from other populations is the result of regional circulation patterns such as gyres and mesoscale eddies (Coley et al. 1996, Palumbi 1994). We should, then, expect much variation, both temporally and spatially, with regards to the degree of "openness" of marine populations. The oceanic circulation pattern around PR is characterized by two west flowing currents along the north and south coast, and the formation of gyres along the west coast (Appeldoorn and Meyers 1993). These gyres may result in the retention of larvae and consequently that a relatively high proportion of locally produced red hind larvae recruit along the west coast of PR.

By assuming an influx of recruits from other populations equivalent to 20% of the local production, we obtained a behavior that is consistent with what the PR red hind population has done in the last 20 years. There are no data that would allow us to assess how valid this assumption is. However, it could be tested by analyzing the genetic structure of red hind populations within the region. An annual influx of recruits equivalent to 20% of the local production would make the PR population genetically undistinguishable from the other populations.

In its broadest sense, a metapopulation can be defined as a set of spatially discrete semi-isolated subpopulations in which migration among them is high enough to have a significant effect on their dynamics and genetic structure (Hanski and Simberloff 1997). Many types of metapopulations have been proposed (see Harrison and Taylor 1997 for review). However, one type of metapopulation model that may be particularly relevant for managing exploited populations is the "source-sink" model. A source-sink metapopulation is one in

which some populations have growth rates of less than one ("sinks") because they occupy low quality and/or exploited sites, and others have growth rates greater than one ("sources") because they occupy good or less exploited sites. Viewing coral reef fish populations as metapopulations has important ramifications for understanding their dynamics and for the development of effective management strategies such as marine reserves (Gubbay 1995, Bohnsack 1993, Roberts and Polunin 1991).

Although our analysis suggests that the western PR red hind population is a "sink", and that recruits from other populations may be keeping the population from going extinct, it also points towards the limitations of "source-sink" management strategies such as the establishment of marine fishery reserves. The model predicts that a protected population with at least twice the number of adult females would be required to restore a heavily exploited population, such as the red hinds in the western shelf of PR, to its original size. Nonetheless, the model also predicts that a relatively small influx of recruits from other populations is enough to keep an exploited population from going extinct. Thus, even though marine fishery reserves may not be very effective in restoring over-fished stocks, they may be very effective in keeping exploited populations from going locally extinct. By itself, this is a very positive impact because it keeps biodiversity high, and helps in maintaining ecosystem function in coral reefs.

In conclusion, the life history traits of red hinds, specifically the importance of high adult survivorship to the population growth rate, makes them very susceptible to fishing mortality. On the other hand, their apparently metapopulation-like regional structure composed of semi-isolated, spatially discrete subpopulations, makes heavily exploited subpopulations, like the one in PR, less susceptible to local extinction.

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